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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Mitteilung an unsere Leser

Mit Beginn des Bandes 55 (1990) werden einige Veränderungen im Bereich der Schriftleitung und im Kreis der Herausgeber wirksam:

Herr Prof. Dr. Harald Schliemann, Hamburg, war seit Juli 1972 als Schriftleiter für die „Zeitschrift für Säugetierkunde" tätig. An seiner Stelle wird nunmehr Herr Priv. Doz. Dr. Peter Langer, Gießen, als zweiter Schriftleiter tätig. Die Federführung in der Schriftleitung liegt nunmehr bei Herrn Prof. Dr. Dieter Kruska, Kiel. Herr Prof. Dr. Harald Schliemann bleibt der Zeitschrift weiter, und zwar nunmehr als Mitglied des Herausgebergremiums, verbunden. Als weiteren neuen Herausgeber hat die Deutsche Gesellschaft für Säugetierkunde zu diesem Zeitpunkt in Abstimmung mit der Verlagsbuchhandlung Paul Parey Herrn Prof. Dr. Wolfgang Maier, Tübingen, berufen.

Der Wechsel von Herrn Prof. Dr. Harald Schliemann von der Schriftleitung in das Herausgebergremium ist dem Verlag Anlaß, ihm wie auch Herrn Prof. Dr. Dieter Kruska für die intensive Tätigkeit in langen Jahren Dank zu sagen. Beide hatten, in Zusammenarbeit mit den Herausgebern, wesentlichen Einfluß darauf, daß die Internationalisierung der „Zeitschrift für Säugetierkunde" gelungen ist und auch die Qualität der veröffentlichten Arbeiten den heutigen Qualitätsansprüchen entspricht. Nur eine weltweit verbreitete und gelesene Zeitschrift bietet bei der heutigen internationalen Verflechtung der Naturwissenschaften für den Verfasser einer Arbeit die Voraussetzung, daß seine Ergebnisse überall zur Kenntnis genommen und zitiert werden. Dafür mußten zwar die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" das Erschwernis in Kauf nehmen, daß ein immer größerer Teil der Arbeiten in englischer Sprache publiziert wird, sie wurden dafür aber mehr als entschädigt durch die internationale Anerkennung für die Qualität der Zeitschrift im Vergleich zu thematisch vergleichbaren Publikationen.

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To our readers

Beginning with volume 55 (1990) the following changes in the office and the editorial board will become effective:

Professor Harald Schliemann, Hamburg, has been a member of the editorial office of the "International Journal of Mammalian Biology" since July 1972. For many years he served the journal as editor-in-chief. Now Priv. Doz. Dr. Peter Langer, Gießen, will replace him in the editorial board and Professor Dieter Kruska, Kiel, will become editor-in-chief. Professor Harald Schliemann will continue in his help for the journal as a member of the editorial board. The "Deutsche Gesellschaft für Säugetierkunde" has also appointed Professor Wolfgang Maier, Tübingen, as a new member of the editorial board in accordance with Paul Parey Scientific Publishers.

The publishers wish to take this opportunity to express their gratitude to Professor Harald Schliemann as well as to Professor Dieter Kruska for all the work they had done in the development of the "International Journal of Mammalian Biology". Through their guidance the journal has a worldwide distribution and is a much quoted research journal well-known to all international scientists in the field of mammalian biology.

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Presence and ecological distribution of *Mus "spretoides"*[1] and *Mus musculus domesticus* in Israel Circum-Mediterranean vicariance in the genus *Mus*

By J.-C. Auffray, E. Tchernov, F. Bonhomme, Giora Heth, S. Simson, and E. Nevo

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Abstract

Described the presence of *Mus "spretoides"* in Israel by morphometric and biochemical analyses. 792 specimens of *Mus* are morphologically studied. These animals were live-trapped or came from museums or owl pellets from all over Israel. By then, distributions of both *Mus "spretoides"* and *Mus musculus domesticus* were established: *Mus "spretoides"* ranges in strictly Mediterranean environments while *Mus musculus domesticus* occurs also in semi-arid environments. Partly competitive exclusions of *Mus "spretoides"* from human dwellings and of *Mus musculus domesticus* from natural environments appear in sympatric area.

The typical Mediterranean range and ecology of *Mus "spretoides"* allows to demonstrate a clear vicariance around the Mediterranean Sea between this eastern species and *Mus spretus* which occurs in the western part of the Mediterranean Basin.

Introduction

Biochemical genetics allows for the recognition of four species of mice in Europe (Bonhomme et al. 1978, 1983; Thaler et al. 1981). Likewise it allows for the establishment of discriminative interspecific morphological criteria in the genus *Mus* on the basis of biochemically discriminated material (Darviche and Orsini 1982; Orsini et al. 1983). Thus, the boundaries of the European species have been established, as well as, their ecological features and distributions.

In Israel, only the house mouse *Mus musculus domesticus* (sensu Thaler et al. 1981) has been described until now (Harrison 1972). The house mouse is common in all areas around the Mediterranean Sea. In this species, the great length of the tail, relative to the length of the body and head as compared to other European species of mice, makes it easy to recognize in the field.

In this study, we report the finding of a short-tailed mouse in Israel which demonstrates the presence of two sympatric species in this part of the Mediterranean Basin. The present study provides original data on the presence and on the range of *Mus "spretoides"* in Israel, the ecological features of the distribution of the two partly sympatric species of mice and the micro ecological partition of the habitat between them.

[1] The oriental Mediterranean mouse has been described under various names. Due to the absence in the international nomenclature of a clear definition of this species (see taxonomy section of the present paper), authors use *Mus "spretoides"* for commodity throughout this paper.

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Material and methods

Material

Apart from the few animals which were live trapped (N = 27), we also studied 242 specimens from all over Israel (deposited at Tel Aviv University Museum and the Hebrew University Museum in Jerusalem). In addition, we analyzed the proportion of both mice (523 mice) in owl pellets involving 12 localities.

Inter-species discrimination

Biochemical study: The trapped animals were dissected and their organs (plasma, hemolysate, kidney, liver, heart) stored at −80 °C. They were subsequently submitted to standard routine protein electrophoresis procedure as described in Pasteur et al. (1987).

Morphological study: The inter-specific discrimination is based on the method of Orsini et al. (1983). Briefly, the recognition of the species is based on:

1. The index of head plus body length/tail length (HB/T) measured on live animals. This measurement is perfectly discriminative between both species and allows for recognition by sight with a little training.
2. The zygomatic index on skulls (ZI: Width of Malar process anterior part/width of Zygomatic arch upper part, Fig. 1). ZI appears to be the best discriminatory parameter among those given by Orsini et al. (1983).

These authors developed this method for Greek and Bulgarian material. Israeli material is first analysed for these two parameters.

Micro-ecological studies

A correspondence analysis, as described by Benzecri et al. (1976) was performed, comparing the proportion of both species in raptor pellets, collected from sites that varied in environmental features.

The proportion of mice for the pellet collections of each location has been calculated from the ZI distribution. The ZI distributions of both species show a small overlap. The average of the two species distribution means was calculated: all the material presenting a ZI above this average was classified as *Mus "spretoides"* and all below as *Mus musculus domesticus*.

We have established 5 categories of specific proportions of the two mice within owls pellets collections as summarized in Table 1.

The correspondence analysis was performed on these categories (each site collection is treated itself as an unactive individual), using the environmental features of the pellet locations as variables. The owl *(Tyto alba)* possesses a small hunting area of 4 km^2 around the nest (Libois 1984). The general features of the environment of the raptors hunting areas is determined by the presence (or lack thereof) of human dwellings (Variable H), agricultural field (A) and natural environment which is unexploited by man (U), and by the location of the hunting area in Mediterranean climatic zone (M) and in the zone of mice sympatry (S).

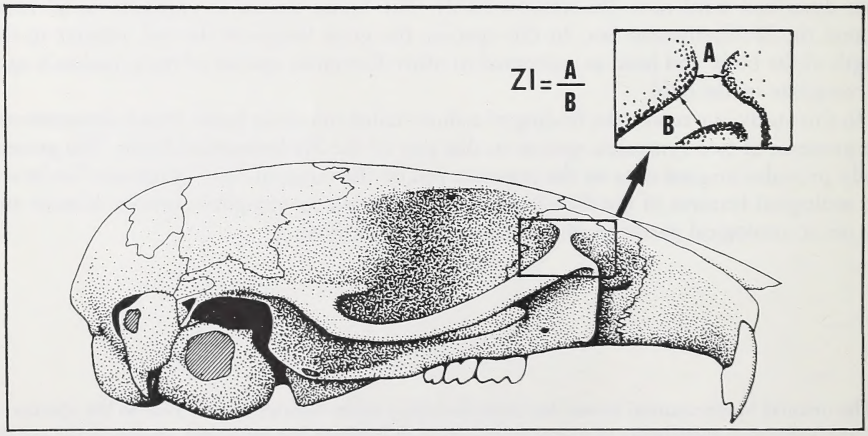


Fig. 1. ZI parameter

Results

Biochemical discrimination

14 individuals could clearly be identified as *Mus "spretoides"* whereas remaining 13 others were to be assigned to *Mus musculus domesticus* without ambiguity according to the diagnostic locus (Car: Carbonic anhydrase) already described for Eastern European mice (Bonhomme et al. 1983). The Israeli samples of the two species were not significantly differing from other Eastern European conspecific populations from a genetical standpoint.

Table 1. **Established categories of specific proportions of *Mus "spretoides"* and *Mus musculus domesticus* within owls pellets collections**

Category	Proportions of *Mus musculus domesticus*	*Mus "spretoides"*
V1	0–20 %	80–100 %
V2	20–40 %	60–80 %
V3	40–60 %	40–60 %
V4	60–80 %	20–40 %
V5	80–100 %	0–20 %

Morphological discrimination

For the HB/T index, only entire animals (trapped ones) could be used. In spite of the small sample size, it is possible to see that discrimination is feasible by this parameter (Table 2). The divergence between European *Mus "spretoides"* described by Orsini et al. (1983) and Israeli one for this parameter comes essentially from the lengthening of the tail in Israeli material (mean 62.1 mm vs 54.4 mm in Europe; $t = 4.42$, $df = 42$, $p < 0.01$).

Table 2. **Values of discriminatory parameters, H + B/T and ZI, for *Mus musculus domesticus* and *Mus "spretoides"***

		Greece Bulgaria*			Israel		
		n	$\bar{x}$	σ	n	$\bar{x}$	σ
H + B/T	*M. "spretoides"*	35	1.49	.10	14	1.28	.08
	M. m. domesticus	15	1.07	.03**	13	1.03	.03**
ZI	*M. "spretoides"*	45	.74	.10	47	.80	.10
	M. m. domesticus	22	.47	.05**	52	.52	.07**

* From Orsini et al. 1983. ** $p < .05$

Concerning the ZI index, Figure 2 presents the histogram of the results obtained with the 792 Israeli mice measured for this parameter. It does not represent a normal distribution (Kolmogorov-Smirnov test: $D = 0.12$, $N = 792$, $p < 0.01$), but rather a bimodal one.

Later, we calculated the average of this trait for each species only for live trapped mice and for museum specimens. For this last category, we used only individuals for which tail, head and body measurements had been recorded, and these were clearly determined by this characteristic as belonging to one of the two species (Table 2). ZI is very discriminatory, too, and may be also used on museum pellet material.

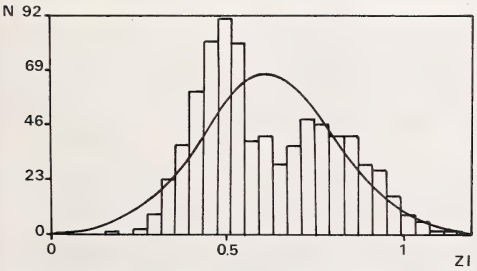
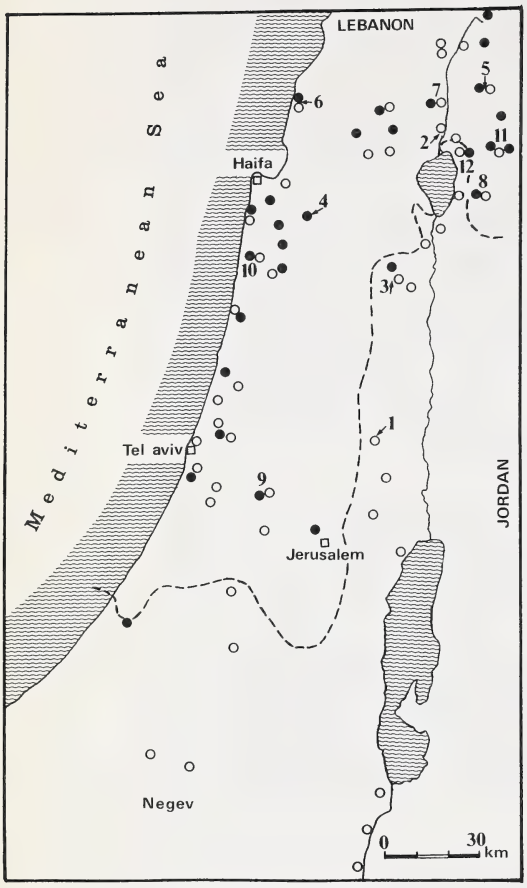


Fig. 2. ZI parameter distribution in mice in Israel

Distribution and habitat of both species of mice in Israel

Mus musculus domesticus occurs throughout Israel, whereas *Mus "spretoides"* occurs on the western coastal plain, hills and



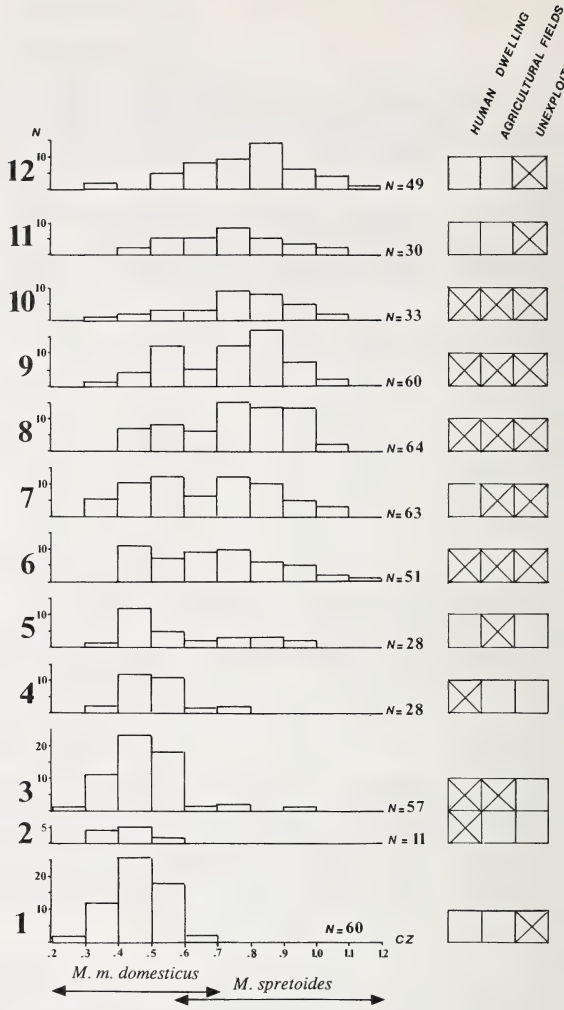


Fig. 3 (left). Presence of *Mus musculus domesticus* (○) and *Mus "spretoides"* (●) in Israel; (1 to 12): Location of owl pellet collections; (---) Annual 400 mm rainfall curve. – *Fig. 4 (right).* Mice ZI distribution within owl pellet collections from 12 locations studied and brief description of the raptors hunting area for each location

mountains of northern Israel. Humidity apparently plays an important role in the distribution of *Mus "spretoides"*, which has its southernmost boundary correlated with the annual 400 mm rainfall curve, which corresponds to the Mediterranean climatic limit (Fig. 3).

Figure 3 shows that these two species are found sympatrically in the Mediterranean climatic zone.

Mus "spretoides" was trapped in two kinds of environments: sandy dunes beaches and, up to an altitude of 500 m, in bushes (especially correlated with *Pistacia lentiscus*). No trapping at higher altitudes was done. This species has never been found in human dwellings which are usually inhabited by *Mus musculus domesticus*. We have not succeeded in trapping the former in cultivated fields, but it may occur there. *Mus musculus domesticus*

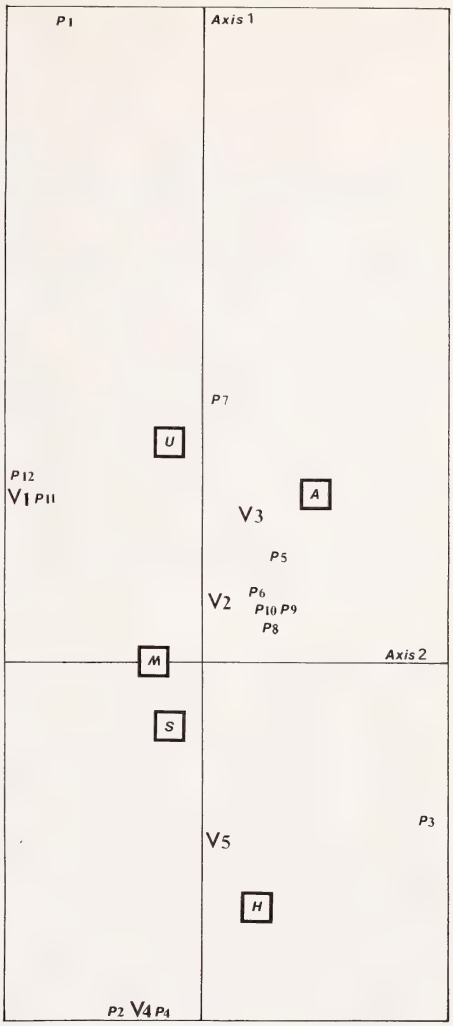


Fig. 5. Axis 1,2 plan of the correspondence analysis (the two first extracted factors account respectively for 68 % and 27 % of the explanation); V 1 to 5: both mice proportions categories in pellets (active individuals of the analysis); P 1 to 12: pellet collections (unactive individuals in the analysis); H, A, U, M, S variables (described in text)

was trapped indoors in the zone of sympatry (Mediterranean climatic zone) and outdoors in the northern Negev desert (N = 8), where no *Mus "spretoides"* occurs.

Figure 4 presents the distribution of ZI of the material derived from owl pellets. The result of the Correspondence Analysis is shown in Figure 5. This associates V4 and V5 proportions (more than 60 % of *Mus musculus domesticus*) with human dwellings, V2 and V3 (between 20 and 60 % of *Mus musculus domesticus* and between 40 and 80 % of *Mus "spretoides"*) with agricultural fields and natural environments and V1 (more than 80 % of *Mus "spretoides"*) with natural environments.

The presence of the two species is strongly correlated with the habitats: *Mus musculus domesticus* occurs in human settlements and agricultural areas (points 2 to 10), whereas *Mus "spretoides"* occurs in agricultural areas and natural environments (points 6 to 12).

The calculation of the percentage of each mice in the total number of prey in owl pellets was possible for 4 points (Table 3).

Table 3. **Percentage of both species of *Mus* in the total number of prey of owl pellets (see location on fig. 3)**

	Percentage of both mice (N)	Percentage of *M. m. domesticus*	Percentage of *M. "spretoides"*
Point 3	16.8 (57)	15.8	1.0
Point 6	42.9 (51)	18.9	24.0
Point 7	15.5 (63)	7.4	8.1
Point 10	14.7 (33)	3.3	11.4

Discussion

Taxonomy

In the last 20 years, *Mus "spretoides"* has been described under various names by several authors. According to the distribution and the ecological, morphological and biochemical features, it seems that all of these authors described the taxa referred to as *Mus "spretoides"* in the present paper. This species has also been called *Mus abboti* (Marshall and Sage 1981), *Mus "4A"* (Bonhomme et al. 1983), *Mus "spicilegus* sud" (Orsini et al. 1983), *Mus "spicilegus tataricus"* (Marshall 1986), *Mus "macedonicus"* (Thaler 1986), or even when its specific status was not clearly recognized, as *Mus "musculus spicilegus"* (Ondrias 1965) or *Mus "hortulanus macedonicus"* (Petrov and Ruzic 1983). Given this great confusion, and according to the fact that clear of type specimens of *Mus abboti* is still to be done, and that all other names could lead to a confusion with its northernmost sibling species (the so-called mound-builder mouse), we prefer to use for commodity *Mus "spretoides"* (Bonhomme et al. 1984) throughout this paper.

Mus "spretoides" has already been described in Bulgaria and Cyprus (Orsini et al. 1983), Greece (Ondrias 1965), Turkey and Iran (Darviche et al. 1979). *Mus musculus domesticus* has been described in the Middle-East, Western Europe, Africa, and America (see Bonhomme 1986 for a review). No study ever revealed any hybrids between these two species in nature. Interspecific breeding, however, is possible under laboratory conditions: Offspring are viable, but F1 males are sterile (Bonhomme et al. 1984).

Habitat partition between *Mus "spretoides"* and *Mus musculus* domesticus in Israel

It appears that there is a correlation between the presence of *Mus musculus domesticus* and *Mus "spretoides"* respectively with human settlements and unexploited environment.

Nevertheless, to assess the presence of permanent feral populations (occurring outdoors throughout the year) for *Mus musculus domesticus,* we consider the percentage of this species in the total number of prey in owl pellets. In Europe, this percentage, in regions where this species is strictly commensal, varies between 1 % to 5 % (Contoli and Sammuri 1978; Barbieri et al. 1975; Lovari et al. 1976; Libois 1984; Chaline et al. 1974). In Southern France, in the Mediterranean climate where *Mus musculus domesticus* is both permanently feral and commensal, its proportion in raptors prey varies from 10 to 30 % (Libois 1984). In some places in Israel it can reach 15.5 % (point 3) or 18.6 % (point 6), and thereby could establish the occurrence of feral permanent populations of the house mouse there. In the zone of sympatry, that is the Mediterranean climate, the feral populations of *Mus musculus domesticus* may occur only in agricultural fields or in close proximity to human settlements, whereas only *Mus "spretoides"* can be found completely independantly of human dwellings (poins 11 and 12). When they occur sympatrically, these two species seem to have established a partition of the environment, and the only place of syntopy could be in cultivated fields.

We noted the presence of feral *Mus musculus domesticus* populations in the northern Negev desert, where we caught 8 feral animals more than two kilometers from the first settlement, or at point 1 (Fig. 2). So, this species occurs as feral populations in semi-arid natural environments where *Mus "spretoides"* is missing but not in Mediterranean zones of sympatry with *Mus "spretoides"*. Also, the occurrence of feral populations of the house mouse in Mediterranean environments in Europe (Orsini et al. 1982) suggests that, in Israel, this species is partly competitively excluded from such type of natural environments by *Mus "spretoides"*.

Besides, we noted a longer tail for *Mus "spretoides"* in Israel, comparing with European material. The inverse relation between tail size and latitudes may be an example of Allen's

rule which states that, within closely related species, the colder environment, the shorter the appendages (reviewed for mice in BARNETT 1965). By living in human dwellings, where their micro-environment is buffered, *Mus musculus domesticus* may not follow Allen's rule.

Circum-Mediterranean vicariance in the genus *Mus*

Our study clearly shows the Mediterranean distribution of *Mus "spretoides"* in Israel. The Mediterranean feature of the distribution of this species is confirmed by its northern distribution: Greece, Bulgaria, Turkey and Iran (see ORSINI et al. 1983 for a review). There, the northern limit of its distribution also corresponds to the limit of the Mediterranean climate. So, this species appears to be Mediterranean on all its known Eurasian distribution (Fig. 6). HARRISON (1972) gives measurements of mice from the Middle East and we note that he reports short-tailed mice in Israel, Lebanon and Syria, but not in Jordan and Saudi Arabia. These data seem to indicate that there is a junction between northern and southern areas of *Mus "spretoides"* still under Mediterranean climate. MARSHALL and SAGE (1981) described a short-tailed mouse in Egypt, but finally assigned this animal to *Mus musculus domesticus* (MARSHALL 1986). So *Mus "spretoides"* does not seem to extend beyond the Mediterranean climate southwards. In Greece and Bulgaria it seems to slightly range out of the Mediterranean zone.

Such a sympatry between *Mus musculus domesticus* and another Mediterranean species of *Mus* occurs in the western part of the Mediterranean region. There, *Mus spretus* occurs as a strictly feral and Mediterranean species (Fig. 6), and is found in shrubs and beaches while *Mus musculus domesticus* is both feral and commensal. So, the partition of habitat in the western Mediterranean Basin is basically very similar to that in Israel. Ecological features concerning the relation between *Mus musculus domesticus* and *Mus spretus* are better known than with *Mus "spretoides"*. Ecology (ORSINI 1982), behavior (CASSAING 1984), population dynamics (CASSAING and CROSET 1985), water balance (SICART et al. 1985), metabolic cold adaptation (AUFFRAY 1988) of these species have comparatively been studied. They confirm the Mediterranean feral nature of *Mus spretus,* as compared with the house mouse. *Mus spretus* is better adaptated to dryness, badly adaptated to cold temperatures, is aggressive and territorial. By contrast, *Mus musculus domesticus* is accustomed to nomadism or aggregative population structures in the sympatric zone of Southern France. Nevertheless, in Israel, some divergences seem to appear in the competition pattern between *Mus musculus domesticus* and the feral species of mice, in this case *Mus "spretoides"*. Indeed, in the Middle-East, *Mus musculus domesticus,* found in semi-arid zone where the feral species is missing, seems to be better adapted to dryness than *Mus "spretoides"*.

It would be valuable to undertake physiological and ethological studies on the pair *Mus musculus domesticus/Mus "spretoides"* to better determine the ecological proximity between this last species and *Mus spretus,* but also to approach the ecological disparities between eastern and western populations of *Mus musculus domesticus* in the Mediterranean Basin.

Both *Mus "spretoides"* and *Mus spretus* are strictly Mediterranean species. Mediterranean climatic zones around the Mediterranean Sea are discontinuous areas. The biggest interruption is the Lybian-Egyptian desertic coast, Cyrenaica being a biogeographic "Mediterranean island". The Mediterranean climate is neither characteristic of the Italian Riviera nor the Po Delta, so the Italian Peninsula can also be considered as a barrier strictly for Mediterranean species. These two interruptions cut the Mediterranean Basin into two biogeographic zones, the occidental (Southern France, Iberic Peninsula and Maghrebi Coast) and the oriental (from Yugoslavian to Israeli Coast and an extension to Iran).

A very clear vicariance between *Mus spretus* and *Mus "spretoides"* is established between these two parts of the Mediterranean Basin. Nevertheless, the Italian Peninsula

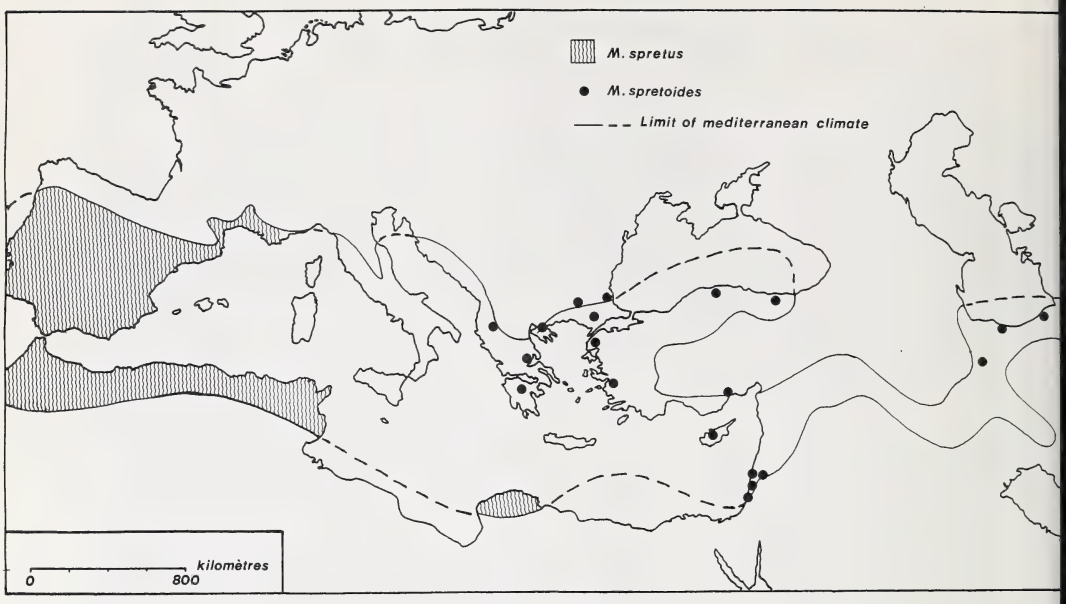


Fig. 6. Circum-Mediterranean distribution of *Mus spretus* and *Mus "spretoides"* (modified from Orsini 1982 and Orsini et al. 1983)

remains free of these two feral mice. On the other hand, Cyrenaica harbors *Mus spretus* (Marshall and Sage 1981). This could be explained by the colonization of *Mus spretus* through northern Africa, at a time when the Sahara was hospitable. After the desertification, an isolated population of *Mus spretus* could have remained as a refuge in this zone. The circum-Mediterranean parcelling out and species vicariance are also illustrated by the distribution of some other mammals, such as *Meriones* and *Crocidura* (see Cheylan 1988 for a review).

The discovery of a new species of mice in Israel is also very interesting from a paleontological point of view. Indeed, Israel presents numerous paleontological and archeological sites from the Lower Pleistocene. Only *Mus musculus* lineage has been described since the Pleistocene (Tchernov 1968, 1986). The presence of the two actual species in this region should occur as a result of two lineages, one for each species. Thaler (1986) stresses the need to study late paleontological material with a biometric discriminatory method complemented by biochemical studies on actual material. The morphological method used in this study on extant material may also be applied to fossil material. The dating of the appearance of the two species and of their colonization of the Middle-East should then be viewed through the perspective of competition in time, and the effects of human appearance on the feral and the commensal species of mice.

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Zusammenfassung

Vorkommen und Verbreitung von Mus "spretoides" und Mus musculus domesticus in Israel
Circum-Mediterrane Vikarianz im Genus Mus

Das Vorkommen von *Mus "spretoides"* in Israel wird morphometrisch und biochemisch belegt. Insgesamt wurden dazu 792 *Mus*-Individuen untersucht, die teils lebend gefangen wurden, teils aus Museen oder Gewöllen aus ganz Israel stammten. Danach ist *Mus musculus domesticus* weiter verbreitet, auch in semiariden Gebieten, wogegen *Mus "spretoides"* auf mediterrane Habitate beschränkt ist. Bei sympatrischem Vorkommen wird offensichtlich durch die Konkurrenz der jeweils anderen Art *Mus musculus domesticus* aus dem Freiland, *Mus "spretoides"* hingegen von menschlichen Siedlungen ausgeschlossen.

Im Mittelmeerraum ist *Mus "spretoides"* die östliche Vikariante der westmediterranen *Mus spretus*.

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Hyoid-dentary articulations in golden moles (Mammalia: Insectivora; Chrysochloridae)

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Abstract

Studied the general structure, topography and possible functions of the hyoid region in nine golden mole species. Unusual in-situ articulations between the enlarged stylohyal bones, and the dentaries, were found in all specimens examined. Osteological evidence suggests that hyoid-dentary articulation is an unique anatomical feature characteristic of all chrysochlorids. Its apparent functions are to enhance manipulatory action of, and support for, the tongue during prey handling and mastication, but this remains to be confirmed.

Introduction

Hyoid-mandible articulations occur in some osteichthyian fishes (de Beer 1937; Hildebrand 1974), but have never been recorded in higher vertebrates. Improved museum preservation techniques recently enabled us to detect conspicuous articulation between the large stylohyal bone and the dentary in the Hottentot golden mole *Amblysomus hottentotus* (A. Smith, 1829). Further investigation revealed that hyoid-dentary articulation (Fig. 1) in situ is an unique characteristic of all chrysochlorids. In this preliminary note,

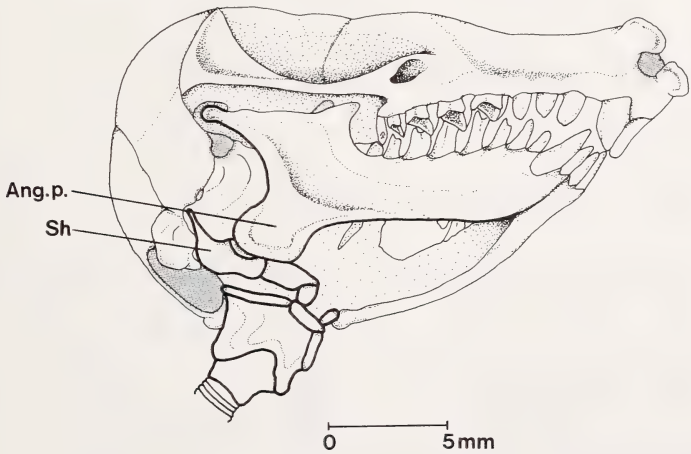

Fig. 1. Skull and hyoid region of an *Amblysomus julianae* Meester, 1972 (TM 39932) showing the articulation between the enlarged stylohyal bone (Sh) and the angular process (Ang. p.) of the dentary

the general structure and possible functions of the hyoid apparati in golden moles are briefly considered.

Golden moles are small, solitary, subterrestrial eutherians about which little is known. Of the 18 species (representing seven genera) endemic to sub-Saharan Africa, 15 are

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restricted to southern Africa (Meester 1974; Meester et al. 1986). Morphologically and ecologically, they show marked convergence with the true moles (Talpidae), and especially the marsupial "mole" *(Notoryctes typhlops)* of Australia (Kuyper 1985; Nevo 1979). Taxonomically, the Chrysochloridae were traditionally associated with the tenrecs (Tenrecidae) of Madagascar (Butler 1956). However, there is no unequivocal evidence favouring a close taxonomic relationship between these families (Butler 1972), and chrysochlorids possess so many unique anatomical features that Broom (1915, 1916), Bugge (1974) and Roux (1947), amongst others, suggested that they should be assigned to a distinct order (the Chrysochloridea).

Materials and methods

Dobson (1882) und Sprague (1944) found that the hyoid apparati of golden moles have an unusual, specialized structure, and while the former author noted a large, concave surface on the anterior aspect of the stylohyal bone, he described this as a site of hyoid-tympanic bulla junction. However, examination of preserved specimens representing eight species (see Table), suggested to us that the anterior surface of the stylohyal articulates not with the auditory bulla, but with the base of the dentary. This was subsequently confirmed by: examination of intact, double-stained *Chrysochloris asiatica* showing the hyoid bones in situ; X-ray photography of five species (*A. hottentotus* – TM 39 201; *A. iris* – TM 29 313; *Chrysochloris asiatica; Chrysospalax trevelyani* – TM 30 262; *Eremitalpa granti* – TM 39 261); and dissection of four *A. hottentotus* (TM 39 200; TM 39 201; TM 39 202; TM 39 205) and one *A. iris* (TM 39 204).

Results and discussion

The hyoid apparati of all species examined, while differing markedly in size, are morphologically similar. Each comprises five pairs of ossified segments that form a chain linking the larynx with the cranium and dentaries (Fig. 2). The basihyal (which is proximal in this discussion) is a small, transverse bar (of paired origin; de Beer 1937) that meets distally with the thyrohyals and hyoid cornua. The long, cylindrical thyrohyals run caudolaterally from the basihyal to join the thyroid cartilage via the chondrohyoid cartilages (which are partly ossified). Each anterior hyoid cornu consists of three bony elements (a condition Howes 1896 termed "integrocornuate"), which in proximal-distal order are: 1. a small, squat ceratohyal that runs rostromedially; 2. a short, rectangular or triangular epihyal that is deflected laterally; 3. a robust, bulbous stylohyal with a tapering distal extremity (the styloid process) which projects rostrodorsally to join with the tympanic bulla via a long, slender tympanohyoid cartilage. As in most other insectivores,

Table 1. **Chrysochlorid specimens in the Transvaal Museum (TM) examined during the study**

Species	TM accession numbers
Chrysospalax trevelyani (Gunther, 1875)	39438, 39927
Chrysochloris asiatica (Linnaeus, 1758)	39235, 39237, 39238, 39239, 39245, 39291, 39293, 39294, 39295
Eremitalpa granti (Broom, 1907)	39261
Chlorotalpa duthiae (Broom, 1907)	39456
Chlorotalpa sclateri (Broom 1907)	39439, 39442, 39445
Calcochloris obtusirostris (Peters, 1851)	39470
Amblysomus iris Thomas & Schwann, 1905	39164, 39165, 39167–39173, 39175, 39176, 39204, 39933
Amblysomus hottentotus (A. Smith, 1829)	39200–39203, 39205, 39206, 39240, 39246–39248, 39260, 39296, 39297, 39422, 39423
Amblysomus julianae Meester, 1972	39769, 39770, 39932

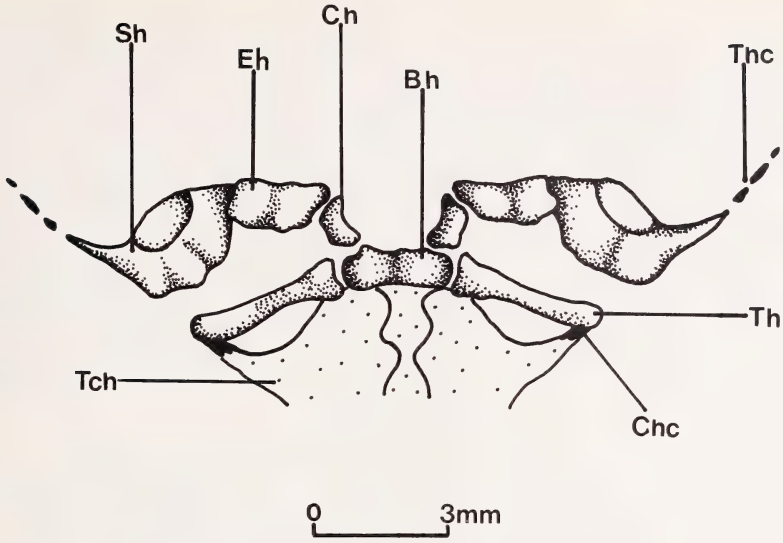

Fig. 2. Hyoid apparatus (ventral view) of *Chrysochloris asiatica.* Bh – basihyal; Ch – ceratohyal; Chc – chondrohyal cartilage; Eh – epihyal; Sh – stylohyal; Th – thyrohyal; Thc – tympanohyal cartilage

the position of attachment to the skull is slightly anterior to the stylomastoid foramen – a condition Howes (1896) termed "protrematic" (but see Sprague 1944 for problems associated with this definition) – and is marked by a tympanophyal pit in *Chrysospalax* (Forster Cooper 1928), and a canal (vagina processus hyoidei) in *Chrysochloris* and *Amblysomus*. The proximal, rostral aspect of the stylohyal contains a large, smooth surface that articulates in situ with the conspicuously broadened and flattened, ventral edge of the angular process on the dentary (Fig. 1). (When hyoid apparati are not available for direct examination, the distinctive, flattened base of the angular process serves as a convenient indicator of hyoid-dentary articulation.) In *Chrysospalax trevelyani,* the articular surface on the stylohyal bone is distinctly concave, and is displaced ventrally relative to all other species examined.

From our dissection, the stylohyal-dentary articulation appears to be a synovial "plane joint" (Hildebrand 1974) that permits independent movement of the mandible and hyoids during the devouring of prey (i.e. as the jaw is opened and closed, and the tongue is protruded and retracted). Associated with this joint are muscles that, inter alia, run from the rostral margins of the stylohyal articular surface to the caudolateral aspects of the dentary, and which seemingly act to tense the hyoid-dentary link, and constrain movement along a dorsoventral plane. The precise action of these muscles is currently under study.

While the hyoid apparati of only nine species were available for direct study, hyoid-mandible joints in all of the (13) chrysochlorid species (representing six genera) currently preserved in the Transvaal Museum were inferred from the presence of conspicuously flattened articular surfaces on the dentaries of preserved specimens. (Only *Cryptochloris* was not available.) No similar articular surfaces were found on the dentaries of rodent mole (Bathyergidae) or tenrec *(Tenrec eucaudatus)* specimens examined, nor have they been described in the literature on other mammals. Hyoid-dentary articulation may therefore be an unique, and characteristic, feature of all chrysochlorids.

Until the interaction of hyoid-associated muscles has been established, function(s) of the hyoid-dentary articulation in golden moles can be only suggested. A role in jaw

suspension, (similar to that played by the epihyal-mandible link of some fishes) can be excluded, since the hyoid-cranial attachment is too tenuous to supplement suspension of the mandible provided by the squamosal-mandibular hinge. A function in the detection and transmission of underground vibrations to the middle ear, similar to the prey-detection mechanisms of some primitive amphibians (see Hildebrand 1974), is also highly unlikely in view of the slender, cartilagenous hyoid-cranial link.

The most likely function of the enlarged hyoid bones and articulation is to enhance support for, and manipulatory ability of, the tongue. During the handling of natural, often writhing, prey (such as earthworms) chrysochlorids sometimes use their foreclaws to press the prey item to the ground, but for the most part rely on agile movements of the tongue, jaws and head. While the tongues of chrysochlorids are not particularly long (Sonntag 1923), they are very muscular, and are well supplied with keratinized and scoop-shaped papillae (Dobson 1882). During mastication, only orthal movement of the mandible is allowed by the tight squamosal-mandibular joint (Parsons 1901), and the zalambdodont cheekteeth serve mainly for the embrasure shearing of food, with little crushing thereof. Pieces of food apparently are then further homogenized between the horny surface of the tongue and the robust palatal ridges, before swallowing. This process involves forceful movement of the muscular tongue, so that a strong base for its support is imperative. The hyoid-cranial link seems too tenuous to provide sufficient support by itself. The hyoid apparatus and articulation, however, are sufficiently robust to provide additional support and suspension for the tongue, whilst also permitting its movement independently of the mandible.

This explanation assumes that hyoid-dentary articulation in golden moles is functionally related to their zalambdodont dentition. The apparent absence of hyoid-dentary joints in other taxa exhibiting zalambdodonty (such as tenrecs and selenodonts), however, suggests that this is only partly true: some other factor unique to the chrysochlorid lifestyle must also have been involved in the development of hyoid-dentary articulation. It is possible that accomodation of the well-developed neck musculature (which powers forceful upthrusts of the head during their unique style of burrow construction; Puttick and Jarvis 1977) may have necessitated a decrease in the size of the chewing muscles (the masseters are relatively small; Dobson 1882), with a concurrent, compensatory shift of emphasis from chewing movement of the jaws to increased masticatory action of the tongue during feeding.

Mammalian hyoid apparati show great morphological plasticity in relation to function (Sprague 1944), and due to their position, are very susceptible to environmental influences (Gasc 1967). For this reason, characters of the hyoid region are generally considered to have little phylogenetic value (Grasse 1955). While the phylogenetic significance of the unusual hyoid structure and topography in golden moles cannot be fully assessed until its functions are demonstrated, the uniqueness of hyoid-dentary articulation adds to the wealth of other anatomical information (Broom 1915; Butler 1972; Bugge 1974; Dobson 1882; Forster Cooper 1928; Roux 1947) indicating that chrysochlorids are extremely specialized mammals which should perhaps be afforded at least subordinal rank within the Insectivora.

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Zusammenfassung

Hyoid-dental-Gelenkungen bei Goldmullen (Mammalia: Insectivora; Chrysochloridae)

Auffällige Gelenkverbindungen zwischen dem Stylohyale des vergrößerten Zungenbeinapparates und den Dentalia des Unterkiefers sind beim Hottentotten-Goldmull, *Amblysomus hottentotus*, festgestellt worden. Bei weiteren Untersuchungen wurde bei allen Gattungen der Chrysochloridae außer *Cryptochloris*, der nicht zur Untersuchung zur Verfügung stand, auf dem Unterteil der Dentalia eine bemerkenswerte Gelenkfläche gefunden. Kontakt, in situ, zwischen dem Stylohyale und der Unterseite der Dentalia ist durch Sezierung *(A. hottentotus, Chrysochloris asiatica),* Röntgenuntersuchung *(A. hottentotus, Chrysospalax trevelyani, C. asiatica, Eremitalpa granti)* und Untersuchungen von aufgehellten, doppelgefärbten, unversehrten Exemplaren von *C. asiatica* bestätigt. Über derartige Gelenkungen ist bisher weder bei Goldmullen noch anderen Säugetieren berichtet worden. Wir kommen daher zu dem Schluß, daß es ein typisches Merkmal der Chrysochloriden ist, mit möglicher systematischer Bedeutung. Wahrscheinlich ist die Funktion eine stärkere Unterstützung der Zunge, die beim Kauen beteiligt ist. Gründliche weitere Untersuchungen der beteiligten Muskulatur könnten die taxonomische, systematische und funktionelle Bedeutung dieses eigenartigen Merkmals der Goldmulle weiter erläutern.

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Untersuchungen am P1 im Gebiß des europäischen Dachses *(Meles meles)*

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Abstract

Numerical and metrical studies on the first premolar in the European badger Meles meles L.

Described are the occurrence, size and position of the first premolar (P1) in the European badger. Information was obtained from 315 badger skulls of known sex, collected in the Swiss midlands during the period 1967 to 1982. 232 of the skulls were aged by counting dentine rings in the lower incisors. 1. 368 of 1260 possible P1 (29 %) were not developed (317 in the upper jaw, 51 in the lower); 2. there was no difference in the occurrence of P1 between males and females, or between the left and right sides of the skull; 3. bilateral absence of P1 was more common than unilateral absence; 4. there was no correlation between absence of P1 and skull length; 5. P1 was characterised by a high degree of variability in its form and position in the tooth row; 6. the distance between C and P2 was shorter in skulls with P1 absent than in skulls where P1 was present. The results are discussed from the point of view of developmental and functional morphology, genetics and taxonomy.

Einleitung

In der säugetierkundlichen Literatur finden sich unterschiedliche Angaben zur Anzahl Zähne im Gebiß des europäischen Dachses *Meles meles* (L. 1758). Diese Unklarheiten beruhen auf verschiedenen Interpretationen des ersten Vorbackenzahnes P1, welcher nicht bei allen Schädeln erkennbar ist. Grundsätzlich lassen sich vier Auffassungen unterscheiden:

1. N = 38. Das Gebiß umfaßt in der Regel 38 Zähne, die P1 gehen aber häufig verloren. „Gebiß 38 Zähne. Der erste Lückenzahn oben und unten . . . fällt in der Regel aus, so daß nur 34 Zähne bleiben" (Blasius 1857). Analoge Angaben finden sich bei Baumann (1949), Gaffrey (1961), Long (1965), Buchalczyk in Pucek (1981). Miller (1912) weist darauf hin, daß der P^1 rascher ausfalle als der P_1.
2. N = 38. Der P1 erscheint häufig nicht. „. . . viel häufiger fehlen sie als echte Anomalien von Geburt an" (Stubbe 1980). Heráň (1971) und Neal (1977) vertreten dieselbe Ansicht.
3. N = 36. In der Regel finden sich erste Prämolaren nur im Unterkiefer, die Zahnzahl beträgt demnach N = 36. „The premolar formula is 3/4" (Colyer 1936). Auch Lee (1977) erachtet N = 36 als Normalfall.
4. N = 34. Beim P1 handelt es sich um einen bei rezenten Dachsen oft zusätzlich angelegten Zahn. Als Zahnzahl wird N = 34 angegeben. „Dental formula of the functional teeth 3.1.3.1./3.1.3.2." (Corbet und Southern 1977). Diese Zahl kann sich aber auf 35 bis 38 erhöhen (Fullagar et al. 1960).

Die Meinungen liegen somit zwischen N = 34 mit häufigen Polyodontien, und N = 38 mit häufigen Oligodontien und/oder sekundärem Verlust durch Trauma. Bemerkenswert ist die Angabe Heptners (1968), wonach erste Prämolaren bei Dachsen aus dem Westen des Artareals viel häufiger vorkommen als bei solchen aus dem Osten.

In der Folge soll eine umfangreiche einheitliche Schädelsammlung zur Klärung dieser unterschiedlichen Ansichten herangezogen werden.

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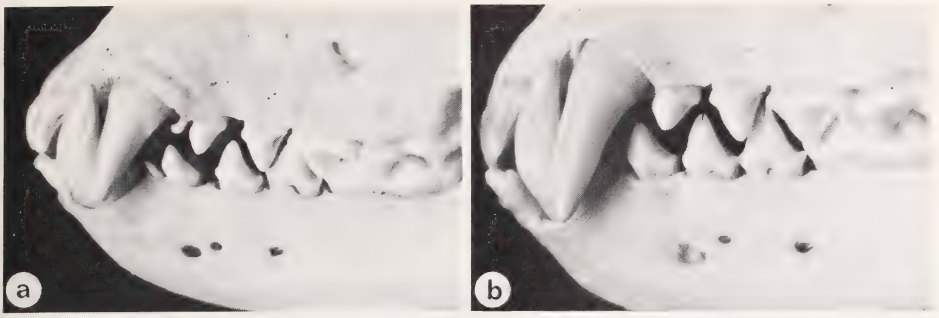

Abb. 1. a: Gebiß mit 4 vorhandenen P1 (♂ 7 Mon., Nr. 285/76); b: mit keinem angelegten P1 (♂ 5 Mon., Nr. 338/73)

Material und Methode

Alle Schädel stammen von Dachsen aus dem Kanton Bern, Schweiz (für Details s. Lüps 1984). Zur numerischen Betrachtung wurden 2 Altersgruppen geschaffen:
a. 20 Schädel von Jungdachsen, bei denen noch nicht alle Ersatzzähne hochgewachsen sind.
b. 315 Schädel (177 ♀, 138 ♂) von Tieren mit vollständig entwickeltem Gebiß.
Die Altersbestimmung erfolgte mit Hilfe der Weite der Pulpahöhle (Graf und Wandeler 1982) und von Zahnschnitten (Graf 1982; Lüps et al. 1987). Für die metrische Analyse fanden 42 ♀ Verwendung, alle älter als 12 Monate (21 mit 4 angelegten P1, 21 mit nur im Unterkiefer angelegten P1; ♀ wurden deshalb gewählt, weil nur bei ihnen für beide Serien eine genügend große Anzahl Schädel vorlag).

Als Vergleich wurden die Daten von 100 Schädeln aus Dänemark herangezogen (B. und P. Lüps, zur Herkunft vgl. Andersen 1954).

Numerische Beurteilung

Bei älteren Tieren ist oft nicht mehr mit Sicherheit zu erkennen, ob ein Zahn nie vorhanden gewesen ist oder ob er früh verlorenging und sich die Alveole gefüllt hat. Zur Klärung diente die Trennung in 2 Altersgruppen (s. oben).

Entsprechend der Ausprägung des P1 wurde in beiden Altersgruppen jede P1-Position einer der folgenden Kategorien zugeordnet:
A. keine Spur eines Zahnes zu sehen, dieser war offensichtlich nicht angelegt
B. Zahn angelegt, Alveole offen oder verwachsen(d), aber noch erkennbar
C. Zahn am Kieferrand abgebrochen, Wurzel noch in der Alveole steckend
D. Zahn intakt vorhanden
E. Überzähliger Zahn (Polyodontie).

Nur leichte Beschädigungen (Absplittern kleiner Teile, Abbrechen von Spitzen) wurden nicht berücksichtigt.

Metrische Analyse

Mit einer Schieblehre wurden Zahnmaße und -abstände (Diastema) auf 0,1 mm genau ermittelt. Als Meßpunkte dienten:
Zahnmaße: größte Kronenlänge (L), geringste Kronenbreite (B), Höhe (H) ab Alveolarrand.
Diastema: Hinterer Rand der C-Alveole, Vorderrand der Alveolen von P1, P2 und M1.

Zähne und Diastema wurden in beiden Kieferhälften gemessen und dann gemittelt (bei einseitigem Fehlen wurde das Maß des vorhandenen Zahnes verwendet, s. dazu Lüps und Roper 1988). Die topographische Lage des P1 in bezug auf die Nachbarzähne und seine Stellung ließen sich sowohl bei vorhandenen wie bei fehlenden Zähnen ermitteln. Bei der Interpretation der Stellung wurden Zähne mit Abweichungen der Zahnachse bis zu rund 30 Grad von einer Senkrechten zur Kieferoberfläche als in Normalstellung befindlich beurteilt. War die Abweichung stärker, wurde der Sektor mit der stärksten Abweichung zur Senkrechten bezeichnet. Nicht berücksichtigt wurde die Drehung des Zahnes in der Alveole, da der Zahn nach der Präparation wohl oft nicht mehr in der ursprünglichen Position eingefügt und verleimt wurde. Aus diesem Grund wurden auch größter und geringster Durchmesser ermittelt und nicht mesiodistaler und buccolingualer Durchmesser (vgl. Hillson 1986).

Bei der Verwendung des Student-t-Tests wurde in allen Fällen das Niveau $p = 0.001$ als Signifikanzschwelle gewählt.

Tabelle 1. **Erscheinungshäufigkeit und Verluste des P1 im Gebiß von 315 Dachsen**

	♂♂ (n = 138)				♀♀ (n = 177)				Total					
	P^1	%	P_1	%	P^1	%	P_1	%	P^1	%	P_1	%	$P^1 + P_1$	%
A	148	53,6	23	8,3	169	47,7	28	7,9	317	50,3	51	8,1	368	29,2
B	8	2,9	9	3,3	16	4,5	21	5,9	24	3,8	30	4,8	54	4,3
C	16	5,8	20	7,2	12	3,4	19	5,4	28	4,5	39	6,2	67	5,3
D	104	27,3	224	81,2	157	44,4	286	80,8	261	41,4	510	80,9	771	61,2
	276	100 %	276	100 %	354	100 %	354	100 %	630	100 %	630	100 %	1260	100 %

A = Zahn nicht angelegt, B = verwachsene/verwachsende Alveole, C = Zahnrest vorhanden, D = Zahn intakt vorhanden

Ergebnisse

Numerische Beurteilung

Milchgebiß und Zahnwechsel

In keinem der untersuchten Schädel von Dachsen mit Milchgebiß fanden sich Spuren, die auf die Anwesenheit des P1 im Milchgebiß hinweisen würden. Neal (1977) gibt für das Milchgebiß die Prämolarenzahl P = 4 je Kieferhälfte an, weist jedoch darauf hin, daß die P1 häufig fehlen: „the first premolar is not always present and if it does occur, it is often shed very early or does not penetrate the gums". Stubbe (1980) erwägt, daß der P1 als Milchzahn beim Dachs fehle, und wirft die Frage auf,„warum sollte es nicht denkbar sein, daß in der Zahnreihe auch vor den Prämolaren monophyodonte Zähne zu finden sind?". Wie bei anderen Carnivoren nachgewiesen (Linhardt 1968; Lüps et al. 1972 für den Rotfuchs; Meyer 1941; Seiferle und Meyer 1942 für den Haushund), erscheint offensichtlich auch beim Dachs der P1 nur in einer Zahn-Generation. Ist er aber bei den genannten Arten von der Größe und Struktur her klar als Ersatzzahn – nicht als spät erscheinender und persistierender Milchzahn – erkennbar, so ist diese Zuordnung beim Dachs nicht ganz einfach.

Im Ersatzgebiß erscheint der P1 im Oberkiefer erst, nachdem alle Schneidezähne und der Eckzahn gewechselt sind, im Unterkiefer nach dem Wechsel der Schneidezähne (Neal 1977; Lüps 1983). Bei 15 Oberkiefern, in denen er erwartet werden durfte, fehlt er in 9, bei 20 entsprechenden Unterkiefern in 3 Fällen.

Gesamtbetrachtung des Ersatzgebisses

Von insgesamt möglichen 1260 P1 sind 771 intakt vorhanden (61,2 %), bei 368 (29,2 %) fehlt jeglicher Hinweis auf einen einmal vorhandenen Zahn. Die übrigen 121 Fälle betreffen verwachsen(d)e Alveolen und vorhandene Wurzelreste. Polyodontien konnten keine nachgewiesen werden (Tab. 1).

Bei ♂ scheint der P^1 zwar häufiger nicht angelegt als bei ♀, der Unterschied ist aber nicht signifikant ($p = 0{,}03$). Beim P_1 ist der Unterschied noch geringer. Damit können bei einer Gesamtbetrachtung ♂ und ♀ zusammengefaßt werden.

Anlage des P1 in Abhängigkeit vom Alter

Völlig verwachsene Alveolen bei Alttieren können zur Interpretation der Nicht-Anlage dieses Zahnes führen. Wäre dies der Fall, so müßte bei Jungtieren der Anteil

Tabelle 2. **Erscheinungshäufigkeit und Verluste in Abhängigkeit vom Alter des Tieres**

	≤ 12 Monate (n = 63 Schädel)				≥ 13 Monate (n = 252 Schädel)			
	P^1		P_1		P^1		P_1	
	n	%	n	%	n	%	n	%
A	75	59,5	10	7,9	242	48,0	41	8,1
B	1	0,8	–	–	23	4,6	30	6,0
C	–	–	–	–	28	5,6	39	7,7
D	50	39,7	116	92,1	211	41,8	394	78,2

A–D: vgl. Tab. 1

der als nicht-angelegt taxierten P1 tiefer liegen als bei Alttieren. Diese Annahme trifft nicht zu (Tab. 2).

Daß verwachsende oder verwachsene Alveolen bei älteren Tieren häufiger vorkommen als bei 1jährigen und jüngeren entspricht der Erwartung.

Der P1 in den beiden Kieferhälften

Um eventuelle asymmetrische Manifestationen zu erfassen, wurden die an 315 Schädeln gewonnenen Daten nach Körperhälften getrennt ausgewertet (ohne Unterteilung nach Alter und Geschlecht).

Weder im Ober- noch im Unterkiefer ließ sich für eine der 4 Kategorien A bis D ein Links-/Rechts-Gefälle feststellen. Eine Trennung nach Kieferhälften ist daher nicht notwendig. Beidseitige Anlage oder beidseitiges Fehlen ist wesentlich häufiger als einseitiges (80 % im Oberkiefer, 95 % im Unterkiefer). Asymmetrisches Vorhandensein sowohl im Ober- wie im Unterkiefer trat nur dreimal auf.

Bei 190 Oberschädeln sind ein oder zwei P1 nicht ausgebildet, wobei die Zahlen derjenigen mit symmetrischem Fehlen des P1 rund doppelt so hoch liegen wie diejenigen mit einseitiger Anlage. Im Unterkiefer weisen 15 Schädel lediglich einen P1 auf, bei 18 fehlten beide. Einseitiges Fehlen des P1 ist in beiden Kiefern seltener als beidseitiges (Tab. 3).

Verteilung der Ausbildung des P1 auf den Gesamtschädel

Bei lediglich 121 Schädeln sind mit Sicherheit alle vier P1 angelegt worden (38,5 %). Bei 12 Schädeln fehlen alle P1 (= 3,8 %). Fehlen beide P1 im Unterkiefer, fehlen sie mit 6 Ausnahmen auch im Oberkiefer (Tab. 4, Abb. 2).

Tabelle 3. **Manifestation und Zustand des P1 in beiden Kieferhälften**

		P1 links		P1 rechts	
		n	%	n	%
Oberkiefer	A	160	50,8	157	49,9
	B	12	3,8	12	3,8
	C	14	4,4	14	4,4
	D	129	41,0	132	41,9
Unterkiefer	A	24	7,6	27	8,6
	B	19	6,0	11	3,5
	C	19	6,0	20	6,3
	D	253	80,4	257	81,6

A–D: vgl. Tab. 1

Tabelle 4. **Schädel mit nicht angelegten P1, ohne Berücksichtigung ob 1 oder 2 Zähne angelegt sind; verlorengegangene und beschädigte Zähne als angelegt taxiert**

	♂♂ (n =138)		♀♀ (n =177)		♂♂ + ♀♀ (n =315)	
Nur im Oberkiefer	75	63,8 %	86	57,6 %	161	60,3 %
Im Ober- u. Unterkiefer	13	10,2 %	16	10,7 %	29	10,5 %
Nur im Unterkiefer	1		3		4	

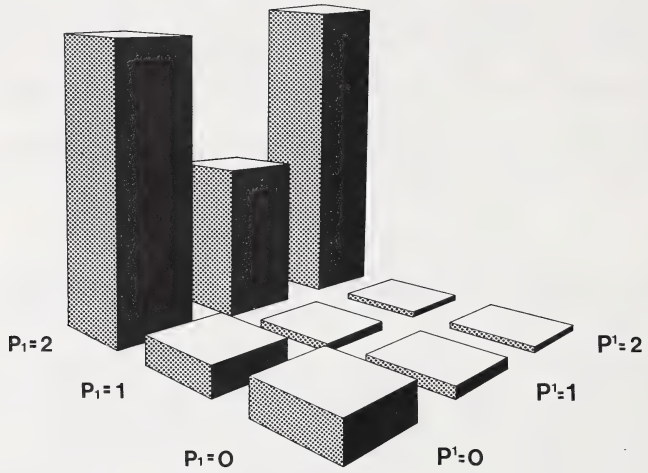

Abb. 2. Manifestation des P1 bei 315 Schädeln

Ausbildung des P1 in Abhängigkeit von der Schädellänge

Unter der Annahme einer höheren Variabilität der Schädellänge im Verhältnis zu derjenigen der Zahngröße müßte der für die Ausbildung der P1 zur Verfügung stehende Raum bei großen Schädeln erweitert sein (s. Lüps und Roper 1988). Bei großen Schädeln könnten damit die P1 häufiger angelegt worden sein, als bei kleinen. Um dies zu überprüfen, wurden 222 Schädel mehr als einjähriger Tiere (> 12 Monate) mit meßbarer Condylobasallänge untersucht. Das Vorhandensein von zwei, einem oder keinem P1 je Kiefer (Ober- und Unterkiefer gesondert betrachtet) wurde nach Geschlechtern getrennt gegen die Schädelgröße aufgetragen. Ein Trend nach häufiger ausgebildeten P1 bei längeren Schädeln läßt sich nicht nachweisen (Abb. 3).

Metrische Analyse

Maße, Größen- und Formvariabilität des P1

Größte Länge und geringste Breite weisen ähnliche Variationskoeffizienten auf (durchwegs zwischen 10 und 13). Deutlich höhere v-Werte weist die Höhe ab Kieferrand auf (v = 12–24), wobei es hier zu berücksichtigen gilt, daß diese Zähne leicht beschädigt oder abgeschliffen sein können und sie nach erfolgter Präparation unterschiedlich tief eingesetzt worden sein können, diesem Maß somit keine allzu große Bedeutung beigemessen werden darf (Tab. 5).

Ein Vergleich von P_1-Maßen bei Schädeln mit und ohne P^1 läßt keine faßbaren Unterschiede erkennen.

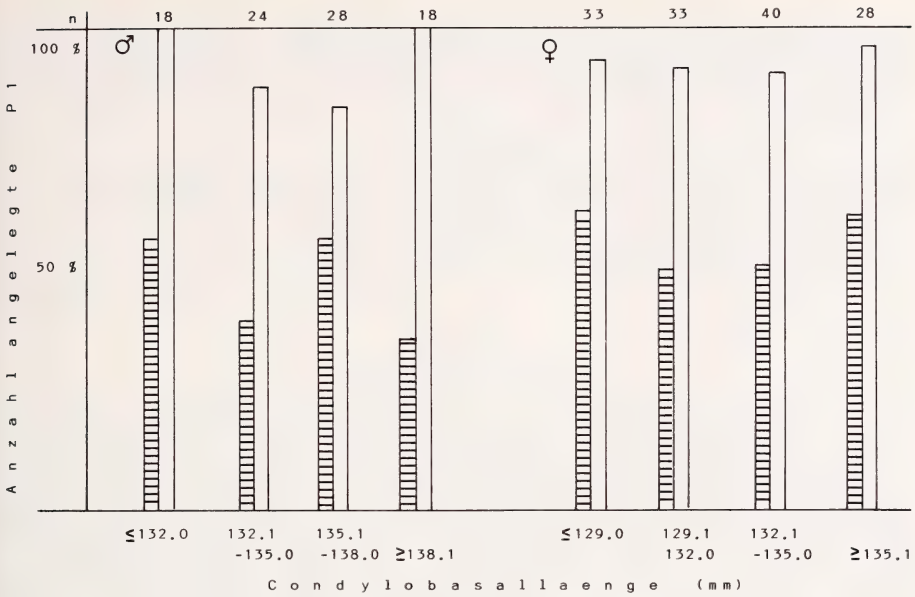

Abb. 3. Die Anlage der P1 in Abhängigkeit von der Schädellänge. Schraffiert: P^1; weiße Säulen: P_1

Ausscheren des P1 aus der Zahnreihe

Im Oberkiefer (n = 21 Schädel) stehen die P1 in 14 der 42 Fälle um bis 1 mm, in den übrigen 28 (= 66,7 %) um mehr als 1 mm lingual zur Backenzahnreihe versetzt. Im Unterkiefer (n = 42 Schädel) sind Abweichungen um mehr als 1 mm nach lingual oder buccal selten (n = 4, = 4,8 %).

Zahnabstände

Die beiden Serien (je 21 mit und ohne P^1) unterscheiden sich weder in der Schädellänge noch in den Abständen vom C zum M1 (alle $p > 0{,}7$) noch in den Abständen des C zu P_1 und P_2 (alle $p > 0{,}09$). Bei Schädeln mit fehlendem P^1 aber ist der Abstand C–P^2 hochsignifikant kleiner als bei solchen mit vorhandenem P^1 ($p < 0{,}001$).

Mit zunehmender Distanz vom C nimmt die Variabilität ab, d. h., daß in beiden Kiefern die Lücke zwischen C und P1 die höchste Variabilität zeigt. Tatsächlich finden sich in beiden Kiefern Abstände von 0 (keine räumliche Trennung der Alveolen von C und P1 am Alveolarrand, d. h., an der Kieferoberfläche bilden sie eine Einheit) bis zu 1,5 mm.

Im Unterkiefer sind die Abstände C–P1 durchschnittlich doppelt so groß wie im

Tabelle 5. **Die Größe des P1 im Ober- und Unterkiefer bei 21 ♀♀ mit 4 angelegten P1**
(Vgl. Tab. 6a; bei 5 Tieren sind die P1 im Ober- und/oder Unterkiefer verlorengegangen; Angaben in mm)

	P^1				P_1			
	n	$\bar{x}$	s	v	n	$\bar{x}$	s	v
Länge	16	1,46	0,15	10,3	16	1,41	0,18	12,8
Breite	16	1,13	0,17	15,0	16	1,18	0,12	10,2
Höhe	16	2,12	0,50	23,6	16	2,30	0,29	12,6

Oberkiefer (Tab. 6). Der Abstand zwischen C und P2 ist im Unterkiefer noch um rund 1 mm größer als im Oberkiefer, beim Abstand C–M1 sind die Abstände praktisch identisch mit einer geringen Variation, die von derjenigen der Condylobasallänge unwesentlich abweicht.

Stellung des P1

Im Oberkiefer weisen 16 P1 (= 38,1 %) eine annähernd senkrechte Stellung im Kiefer auf, 14 sind nach vorn gerichtet, 10 nach außen und 2 nach innen.

Im Unterkiefer stehen lediglich 9 P1 annähernd senkrecht, 4 weisen nach außen, die übrigen 71 nach vorn (= 84,5 %).

Diskussion

Morphologische Aspekte

Beim P1 handelt es sich sowohl im Ober- wie im Unterkiefer um den in allen Dimensionen kleinsten Zahn im Gebiß des europäischen Dachses. Er weist eine deutlich höhere Variabilität (ausgedrückt als Variationskoeffizient v) auf als die andern Zähne (Lüps und Roper 1988). Ebenfalls sehr variabel sind seine Abstände zu C und P2, seine Lage in bezug auf die Backenzahnreihe und die Stellung im Kiefer in bezug auf die Senkrechte. Diese Punkte sind bei Berücksichtigung seiner Stellung als Endglied der Prämolarenreihe verständlich. Er zeigt alle Merkmale eines stammesgeschichtlich (Quinet 1966; Gingerich und Winkler 1979; Pengilly 1984; Wolsan et al. 1985) oder durch Rassenzucht bedingten (Grüneberg 1963), sich in Reduktion befindlichen Zahnes. Diese Feststellung wird durch das sehr häufige Fehlen, nicht infolge Verlust durch Trauma, sondern durch das Fehlen einer Anlage oder deren nicht erfolgte Ausgestaltung unterstrichen. Es handelt sich um einen klassischen Fall fortschreitender echter Oligodontie. Für diese u. a. auch von Heráň (1971), Neal (1977), Stubbe (1980) und Vítaz (1986) vertretene Ansicht sprechen sehr viel mehr Fakten als für die durch Fullagar et al. (1960) und Corbet und Southern (1977) erwähnte Alternative einer zusätzlichen Anlage (Polyodontie). Polyodontien treten bei Dachsen selten auf (Fullagar et al. 1960; Heráň 1971; Stubbe 1980; Lüps 1986) und lassen allgemein kein einheitliches Bild erkennen, wie dies beim P1 der Fall ist.

Der Vergleich zwischen Ober- und Unterkiefer läßt im Oberkiefer eine stärkere Reduktionstendenz erkennen als im Unterkiefer. Hinweise sind ein häufigeres und etwas stärker asymmetrisches Fehlen des P^1, sein stärkeres Ausscheren aus der Zahnreihe und das ausgeprägtere Abweichen von der häufigsten Zahnstellung. Diesem Trend entsprechende geringere Unterschiede in der absoluten Größe und eine erhöhte Variation im Oberkiefer liegen aber nicht vor. Möglicherweise ist bereits die Schwelle erreicht, bei deren Unter-

Tabelle 6. **Zahnabstände bei je 21 ♀♀**

A: Tiere mit 4 angelegten P1, B: Tiere mit nur im Unterkiefer angelegten P1. (Angaben in mm)

		Oberkiefer				Unterkiefer		
	n	x̄	s	v	n	x̄	s	v
A. C–P1	21	0,23	0,24	104,3	21	0,50	0,37	74,0
C–P2	21	1,44	0,49	34,0	21	2,54	0,49	19,3
C–M1	21	21,78	1,09	5,0	21	21,28	1,10	5,2
Condylobasallänge	21	132,29	4,58	3,46				
B. C–P1	–	–	–	–	21	0,66	0,38	57,6
C–P2	21	0,87	0,34	39,1	21	2,78	0,40	14,4
C–M1	21	21,63	0,76	3,5	21	21,14	0,64	3,0
Condylobasallänge	21	132,89	2,98	2,2				

schreitung die Anlage eines Zahnes ausbleibt (vgl. Grüneberg 1963), was im Oberkiefer häufiger geschieht als im Unterkiefer. Aufgrund dieser Befunde darf auf eine stärkere Konzentration des Zahnmaterials und damit der kau-wirksamen Fläche im Oberkiefer geschlossen werden, wie dies auch anhand der Messungen an den übrigen Zähnen postuliert wurde (Lüps und Roper 1988).

Zwei Erklärungen bieten sich an für die Unterschiede in der Diastemlänge C–P2 bei Tieren mit und solchen ohne P^1: 1. Das Fehlen einer P^1-Anlage bietet dem P^2 mehr Platz zum Wegrücken vom P^3, was zu einer lockereren Stellung innerhalb der gesamten Backenzahnreihe führen kann; 2. der geringe Abstand C–P^2 verunmöglicht das Erscheinen eines P^1. Die erste Erklärung ist wahrscheinlicher, eine Überprüfung anhand des vorliegenden Schädelmaterials ist aber nicht möglich.

Funktionelle Aspekte

Die recht kräftigen Eckzähne belegen die stammesgeschichtliche Herkunft des Dachses als Vertreter der Carnivora, die breiten und höckerigen ersten Molaren aber weisen auf den „Allesfresser" hin. Detailliertere Angaben zum Gebrauch der einzelnen Zähne des Dachsgebisses liegen aber kaum vor. Immerhin verweisen Kruuk (1978) und Macdonald (1980) auf den Einsatz der Schneidezähne beim Fangen von Regenwürmern *Lumbricidae*. Lüps und Roper (1988) bringen die Eckzähne mit intraspezifischen Auseinandersetzungen in Zusammenhang. Daß die Molaren der Zerkleinerung der Nahrung dienen, geht aus deren oft sehr starken Abkauung (Stubbe 1965; Neal 1977) und der Beobachtung zerquetschter Speisereste (z. B. Weizen, Roper und Shepherdson briefl.) hervor, auch wenn andere Nahrungspartikel unzerkaut geschluckt werden (z. B. Kirschsteine, eigene Beob.). Über die Bedeutung des P1, dem ihm möglicherweise Schutz gegen mechanische Beschädigung gewährenden Eckzahn unmittelbar anschließend, liegen keine Angaben vor. Der P1 geht nur unwesentlich häufiger verloren als der I1 (Lüps 1986). Wesentlich ist die Beobachtung, daß die P1 das Zahnfleisch kaum überragen und bisweilen nur mit einem harten Gegenstand ertastbar sind.

Geographische Variation

Heptner (1968) hat auf ein West-Ost-Gefälle in der Erscheinungshäufigkeit des P1 hingewiesen: Die ersten Lückenzähne fehlen bei fernöstlichen Unterarten von *Meles meles* völlig, erscheinen nach Westen mit zunehmender Häufigkeit und sind in Mitteleuropa zu mehr als 75 % vorhanden (vgl. auch Heptner und Naumov 1974). Es gilt allerdings zu berücksichtigen, daß seine Serien zum Teil nur wenige Individuen umfassen, bei der Interpretation eine gewisse Zurückhaltung am Platze ist. Da kaum eine der in den letzten Jahren veröffentlichten Arbeiten die Angaben Heptners berücksichtigt, sind seine Angaben in Abb. 4 auszugsweise wiedergegeben. Inzwischen sind aus Mittel- und Osteuropa weitere Serien auf den numerischen Zustand des Gebisses hin untersucht worden. Da sich einige als nicht sehr umfangreich (z. B. Ratcliffe 1971; Stubbe 1980; Vítaz 1986) oder als sehr heterogen zusammengesetzt präsentieren (z. B. Spittler und Jansen 1985), werden hier nur diejenigen berücksichtigt, die durch ihre Herkunft eine repräsentative Stichprobe gewährleisten. Der Vergleich der Daten Heptners (1968) mit einer differenziert zusammengesetzten Übersicht aus West- und Mitteleuropa bestätigt die Pauschalbeurteilung „Europa" dieses Autors mit 69,3 % angelegten P1 weitgehend. Innerhalb weiter Teile Europas (für Südeuropa fehlen Vergleichswerte weitgehend) liegt aber kein klares Bild vor. So weisen die benachbarten Populationen aus dem Hakel (Stubbe 1980), aus der Slowakei (Vítaz 1986) und aus Böhmen (Heráň 1971) recht unterschiedliche Werte auf. Die geringste Zahl angelegter P1 und am wenigsten Schädel mit 4 P1 fand Hancox (cit. in Neal 1977). Eine Mittelstellung nehmen die 100 Schädel aus Dänemark *(Meles m. danicus)*

Abb. 4. Manifestationshäufigkeit des P1 im eurasischen Raum. Gerasterte Kreissegmente: Prozent angelegte P1 pro Serie. A = vorliegende Daten (n = 315); B = Großbritannien (n = 212, Hancox, cit. in Neal 1977); C = Dänemark (n = 100, s. Text); D = Hakel/DDR (n = 82, Stubbe 1980); E = Rumänien (n = 47); F = mittlerer und östlicher Teil der europ. UdSSR (n = 105); G = Gebirgssysteme Mittelasiens (n = 23); H = Tien-Tsin (n = 30); I = Transbaikal und Ussuri (n = 33). E–I aus Heptner (1968)

ein, sowohl was die Gesamtzahl angelegter P1 (70 %), wie die Anzahl Schädel mit P1 = 4 anbetrifft. Es handelt sich bei diesen Schädeln aus Dänemark um die einzige Serie, die mit der in dieser Arbeit untersuchten aus methodischen Gründen uneingeschränkt verglichen werden darf, da die Datenaufnahme (und Interpretation) durch denselben Bearbeiter erfolgt ist.

Folgerungen

Häufiges Fehlen (Oligodontie) und eine hohe Variabilität in Größe, Form, Lage und Stellung lassen den P1 im Gebiß des Dachses als typischen Fall eines sich in Reduktion befindlichen Endgliedes der Backenzahnreihe erkennen. Die Hypothese einer Polyodontie muß wegen des häufigen Auftretens verneint werden. Diese Reduktion ist in Zusammenhang mit einer starken Konzentration des Zahnmaterials auf den M1 hin (Pocock 1920; Petter 1976) zu betrachten. In dem für die Reihe M1–P2 festgestellten Gradienten in beiden Kiefern (Lüps und Roper 1988) bildet der P1 das Endglied mit allen Konsequenzen. Mitteleuropäische Dachse zeigen diese Reduktion wesentlich weniger ausgeprägt als diejenigen weiter östlich beheimateter Populationen (Daten allerdings nur numerisch, ohne metrische Angaben, Heptner 1968). Einen ähnlichen Trend in der Variation beschreiben u. a. Glass und Todd (1977) für den zweiten oberen Backenzahn bei *Felis bengalensis*. Die Autoren messen dieser quasi-kontinuierlichen Merkmalausbildung keinen diagnostischen Wert bei. Matjuschkin (1978), Werdelin (1981), Kurtén und Werdelin (1984) andererseits befassen sich mit systematischen Fragen im Zusammenhang mit Zahnpolymorphismen beim Genus *Lynx*. Eine Diskussion über die Irreversibilität stammesgeschichtlich

verlorengegangener Merkmale (Wolsan 1984; Kvam 1985; Werdelin 1987) erübrigt sich bei den hier vorgelegten Daten für den Dachs. Über die Stabilität eines solchen phänotypischen Polymorphismus im europäischen Raum können allerdings keine Aussagen gemacht werden, da genetische Untersuchungen zu diesem Fragenkomplex, wie sie dazu notwendig wären (vgl. Villwock 1984), bislang nicht vorliegen. Für den Prämolarenverlust beim Deutschen Schäferhund vermutet Rosin (1949) einen rezessiven Erbgang mit schwankendem Ausprägungsgrad. Auch Horak (1988) weist auf einen rezessiven Erbang für Prämolarenverlust bei Haushunden hin. Die bei Labormäusen und beim Menschen gewonnenen Erkenntnisse (vgl. Hillson 1986) weisen auf eine hohe Komplexität hin, die auch bei diesen, anhand von Stammbäumen rekonstruierbaren Beispielen nicht klar durchschaubar ist.

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Zusammenfassung

Das Vorhandensein, die Größe, Lage und Stellung der ersten Vorbackenzähne P1 im Ober- und Unterkiefer wurde bei 20 Jungdachsen mit noch nicht abgeschlossenem und 315 Dachsen mit vollständig abgeschlossenem Zahnwechsel numerisch und metrisch erfaßt. Da in keinem untersuchten Kriterium geschlechtsspezifische Unterschiede vorlagen, wurden ♂♂ und ♀♀ für die meisten numerischen Abklärungen als Einheit gewertet. Resultate:

1. Der P1 erscheint im Milchgebiß nicht.
2. Bei jungen Dachsen (≤12 Monate) ist der P1 nicht häufiger vorhanden als bei älteren. Sein Fehlen ist in den meisten Fällen als echte Oligodontie zu werten.
3. Der P^1 fehlt zu 50 %, der P_1 zu 8 %.
4. Zwischen linker und rechter Kieferhälfte finden sich keine Unterschiede in der Häufigkeit des Erscheinens und in den Maßen.
5. Beidseitiger P1-Mangel ist sowohl im Ober- wie im Unterkiefer häufiger zu beobachten als einseitiger.
6. Eine Abhängigkeit von der Schädelgröße läßt sich nicht nachweisen.

Diese Befunde werfen morphologische, funktionelle und geographische Fragen auf. Über die genetischen Grundlagen können vorläufig keine Aussagen gemacht werden.

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Contribution à l'éco-éthologie du Molosse de Cestoni, *Tadarida teniotis* (Chiroptera), dans les Alpes valaisannes (sud-ouest de la Suisse)[1]

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Abstract

Contribution to the eco-ethology of the European free-tailed bat, Tadarida teniotis (Chiroptera, Molossidae), in the Alps of the Valais (south-western Switzerland)

Studied roosts and seasonal activity of the European free-tailed bat *(Tadarida teniotis)* in the Swiss Alps from 1985 to 1988. *T. teniotis* has been caught repeatedly (1958–1988; 32 times) in the nets of ornithologists on the Franco-Swiss passes of Balme and Bretolet, and was presumed to be a migrant or a vagrant in the north-western Alps. Acoustic and visual observations resulted in the discovery of 4 rock-inhabiting colonies. The day-time roosts are located between 570 and 1100 meters above sea-level at the foot of tall vertical, limestone cliffs, well exposed to sunshine. The bats roost in narrow vertical crevices under slabs of rocks parallel to the main rock mass, the opening being oriented downwards. Two major facts concerning the biology of the Free-tailed bat were evidenced: a sedentary status and intermittent hunting activity in winter. The topographical configuration as well as microclimatic conditions are probably two factors allowing this species to subsist the year-round above 46° latitude north. Observations of *T. teniotis* hunting on the passes of Bretolet and Balme suggest that the species ascend to the passes to feed on the multitude of migratory insects.

Introduction

Chauve-souris méridionale qui atteint dans les Alpes la limite nord de son aire de répartition paléarctique, *Tadarida teniotis* est le seul représentant de la famille des Molossidés qui ait colonisé le continent européen. Dans leurs monographies, Aellen (1966) et Kock et Nader (1984) ont déjà traité en détail les questions relatives à la systématique, à la taxonomie, à la paléontologie et à la biogéographie du Molosse de Cestoni.

En Suisse, à part deux anciennes mentions de Bâle et du col du Saint-Gothard, en 1869 et 1872 respectivement (Aellen 1966), l'espèce a été capturée régulièrement sur les cols de Bretolet (1920 m) et de Balme (2200 m), à la frontière franco-suisse, dès la fin des années 1950 (Aellen 1962; Catzeflis 1980). Parallèlement à ces découvertes en altitude, Helversen (in Zbinden et Zingg 1986), puis Lehmann et al. (1981) et enfin Zbinden et Zingg (1986) ont réalisé une série d'observations dans le canton du Tessin (sud-est de la Suisse) de 1969 à 1984, entre 230 et 600 m d'altitude; cependant, aucune capture n'a été réalisée jusqu'ici au sud des Alpes, sur territoire helvétique, et les mentions tessinoises concernent exclusivement des contacts visuels crépusculaires ou des individus entendus, voire enregistrés, lors de leurs parties de chasse nocturnes (fig. 1).

Quoique régulières – puisqu'elles constituent 2.2 % du total des chauves-souris baguées sur le col de Bretolet (Aellen, in litt.) et 8.6 % des captures du col de Balme (Catzeflis 1980), [cf. tabl. 1 et fig. 1] – les apparitions de *T. teniotis* sur les cols alpins ont longtemps passé pour des incursions sporadiques d'individus erratiques, voire migrateurs (Aellen 1962, 1966).

[1] Ce travail est dédié à Jürgen Gebhard.

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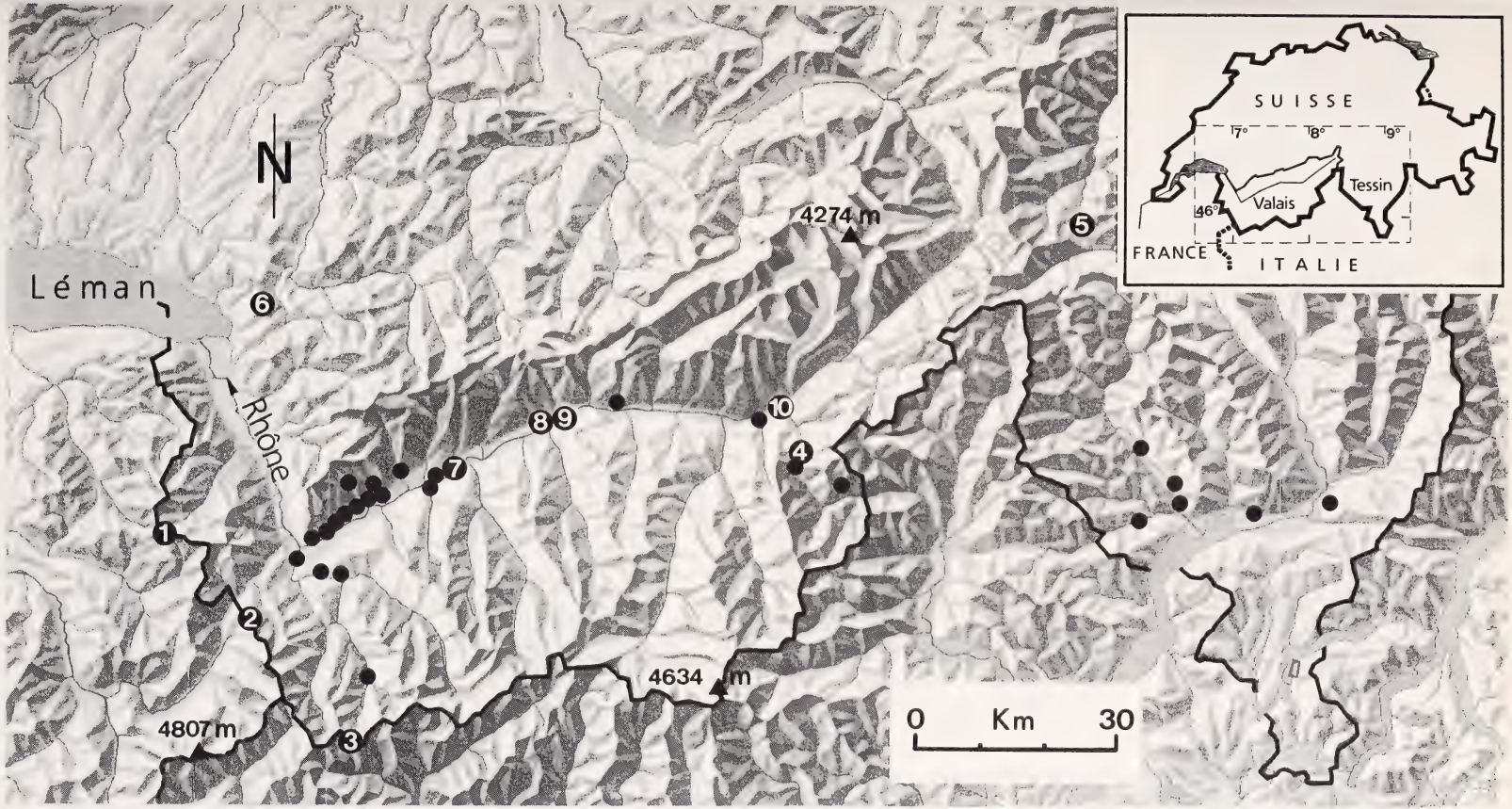

Fig. 1. Situation géographique du Valais (encart) et aire de répartition de *Tadarida teniotis* en Suisse:
• Valais: observation acoustique et/ou visuelle ainsi que capture; Tessin: enregistrement d'individus en chasse [Zbinden et Zingg (1986)]
● 1. col de Bretolet, 1920 m (29 captures)/2. col de Balme, 2200 m (3 captures)/3. col du Grand Saint-Bernard, 2470 m/4. col du Simplon, 2005 m/5. col du Saint-Gothard, 2000 m (une mention)/6. col de Jaman, 1512 m/7. Sion, 500 m/8. Sierre, 540 m/9. Bois de Finges/10. Brig, 680 m
(Reproduit avec l'autorisation de l'Office fédéral de topographie du 23. 9. 1988)

Cadre de l'étude

Profonde vallée intra-alpine d'orientation est-ouest, le Valais jouit d'un régime climatique fort singulier. Relativement humide dans sa partie avale, le climat devient très sec dans le Valais central où a été enregistré le minimum absolu de précipitations annuelles dans l'ensemble du massif alpin (450 mm, Ozenda 1985). Dans l'ouest du canton, le régime pluvial est de type continental, avec un pic caractéristique en période estivale; dans le Haut Valais, soit en amont du Bois de Finges, le déficit estival traduit par contre l'influence notoire d'un régime saisonnier méditerranéen (Roten 1964). Le Valais est l'une des régions de Suisse où la nébulosité est la plus faible, les nappes de brouillard hivernal s'avérant particulièrement rares dans la plaine du Valais central (en moyenne 5–10 jours l'an). L'insolation absolue y est ainsi l'une des plus intenses de Suisse: entre 2000 et 2100 heures annuelles en moyenne dans le centre du canton. Un des caractères les plus frappants de cette insolation réside dans ses valeurs hivernales élevées: 300 heures pour les trois mois d'hiver, alors que le Plateau vaudois

Tableau 1. **Molosses capturés sur les cols franco-suisses de Bretolet (1958–1988: 29 individus) et de Balme (1973–1974: 3 individus); noter la nette prédominance de mâles**

Date	sexe	collection/No bague	heure	poids [gr]	observateur
A. Col de Bretolet, 1920 m d'altitude					
11.08.58	mâle	Mus. Genève 946.1	04.00		M. Godel
27.08.58	mâle	Mus. Genève 949.7	00.45	33	F. Vuilleumier
19.08.61	mâle	623 A	24.00	28	F. Vuilleumier
04.09.62	mâle	626 A	02.00	34.5	V. Dorka
19.09.63	mâle	Mus. Genève 1044.12		36	A. Meylan
22.09.63	mâle	Mus. Genève 1044.13			A. Meylan
05.10.64	mâle	Mus. Genève 1065.90	22.30	42.5	
??.??.64	?	Mus. Lausanne			J. Aubert
08.09.68	?	Coll. A. Brosset	09.00		J. Aubert
19.09.68	mâle	641 A			
07.08.70	mâle	642 A	22.30		W. Kübler
31.07.72	mâle	644 A	05.00	36	R. Winkler
05.08.72	mâle	646 A	05.00	32	R. Winkler
12.08.72	mâle	647 A	04.30	32	R. Winkler
08.09.72	mâle	651 A	22.30	35	R. Winkler
03.10.72	mâle	652 A	06.00	35	R. Winkler
23.08.73	mâle	654 A	03.30	32	R. Winkler
23.08.73	mâle	655 A	03.30	31	R. Winkler
04.09.73	mâle	656 A	03.00	28	R. Winkler
14.09.73	mâle	658 A	01.00	30	R. Winkler
01.08.74	mâle	659 A	01–05.00	36	R. Winkler
03.08.74	mâle	660 A	02.30	33	R. Winkler
23.09.76	mâle	666 A	00.30	35	R. Winkler
11.09.77	mâle	675 A	22.45	31	L. Jenni
08.09.80	mâle		04.00	42	L. Jenni
01.10.81	mâle	712 D	23.00	45	L. Jenni
16.07.82	mâle	713 D	02.00	31	L. Jenni
25.08.82	mâle	715 D	22.30	34	L. Jenni
06.08.88	mâle	809 E	01.00	33	M. Leuenberger
B. Col de Balme, 2200 m:					
29.07.73	mâle	426 B			F. Catzeflis
20.08.73	mâle	427 B			F. Catzeflis
25.08.74	fem.	428 B			F. Catzeflis

voisin n'en connaît que 180. Le Valais est également soumis à un régime de foehn, vent du sud chaud et sec qui entraîne de fréquents redoux, particulièrement sensibles en période hivernale. A Sion, la moyenne des températures du juillet atteint environ 20° alors que celle de janvier est proche du 0 °C (Bouet 1978; Imhof 1965–78; Schüepp 1961, 1962, 1963; Uttinger 1965).

D'un point de vue faunistique, cette région abrite, aux côtés de reliques boréo-alpines, des populations d'animaux orientaux et méditerranéens à la frange de leur aire de répartition médioeuropéenne. Les espèces de chauves-souris trouvées jusqu' ici en Valais sont: *Rhinolophus hipposideros, R. ferrumequinum, R. euryale* (à l'état subfossile, 3870 ± 60 ans B.P.), *Myotis daubentonii* (morphotype *nathalinae* inclus), *M. brandtii, M. mystacinus, M. emarginatus, M. nattereri, M. bechsteinii, M. myotis, M. blythi, Nyctalus noctula, N. leisleri, N. lasiopterus, Eptesicus serotinus, E. nilssoni, Vespertilio murinus, Pipistrellus pipistrellus, P. nathusii, P. kuhlii, P. savii, Plecotus auritus, P. austriacus, Barbastella barbastellus, Miniopterus schreibersi* et *Tadarida teniotis* (Arlettaz 1986 et obs. pers. inédites).

Matériel et méthodes

Cet article présente une synthèse des observations réalisées entre le 2 septembre 1985 et la fin août 1988. Durant ce laps de temps, des contacts ont été recherchés et/ou obtenus sur 117 jours au total. Un peu plus du quart de ces contacts avec *T. teniotis* sont le fruit du hasard; parmi les journées d'excursion consacrées spécialement à l'espèce, plus de 80 % se sont soldées par un succès de contact. Au total, 104 jours ont fourni des observations positives.

Détection acoustique

Les diverses descriptions des manifestations vocales de *T. teniotis* (König et König 1961, Schilling et al. 1986, etc.) ainsi que l'écoute de prises de son procurées à titre d'illustration par P. Zingg (cf. Zbinden et Zingg 1986) ont servi de référence préable aux investigations sur le terrain. L'enregistrement de divers types de cris – lancés par des animaux tournant devant les falaises, s'agitant à l'intérieur des failles ou chassant à distance des gîtes répertoriés – a été effectué avec un magnétophone équipé d'un micro dynamique monté sur une parabole. Les bandes magnétiques ont été gracieusement analysées sur un oscilloscope par P. E. Zingg; cette méthode a permis de confirmer la validité des critères utilisés pour la détermination de *T. teniotis* à l'oreille nue.

Observation visuelle

Parallèlement aux efforts d'écoute crépusculaire et nocturne, des contacts optiques avec *T. teniotis* ont été recherchés. Les observations se font à l'oeil nu ou aux jumelles, en balisant systématiquement les lignes de crête au crépuscule et, dans une moindre mesure, à l'aube; le recours à un phare halogène de 100 W, branché sur une batterie transportable de 12 V, s'est avéré nécessaire pour l'observation directe des animaux en dehors des phases crépusculaires; souvent deux projecteurs ont même été utilisés: le premier envoyant un faisceau fixe sur un point donné de l'espace ou des parois rocheuses (sur un gîte potentiel par exemple), le second, tenu en main, servant à suivre les Molosses en vol. Lors des factions au pied des parois habitées, en plus de jumelles 10 × 40, un binoculaire 25 × 80 monté sur trépied s'est avéré fort utile; l'appareil optique était alors dirigé en permanence sur le site, dans le faisceau créé par le projecteur fixe. Enfin, une série de clichés photographiques montrant différentes attitudes de Molosses abordant leur gîte au petit matin a pu être réalisée (fig. 2).

Capture

Une trappe telle que décrite par Gaisler et al. (1979) et Perrin (1985) a été construite afin de tenter une capture de *T. teniotis* au gîte; elle n'a jusqu'ici été utilisée qu'une seule fois en Suisse. L'installation de la trappe dans la paroi a nécessité le recours à un varappeur expérimenté. Lors de la tentative de capture, le piège était maintenu en place par un système de cordages légers assuré par deux mousquetons fixes scellés dans la roche au-dessus du gîte (Arlettaz 1987). L'opération se déroula le 26. 09. 86; elle permit de capturer un mâle adulte au pelage gris argenté, d'un poids de 54 grammes (!) pour une envergure de 42 cm. Ses avants-bras mesuraient 61.9 et 62.1 mm.

Le 07. 08. 88, à 01h00 [l'heure indiquée tout au long de ce travail est l'heure d'hiver (HEC)], un second mâle adulte fut capturé au filet sur un plan d'eau où il venait s'abreuver; il pesait 36 gr. et ses avant-bras mesuraient 57.7 et 58.1 mm; son pelage était brun sombre terne avec quelques nuances de gris.

Les deux animaux (ainsi que l'individu capturé à Bretolet le 06. 08. 88, cf. tabl. 1) furent munis d'une bague en aluminium sur la face inférieure de laquelle a été fixé, au moyen d'une colle de contact, un bout de bande adhésive réfléchissante de couleur rouge ou blanche.

Résultats

Critères de détermination in natura

Cris de chasse et émissions sonores

Les cris de chasse du Molosse sont compris entre 9 et 15 kHz, soit inclus entièrement dans les limites de l'amplitude auditive d'un homme normal (Zbinden et Zingg 1986); brefs et cinglants, ils rappellent ceux que la grive musicienne, *Turdus philomelos,* lance en vol (voir également König et König 1961); à deux reprises, des cris de Molosse ont été perçus depuis l'intérieur d'une automobile en marche, malgré le ronronnement du moteur, ce qui donne une idée de leur vigueur! Lorsqu'on perçoit ces sons, ce qui frappe d'emblée c'est à la fois l'altitude relativement élevée, la rapidité et la trajectoire de vol rectiligne du chiroptère qui les émet. Quand ils volent, les Molosses lancent des cris de croisière à raison d'un peu plus d'une émission par seconde; cependant, leur enchaînement s'accélère soudainement («buzz», cf. Zbinden et Zingg 1986) lorsque l'animal prend en chasse une proie de taille. Lors de leur retour matinal au gîte, les Molosses exécutent une série d'environ 3 à 20 tentatives d'abordage avant de pénétrer dans leur faille; au cours de ces manoeuvres, ils décrivent de vastes orbes devant leur cirque rocheux, tout en accélérant leurs pulsions sonores lorsqu'ils s'approchent de la paroi, probablement afin d'accroître l'acuité de leur détection. *T. teniotis* ne crie pas en permanence lorsqu'il vole; au crépuscule et à l'aube, des Molosses ont été vus à maintes reprises sans qu'aucun son ne soit perceptible sur de longs tronçons de vol. Les Molosses sont très bavards au gîte, plus particulièrement à l'aube; ils émettent alors de véritables cascades de sons suraigus, des sortes de crépitements stridents. Des cris grinçants, «liquides» et plus graves, provenant de l'intérieur des fissures occupées, ont également été enregistrés.

Vol et silhouette

L'observation crépusculaire ou nocturne, en l'occurrence au moyen d'un phare ou dans le halo des violents éclairages des stades de football, a permis à plusieurs occasions de suivre visuellement les Molosses lors de leurs déplacements aériens. En principe, ces chiroptères

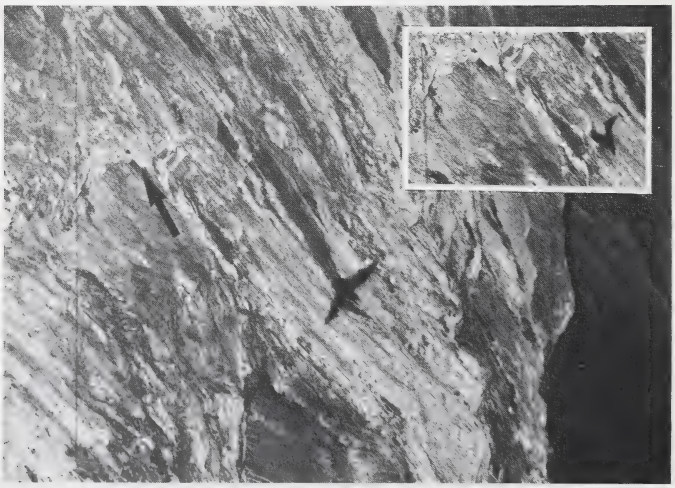

Fig. 2. Silhouette d'un Molosse volant devant sa falaise à l'aube. La flèche indique l'emplacement de la fissure occupée; on devine au-dessus de la faille un des deux mousquetons qui servent à l'arrimage de la trappe et sur la gauche les fils de pêche qui permettent son ascension dans la paroi. Encart: le même individu accostant son gîte au petit matin. Clichés R. Arlettaz

chassent à une hauteur de 10 à 50 m au-dessus du sol, voire davantage; cependant, lors de la poursuite d'un insecte de taille, un papillon nocturne par exemple, ils plongent parfois à 2–5 m seulement au-dessus du sol afin de maîtriser leur proie; lors de ces piqués, on peut entendre, à faible distance, un froissement d'ailes caractéristique. Leur vol suit généralement une trajectoire éminemment rectiligne, sans les brusques crochets qui caractérisent les évolutions de la Noctule, *Nyctalus* sp. Les battements d'ailes du Molosse sont stéréotypiques et peu profonds, paraissant aussi rigides que ceux des Martinets (par exemple *Apus melba*), seul le dactylopatagium étant très mobile (Hill et Smith 1985); s'ils manquent singulièrement d'ampleur, ils sont par contre très énergiques et rapides, semblables sous cet aspect à ceux du Faucon pèlerin, *Falco peregrinus,* voire d'un Limicole. Le vol battu est de règle; parfois cependant, les Molosses interrompent brièvement leur vol actif et se laissent glisser sur leurs ailes étendues. En vol, le corps paraît d'autant plus massif que les ailes sont longues et étroites, mais ce sont ses immenses oreilles qui constituent le caractère le plus frappant de la silhouette de *T. teniotis* (fig. 2; König et König 1961), d'autant plus que la queue semble impossible à discerner chez un individu en vol. Cette particularité écarte d'emblée tout risque de confusion avec les autres grandes espèces de chauves-souris d'Europe (Klawitter et Vierhaus 1975).

Gîtes rupestres

Situation

C'est grâce à des séances d'observation au pied de différents complexes rocheux a priori propices que les falaises préférées des Molosses ont été repérées à la belle saison. Les bruyantes allées et venues que les animaux exécutent à l'aube avant de regagner leur gîte permettent sans trop de peine de localiser précisément les fissures habitées, généralement en suivant les chiroptères dans le faisceau du phare halogène.

Falaise A, site 1. Ce site est situé à 800 m d'altitude, dans un cirque rocheux s'étendant sur plus de 6 km, entre 500 et 3000 m d'altitude. A l'emplacement du gîte, l'orientation générale de la paroi (haute d'environ 530 m) est le sud-ouest, tandis que la section de falaise qui abrite *T. teniotis* est exposée au sud-sud-ouest. La faille habitée par les Molosses est située à environ 30 m au-dessus du sol; au pied dés rochers s'étendent de fins pierriers très déclives que les buissons ont grand peine à coloniser. Cette imposante paroi est essentielle-

Fig. 3. Falaise calcaire abritant les sites 1 et 2; les flèches indiquent leur position respective. D'après dia P.-A. Oggier

ment constituée de calcaires massifs ou lités et d'alternances de marnes et de calcaires argileux qui représentent des dépôts du Jurassique supérieur (Malm), du Crétacé inférieur et du Nummulitique (Eocène supérieur). Selon la saison, un à cinq Molosses (ou plus?) ont occupé ce gîte en 1985, 1986 et 1987 (fig. 2 et 3).

Falaise A, site 2. Découvert en avril 1987 par A. Sierro, ce site se trouve au sud-est et à 900 m à vol d'oiseau du précédent; il appartient à la même unité tectonique et présente une lithologie en tout point similaire. La falaise de même que le gîte sont orientés au sud-sud-ouest. Les deux failles occupées, situées l'une au-dessus de l'autre à une distance d'environ un mètre, se trouvent à 570 m d'altitude, soit à 20–30 m au-dessus du vignoble qui grimpe sur le glacis du pied de la paroi. Un à trois individus y ont été notés (fig. 3).

Falaise B, site 3. Egalement découvert en avril 1987, ce gîte se trouve environ à 3 km au sud-ouest des précédents; la paroi qui l'abrite appartient à la même nappe de roches sédimentaires; cependant, la lithologie est ici constituée de grès siliceux et d'alternances de calcaires et de marnes; elle représente le Jurassique inférieur (Lias). Le site habité est orienté plein sud, à environ 830 m d'altitude, tandis que la falaise sétend sur 2 km de 580 à 1500 m d'altitude; la faille se trouve à environ 20 m du sol. Deux individus au moins volaient devant le gîte en question le 17 avril 1987.

Falaise C, site 4. Les difficultés d'accès au pied de cette autre gigantesque paroi ainsi que le danger de chutes de pierres n'ont pas encore permis de localiser exactement la faille rupestre occupée. Cependant, les allées et venues matinales d'au moins 2–3 Molosses fournissent des indications sur la position de celui-ci. Ce gîte est situé 13 km au sud-sud-ouest de la falaise B, à 1100 m d'altitude et à 30–40 m du pied du cirque qui présente, en plusieurs palliers successifs, un développement vertical de 1150 m (660–1805 m) pour une longueur totale d'un peu plus de 2 km. Le complexe rocheux et le site, d'orientation générale sud-ouest, font partie de la zone des racines des Nappes helvétiques; le site proprement dit est taillé dans une épaisse barre de Malm constituée de calcaires massifs.

Falaises diverses. La présence de Molosses a été notée en d'autres lieux rupestres, cependant sans que leur comportement puisse laisser subodorer l'existence de gîtes occupés de façon permanente. Durant l'hiver 1987/88, des *T. teniotis* ont été notés à leur envol crépusculaire auprès de trois autres falaises situées entre 500 et 900 m d'altitude; il s'agissait peut-être en l'occurrence de gîtes qui ne sont utilisés qu'à la mauvaise saison.

Malgré une propection minutieuse de plusieurs falaises taillées dans des massifs cristallins et présentant des conditions d'exposition et une configuration a priori propices à *T. teniotis,* sa présence n'y a jusqu'ici jamais été décelée.

Configuration des gîtes

Les trois gîtes précisément localisés présentent une structure similaire; situés dans des falaises à pic, par conséquent quasiment dépourvues de végétation, ce sont des fissures exiguës qui lézardent le roc parallèlement à la face et s'ouvrent verticalement vers le bas; leur partie distale forme de la sorte une gigantesque écaille qui paraît décollée de la masse rocheuse et revêt à son extrémité l'aspect d'une lèvre de plusieurs centimètres d'épaisseur (fig. 2). Les Molosses se réfugient à l'intérieur de cette étroite poche suspendue. Sur le site 2, il a été possible de discerner un Molosse dans sa faille, en plein jour, avec des jumelles longue focale, en éclairant l'intérieur de la fissure depuis le pied de la falaise.

Activité saisonnière

Sédentarité et activité de chasse hivernale

Un suivi régulier des gîtes répertoriés, principalement ceux de la falaise A, permet d'affirmer que les Molosses qui les habitent sont de moeurs sédentaires. Les contacts sont cependant beaucoup plus sporadiques durant les mois froids, ce qui trahit selon toute

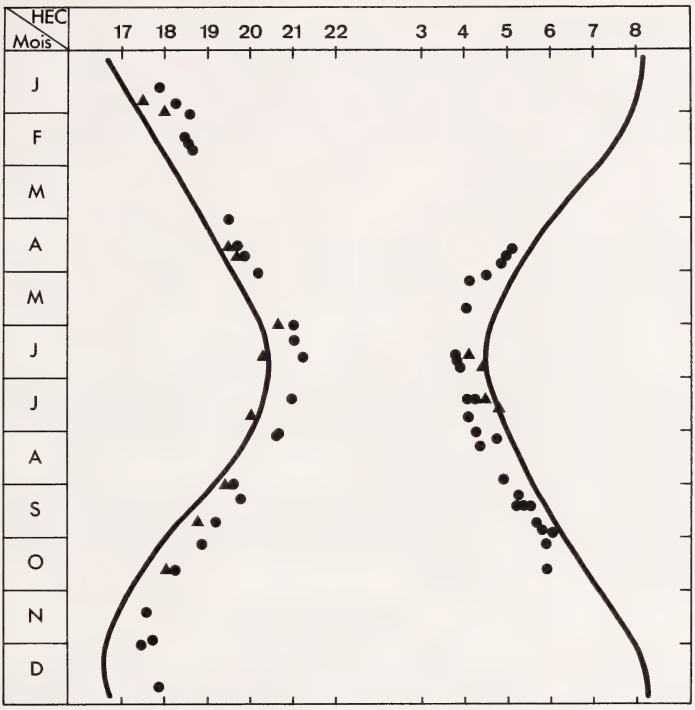

Fig. 4. Rythmes circadiens:
● *Tadarida teniotis:* essor vespéral et retour au gîte à l'aube
▲ Chiroptera sp. (*Pipistrellus* sp.?): premiers et derniers contacts à proximité des mêmes falaises
– coucher et lever du soleil
HEC = Heure Europe Centrale (heure dite «d'hiver»)

vraisemblance une activité hivernale intermittente qui coïncide apparemment avec les périodes de redoux (voir Avery 1985). Voici relatées quelques observations vespérales par basse température extérieure: 1° le 25 janvier 1987, un Molosse est entendu au site 1 entre 18h15 et 18h54; le thermomètre indique 0.5 °C à 17h30 et 0 °C à 19h00; 2° le 1er février 1987, le thermomètre digital affiche 0.7 °C à 18h30 lors du passage d'un Molosse; 3° le jour de Noël, 25 décembre 1987, un Molosse émerge de la paroi, alors qu'il fait 0°C. D'autres factions au crépuscule par température ambiante inférieure à 0 °C se sont en revanche révélées négatives; le 31 janvier 1987, par exemple, il fait −0.5 °C et les Molosses ne se manifestent pas. De même, les rares visites effectuées à l'aube en période hivernale n'ont jamais permis de détecter un quelconque signe d'activité (fig. 4 et 5); l'important contraste thermique nocturne en est probablement la cause: dans la plaine du Rhône, les brises descendantes entraînent la formation d'une nappe d'inversion thermique, c'est dire que la température atmosphérique chute progressivement entre le crépuscule et l'aube.

Lors de ces observations hivernales positives, des vols d'insectes isolés (entre autres de lépidoptères nocturnes) ont été constatés, plus rarement le va-et-vient de petits chiroptères (*Pipistrellus* sp.?) le long des parois. Il n'a néanmoins pas été possible de déceler une véritable activité de chasse de *T. teniotis* de la mi-décembre à fin janvier (absence de «buzz»). Par contre, en date du 15 février 1988, la capture de proies est confirmée: 5 Molosses au minimum chassent sur un stade de football, à 460 m d'altitude, de 19h15 à 20h30 environ (heure d'extinction des projecteurs), par une température voisine de 5 °C. Ce soir-là, quelques rares «buzz» accompagnaient la poursuite de papillons de nuit;

Tableau 2. **Décalage, en minutes, entre le coucher/lever astronomique du soleil et le premier contact au crépuscule/dernier contact à l'aube auprès des gîtes occupés par *T. teniotis* (observations acoustiques et optiques)**

Les premiers et derniers contacts optiques avec de petites chauves-souris indéterminées cohabitant dans les mêmes falaises sont indiqués à titre de comparaison.

Espèce	nombre d'observations	moyenne	minimum	maximum
T. teniotis	54	39′ ± 11′	20′	71′
Chiroptera sp. (*Pipistrellus* sp.?)	15	13′ ± 14′	−20′	30′

toutefois, le comportement des Molosses indiquait semble-t-il surtout une chasse soutenue aux petits insectes qui gravitaient nombreux autour des lampadaires; ces derniers étaient probablement gobés sans qu'une véritable prise en chasse ne s'avère nécessaire, c'est-à-dire sans qu'aucun «buzz» ne soit perceptible.

Le Molosse est actif non seulement par basse température, mais également par temps maussade: le 13 mars 1988, un Molosse chasse durant plus de 20 minutes, par pluie battante et brise forte, au-dessus d'une autre place de sport (465 m) en poussant de fréquents «buzz» qui signalent l'attaque de gros insectes.

Rythmes nycthéméraux

Les Molosses prennent leur essor relativement tard dans la soirée et leur retour au gîte à l'aube est hâtif; en moyenne, ils quittent ou regagnent leur faille 39 minutes respectivement après ou avant le coucher ou lever astronomique du soleil; leur activité crépusculaire est en outre sensiblement plus réduite que celle des autres petites espèces de chiroptères (*Pipistrellus* sp.?) qui cohabitent dans les mêmes falaises (cf. tabl. 2 et fig. 4) ou des Noctules, *Nyctalus noctula,* en général (voir par exemple Stutz et Haffner 1985–1986, Perrin 1988). Il n'y a pas de différence notoire de décalage entre soir et matin. Notons enfin que les émergences tardives paraissent plus fréquentes en décembre et janvier (fig. 5).

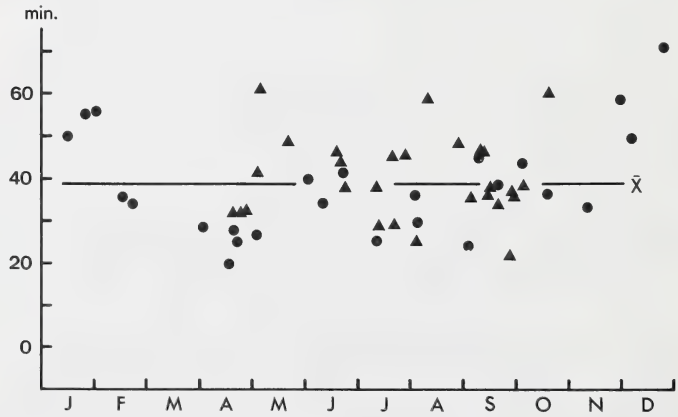

Fig. 5. Décalage (en minutes) entre le lever ou coucher du soleil (= 0) et le premier (● = contact vespéral) ou dernier (▲ = contact matinal) indice d'activité auprès des gîtes occupés (observations acoustiques et optiques)

Mobilité spatiale

Deux seuls *T. teniotis* ont été capturés et bagués jusqu'ici dans la plaine valaisanne; la bague réflectrice dont a été affublé le spécimen capturé au gîte a permis de le repérer à deux reprises au moyen du phare; capturé le 26 septembre 1986, ce mâle est observé ibidem le 23 avril 1987 (poursuivant un second individu), enfin il est contacté le 28 août 1987 tandis qu'il chasse sur le village voisin, à 850 m de distance et 250 m de dénivellation du gîte qu'il occupe traditionnellement.

Les Molosses chassent en solitaire ou en petite troupe; ils parcourent vraisemblablement de vastes espaces, s'arrêtant ici ou là pour exploiter une concentration locale d'insectes durant des phases de chasse qui peuvent durer de quelques dizaines de secondes à plusieurs heures, à la façon des Martinets alpins, *Apus melba.* Ainsi, le 17 août 1987, au moins deux Molosses chassent au-dessus d'un village situé à l'amont du coude du Rhône de 20h45 à 22h15, puis de 23h00 à 23h45; cette nuit-là, une singulière concentration de papillons nocturnes est effectivement notée et le phare permet de repérer, non sans difficulté, les Molosses qui les harcèlent inlassablement («buzz» incessants). Les individus qui chassent très fréquemment dans cette zone, propice car abritée du vent, proviendraient d'un cirque calcaire distant de 6 km (falaise C): il n'existe en effet pas d'autre falaise habitée plus proche, sachant que le secteur de chasse en question est situé au coeur d'un massif cristallin où l'espèce est absente, faute de parois propices (cf. discussion).

Plusieurs nuits passées à Balme et à Bretolet ont permis d'étudier l'activité de *T. teniotis* sur ces cols. Les 22–23 septembre 1987 par exemple, nous notons des cris de chasse d'au moins deux *T. teniotis* sur le col de Bretolet presque sans arrêt entre 19h27 et 05h01, soit durant près de dix heures. Or, à cette même période, les Molosses de la plaine du Rhône émergent à 19h12 au crépuscule (20 septembre 1987) et regagnent leur fissure vers 05h40 (20 septembre 1985) [cf. fig. 4]. Le faible écart entre l'émergence des Molosses hors de leur gîte diurne et le premier contact sur le col (15 minutes) – ou entre le dernier contact d'altitude et l'ultime signe d'activité aux alentours des failles (40 minutes) – suggère que les gîtes où certains de ces Molosses logent à cette époque de l'année se trouvent à quelques kilomètres seulement du col, sur territoire helvétique ou français. Notons que la falaise valaisanne la plus proche de Bretolet connue pour abriter *T. teniotis* en est distante de 27 km (site 4): il est par conséquent peu probable qu'ils s'agisse des mêmes individus, puisqu'avec une vitesse de croisière estimée à 40–60 km.h^{-1}, certains au moins des Molosses entendus à Bretolet gîteraient potentiellement dans un rayon de 10 à 15 km du col.

A l'étage subalpin, plusieurs observations de Molosses en chasse ont été réalisées dans d'autres secteurs du Valais: le 23 juin 1986 dans la soirée, un Molosse chasse au-dessus de Bourg-St-Pierre (1640 m d'altitude), village situé au pied du col du Grand-St-Bernard; durant la nuit du 2 au 3 août 1988, deux individus au moins sont entendus près du col du Simplon, vers 1900 m d'altitude; les 3–4 août 1988, quelques individus évoluent au crépuscule et à l'aube, à 1600 m d'altitude, sur des pâturages situés à 8 km au sud-est du col du Simplon (cf fig. 1).

En revanche, *T. teniotis* n'a jamais été pris sur le col de Jaman (situé à 1512 m d'altitude et à 37 km au nord-nord-est de Bretolet, fig. 1), alors que des dizaines de chiroptères y ont été capturés dans les filets des ornithologues depuis 1967 (Gillieron et collaborateurs, comm. pers.). Des séances d'écoute sur place en 1987 et 1988 se sont également révélées négatives.

Discussion

Détermination acoustique

L'essentiel des cris et manifestations vocales de *T. teniotis* appartient au domaine audible (Zbinden et Zingg 1986); cette aubaine permet la détermination de cette espèce à l'oreille

nue, c'est-à-dire sans qu'il y ait besoin de recourir à un diviseur de fréquence pour l'enregistrement des sons, puis à un fastidieux travail d'analyse en laboratoire. Il faut cependant garder à l'esprit que plusieurs espèces de chiroptères européens lancent au vol des cris qui sont naturellement perceptibles par l'homme (*Pipistrellus* spp., *Nyctalus* spp., *V. murinus,* etc.). *Nyctalus noctula,* par exemple, émet ses fréquences les plus basses en limite supérieure de notre spectre acoustique; ses cris sont ainsi partiellement audibles pour les personnes qui disposent d'une bonne ouïe, les jeunes observateurs en particulier (voir König et König 1961). Le risque de confusion étant réel, l'observateur néophyte qui pense être en présence de *T. teniotis* évitera toute identification acoustique intempestive en recourant parallèlement à diverses approches (cf. matériel et méthodes). La détermination acoustique du Molosse exige en effet non seulement de bonnes facultés auditives mais aussi une certaine expérience de terrain.

Les cris de *T. teniotis* sont en fait familiers à l'auteur depuis ses débuts avec les chauves-souris, soit 1979; jusqu'en 1985 cependant, ces manifestations vocales étaient faussement attribuées à des Pipistrelles, *Pipistrellus* sp. Il est intéressant de noter qu'Aellen (1962) confondait lui aussi les cris de *T. teniotis* avec ceux de *Vespertilio murinus:* «Elle (= la Sérotine bicolore) est fréquente au col de Bretolet (...). Il est certain qu'un très grand nombre d'animaux passent le col largement au-dessus des filets; cette assertion est basée sur l'observation répétée de son cri, puissant et prolongé, assez aisément reconnaissable au vol. Les Vespertilions bicolores se font ainsi entendre certaines nuits presque continuellement, du coucher au lever du soleil.»

Morphologie et silhouette

A l'examen d'un Molosse vivant, on remarque que l'uropatagium enserre la queue à la manière d'un fourreau mobile et présente la caractéristique d'être extensible longitudinalement; de la sorte, si la queue dépasse de près de 30 mm chez un animal au repos, sa longueur libre n'atteint que 9 mm lorsque la membrane interfémorale est tirée vers l'arrière. Cette faculté, également notée par Noblet (comm. pers.), joue peut-être un rôle dans la navigation spatiale de cette espèce; elle expliquerait en outre la difficulté de discerner la queue chez un Molosse en vol. Mais la fonction de cette queue est peut-être avant tout celle d'un organe tactile: lorsqu'un Molosse s'enfonce dans une fissure, effrayé par la violence d'un projecteur par exemple, il progresse à reculons, accompagnant son mouvement de fuite par des tâtonnements de la queue.

Sex ratio

Le sex ratio des Molosses capturés en Valais est au premier abord déroutant: une seule femelle pour 33 mâles! Cependant, comme la majorité des captures a été réalisée à Bretolet (85.3 %), cette prédominance de mâles ne reflète peut-être que la situation qui prévaut sur ce col. Deux hypothèses, par ailleurs complémentaires, pourraient expliquer un tel déséquilibre: 1° chez la plupart des chiroptères, les mâles adultes vivent en principe à la périphérie des colonies de mise-bas; dans les régions au relief accusé, ce phénomène entraîne une probabilité d'occurrence des mâles nettement accrue en altitude (en tout cas chez les espèces dont les colonies de parturition sont exclusivement implantées à basse altitude); une telle règle s'appliquerait a fortiori à une espèce aussi méridionale que *T. teniotis.* 2° Bretolet se situe en limite de l'aire de répartition géographique de *T. teniotis*, ce que suggérerait l'absence totale de l'espèce au col de Jaman voisin (cf. résultats); «l'effet de marge» évoqué sous 1° agirait ici dans une perspective géographique (i.e. horizontale) et non plus altitudinale, avec pour conséquence logique une sous-représentation des femelles aux confins de l'aire de distribution puisque ces dernières n'établissent selon toute vraisemblance pas de colonies de parturition en position aussi excentrique, en raison

notamment des conditions écologiques suboptimales qui y règnent. La présence d'une femelle parmi les trois captures de Balme cautionnerait d'ailleurs cette seconde hypothèse puisque ce col occupe une position moins marginale que le précédent (voir fig. 1).

Structure et microclimat des sites rupestres

Les falaises cristallines prospectées en Valais n'ont jusqu'ici révélé aucun indice de présence de *T. teniotis;* il semblerait donc que le calcaire réponde mieux aux exigences écologiques de cette espèce (qualité thermique et/ou microstructures créant des gîtes adéquats).

Les gîtes découverts par P. Medard dans le sud-ouest de la France présentent des caractères identiques à ceux du Valais; ils sont néanmoins situés sur les flancs d'un cañon, dans la partie faîtière de falaises qui ont une hauteur n'excédant pas une cinquantaine de mètres. Il est vraisemblable que l'épaisseur (5 à 30 cm environ) de l'écaille rocheuse sous laquelle ces chiroptères se réfugient, en tout cas durant la belle saison, réponde à des exigences thermiques précises (conductibilité optimale de l'énergie solaire captée en surface); ces failles, situées dans des falaises très exposées au rayonnement solaire, joueraient en outre le rôle d'une cloche dans laquelle l'air chaud qui s'élève à fleur de paroi est piégé (voir aussi Perrin 1988). La température régnant dans ces gîtes avoisinerait par conséquent les maxima concevables en milieu rupestre.

König et König (1961) et Aellen (in litt.) ont observé des Molosses gîtant sous les arcades du Pont du Gard, en Provence. Enfin, dans le nord du Vercors (gorges de la Bourne, Isère), Desmet et Noblet (1976) ont découvert les restes d'au moins 18 Molosses dans un pierrier à l'aplomb d'un vaste porche de grotte fissuré. Contrairement aux gîtes du Valais et du Roussillon, ces derniers ne sont pas situés à flanc de paroi mais surplombent totalement le vide.

Le choix de fissures exiguës béant vers le bas semble propre à plusieurs grandes espèces de chiroptères rupicoles [Molossidés, Brosset (1966); *N. noctula,* Perrin (1988)] qui ont coutume de se laisser choir dans l'espace lors de leur essor vespéral.

L'activité restreinte des Molosses durant les mois les plus froids n'a pas permis de déceler si les gîtes habités à la mauvaise saison sont ces mêmes failles superficielles ou si ce sont des anfractuosités structurellement différentes, par exemple plus profondes; celles-ci seraient a priori plus propices au maintien d'un état torpide, même temporaire, puisque peu sujettes aux aléas des conditions météorologiques extérieures (Perrin 1988). Une chose est sûre: certains sites d'hiver se trouvent dans le proche voisinage de ceux qui sont occupés du printemps à la fin de l'automne.

Mobilité spatiale

Plusieurs faits prouvent que les Molosses ne sont pas des chiroptères en migration sur les cols alpins de Bretolet et de Balme et qu'ils s'y rendent dans le seul but d'exploiter les concentrations d'insectes en transit migratoire automnal: 1° l'aire de répartition géographique de *T. teniotis* ne s'étend pas au nord de la chaîne alpine; si le Molosse était un migrateur transalpin, seules les populations du massif seraient susceptibles de franchir les cols, or les Molosses des Alpes valaisannes sont sédentaires; 2° *T. teniotis* a été observé à proximité du Simplon, col qui ne constitue pas un axe pour la migration automnale (cf. résultats); 3° des contacts acoustiques d'individus en chasse ont été notés non loin d'un col qui constitue bel et bien un axe secondaire de migration, mais en dehors des périodes de passage printanier ou automnal (23 juin, au pied du col du Grand-St Bernard, cf. résultats); 4° l'absence de cette espèce sur le col de Jaman, si proche pourtant de Bretolet, constitue un quatrième argument: si les Molosses de Bretolet étaient migrateurs, ils se seraient également manifestés sur le col de Jaman, comme c'est le cas pour la plupart des autres espèces de chauves-

souris réputées migratrices (voir Aellen 1962). On peut en conclure que le col de Jaman, situé dans les Préalpes du nord, se trouve en dehors de l'aire de répartition de *T. teniotis* (cf. 1°).

Convergence avec le Martinet à ventre blanc

Le Molosse de Cestoni et le Martinet alpin, *Apus melba,* présentent d'indéniables convergences morphologiques et écologiques: ce sont des insectivores avides d'espace aux moeurs essentiellement rupestres. Ce parallèle comporte cependant une restriction majeure: *T. teniotis* est sédentaire tandis que *Apus melba* est un migrateur au long cours. Leur comportement sédentaire rend les Molosses septentrionaux tributaires d'un microclimat hivernal propice puisque cette espèce n'a pas la faculté d'effectuer des léthargies prolongées (Brosset 1966, cf. infra). Cette contrainte draconienne suffirait d'ailleurs à expliquer que *T. teniotis* n'a pas colonisé les falaises helvétiques situées au nord de l'arc alpin qui sont pourtant habitées par le Martinet à ventre blanc. Les Molosses seraient par conséquent géographiquement plus limités que les Martinets à ventre blanc dans le choix de leurs gîtes et secteurs de chasse.

Les falaises valaisannes habitées par le Molosse abritent toutes également des colonies de Martinets alpins; c'est aussi le cas des sites occitans (P. Medard, comm. pers.) et d'autres localités traditionnelles de France méridionale (Pont du Gard par exemple, König et König 1961, Hainard 1987) et d'Espagne (obs. pers.). En Valais, les Molosses logent principalement au pied des parois calcaires, alors que les failles habitées par les Martinets se situent toujours dans leur partie sommitale (des recherches de gîtes dans le haut de ces parois n'ont donné aucun résultat tangible à ce jour); cette différence notable n'est pourtant plus perceptible dans les petites parois des cañons du Roussillon (Medard et Arlettaz, obs. inédites) et de Navarre, Espagne (obs. pers.), où Molosse de Cestoni et Martinet alpin logent côte à côte dans la même fissure.

Comportement sédentaire, activité de chasse hivernale et répartition géographique

La sédentarité et l'activité alimentaire hivernale des Molossidés ne constituent pas en soi des faits nouveaux; de tels comportements n'ont cependant jamais été signalés chez l'espèce *T. teniotis* dont la biologie reste floue. Brosset (1966) décrit les Molosses en général comme des chauves-souris robustes, capables de supporter le manque d'eau et de nourriture, d'endurer des températures extrêmes. Il suggère également, sur la base d'observations et d'expérimentations, que les chiroptères du genre *Tadarida* présentent en revanche une «régulation thermique déficiente»; ils doivent par conséquent se contenter de torpeurs, i.e. de phases léthargiques impossibles à prolonger au-delà d'un certain seuil: «... les Molosses ne paraissent pas aptes à l'hibernation saisonnière continue, et c'est de toute évidence cette particularité physiologique qui détermine leur répartition géographique et leurs mouvements migratoires» (citant le cas de *T. brasiliensis*). La topographie et le climat du Valais central expliqueraient la présence de ce chiroptère à plus de 46° de latitude nord tout au long du cycle annuel; en effet, les falaises, les affleurements rocheux et les versants situés sur la rive droite du Rhône, exposés quasi perpendiculairement au rayonnement solaire hivernal, se réchauffent rapidement à la mauvaise saison. De telles conditions stimulent l'activité hivernale des insectes, permettant ainsi aux Molosses de se sustenter dans un environnement climatique pourtant fortement marqué par la continentalité. Enfin, il est possible que cet ensoleillement hivernal exceptionnel pourvoie à l'entretien de l'inertie calorifique des massifs calcaires et favorise un microclimat adéquat dans certains gîtes rupestres (voir Perrin 1988). La stratégie adoptée par la Molosse pour passer la mauvaise saison agirait donc en tant que facteur limitant de son aire de répartition géographique [comme le suggérait déjà Brosset (1966) pour le genre *Tadarida*]. Le Valais semble constituer, au vu de nos connaissances actuelles sur la biogéographie de l'espèce, le bastion

septentrional habité par le Molosse de Cestoni dans l'ensemble du domaine paléarctique; nous pouvons donc présumer que *T. teniotis* est de moeurs virtuellement sédentaires dans toutes les régions d'Europe qu'il a colonisées.

Conclusion

S'il est vrai que leurs émissions sonores permettent de repérer aisément les Molosses, leur capture exige en revanche un investissement d'énergie colossal. Cette situation explique le peu de données dont nous disposons actuellement sur la biologie de ce chiroptère. Il serait particulièrement pertinent de: 1° prouver la reproduction de l'espèce dans les Alpes suisses; 2° étudier le bilan énergétique de ces chauves-souris durant l'hiver; 3° définir plus précisément leurs stratégies spatiales; 4° rechercher *T. teniotis* dans d'autres régions d'Europe centrale afin de mieux cerner les limites de son aire de répartition géographique.

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Résumé

Capturé à maintes reprises (1958–1988, 32 mentions) dans les filets des ornithologues sur les cols franco-suisses de Balme et de Bretolet, le Molosse était jusqu'ici présumé migrateur ou erratique dans les Alpes nord-occidentales. Des observations acoustiques et visuelles (1985–1988) ont permis de découvrir 4 sites rupestres abritant cette espèce. Les gîtes diurnes sont situés entre 570 et 1100 m d'altitude, au pied de gigantesques et vertigineuses parois calcaires très exposées au rayonnement solaire; ce sont d'étroites failles verticales qui forment une sorte d'écaille décollée parallèlement à la surface de la masse rocheuse et dont l'ouverture est orientée vers le bas. Deux faits majeurs de la biologie du Molosse ont été mis en évidence: un comportement sédentaire et une activité de chasse intermittente en période hivernale. La configuration topographique (relief tourmenté d'une grande vallée encaissée avec un versant exposé au sud) et les conditions microclimatiques (ensoleillement hivernal exceptionnel et redoux induits par le foehn) sont probablement deux facteurs qui permettent l'existence durant toute l'année de cette espèce à plus de 46° de latitude nord. L'observation des Molosses chassant à Bretolet et à Balme (1920 et 2200 m d'altitude), suggère que ceux-ci se rendent sur les cols dans le seul but d'exploiter les nuées d'insectes en transit migratoire.

Zusammenfassung

Beitrag zur Öko-Ethologie der Bulldoggfledermaus, Tadarida teniotis (Molossidae), in den Walliser Alpen (Südwestschweiz)

Die Bulldoggfledermaus wurde auf den französisch-schweizerischen Grenzpässen Balme und Bretolet zwischen 1958 und 1988 insgesamt 32mal in von Ornithologen gestellten Netzen gefangen. Die Funde von *T. teniotis* in den nordwestlichen Alpen wurden bisher migrierenden oder umherirrenden Tieren zugeschrieben. Hör- und Sichtbeobachtungen in den Jahren 1985–1988 führten im Wallis zur Entdeckung von vier Felsstandorten mit Tagesquartieren der Bulldoggfledermaus. Die Quartiere befinden sich auf 570 bis 1100 m ü. M., am Fuße von mächtigen vertikalen, stark sonnenexponierten Kalkfelswänden. Die Quartiere bestehen aus senkrechten Felsspalten, gebildet durch eine parallel zur Oberfläche der Wand abstehende Felsplatte, die gegen unten eine Öffnung bildet. Die bisherigen Beobachtungen im Wallis zeigen, daß *T. teniotis* hier seßhaft ist und auch im Winter zur Nahrungsaufnahme ihr Quartier verläßt. Die topographischen Gegebenheiten und die mikroklimatischen Bedingungen sind zwei wahrscheinliche Faktoren, die die Existenz von *T. teniotis* über 46° nördlicher Breite

während des ganzen Jahres ermöglichen. Die Beobachtung von jagenden Bulldoggfledermäusen auf den Pässen Bretolet und Balme (1920 bzw. 2200 m ü. M.) läßt annehmen, daß diese ausschließlich zur Erbeutung durchziehender Insekten zu den Pässen fliegen.

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Chromosomal variation in two populations of the genus *Ctenomys* (Rodentia, Octodontidae) from Uruguay

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Abstract

Analysed the karyotypes from two populations of the *Ctenomys pearsoni* complex sensu Altuna and Lessa (1985) with 2n = 70, FN = 80 corresponding to *C. pearsoni* and 2n = 56, FN = 78 corresponding to *C.* sp. aff. *C. pearsoni*, revealed variation in karyotype composition. Of nine specimens of *C. pearsoni* one presented a karyotype with 2n = 68, FN = 80. Of nine specimens of *C.* sp., five presented the same diploid number (2n = 56) but different FN values (FN = 77, 78, 79). C-band staining of the karyotypes with different FN values revealed that, the differences observed in karyotype composition are not due to heterochromatin shifts.

Introduction

Among rodents of the Neotropical region, the subterranean genus *Ctenomys* exhibits extensive karyotypic variability with chromosome number ranging from 2n = 22 to 2n = 70 (Reig and Kiblisky 1969; Kiblisky et al. 1977; Gallardo 1979). In this paper we report intrapopulation chromosome variation in two population of the *C. pearsoni* complex with modal numbers of 2n = 56 and 2n = 70 (Novello and Lessa 1986).

Materials and methods

Animals were captured alive using Oneida Victor traps N° 0 in Carrasco (34° 53′ S, 56° 02′ W, Dpto. de Montevideo) and Autódromo Nacional (34° 25′ S, 56° 26′ W, Dpto. de San José). Two hours prior to sacrifice, the animals were injected i.p. with colchicine (0.1 % colchicine, 0.2 ml/100 g of body weight). Chromosome preparations were obtained from bone marrow cells after hypotonic treatment and ethanol acetic-acid fixation. Chromosome counts were made under the microscope and using enlarged photograph of selected metaphases stained with Giemsa. The Arrighi and Hsu (1971) method was applied to stain C-bands. NOR staining was carried out incubating slides in $AgNO_3$ 50 % in deionized water for 2–3 hours at 60 °C.

The specimens were stored in the collection of the Dpto. de Zoología Vertebrados de la Facultad de Humanidades y Ciencias de Montevideo, Uruguay.

Results

Sample from Carrasco (*C.* sp. 2n = 56, FN = 78)

Of the nine specimens studied four presented the modal karyotype composed by: one subtelocentric pair, 11 metacentric and submetacentric pairs, 15 telocentric pairs, a metacentric X and a subtelocentric Y (Fig. 1a). The remaining specimens presented the same 2n value but variable FN value (Table 1). Three specimens (EL 51, EL 91 and EL 43) presented two unpaired chromosomes: a medium sized submetacentric and a telocentric one (Fig. 1b, 1c). The other two specimens (EL 49 and EL 52) presented two unpaired telocentric chromosomes of short and medium size (Fig. 1d).

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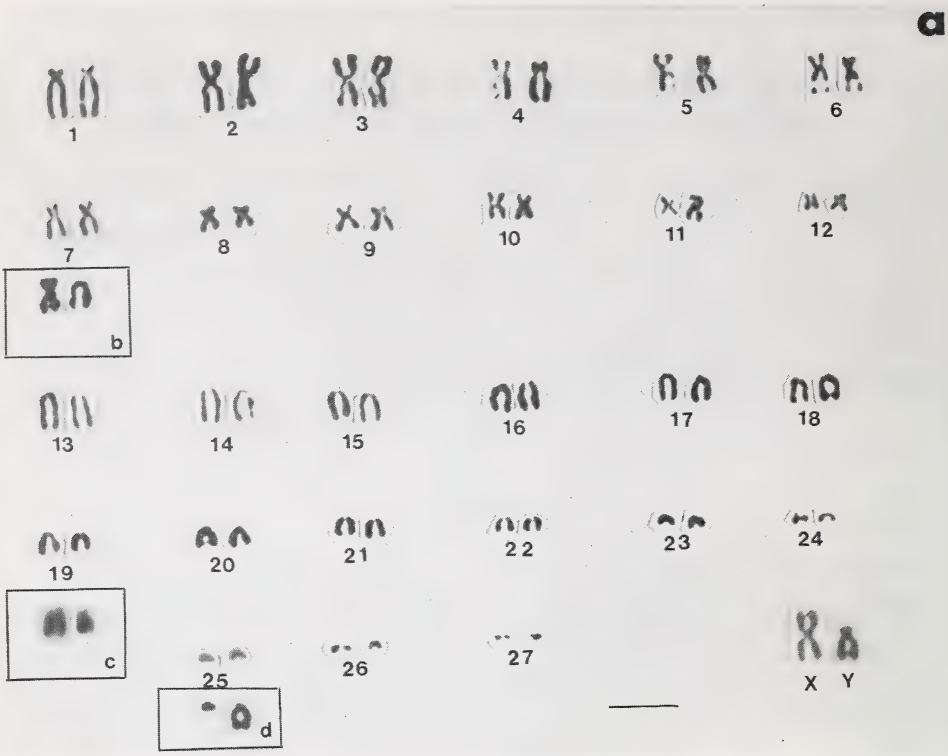

Fig. 1. a. Standard karyotype of *C.* sp. (FN = 78); *b.* Heteromorphic pair present in the specimen EL 43; *c.* Heteromorphic pair present in the specimen EL 51; *d.* Heteromorphic pair present in the specimen EL 52. In all figures bar represents 10 microns

Table 1. **Karyotypic variation observed in the *C.* sp. (2n = 56) population from Carrasco**

Karyotypes marked with asterisk present heteromorphic chromosomes

Specimen	biarmed	uniarmed	FN
CA 52	24	30	78
EL 43*	23	31	77
EL 51*	25	29	79
EL 52*	24	30	78

Sample from Autódromo Nacional (*C. pearsoni* 2n = 70, FN = 80)

Of the nine specimens analysed eight presented the modal karyotype composed by: one subtelocentric pair, 5 metacentric and submetacentric pairs, 28 telocentric pairs, a metacentric X and a subtelocentric Y (Fig. 2). The remaining specimen had 68 chromosomes and FN = 80. We observed three different features in this karyotype: a) the presence of a long metacentric chromosome absent in the modal karyotype; b) an unpaired short metacentric chromosome; c) heteromorphism of the pair bearing the secondary constriction. This karyotype has only 27 telocentric chromosome pairs (Fig. 3).

After C-banding, the karyotype of *C. pearsoni* showed positive staining in the pericentric region of the pair bearing the secondary constriction and in a medium sized telocentric pair (Fig. 4a). The modal karyotype of *C. sp.* (2n = 56, FN = 78) showed positive C-band staining in the pericentric region of the pair bearing the secondary constriction (Fig. 4b). Both karyotypes presented positive staining of the long arm of the Y chromosome.

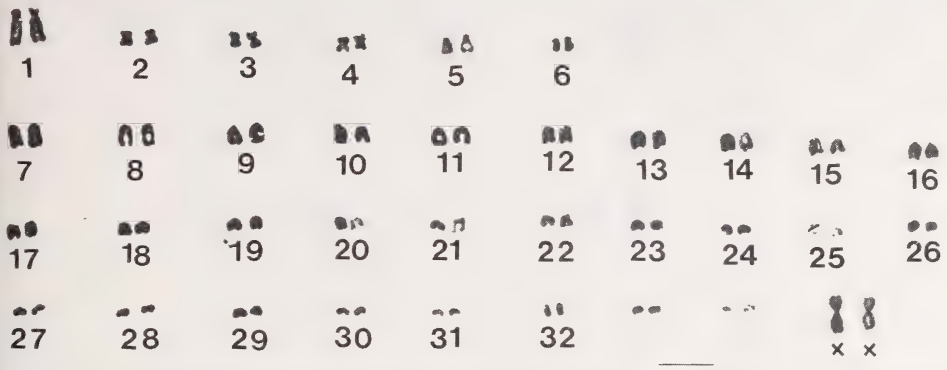

Fig. 2. Standard karyotype of *C. pearsoni* from Autódromo Nacional

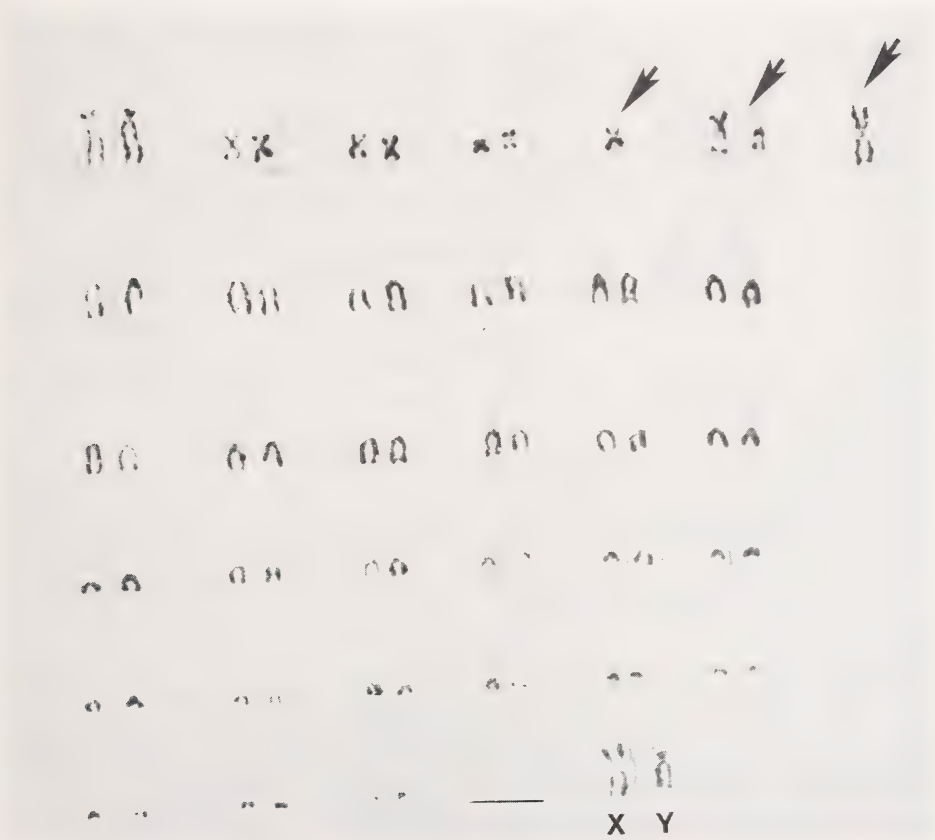

Fig. 3. Heteromorphic karyotype of the specimen CA 58 *(C. pearsoni);* Heteromorphic chromosomes marked with arrow

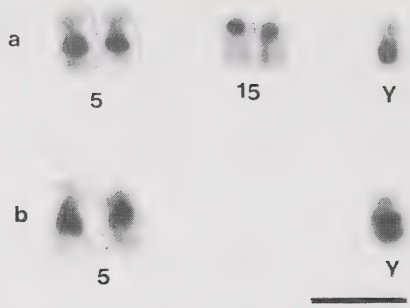

Fig. 4. a. Unique positive C-banded chromosomes of *C. pearsoni; b.* Unique positive C-banded chromosomes of *C.* sp. (2n = 56, FN = 78)

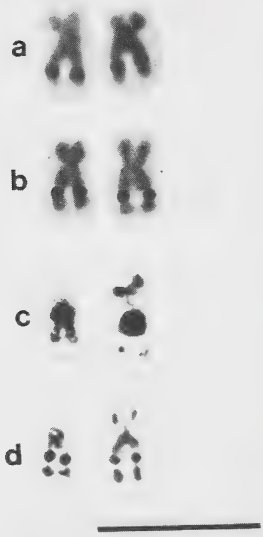

Fig. 5. a. Unique positive silver stained chromosomes in the *C. pearsoni* karyotype. *b.* Unique positive silver stained chromosomes in the *C.* sp. (2n = 56, FN = 78) karyotype; *c.* heteromorphic chromosomes of the specimen CA 58 after C-banding; *d.* heteromorphic chromosomes of the specimen CA 58 after silver staining

After silver staining the karyotype of *C. pearsoni* showed positive staining in the area of the secondary constriction of the pair N° 5 (Fig. 5a). In the *C. sp.* (2n = 56, FN = 78) karyotype, positive silver staining was observed in the secondary constriction presents in the pair N° 6 (Fig. 5b).

The heteromorphic chromosomes of the specimen CA 58 (*C. pearsoni*) presented positive C-band staining in the pericentric region of the two homologous chromosomes (Fig. 5c), and positive silver staining in the secondary constriction of the same chromosome pair (Fig. 5d).

Discussion

The specimens of *C.* sp. EL 49 and EL 52 have the same 2n and FN values as the modal karyotype (2n = 56, FN = 78). A plausible explanation for the difference in size of the two telocentric chromosomes could be the loss or addition of chromatin. The remaining karyotypes of this population showed a different pattern of karyotypic variation. The change in the FN value without a corresponding change in the 2n value suggests whole arm pericentric inversion. In specimen EL 43 pericentric inversion could be causing the transition from a biarmed to a uniarmed chromosome. In EL 51 and EL 91 karyotypes the same change

in opposite direction could be postulated. The heteromorphic karyotype of *C. pearsoni* presents a complex picture. The variation of the 2n value can be due to a Robertsonian translocation resulting in the long metacentric absent in the modal karyotype. In spite of the heteromorphism observed in the pair bearing the secondary constriction neither the C-band nor the nucleolar organizing region are implicated in karyotype variation in *C. pearsoni* nor *C.* sp. (FN = 77, 78, 79). This fact leads us to propose that in karyotypes EL 49 and EL 52 the difference in length of the telocentric chromosomes is due to a euchromatin shift. A similar phenomenom was reported by Gallardo (1983) in *Thomomys bottae*.

Chromosome variation within population of *Ctenomys* has been reported by Reig and Kiblisky (1969) in Argentina and Gallardo (1979) in Chile. In the later animals with heteromorphic chromosomes inhabit a peninsular zone isolated from the remaining territory by absence of vegetation and water. In our case, individuals of the *C.* sp. population with heteromorphic chromosomes (FN = 77, 78, 79) were collected in an area less than 2500 m^2 without visible barriers from specimens with modal karyotypes.

The variation observed in these populations is difficult to explain. The chromosomal variation observed in the FN values of the *C.* sp. population suggests that these chromosome rearrangements do not cause severe negative heterosis. This could be due, at least in karyotypes with heterocygotic whole arm inversion (EL 43, EL 51, EL 91), to pairing at meiosis without the presence of inversion loops. According to Ford (1969), inversion loops were never observed in meiosis in mammals, not even in man.

High amount of variation in *C.* sp. can be due to diverse factors associated with subterranean life such as: low vagility, solitary occupation of the burrow, high inbreeding and the effect of drift (Patton 1983). The populations surveyed here share all these characteristics (Altuna 1985). Unfortunately, the populations studied were destroyed by severe damage of their habitat by man before G-band analysis could be performed. Work is in progress to etablish the existence of chromosome variation in neighbouring populations.

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Zusammenfassung

Chromosomale Abweichungen bei zwei Populationen des Genus Ctenomys (Rodentia, Octodontidae) aus Uruguay

Die Karyogramme aus zwei Populationen von Kammratten *(Ctenomys)* der *C. pearsoni*-Gruppe aus Uruguay werden beschrieben. In der einen Population besaßen 8 von 9 Exemplaren 2n = 70 Chromosomen. Das neunte Tier hatte bei gleicher FN 80 nur 68 Chromosomen. In der zweiten Population hatten alle 9 untersuchten Kammratten 2n = 56 Chromosomen. FN war in 6 Fällen 78, einmal 77 und zweimal 79. Bei zwei der sechs Tiere mit FN 80 war je ein Autosom im Vergleich zu Normaltieren größer.

Eine C-Bandenfärbung ergab, daß Heterochromatin an den geschilderten Unterschieden nicht beteiligt war.

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Food transit times and carbohydrate use in three Phyllostomid bat species

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Abstract

Studied were the food transit times and carbohydrate use in three species of frugivorous microchiroptera. Food passed through the digestive tract very quickly, averaging from 22.3 ± 4.2 minutes in *Carollia perspicillata* to 33.6 ± 3.4 minutes in *Phyllostomus discolor* (mean ± S.D.; N = 12 trials respectively). The mean value of "additional load", i.e. the amount of food consumed before starting to defecate, was 3.95 ± 0.4 g of banana in *Carollia* (mean ± S.D.; N = 40 trials), corresponding to 22 % of body weight.

The highest uptake of the soluble carbohydrates sucrose, glucose and fructose was found in *Sturnira lilium* (92.9 %), the poorest in *Phyllostomus* (86.6 %). Lactating female *Carollia* displayed a higher degree of sugar uptake (91.5 %) than conspecifics (89.2 %) while food transit times were unchanged.

A suboptimal but still satisfactory use of carbohydrates in combination with remarkably short food transit times seems to be the best strategy to maximize energy gain in frugivorous Phyllostomids eating a low-quality diet.

Introduction

Homoeothermy and locomotion by active flight are properties that imply a high metabolic rate. While many studies have investigated the composition and variety of diet in bats (Wilson 1973; Gardner 1977) there is only sparse information about the uptake of food by the digestive system (Keegan 1975).

Active fliers should have to minimize their mass intake of food but at the same time maximize their energy intake. Optimal foraging is one important factor helping to solve this dilemma (Fleming and Heithaus 1986; Fleming et al. 1977). Concerning a second factor, i.e. the digestive abilities of a bat, two different strategies are possible to maximize the energy yield from food: 1) Either small quantities of food are consumed at a time and totally processed or 2) large amounts are passed through the intestine quickly with suboptimal uptake.

These two strategies are not exclusive, but mark extremes on a continuum of possible behaviors, which are influenced by the abundance of high- or low-quality food.

I became aware of this problem through the observation that frugivorous bats already begin defecating a few minutes after the start of a food-rewarded flight training. The purpose of this study was to systematically investigate food transit times through the alimentary canal and determine energy uptake in order to clarify, which of the above mentioned strategies are used by frugivorous bats on a given diet.

Material and methods

Animals of the three phyllostomid bat species *Carollia perspicillata* (3 ♂; 3 ♀), *Phyllostomus discolor* (3 ♂; 3 ♀) and *Sturnira lilium* (2 ♀) were taken from captive colonies maintained at the Zoological Institute of Bonn University.

I measured the food transit times of animals which were transferred daily into solitary cages. At

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the same time of day (one hour after the dark cycle began) mashed ripe banana was offered as food ad libidum. Every other day this mash was stained with a commercial food dye ("chocolate brown" by Fa. Brauns-Heitmann, Warburg) to indicate the transit of freshly consumed food.

I observed the animals' feeding behavior and determined food transit times using an infra-red nightvision scope.

The maximal "additional load", i.e. the quantity of food a bat swallowed before starting to defecate, was determined in 4 male *Carollia*. These animals were exclusively fed during a flight-training and rewarded with pieces of banana (150 ± 10 mg) in every test trial which allowed exact correlation of consumed quantities and times of intestinal passage.

The percentage of the carbohydrates sucrose, glucose and fructose in the banana and in the feces of the animals was analysed by UV-spectral photometry. For this the samples were dehydrated, ground, dissolved in aqua dest. and the following enzymatic preparation (Boehringer 1973) applied:

1. Sucrose + H_2O → β-Fructosidase → Glucose + Fructose
2. Glucose + ATP → HK → G-6-P + ADP
3. Fructose + ATP → HK → F-6-P + ADP
4. G-6-P + $NADP^+$ → G-6-P-DH → Gluconat-6-P + NADPH + H^+
5. F-6-P → PGI → G-6-P

The amount of NADPH is proportional to the amount of glucose and was measured at 340 nm.

The degree of sugar uptake is expressed in terms of the percentage ratio between the sugar contents of food and feces. This is a valid approximation of the real sugar uptake as the dry weight composition of food and feces in this case is nearly identical.

In order to investigate a possible influence of lactation or temporal reduction of food access on food transit times and digestion, two additional experimental groups of *Carollia* were examined: Group "L" consisted of two lactating females (8 to 14 days post-partem), group "F" of two males being accustomed to a shortened food access of only three hours per day.

I report all the data as means ± S.D.

Results

The food transit times of the three species investigated are significantly different (ANOVA $F = 31.674$; $p < 0.001$; LSD-test: C./S.: $p < 0.05$; S./P.: $p < 0.01$) (Table 1).

Compared to insectivorous species (Buchler 1975; Luckens et al. 1971) the retention time of food in the digestive tract of frugivorous bats are lower. Within the frugivores there seems to be a positive correlation between food transit time and body mass.

In contrast to the findings in *Myotis lucifugus* (Buchler 1975), no connection between the value of transit time and the level of activity in *Carollia* was found. Animals exclusively feeding during a flight training did not exhibit statistically different values for intestinal passage compared to caged conspecifics (24.4 ± 4.5 minutes; N = 40 trials / 22.3 ± 4.2 minutes; N = 12 trials; $t = 1.438$; $p > 0.10$).

There were no sex-dependent differences in food transit times for either *Carollia* (♂ = 23.3 ± 4.3 min; ♀ = 21.3 ± 4.2 min; N = 6 per group; $t = 0.815$; $p > 0.20$)

Table 1. **Food transit times in three Phyllostomid bat species compared to data by other authors**

	transit time (min)	body weight (g)	feeding habit
Carollia perspicillata	22.3 ± 4.2	18	F
Sturnira lilium	25.7 ± 3.0	20	F
Phyllostomus discolor	33.6 ± 3.4	35	O
Rousettus aegyptiacus	46	130	F (Keegan 1977)
Artibeus jamaicensis	30	50	F (Morrison 1980)
Eptesicus fuscus	122	20	I (Luckens 1971)
Myotis lucifugus	46–144	8	I (Buchler 1975)

Results are shown in terms of mean ± S.D.
N = 12 trials per group; F = Frugivorous; I = Insectivorous; O = Omnivorous

or *Phyllostomus* (♂ = 33.7 ± 2.9 min; ♀ = 33.5 ± 4.2 min; N = 6 per group; t = 0.096; p > 0.20).

I also found no evidence for variation in food transit time with reproductive conditions or under conditions of food limitation. Lactating females (group "L") of *Carollia* show no statistically significant longer passage times than non-lactating conspecifics (23.7 ± 4.6 minutes; N = 6 trials / 21.3 ± 4.2 minutes; N = 6 trials; t = 0.944; p > 0.20). The contrary is reported for the insectivorous *Myotis lucifugus* (Buchler 1975).

The experimental group "F" of male *Carollias* likewise showed no significant differences in transit times compared to normal males having food access during the whole dark cycle (22.4 ± 4.2 minutes; N = 6 trials / 21.3 ± 4.2 minutes; N = 6 trials; t = 0.454; p > 0.20).

Carollia starts to defecate after having consumed an amount of 3.95 ± 0.4 g banana on the average (N = 40 trials) (Fig. 1). This corresponds to an "additional load" of 22 % of body mass. The maximum value found was 4.8 g, equivalent to 27 % of body mass. As *Carollia* is able to fly even with a load of about 50 % – this is the case while carrying a three-week-old pup – the observed momentary maximum of nutritive load seems to be due to a complete filling of the alimentary canal.

No significant interindividual differences were found in this respect. However, there is a significant relation (y = 8.5x – 9.06; r = 0.77) between the mass of food ingested and transit time. Food staining indicated that all three species empty their digestive tracts completely prior to the next day's meal, unlike the insectivorous *Eptesicus fuscus,* whose first fecal pellets consist of the final remains of the previous day's food (Luckens et al. 1971). The quantitative ratio of the three saccharids in the banana correspond (Table 2) well with data found by other authors (Forsyth 1980). The same is true for the water content in the ripe fruit.

The three bat species differ significantly in the degree of sugar uptake (ANOVA F = 18.86; p < 0.001; LSD-test: C./S.: p < 0.01; C./P.: p < 0.05).

The soluble carbohydrates are best exploited by *Sturnira* (92.9 %) while *Phyllostomus* displays the poorest degree of sugar uptake (86.6 %). Considering the very short transit times the data suggest a highly efficient carbohydrate resorption in the intestine.

With *Carollia,* showing an average sugar uptake of 89.2 %, the experimental group "F" proved to be unimpaired (89.0 %) in its digestive abilities. Lactating females of *Carollia* (group "L") seem to score better (91.5 %) than their conspecifics. This fact is probably due to milk production, just like the distinctly decreased water content of their feces.

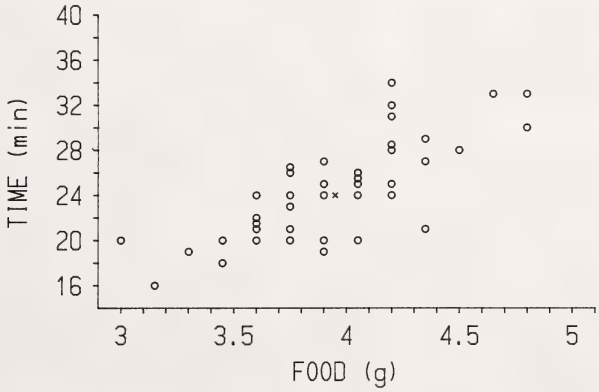

Fig. 1. Distribution of food transit times as a function of the amount of food consumed before starting to defecate in *Carollia perspicillata.* × indicates the mean value of the "additional load"

Table 2. **Percentage of soluble carbohydrates and water content in food and feces of Phyllostomid bats**

	sucrose	glucose	fructose	sugar total	sugar uptake (%)	water content
Banana	19.9 ± 1.2	7.9 ± 2.3	8.8 ± 1.7	36.6 ± 5.1		74.5 ± 1.3
Carollia perspicillata	0.65 ± 0.09	1.07 ± 0.10	2.23 ± 0.18	3.96 ± 0.22	89.2	79.8 ± 1.3
Phyllostomus discolor	1.33 ± 0.41	1.78 ± 0.48	1.81 ± 0.38	4.91 ± 0.82	86.6	79.9 ± 2.0
Sturnira lilium	0.57 ± 0.07	1.56 ± 0.15	0.46 ± 0.29	2.60 ± 0.37	92.9	76.4 ± 2.4
Carollia "F"	0.77 ± 0.15	1.23 ± 0.20	2.04 ± 0.33	4.04 ± 0.31	89.0	79.1 ± 1.9
Carollia "L"	0.44 ± 0.18	0.91 ± 0.09	1.75 ± 0.28	3.10 ± 0.36	91.5	76.3 ± 2.0

Results are shown in terms of mean ± S.D.; N = 4 trials per group. Sugar values in % dry weight; water content in % fresh weight. Sugar uptake in terms of percentage ratio between sugar contents of food and feces.

In each of the five experimental groups a urine sample was analysed. None of them contained soluble carbohydrates.

Discussion

Neotropical bats feed on a variety of fruits and parts of plants but prefer certain species. This could be due to a preference for high- or low-abundant fruits (Bonaccorso and Gush 1982). *Carollia* may specialize on less-abundant *Piper* and *Muntingia* fruits, but show a fast, efficient and intermittent feeding behavior (Bonaccorso and Gush 1981). *Artibeus jamaicensis* prefers super-abundant *Ficus* fruits and is a slow constant feeder, which achieves a high degree of energetic economy by efficiently sucking fruits dry instead of swallowing them (Morrison 1980). This unusual mode of obtaining calories is also reported for some Megachiroptera (Wolton et al. 1982).

Apart from the abundance of fruits their nutritive value can control the bats' feeding behavior (Thomas 1984). Tropical fruits generally have a high percentage of carbohydrates, but often lack proteins and lipids (Morton 1973). In this respect banana is representative for the food supply of tropical frugivores, showing a dry weight percentage of up to 70 % soluble carbohydrates but only 1.2 % proteins and 0.2 % lipids.

The soluble sugars sucrose, glucose and fructose make up more than 95 % of the digestible energy in ripe banana fruits (Marriott and Lancaster 1983).

The strikingly short food transit times found in this investigation at first suggest that bats use the second strategy of low efficiency high bulk food processing. The fact that the length of the intestine of frugivorous microchiroptera is only ⅓ to ⅕ of that of a rodent of comparable body weight (Klite 1965) adds to this idea. The high values of carbohydrate uptake however, suggest that this extreme strategy is not applied. It appears to be advantageous for frugivorous bats to do without a complete (i.e. 100 %) sugar exploitation, but to keep it on a sufficiently high level in order to avoid the need for large quantities of food.

The daily energy budget of a bat can be estimated by measurements of oxygen consumption (McNab 1969) and results in the following for the species of this investigation:

Carollia perspicillata	5.2 (+1.3) Kcal/d
Sturnira lilium	6.4 (+1.6) Kcal/d
Phyllostomus discolor	5.8 (+1.5) Kcal/d

The values in parentheses give the additional amount of energy needed for a net flying time of 30 minutes per night. They are based on the assumption that flight metabolism is approximately the 12-fold of the basal metabolic rate (Thomas et al. 1984). As ripe banana fruit contains 96 Kcal/100 g of edible material, a daily minimum requirement of 6.8 g *(Carollia)*, 8.3 g (*Sturnira*) and 7.6 g banana (*Phyllostomus*) can be calculated for freely flying animals. 5.4 g of banana, which is equivalent to the basal rate of metabolism in *Carollia*, corresponds well with the finding that caged animals of this species need about 5 g of this fruit per day to maintain their body weight when supplied with protein once a week (Laska and Schmidt 1986).

I conclude that a suboptimal but still satisfactory use of carbohydrates in combination with strikingly short food transit times seems to be the best strategy to economize with energy in frugivorous Phyllostomids feeding on a low-quality diet.

The possible effects of a change of diet still have to be investigated.

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Zusammenfassung

Dauer der Nahrungspassage und Kohlenhydratverwertung bei Carollia perspicillata, Phyllostomus discolor und Sturnira lilium (Phyllostomatidae, Chiroptera)

Bei drei fruchtfressenden Fledermausarten der Neotropen wurden die Verweilzeiten der Nahrung im Verdauungstrakt und die dabei erzielte Kohlenhydratausbeute untersucht. Anhand gefärbten Futters wurden sehr kurze Darmpassagezeiten nachgewiesen, die von 22.3 ± 4.2 Minuten bei *Carollia perspicillata* bis zu 33.6 ± 3.4 Minuten bei *Phyllostomus discolor* reichten (x ± s; jeweils N = 12).

Die maximale Futtermenge, die vor Einsetzen der Defäkation aufgenommen wurde, betrug bei *Carollia* im Mittel 3.95 ± 0.4 g Banane. Dies entspricht 22 % des Körpergewichtes.

Die höchste Resorptionsrate der Kohlenhydrate Saccharose, Glucose und Fructose erzielte *Sturnira lilium* mit 92,9 %, die niedrigste *Phyllostomus discolor* mit 86,6 %. Laktierende *Carollia* zeigten eine höhere Zuckeraufnahme (91,5 %) als ihre Artgenossen (89,2 %), wobei die Transitzeiten der Nahrung unverändert blieben.

Eine suboptimale, aber hinreichend hohe Ausnutzung der Kohlenhydrate scheint im Zusammenspiel mit sehr kurzen Verweilzeiten der Nahrung im Körper die ökonomischste Strategie zur Energiegewinnung bei frugivoren Phyllostomatiden zu sein.

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A comparative restriction endonuclease analysis of nuclear DNA from Austrian *Apodemus* species: Intraspecific variability in middle repetitive DNA families contrasts isoenzyme data

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Abstract

Studied middle repetitive DNA families in three Austrian *Apodemus* species (*Apodemus sylvaticus, Apodemus flavicollis* and *Apodemus microps*) using several type II restriction endonucleases and agarose gel electrophoresis. Three endonucleases, BstEII, EcoRI and HindIII revealed defined banding patterns due to specific repetitive DNA families. HindIII digested DNA samples from *Apodemus microps* differ from both *Apodemus sylvaticus* and *Apodemus flavicollis* DNA samples. Differences between the latter two species could be revealed with BstEII in only one of the populations under investigation. This finding indicates intraspecific variability even in the existance of middle repetitive DNAs in the latter species. This contrasts with the analysis of 16 isoenzyme loci, which exhibited only monomorphic patterns.

Introduction

The reconstruction and characterization of phylogenetic relationships is one of the most fascinating approaches of biology. The characterization of DNA by various means was found to be a reliable and helpful method in phylogenetic analysis. The large number of rodent species showing different degrees of divergence, together with high abundance, make them very useful for phylogenetic studies at the molecular level. For identification of sibling species, simple DNA analysis as presented in this paper may provide a powerful basis for finding new species characters and can help to elucidate the species state of the particular specimen.

The Austrian members of the Eurasian genus *Apodemus, Apodemus sylvaticus, Apodemus flavicollis* and *Apodemus microps,* belong to the most common small mammals in their area of distribution. Both similarity and high variability in their morphological characters have often led to a controversial discussion of their species state, possible introgression and natural hybridization (see Niethammer 1978a, b; Steiner 1978 for a review).

Chromosomal analysis (Engel et al. 1978; Csaikl 1980; Vujosevic et al. 1984) and isoenzyme studies (Engel et al. 1978; Csaikl et al. 1980, 1986; Gemmeke 1980, 1983) strengthen the picture of a very close phylogenetic relationship among these three species.

Studies on the nuclear DNA of these species are rather rare and mainly subject to molecular biology than to phylogenetic and systematic considerations (McLaren and Walker 1970; Cooke 1975; Brown and Dover 1979; Catzeflies et al. 1987). Furthermore, most of these studies are done with specimens of unknown origin or based on analysis of a single animal. This prompted us to study the nuclear DNA at the population level with various restriction endonucleases.

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Table 1. **Geographic area and external measurements of *Apodemus* species**
"Wiener Becken": 16° 20′–16° 25′/47° 53′–47° 56′; "Seewinkel": (16° 45′–17°/47° 45′–48°)*

	body			tail			hindfoot			ear		
	min	mean	max	min	mean	max	min	mean	max	min	mean	max
"Wiener Becken":												
A. s. (n=1)		83.0			73.0			21.0			14.3	
A. f. (n=7)	90.0	96.0	104.0	86.0	92.8	104.0	22.0	23.7	25.0	16.3	17.5	18.4
„Seewinkel":												
A. m. (n=9)	75.0	81.4	86.0	75.0	82.1	90.0	18.0	18.5	19.5	13.5	13.8	14.0
A. s. (n=5)	70.0	81.8	90.0	78.0	82.4	87.0	18.0	20.3	22.0	13.5	15.7	16.6
A. f. (n=3)	93.0	97.0	105.0	92.0	100.7	108.0	23.0	23.8	24.5	17.2	18.0	18.5

* Name and coordinates of the geographic area.
A. m.: Apodemus microps, A. s.: Apodemus sylvaticus, A. f.: Apodemus flavicollis. n-number of each species are given in brackets. Values are given in mm

Materials and methods

Animals

All animals used in this study were caught alive by help of wooden traps using peanut butter as bait. Most animals were kept alive in cages for at last six months with an offer of oats and apples ad libidum. Species determination was done by correlation of the length values of hind foot and ear. Values for external characters and geographical area are given in Table 1. Additionally, LDH isoenzymes were used to confirm the species-affiliation (Csaikl et al. 1980). All experiments were carried out with samples obtained from a single specimen.

Isoenzymes

The enzymes LDH (loci A and B, EC 1.1.1.27), NAD-MDH (loci s and m, EC 1.1.1.37), NADP-MDH (locus s, EC 1.1.1.40), 6-PGD (locus A, EC 1.1.1.42), G-6-PD (locus A, EC 1.1.1.49), SOD (locus A, EC 1.15.1.1), AAT (loci s and m, EC 2.6.1.1), CPK (loci A and B, EC 2.7.3.2), AK (locus A, EC 2.7.4.3), ACY-1 (locus A, EC 3.5.1.14), ADA (locus A, EC 3.5.4.4), and PGI (locus A, EC 5.3.1.9) were studied in homogenized muscle samples as described previously (Csaikl et al. 1980, 1986).

Nuclear DNA extraction

Livers of freshly killed individual mice were minced into small pieces and homogenized with a Potter-Elvenhjem-homogenizer using icecold MSB-CA^{++} (Lansman et al. 1981). To avoid contamination with mitochondria, the crude nuclear pellet was washed three-times with MSB-EDTA (Lansman et al. 1981) and recollected by centrifugation at 700xg (5 min, 4 °C). This pellet was used for the actual DNA extraction according to Flamm et al. (1966). Quality and amount of DNA was checked both with a photometer and with agarose gel electrophoresis (Maniatis et al. 1982).

Restriction endonuclease analysis

All endonucleases used (AluI, BamHI, BstEII, EcoRI, HaeIII, HindIII, HpaII and MspI) were obtained from Bethesda Research Laboratories (BRL), Eggstein, FRG. Digestions were carried out using 40 µl reaction mixtures under conditions recommended by the vendor. A HindIII-digest of phage lambda DNA was used as molecular weight marker in every gel. Restricted DNA samples were electrophoresed on agarose (Seakem Co.) in the presence of ethidium bromide (Maniatis et al. 1982). The gels were photographed under UV-light with a Kodak Technikal Pan 2415 using a standard Leica/Elmar 65 Photographic equipment.

Results and discussion

With the discovery and purification of a number of type II restriction endonucleases, an easy and reliable method for coarse comparisons of nuclear DNA from species of interest is available. These enzymes cleave duplex DNA at a specific recognition site, which is typically four or six nucleotides of length. With the help of agarose gel electrophoresis it is possible to compare samples from different species but restricted with the same restriction endonuclease. DNA sequences existing to a higher than average degree with equal length boardered by the same recognition sequence, can be identified with the appropriate restriction endonuclease. They are revealed as a distinct band upon a smear of different sized DNA fragments in an ethidium bromide stained agarose gel (Fig. 1). Those bands are calculated to contain 20,000 copies per genome and are called middle repetitive DNA (Brown and Dover 1981). Therefore restriction endonuclease comparisons can give valuable information on repeated sequences, which seem to be a general feature of the eukaryote genome (Britten and Kohne 1968).

Nuclear DNA from 25 individual mice of the three *Apodemus* species, *Apodemus sylvaticus, Apodemus flavicollis* and *Apodemus microps* was digested with a panel of eigth restriction endonucleases: AluI, BamHI, BstEII, EcoRI, HaeIII, HindIII, HpaII and MspI. Different restriction endonuclease concentrations revealed the same DNA banding pattern only varying in the intensity of the bands. AluI and HaeIII produced fragment classes of lower molecular weight, which are difficult to resolve and to interprete under standard conditions. BstEII, EcoRI and HindIII produced reproducible predominant bands. No middle repetitive DNAs could be detected with the other restriction endonucleases used. A representation of the different digestions are shown in Fig. 1 and the results are summarized in Table 2. EcoRI digestions gave the same digestion pattern in all three species with bands of 1.8 kb, 1.3 kb, 0.5 kb and 0.4 kb. HindIII digestions revealed three bands of 1.2 kb, 0.75 kb and 0.40 kb in *Apodemus sylvaticus* and *Apodemus flavicollis* but only two (1.2 kb and 0.40 kb) appeared in *Apodemus microps.* Interestingly, BstEII revealed a weak DNA band of 2.4 kb only in the three individuals from the „Seewinkel"-population of *Apodemus flavicollis.* In specimens caught in the „Wiener Becken", this 2.4 kb band was absent. Additionally a comparison with published results reveals differences

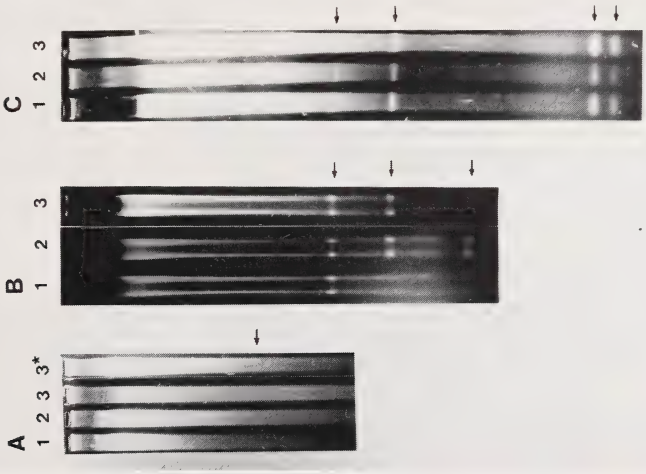

Fig. 1. Middle repetitive DNA in *Apodemus* species: Nuclear DNA was digested using A: BstEII; B: HindIII and C: EcoRI. Lanes 1: *Apodemus microps;* lanes 2: *Apodemus sylvaticus;* lanes 3: *Apodemus flavicollis* population I and II (II indicated by star)

in HindIII digested DNA of *Apodemus microps* (Cooke 1975). While in *Apodemus microps* samples from Czechoslovakia, the same three bands as in *Apodemus sylvaticus* and *Apodemus flavicollis* exist, whereas in our material from the „Seewinkel", the 0.75 kb band is absent. This points to a geographical variability in the existance of middle repetitive DNA families. To our knowledge this is the first description of diversity in the appearance of middle repetitive DNAs in different populations of a species. Analysis of mitochondrial DNA from the same *Apodemus* populations in Eastern Austria revealed also a high degree of intraspecific variability (Csaikl et al. in prep.). Additional support for this findings comes from cytogenetic results. With C-banding techniques several authors (Engel et al. 1978; Vujosevic et al. 1984; Habenicht 1978) could detect variability in the heterochromatin of *Apodemus flavicollis* chromosomes from different geographic populations. In contradiction to cytogenetic, mitochondrial and nuclear DNA data, isoenzyme analysis of this species from us and others (Csaikl et al. 1980; Gemmeke et al. 1987) showed no geographic variation. The analysis of 16 different enzymatic loci revealed no intraspecific variability in the specimes studied for middle repetitive DNA. All samples were homozygous for the same „frequent" allele described previously (Csaikl et al. 1980, 1986).

We consider our results on middle repetitive DNA presented in this paper to be a useful tool to distinguish between *Apodemus microps* on one hand and *Apodemus sylvaticus* and *Adpodemus flavicollis* on the other in Eastern Austria. A separation of *Apodemus sylvaticus* vs. *Apodemus flavicollis* is only possible in the „Seewinkel"-population, thus indicating that intraspecific variability is reflected also in nuclear DNA families. Our results indicate also that this type of nuclear DNA families are subjected to intraspecific variation.

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Zusammenfassung

Restriktionsendonuclease-Vergleich von Kern-DNA in Österreich vorkommender Apodemus Arten: Nachweis von intraspezifischer Variabilität in mittelrepetitiven DNA-Familien bei fehlender intraspezifischer Isoenzymvariabilität

Untersuchungen über mittelrepetitive DNA Familien der drei in Österreich vorkommenden *Apodemus* Arten, *Apodemus sylvaticus, Apodemus flavicollis* und *Apodemus microps* werden vorgestellt.

Table 2. **Middle repetitive DNA classes of *Mus musculus (M. m.), Apodemus sylvaticus (A. s.), Apodemus flavicollis (A. f.)* and *Apodemus microps (A. m.)* appearing after digestions with some restriction endonucleases (R. E.)**

species / R.E.	*M. m.*	*A. s.*	*A. f.* I	*A. f.* II	*A. m.*
EcoRI	–	1.80 kb	1.80 kb	1.80 kb	1.80 kb
	1.30 kb	1.30 kb	1.30 kb	1.30 kb	1.30 kb
	–	0.50 kb	0.50 kb	0.50 kb	0.50 kb
	–	0.40 kb	0.40 kb	0.40 kb	0.40 kb
HindIII	–	1.20 kb	1.20 kb	1.20 kb	1.20 kb
	–	0.75 kb	0.75 kb	0.75 kb	–
	–	0.40 kb	0.40 kb	0.40 kb	0.40 kb
BstEII	–	–	–	2.40 kb	–

Type *A. f.* I was found in the "Wiener Becken", type *A. f.* II in the "Seewinkel".

Unter Verwendung mehrerer Typ II Restriktionsendonucleasen konnten definierte Bandenmuster auf Grund spezifischer mittelrepetitiver DNA Familien festgestellt werden. HindIII verdaute DNA von *Apodemus microps,* unterscheidet sich von DNA der beiden anderen Arten *(Apodemus sylvaticus, Apodemus flavicollis).* Ein Unterschied in BstEII verdauter DNA zwischen beiden letzteren Arten konnte nur in einer der untersuchten Populationen nachgewiesen werden. Dieses Ergebnis belegt die Existenz von intraspezifischer Variabilität von mittelrepetitiver DNA bei *Apodemus flavicollis.* Die Untersuchung von 16 Isoenzymloci ergab hingegen nur monomorphe Muster.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Possible thermoregulatory behaviour in *Giraffa camelopardalis*

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Giraffe, *Giraffa camelopardalis,* are widespread in dry woodlands and savannas in Africa (Smithers 1983) even where ambient temperatures exceed 40 °C during summer. Their independence of free water (Dagg and Foster 1976) thus indicate physiological and behavioural adaptations to reduce water loss.

Although Brownlee (1963) considered the giraffe's shape the most efficient for distribution of the large body weight in a hot climate, to give a large surface area for the dissipation of heat, Innis (1958) and Dagg (1970) found no definite thermoregulatory behaviour in wild (eastern Transvaal, South Africa) and captive (Taronga Zoo, Sydney, Australia) giraffe. However, observations of free-ranging giraffe in the Etosha National Park, Namibia (18° 35′ to 19° 33′ S, 14° 24′ to 17° 08′ E), suggested the contrary.

During July 1987 (winter) the body orientation of stationary giraffe in relation to the sun was noted, by scanning at five minute intervals at waterholes. In December 1988 (summer, the rainy season) fewer giraffe visited waterholes and the body orientation of each individual encountered when driving along roads through woodland and on the fringe of the Etosha Pan were recorded. On all occasions during both seasons ambient temperature and wind speed was also noted. Four main categories of body orientation were used: 1. lateral (long axis of giraffe at right angles to the sun); 2. anterior (facing the sun directly); 3. posterior (facing away from the sun); 4. shadow. Categories 2. and 3. were grouped as "longitudinal".

Some 660 observations on ca. 290 giraffe (including possible resightings of the same individuals) were obtained, most at temperatures similar to the mean prevailing summer (35 °C) and winter (16 °C) temperatures. Wind seemed to have little effect on giraffe, apart from on drinking behaviour. The orientation of giraffe was therefore best observed at low windspeeds (< 5 m.s^{-1}) in winter. As giraffe away from waterholes were observed in summer, windspeed did not influence observations.

At temperatures below 20 °C, only 5 % of the observed giraffe selected shadow, 35 % faced the sun with their longitudinal axis and 60 % were standing parallel to the sun's rays (Fig. 1). This pattern was reversed at high T_a (> 30 °C), where most giraffe (91 %) preferred shadow or faced the sun longitudinally, therefore reducing the body surface area exposed to the sun.

The percentage of giraffe standing at right angles to the sun decreased from 60 % to 9 % over the temperature range < 20 °C–37 °C, with the reserve true for the percentage of giraffe facing the sun longitudinally, or selecting shadow. At $T_a > 34$ °C relatively more giraffe preferred shadow.

A significant deviation from the expected frequency of orientation (i.e. equal number of animals in all directions) was found using the Chi-Square Goodness-of-Fit Test. In the temperature range 25–30 °C, however, no significant difference occurred (Chi-square = 4.88, $p > 0.05$, df = 3, n = 150), possibly indicating this as the thermoneutral zone of giraffe.

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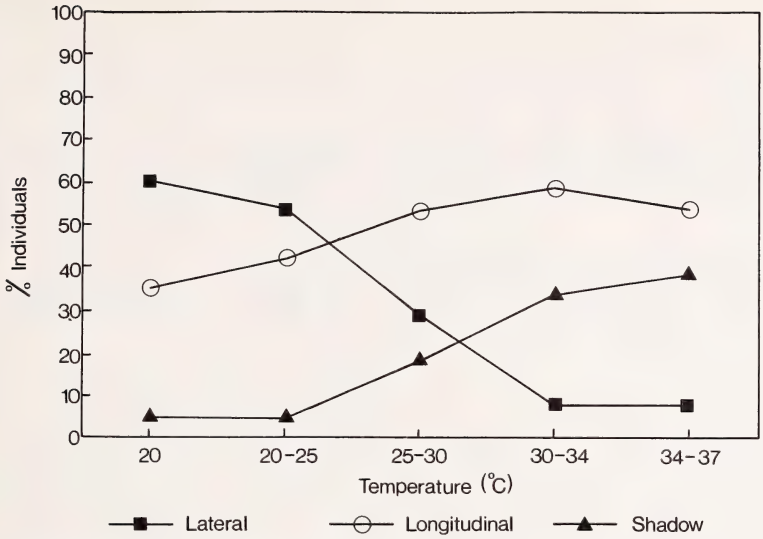

Fig. 1. Body orientation of giraffe relative to the sun over different temperature ranges

Significant differences in body orientation between the sexes and age groups were observed at $T_a > 30\,°C$ (Chi-square = 14.77 for "lateral", 271.99 for "longitudinal" and 128.84 for "shadow"; $p < 0.001$; df = 2). More than 80 % of the adult males faced the sun longitudinally, but only 60 % of the adult females and less than 20 % of the calves. Approximately 70 % of the calves selected shadow in this temperature range, against the 32 % and 13 % of the female and male giraffe respectively.

Physiological adaptations enabling giraffe to tolerate heat and arid conditions include a mechanism for cooling the exhaled air by the mucosa in the nasal passages (Langman et al. 1979), and a carotid rete mirabile which might have a thermoregulatory function as in other artiodactyls (Taylor and Lyman 1972; Mitchell et al. 1980).

Anatomical adaptations include large size and mass, thick skin (Dagg and Foster 1976), long neck and legs, and short body ovoid in cross section. Our data indicate that giraffe also make use of behavioural thermoregulation (Fig. 1). At lower ambient temperatures giraffe tend to position themselves so as to absorb heat over the largest possible body surface, while minimizing heat uptake at high T_a by positioning themselves with their longitudinal axis towards the sun, or seeking shadow.

Size also influences thermoregulatory behaviour. Adult males and females and calves all react in a similar way to high T_a. The taller and heavier males, however, are able to effectively make use of different orientations towards the sun, while the females and especially the calves select shadow. This substantiates Brownlee's (1963) theory of the effective distribution of body mass as well as the theory of a big body, in conjunction with a labile body temperature, acting as a "heat sink".

Giraffe would thus appear to be physiologically and anatomically well adapted to hot arid conditions. This, in conjunction with thermoregulatory behaviour would explain their success in exploiting open woodland and savanna habitats in Africa.

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Constitutive heterochromatin in the fallow deer *(Cervus dama)*

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Previous investigations on the karyotype of *Cervus dama* L. used conventional staining techniques (Gustavsson 1965; Hsu and Benirschke 1967; Wurster and Benirschke 1967; Gustavsson and Sundt 1968) and found a somatic, diploid chromosome number of 2n = 68, XX resp. XY. More recently, fluorescence and banding techniques which allow to differentiate between single chromosomes were used by Neitzel (1982), Wang and Du (1983), Karlik (1984) and Mayr et al. (1987a, 1987b). These investigators have used a wide spectrum of banding techniques, but one of the most helpful techniques for studying the constitutive heterochromatin, the C-banding-technique, has not been applied. The purpose of the present paper is to study the constitutive heterochromatin of *Cervus dama* with this technique and to compare the results with the relatively large ammount of data published for the red deer (*Cervus elaphus*, Goldoni et al. 1984; Herzog 1985, 1987b).

Lymphocyte cultures of 25 fallow deer (*Cervus dama* L.) from Niedersachsen (Federal Republic of Germany) were laid out in order to obtain metaphase chromosomes. The procedures of blood culture and chromosome analysis followed modified standard protocols, described in detail by Herzog (1988).

The somatic, diploid chromosome set of all animals studied consists of 68 chromosomes, namely 66 autosomes and two gonosomes (2n = 68, XX resp. XY; fig. 1). 32 autosome paris and the X-chromosomes are telocentric (according to the terminology of Nagl 1980) with an arm length ratio less than 1:4, whereas the Y is small and submetacentric. One autosome pair is metacentric.

The centromeric index (c.i.) is not useful for the characterisation of the chromosomes, because the p-arms of the telocentrics are very small, to identify only in good preparations and therefore not unequivocally measurable. In addition, the chromosome lengths of the related chromosome pairs show only slight differences (see Fig. 1).

All telocentric autosomes as well as the X-chromosome exhibit distinct C-bands of different size in the centromeric region. The Y shows no distinct C-bands, but the whole chromosome is relatively dark stained i.e. heterochromatic. The metacentric autosome pair shows only slight C-bands.

C-banding reveals a high degree of congruence between fallow deer and red deer; the karyotypes of both species show only slight differences, especially in the form of the Y-chromosome. Similar results have been obtained by Mayr et al. (1987b) for the G-banded karyotype. As the proposition for a C-banded idiogram shows, the differences in the C-banding pattern between both species are of the same magnitude as between different individuals of one species or even different metaphases of the same individual.

The metacentric autosome pair ("pair 1") is also detectable in red deer (*Cervus elaphus,* Goldoni et al. 1984; Herzog 1985, 1987b) and sika deer (*Cervus nippon*, Herzog 1985, 1987a). The C-banded telocentric autosomes are very similar to those of the red deer (fig. 1). The male gonosome was found to be metacentric in red deer from Western Germany (Herzog 1985, 1987b) and unknown origin (Mayr 1987b), but acrocentric in deer from

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Fig. 1. C-banded karyotype (example) of a male *Cervus dama* from Niedersachsen (West Germany). The designation of the chromosome 1 and the gonosomes follows a standardized idiogram of *Cervus elaphus* (Herzog 1987b)

Italy (Goldoni et al. 1984), whereas in fallow deer it has been described as submetacentric in the present study as well as by all previous authors.

The results of the karyotype comparison between red deer and fallow deer are surprising insofar as e.g. the red and the sika deer, two easily interbreeding species (e.g. Harrington 1979), differ much more in their karyotypes than the red and the fallow deer, but no hybrids are reported between fallow and red deer. This means that a reproductive barrier between them may not primarily be caused by karyological incompatibility but by other physiological (e.g. immunological) or behavioral factors.

Acknowledgements

The author is greatly indepted to Prof. Dr. K. Fischer, I. Zoologisches Institut, Universität Göttingen, for providing the blood samples. The studies were supported by the Deutsche Forschungsgemeinschaft and the author was receipient of a grant from the Land Niedersachsen.

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WISSENSCHAFTLICHE KURZMITTEILUNG

Identity of *Apodemus sylvaticus* (Linnaeus, 1758) recorded from Qatar (Rodentia: Muridae)

By D. Kock and I. A. Nader

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Receipt of Ms. 14. 3. 1989

Madkour (1982) reported 4 ♂♂ *Apodemus sylvaticus arianus* (Blanford 1881) from a single burrow containing a nest at Om Selal Mohammad, 15 km W of Doha, Qatar, as a first record for the Arabian Peninsula south of Lebanon. This was accepted by Corbet (1984: 22) as "apparently first record of this or any other species of *Apodemus* in the Arabian Peninsula". However, independant collecting in Qatar (Nader 1984) did not yield any further *A. sylvaticus* and this species was not included in a checklist of ten species recorded from this country.

In his paper, Madkour (1982) mentions some characters which may have led him to identify his mice as *A. sylvaticus* (Linnaeus 1758): smaller size than other *Apodemus* sp. in the NW of the Arabian Peninsula, white underside of body, pectoral spot present (no colouration described), hands and feet white, the hind foot (as considered by him) relatively long.

The measurements (n = 4) given by Madkour (1982) however are too small for an *Apodemus* sp.: HB 54-77, T 70-89, E 11-14, HF 12-17. Such measurements (small body with tail longer than HB, very short feet) indicate a misidentification of *Mus* sp.

The skull as illustrated by Madkour (1982: fig. 2) shows the specimen pictured to be at least subadult (basioccipital suture widely open), with skull proportions (rostrum length: skull length) typical for *Mus,* with small auditory bullae and reduced upper and lower third molars, differentiating the genus *Mus* from other Murinae in this part of the Palaearctic.

Madkour (1982: fig. 1) remarks that the baculum of his specimens differs from the genus *Apodemus* as illustrated by Harrison (1972: fig. 192). His own illustration of the baculum, without differentiation between the Corpus ossis penis and the Dens ossis penis, agrees well with the genus *Mus* (see Niethammer and Krapp 1978: fig. 7b).

The above analysis of information contained in Madkour (1982) leaves no doubt that the record of *Apodemus sylvaticus* in fact concerns *Mus musculus* Linnaeus, 1758. A more detailed identification of this outdoor house mouse has to be postponed until specimens are available for comparison. Harrison (1981) records the tiny subspecies *M. m. gentilulus* Thomas, 1919 from neighbouring Bahrain and the UAE, and the larger *M. m. praetextus* Brants, 1827 from Hofuf/Saudi Arabia and northwards.

Together with additional records of a bat (Madkour 1986: *Otonycteris hemprichi* Peters, 1859) and a rodent (Madkour 1983, 1984: *Gerbillus cheesmani* Thomas, 1919) the mammal fauna of Qatar presently comprises 13 species only. Compared to similar regions (e.g. Clayton 1983: 23–24 species in Kuwait) this number is rather low, very probable due to lack of field work.

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BEKANNTMACHUNG

Einladung

Die 64. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. findet von Sonntag, den 23. September, bis Donnerstag, den 27. September 1990, in Osnabrück statt.

Vorläufiges Programm

Sonntag, 23. September:	Anreise	
	17.00 Uhr:	Vorstandssitzung
	19.00 Uhr:	Zwangloser Begrüßungsabend im Remarque-Saal des Hotels Hohenzollern, am Hauptbahnhof
Montag, 24. September:	9.00 Uhr:	Begrüßung und Eröffnung der Tagung durch den 1. Vorsitzenden im Hörsaal der Biologie am Westerberg, Barbarastr. 11
	9.30 Uhr:	Hauptvortrag und Vorträge zum Schwerpunkt „Ökologie“
	14.30 Uhr:	Vorträge
	17.00 Uhr:	Mitgliederversammlung
	20.00 Uhr:	Forumsdiskussion in der Aula des Schlosses: Strategien zur Rettung vom Aussterben bedrohter Säugetierarten
Dienstag, 25. September:	9.00 Uhr:	Hauptvortrag und Vorträge zum Schwerpunkt „Ontogenese“
	11.00 Uhr:	Posterdemonstration
	14.30 Uhr:	Vorträge
	17.00 Uhr:	Empfang durch die Stadt Osnabrück im Friedenssaal
	20.00 Uhr:	Video- und Film-Referate
Mittwoch, 26. September:	9.00 Uhr:	Hauptvortrag und Vorträge zum Schwerpunkt „Ernährung und Verdauung“
	14.00 Uhr:	Vorträge
	16.00 Uhr:	Führung durch den Zoo Osnabrück
	18.30 Uhr:	Geselliger Abend
Donnerstag, 27. September:		Besuch der Seehundaufzuchtstation Norden/Norddeich und eine Bootsfahrt in das niedersächsische Wattenmeer (geplant)

Alle Interessenten sind zu der Tagung herzlich eingeladen. Neben den angekündigten Schwerpunkten werden wir auch diesmal wieder der Vielfalt der säugetierkundlichen Arbeitsgebiete Rechnung tragen (Vorträge und Poster-Demonstrationen).

Das Programm mit der Vortragsfolge wird allen Mitgliedern, und auf Anfrage auch Nicht-Mitgliedern, rechtzeitig vor der Tagung zugesandt. Falls persönliche Einladungen gewünscht werden, wenden Sie sich bitte an den 1. Vorsitzenden der Gesellschaft, Prof.

Dr. E. Kulzer, Institut für Biologie III, Auf der Morgenstelle 28, D-7400 Tübingen.

Bitte melden Sie die Vorträge, die nicht länger als 15 Min. dauern sollen, und Poster-Demonstrationen beim Geschäftsführer der Gesellschaft Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, D-5300 Bonn 1, Tel. 02 28/73 54 68, möglichst frühzeitig, jedoch spätestens bis zum 30. April 1990 (Ausschlußfrist) an.

Fragen zum Tagungsort und zur Organisation sind zu richten an: Prof. Dr. R. Schröpfer, Universität, FRB Biologie/Chemie: Ethologie, Barbarastr. 11, D-4500 Osnabrück, Tel. 05 41/6 08-28 47.

BUCHBESPRECHUNGEN

Hunter, R. H.. F.: **The Fallopian Tubes.** Their Role in Fertility and Infertility. Berlin – Heidelberg – New York – London – Paris – Tokyo – Hong Kong: Springer 1988. 191 pp., 55 figs. DM 198,–. ISBN 3-540-18436-8

Die Entwicklung zahlreicher neuer Methoden auf allen Gebieten der Biologie und Medizin hat eine Fülle neuer Detailkenntnisse gebracht, die für die Physiologie der Fortpflanzungsorgane und für die praktische Anwendung in Medizin und Veterinär-Medizin von erheblicher Bedeutung sind. Die vorliegende Monographie ist eine sehr nützliche Zusammenfassung unserer derzeitigen Kenntnisse über die Biologie der Tuba ovarica des Menschen, unter Berücksichtigung morphologischer und experimenteller Befunde an Haus- und Labortieren. Nach einer kurzen historischen Einleitung werden Anatomie und Entwicklung der Tuben unter funktionellen Gesichtspunkten behandelt. Die Bedeutung der Tube und ihrer Sekrete für Befruchtung, Transport und Lebensdauer der Gameten, die Vorgänge bei normaler und abnormer Befruchtung finden ebenso Berücksichtigung wie die wechselseitigen Beeinflussungen zwischen mütterlichem Organismus und noch nicht implantiertem Keim. Die abschließenden Kapitel behandeln Mißbildung der Tuben und deren chirurgische Behandlungsmöglichkeiten sowie Techniken bei der *in vitro* Befruchtung und bei der Transplantation von Eiern bzw. Keimlingen. Die Darstellung ist knapp, klar und umfassend. Sie wird durch ausgezeichnete Abbildungen ergänzt. Das Buch ist für alle, die als Mediziner, Veterinäre oder Biologen an der Fortpflanzungs-Biologie interessiert sind, von hohem Wert. D. Starck, Frankfurt/M.

Meyer, H.; Röhrs, M. (Hrsg.): **Studium Generale.** Vorträge zum Thema „Mensch und Tier". Band VI. Hannover: M. und H. Schaper 1989. 102 S. DM 19,50. ISBN 3-7944-0158-1

Der erste Beitrag (v. Engelhardt) behandelt unter vergleichenden Gesichtspunkten Fragen der Leistungsphysiologie des Sportpferdes und bietet einen ausgezeichneten Überblick über grundsätzlich physiologische Unterschiede bei verschiedenen Anpassungstypen bei Säugetieren. Der folgende Vortrag (Rohse) wirft die Frage auf, ob Hominisation im Sinne der biologischen Herkunft des Menschen aus subhumanen Primaten auch als Humanisation verstanden werden kann. Im wesentlichen handelt es sich um eine Analyse dieser Frage in der Roman-Literatur der Zeit nach Darwin (W. Busch, W. Raabe, F. Kafka, A. Huxley). Wissenschaftliche Aussagen der Evolutionsforschung und der Verhaltensforschung aus den letzten 50 Jahren werden nicht erwähnt. Gärtner bringt in seinem hoch interessanten Beitrag nach einer Einführung über populationsbiologische Analysen an Versuchskollektiven Ergebnisse einer, mit Methoden der empirischen Sozialforschung durchgeführten Untersuchung an einer modernen Großstadtbevölkerung über das Verhältnis der Menschen zum Tier. Ein kenntnisreicher Beitrag des W. Busch – Kenners Guratzsch behandelt die Beziehungen und die Einstellung von W. Busch als Künstler und als Privatmann zum Tier und zur Evolution. In sehr klaren und überzeugenden Darlegungen, die auch dem Nicht-Biologen verständlich sein dürften, berichtet Winnacker über Herstellung und Bedeutung transgener Tiere für die Gentechnologie. Notwendigkeit und Nutzen für biologische Erkenntnisse und Medizin (Tumorforschung, Herstellung von Wirkstoffen etc.) werden, – unter voller Beachtung der Ängste bei Laien und der viel diskutierten ehtischen Fragen, – mit großem Ernst besprochen. D. Starck, Frankfurt/M.

PENZLIN, H.: **Lehrbuch der Tierphysiologie.** 4. Aufl. Stuttgart, New York: G. Fischer 1989. 657 S., 418 Abb., 75 Tab. DM 54,–. ISBN 3-437-20392-4

9 Jahre nach der 3. liegt nun die 4., überarbeitete und erweiterte Auflage dieses bekannten Lehrbuchs der Tierphysiologie vor. Das Konzept zur Vermittlung des Lehrinhalts ist in den großen Kapiteln folgender Themenkreise beibehalten worden: Dynamik und Energetik lebender Systeme; Integration und Kommunikation in lebenden Systemen; Stoffaufnahme und -verteilung; inneres Milieu und Homöostase; Informationsaufnahme und -verarbeitung; Physiologie der Effektoren; Physiologie des Verhaltens. Innerhalb dieser Kapitel finden sich jedoch einige Umstellungen sowie Modernisierungen und Erweiterungen von verschiedenen Themen. Mehrere Abbildungen sind entfallen und neue wurden aufgenommen. Neu sind ferner Kontrollfragen am Ende jedes Kapitels und Antworten, die dem Benutzer ein Überprüfen seines Wissensstandes ermöglichen. Insgesamt ist der Umfang des Buches um 91 Seiten erweitert.

Der Text auch dieser Auflage ist konzentriert und verständlich abgefaßt. Die Darstellung der Themen beschränkt sich auf das Wesentliche, Vertiefungen in bestimmte Fragen werden durch Literaturverweise ermöglicht. Insgesamt ist die Neuauflage dieses Lehrbuchs zu begrüßen.

D. KRUSKA, Kiel

HUNTINGFORD, F.; TURNER, A.: **Animal conflict.** Cambridge: Univ. Press 1987, 448 pp. £ 14.95. ISBN 0-412-28750-1

In 12 Kapiteln bietet das Werk eine gediegene, wissenschaftlich fundierte und didaktisch geschickte Gesamtdarstellung der Biologie von Konflikt und Aggression im Tierreich. Jedes Kapitel behandelt ein Teilproblem, beginnt mit einer klar formulierten Fragestellung und endet mit einer präzisen Zusammenfassung. Die Einzelprobleme werden an zahlreichen Beispielen aus dem ganzen Tierreich, von Protisten bis zum Menschen, erläutert (zahlreiche Abb., Strichzeichnungen). Vögel und Säugetiere sind bevorzugt vertreten.

Einleitend werden Definitionen, Terminologie und die Untersuchungsmethoden behandelt. Es folgt eine allgemeine Übersicht über Erscheinungsformen von Konflikt und Aggression in den einzelnen Tierklassen und über Waffen der Tiere und die Art, wie diese benutzt werden. Spezifische Verhaltensweisen und Möglichkeiten von alternativem Verhalten werden besprochen (Tötungs- und Ritualkämpfe, Dominanz und Unterwerfung, Territorialität). Kapitel 4–6 behandeln die Ursachen agonistischen Verhaltens gegliedert nach: Verhaltensmechanismen – hormonale Einflüsse – neurale Mechanismen.

In den beiden folgenden Kapiteln wird das wichtige Problem der genetischen Grundlage und der ontogenetischen Entwicklung agonistischer Verhaltensweisen untersucht und der mögliche Einfluß von Umweltfaktoren (soziale Umwelt) und die Möglichkeit der Modifizierung durch diese Faktoren besprochen.

Eine ausführliche Besprechung der Konsequenzen agonistischen Verhaltens auf Fitness und in Hinblick auf evolutive Änderungen sind der Inhalt von Kap. 9–12.

Das Schlußkapitel bringt eine ausgewogene Besprechung der Aggression beim Menschen und prüft die Frage, ob und inwieweit auch beim Menschen eine endogene (genetische) Grundlage von Aggressivität nachzuweisen ist. Die Antwort lautet unter Berücksichtigung von Untersuchungen an Kleinkindern aus verschiedenen Kulturkreisen, von Zwillingsuntersuchungen und von Studien an vorindustriellen und industriellen Gesellschaften, daß eine genetische Grundlage für den Menschen wahrscheinlich ist, daß aber kulturelle Faktoren bei weitem wichtiger sind als genetische. Vor allem die lange Lernphase und der Erwerb der artikulierten Lautsprache als humanes Spezifikum stehen im Vordergrund. Der gelegentlich vermutete Aggressionstrieb des Menschen existiert nicht.

Die gesamte Darstellung ist ein nüchterner Bericht über die biologischen Fakten und als solcher von großem Wert. Fragen der Ethik, der Moral, der Religion und der politischen Beeinflussung bleiben bewußt ausgeklammert. Dem Buch ist ein ausführliches Schrifttumsverzeichnis (67 S.), leider nur englisch-sprachiger Literatur, beigegeben. Wichtige Ergebnisse aus anderen Sprachen, – so etwa die Studien zum Verhalten beim Hulman (CH. VOGEL) u. a. m. – werden nicht berücksichtigt. Im Text finden sich ausschließlich englische Tiernamen. Die wissenschaftlichen Namen sind aus einem besonderen Register zu entnehmen.

Das Buch setzt basale, biologische Kenntnisse voraus, eignet sich kaum als Einführung für Anfänger. Es ist aber ein sehr nützliches Werk für fortgeschrittene Studenten und als Informationsquelle für Biologen und Interessenten aus Nachbardisziplinen zweifellos von sehr großem Nutzen und kann empfohlen werden.

D. STARCK, Frankfurt/M.

DYBAN, A. P.; BARANOV, V. S.: **Cytogenetics of Mammalian Embryonic Development.** Oxford: Clarendon Press 1987. 361 p., 37 Sigs., 36 tables. £ 35.00. ISBN O-19-854584-3

Cytogenetik als Grenzgebiet zwischen Genetik und Entwicklungsbiologie umfaßt heute im wesentlichen Untersuchungen an Chromosomensätzen und Chromosomenaberrationen, deren Ursache und Folgen. Im vorliegenden Werk werden auf recht breiter Basis Untersuchungen an Mäusestämmen vorgelegt. Eingehend behandelt werden Haploidie, Triploidie, Tetraploidie und die Vorgänge, die zu numerischen Abweichungen im Chromosomenbestand und zu Strukturaberrationen individueller Chromosomen bei Säugetieren führen. Vergleiche mit karyotypischen Anomalien beim Menschen werden eingehend besprochen. Ein Kapitel befaßt sich mit den Auswirkungen chromosomaler Abweichungen auf die Funktion des Gehirns (bedingte Reflexes, Verhalten). Der Einfluß chromosomaler Kontrolle auf frühembryonale Entwicklungsvorgänge wird diskutiert.

Das Buch ist eine umfassend überarbeitete und ergänzte englische Ausgabe einer russischen Arbeit von 1976. Sie ermöglicht Information über die Forschungsergebnisse des Arbeitskreises an der Medizinischen Akademie Leningrad und hat als übersichtliche Zusammenfassung vor allem Bedeutung für Humangenetiker und Cytobiologen. Dem Buch ist ein umfangreiches Schrifttumverzeichnis beigegeben. D. STARCK, Frankfurt/M.

SCHULZE, G.: **Die Schweinswale.** Die Neue Brehm-Bücherei 583. Wittenberg-Lutherstadt: A. Ziemsen 1987. 167 S.; 116 Abb. 21,40 DM. ISBN 3-7403-0048-5

Nur wenige Arten körperkleiner Zahnwale werden in der Familie Phocoenidae vereinigt. Bekanntester Vertreter mit der weitesten Verbreitung im Atlantik, nördlichen Pazifik und Nebenmeeren ist *Phocoena phocoena*, der Schweinswal oder Kleintümmler. Gerade an dieser Art haben bereits frühere Forschungen wesentliche Erkenntnisse erbracht und zu unserem Grundwissen über biologische Besonderheiten der Wale schlechthin beigetragen. G. SCHULZE stellt daher in der vorliegenden Neuerscheinung der bekannten Neuen Brehm-Bücherei insbesondere *Phocoena phocoena* vor und berichtet sehr detailliert über dessen Erforschungsgeschichte, Benennungen, Merkmale, Verbreitung, Körperbau, Nahrung, Fortpflanzung, Verhalten, Feinde und Todesursachen. Dem früher ausgeübten Fang und der Verwertung dieser kleinen Meeressäuger in unseren Breiten ist ein weiterer Abschnitt gewidmet, und alte und neuere Erkenntnisse zur Haltung werden ebenfalls dargelegt. Wiederum wird hier eine Art gekennzeichnet, deren Bestände, obwohl nicht bejagt, zunehmend schrumpfen.

Im Anschluß werden die übrigen sicheren Arten *Phocoena dioptrica, Phocoena sinus, Phocoenoides dalli* und *Neophocaena phocaenoides* in Kürze charakterisiert sowie die erst 1972 bzw. 1975 zu gesonderten Arten erhobenen *Neophocaena asiaeorientalis* und *Neophocaena sunameri.*

Diese Neuerscheinung ist informativ geschrieben, mit zahlreichen Abbildungen versehen und flüssig zu lesen. Sie beruht auf einer ungewöhnlich umfangreichen Literaturdurchsicht alter bis neuester Quellen, die sicherlich bei vertiefenden Fragestellungen zu beachten sind. Dem Autor ist hier jedoch eine schöne Zusammenschau über die Biologie dieser Meeressäuger gelungen. D. KRUSKA, Kiel

KLIMA, M.: **Early Development of the Shoulder Girdle and Sternum in Marsupials (Mammalia: Metatheria).** Advances in Anatomy, Embryology and Cell Biologie Vol. 109. Berlin, Heidelberg, New York, London, Paris, Tokyo: Springer Verlag 1987. 88 pp., 33 figs. DM 88,–. ISBN 3-540-18358-2

Das Vorkommen einer ausgedehnten ventralen Knorpelplatte (Ventralplatte: Coracoid), die bei einigen Arten das Sternum erreichen kann, war von einigen Einzelstadien von Beuteljungen bekannt und wurde in der Regel als altes Reptilerbe, als rudimentäre Bildung gedeutet. Die vorliegende Arbeit bringt erstmals eine umfassende und vollständige Beschreibung der Morphogenese des Schultergürtels bei Beuteltieren (11 Species, über 100 Schnittserien, HUBRECHT Laboratorium, HILL-Collection). Der Schultergürtel der Feten und frühen Beuteljungen zeigt in der Tat starke Anklänge an die Zustände bei Monotremata, während er im adulten Zustand nicht grundsätzlich von dem der Eutheria abweicht. Die Formentwicklung des Gürtels und seiner einzelnen Skelettelemente wird an Hand kontinuierlicher Stadienreihen beschrieben und durch Rekonstruktionen erläutert. Besonders reich vertreten sind *Dasyurus* und *Trichosurus.* Wichtig ist die Feststellung, daß der ventrale Teil des primären Schultergürtels seine maximale Ausbildung zum Zeitpunkt des Geburtstermins zeigt und kurz nach der Geburt bereits rückgebildet wird. Die Tatsache, daß das Neugeborene sofort nach der Geburt den Weg von der mütterlichen Genitalöffnung zum Marsupium und zur Zitze aus eigener Kraft mit Hilfe der Vordergliedmaßen bewältigen muß, zeigt in diesem Zusammenhang, daß die Ausbildung der Ventralplatte als funktionell wichtige Struktur zur Abstützung der Vordergliedmaße verstanden werden muß und als eine Adaptation im Rahmen des gruppenspezifischen Fortpflanzungsverhalten zu deuten ist. Dabei wird Material alter Skelettelemente zum Ausbau einer neuen Konstruktion herangezogen. D. STARCK, Frankfurt/M.

BIBIKOW, D. I.: **Der Wolf, *Canis lupus*.** Die Neue Brehm-Bücherei 587. Wittenberg Lutherstadt: A. Ziemsen 1988. 198 S., 10 Tab., 88 Abb., 23,– DM. ISBN 3-7403-0155-4

Mit dem Ziel, Wölfe in den noch verbliebenen Naturräumen der gesamten Verbreitung möglichst zu erhalten, gingen seit den 70er Jahren von der IUCN Bestrebungen aus, Forschungen zur Ökologie dieser Säugerart staatenübergreifend, vor allem in der UdSSR zu koordinieren. Als Basis zur Bewertung der momentanen Situation und als Grundlage für eine Diskussion über zukünftige Aufgaben erschien 1985 eine, von einem Autorenkollektiv verfaßte Monographie über den Wolf in der Reihe „Tiere der UdSSR und der angrenzenden Länder" in russischer Sprache. Im vorliegenden Band der bekannten Brehm-Bücherei legt der russische Zoologe BIBIKOW in deutscher Sprache eine Erweiterung dieser Studie vor, in der die Verhältnisse in Europa und Nordamerika zusätzlich integriert sind. Der Wolf wird in folgenden Kapiteln beschrieben: Morphologische Besonderheiten, Abstammung und Entwicklungsgeschichte; Systematik; Areal- und Bestandsveränderungen; Lebensraum; Nahrung; Stellung in der Biozönose; Verhalten und soziale Organisation; Fortpflanzung und Populationsstruktur; Mensch und Wolf; Maßnahmen zur Bestandsregulation. Die ersten Kapitel werden vergleichsweise kurz abgehandelt, ökologische und ethologische Ergebnisse stehen im Vordergrund. Besonders interessant erscheinen die modernen Erkenntnisse an Populationen, die über längere Zeiträume in der UdSSR verfolgt wurden. Sie sind durch sehr viel Zahlenmaterial, Skizzen und Abbildungen belegt. Auf die Beziehungen zwischen Mensch und Wolf in anderen Kulturkreisen und die Problematik der Bastardierung von Wölfen und verwilderten Hunden wird ebenfalls eingegangen. Das umfangreiche Literaturverzeichnis läßt zwar einige Studien vermissen und auch Text und Darstellung lassen wenige Mängel erkennen, dennoch stellt dieses Buch eine interessante Zusammenstellung dar, vor allem deshalb, weil hier dem deutschkundigen Interessenten viele Erkenntnisse aus einem anderen Sprachraum zugänglich gemacht werden. D. KRUSKA, Kiel

FLEAGLE, J. G.: **Primate Adaptation and Evolution.** San Diego, New York, London: Academic Press 1988. 486 S., 54 Tab., 271 Abb., 107,– DM. ISBN 0-12-260340-0

Endlich liegt ein umfassendes, primatologisches Lehrbuch vor, nachdem man in der Vergangenheit nur eine große Anzahl einschlägiger Spezialliteratur zur ausgewählten und deshalb unerschwinglichen vorlesungsbegleitenden Lektüre empfehlen konnte. Der Autor, gleichermaßen anatomisch, paläontologisch, systematisch und verhaltensbiologisch versiert, hat seine Erfahrungen in langen Jahren offensichtlich systematisch zur Vorbereitung dieses wertvollen Buches in seine Lehrveranstaltungen eingebaut. Die ersten drei Kapitel behandeln systematische, anatomische, ökologische und verhaltensbiologische Grundlagen, wobei unter vielem anderen positiv auffällt, daß der Mensch in diesem primatologischen Werk selbstverständlich einbezogen ist, ein Mangel vieler anderer Bücher. Sollte eingewandt werden, das Verhalten käme mit nur einem von 16 Kapiteln zu kurz, so muß man entgegenhalten, daß wohltuend und lehrreich verhaltensbiologische Aspekte immer wieder explizit und implizit in den anderen Kapiteln berücksichtigt sind. Gerade diese Integration verschiedener Aspekte der Primatenbiologie macht das Buch so wertvoll.

Es folgen vier systematisch thematisierte Kapitel zur Biologie und Evolution der Privaten, eines ist speziell den verschiedenen Adaptationen gewidmet, obwohl auch diese immer wieder im sonstigen Text Berücksichtigung finden. Die Kapitel 9 bis 16 des Bandes behandeln zwar nach ihren Titeln ausschließlich die Fossilgeschichte, doch dies geschieht erstens so präzis, umfassend, knapp und auf dem aktuellen Stand der Diskussion, daß schon diese zweite Hälfte das Buch konkurrenzlos macht. Zweitens wird der integrative Ansatz konsequent verfolgt, so daß wir es trotz paläontologischer Inhalte stets mit sehr lebendiger Primatologie zu tun haben.

Das großformatige Buch im Hartdeckel ist trotz eng bedruckter Seiten leicht zu lesen, da der Text zweispaltig angelegt ist. Das Buch enthält ein Glossar und ein recht umfängliches, praktisches Register. FLEAGLE verwendet Zeichnungsvorlagen von Dias seiner Vorlesungen als Abbildungen, so daß mit wenigen Ausnahmen didaktisch ausgezeichnete Bebilderung vorliegt. Sowohl die angewandte Reprotechnik als auch das sehr gute Papier des Buches hätten ausgezeichnete Fotowiedergaben erlaubt; das schlechte handwerkliche Können des Verlagsfotografen hat dies leider manchmal verhindert.

Diese kleinen Mängel bedeuten keine Einschränkung für die Empfehlung des Buches an sich. Nur ist schade, daß es nicht in deutscher Sprache wird erscheinen können. Trotzdem ist das Werk nicht nur den an Säugetieren allgemein und an Primaten speziell interessierten Studenten gleichermaßen zu empfehlen; alle Fachkollegen, ob sie über Säugetiere, Primaten oder humanbiologisch arbeiten, alle Evolutions- und Verhaltensbiologen sollen dieses Buch lesen. C. NIEMITZ, Berlin

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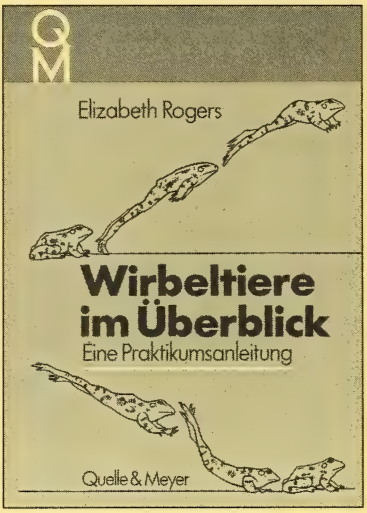

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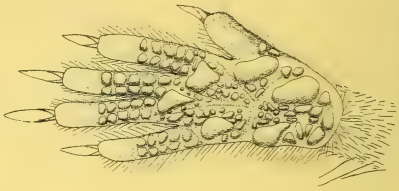

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Body temperature and fur quality in swimming Water-Shrews, *Neomys fodiens* (Mammalia, Insectivora)

By P. Vogel

Institut de Zoologie et d'Ecologie animale, Université de Lausanne

Receipt of Ms. 05. 10. 1988

Abstract

Body temperature of the European water-shrew *Neomys fodiens* was reinvestigated with intraperitoneally implanted radiotransmitters. Two animals, caged in outdoor conditions, were tested during February and March. Mean body temperature (Tb) during rest was 37.0 °C, during activity 37.5 °C. During stress of capture Tb increased to 38.4 °C, and during a social confrontation mean Tb was 39.4 °C.

During forced swimming Tb decreased at a rate of 1.1 °C per minute in an animal with wet fur. However, when kept in adequate conditions, animals could maintain their body temperature at a level of about 37 °C in most of the tested situations. In water of 2.6 °C, mean Tb after 6 min of forced swimming or diving was 37.4 °C, comparable to Tb during terrestrial activity. In these animals the fur remained dry even on its surface. The pelt of these shrews has a hydrophobic property which seems to be unique compared to other semiaquatic mammals.

Introduction

European and American water-shrews (*Neomys fodiens* and *Sorex palustris*) have a body weight of 10–20 g and are the smallest semiaquatic mammals. The degree of their adaptation to swimming and diving is a matter of discussion but most authors consider it to be rather weak. This statement can be substantiated for *N. fodiens* by some selected references: An extensive analysis of faeces, sampled over a two years period by Churchfield (1985) showed, that only 50 % of the food items of the water-shrew are aquatic organisms. After Ruthardt and Schröpfer (1985), the water-shrew is only weakly adapted for locomotion in water. Moreover, most of the measured diving sequences in captivity last only 3 to 10 seconds (Köhler 1984; Churchfield 1985; Ruthardt and Schröpfer 1985). The rows of bristles on hands and feet are doubtless an adaptation for swimming, but several authors state that, in swimming water-shrews, the surface of the fur gets wet (Köhler 1984; Ruthardt and Schröpfer 1985). The resulting physiological consequences have been shown by Lardet (1988) to be that during moderate activity in water, the body temperature (Tb) decreases strongly and therefore, extended activity in cold water seems to be impossible for this strict homeothermic shrew.

Similar observations have been published on the American water-shrew *S. palustris*. The surface of the fur also gets wet and in water of 10–12 °C the Tb drops during swimming by 2.0 °C per minute (Calder 1969).

My own experience with the European water-shrew under laboratory conditions (Vogel 1972a, 1972b) and direct observations in nature (Weissenberger et al. 1983) lead me to consider the wetting of the fur to be a consequence of conditions of captivity and experimental design. Therefore, Tb was reinvestigated in a small experimental study, carried out during winter conditions in low water temperature, paying particular attention to the captivity conditions and the technique of temperature monitoring. For comparison, it was also necessary to determine the Tb during rest and activity on land.

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Material and methods

The experiments were carried out with two *Neomys fodiens* (Pennant, 1771), a male (Nr. 1) and a female (Nr. 2) caught in autumn and kept during the experimental period from February to March in an animal house under "outdoor conditions". During the experimental period, both animals had a weight of 16 ± 1 g.

The body temperature was monitored with radio transmitters (Model X of Mini-Mitter Inc., Sunriver, Oregon, USA) with a range of about 30 cm and a battery life of 3 months. Coated with paraffin, their weight is 1.3 g. The recording was carried out with a special receiver (developped by Lavanchy Electronic, CH 1008 Prilly), a timer-counter (Philips, PM 6671) with a frequency-voltage converter and a paper recorder (Tarkan, W+W Recorder 600).

The intraperitoneal implantation was carried out under 2.5 % Fluothan anaesthesia, after the technique of Heldmaier and Steinlechner (1981). In the case of the male, the transmitter stopped after 5 days and had to be replaced. As a consequence of two consecutive operations, the physiological state of this animal was not optimal. The female, caught the 6. XII. 1986, was implanted on 30. XII. 1986. The battery stopped on the 4. IV. 1987. In the night of 4/5. VI, she was paired with a male and on the 24.VI, after a gestation of 20 days (confirming Vogel 1972a), she gave birth to 6 young which were raised successfully. The transmitter was explanted on the 14. IX and the shrew released at the point of capture on the 8. XI. 1987. This life history proves that the transmitter may not disturb fundamental physiological functions such as reproduction and longevity.

Before and after implantation the animals were firstly kept in standard Macrolon cages (40 × 25 cm) and from the onset of the experiments housed in two large PVC terrariums divided into a terrestrial and an aquatic part. The dimension of the terrestrial part was 95 × 55 cm; the bottom was filled up with 10 cm of humid soil composed of earth and turf, and covered with a litter of moss and dead leaves. The aquatic part had the same dimensions and the water was kept at a depth of 15 cm. Bricks and water cress plants gave a rich infrastructure. Large quantities of *Gammarus* were added regularly and exerted a high attraction. A small aquarium heater did not suppress ice formation but prevented total freezing of the water body.

Three types of swimming experiments were conducted:

1. The shrew was released in the aquatic part of the enclosure where it had to swim or dive without possibility of relaxation. As in the experiments of Calder (1969) and Lardet (1988), the time was limited to 6 minutes.
2. The shrew was released during 30 min in the aquatic part and was provided with an opportunity to relax on a stone, the top of which lay 2 cm beneath the water surface.
3. The shrew was totally immersed, with exception of its nose, during at least 10 minutes. For this experiment, a special diving aquarium (50 × 30 × 30 cm) joined to a terrarium (45 × 45 × 30 cm) was used. The passage to the aquarium lay under water and could be closed behind the passing shrew by means of a slide. The surface of the water was covered by a wire mesh which allowed the shrew to breath by pushing its nose through the mesh. In this confinement, the shrew dove for *Gammarus* several hundred times per day, even if the daily food (minced beef and fish) was present in the terrestrial part. As a consequence, even after closure of the slide, the shrew was not very stressed. Special experimental conditions, ambient temperature (Ta), water temperature (Tw) and requisites are mentioned together with the results.

For the determination of a reference body temperature of *Neomys fodiens* during rest and activity in the terrestrial habitat, 6 periods of 24 h were recorded at Ta from −7 to 21 °C. Herein unambigous sequences of behaviour were selected in which the Tb values were taken every 10 minutes. From these data daily mean values with standard deviation were calculated and the significance levels for differences between mean temperatures determined using a t-test.

Results

Body temperature in the terrestrial habitat

The sequence shown in Fig. 1 indicates that the body temperature during rest remains relatively stable, but varies strongly during activity. In cold environments, about 10 min before leaving the nest, the Tb decreases often as much as 1 °C and then increases rapidly. As a consequence of arousal, colder peripheral blood is put in circulation and cools the central part, an effect which is immediately counterbalanced by active thermoregulation.

The mean Tb of the two shrews in different conditions are presented in Table 1. The difference of Tb between activity and rest is significant. The difference between the two

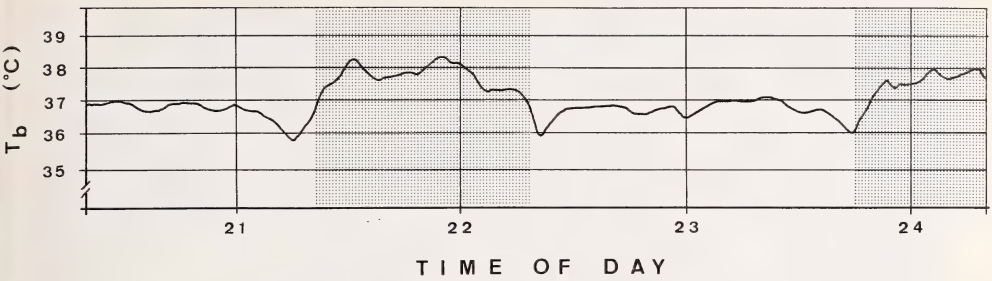

Fig. 1. Body temperature (Tb) of *N. fodiens* kept in outdoor conditions during rest (white part) and during activity (shaded part). Ambient temperature (Ta) is 3 °C

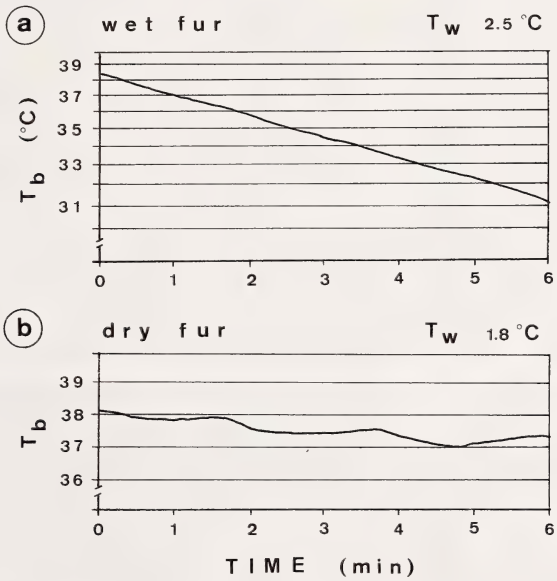

Fig. 2. Body temperature (Tb) of *N. fodiens* during a swimming experiment of 6 min: *a.* Animal with wet fur; *b.* animal with dry fur. Tw: water temperature. The different scales of Tb are dependent of the transmitter

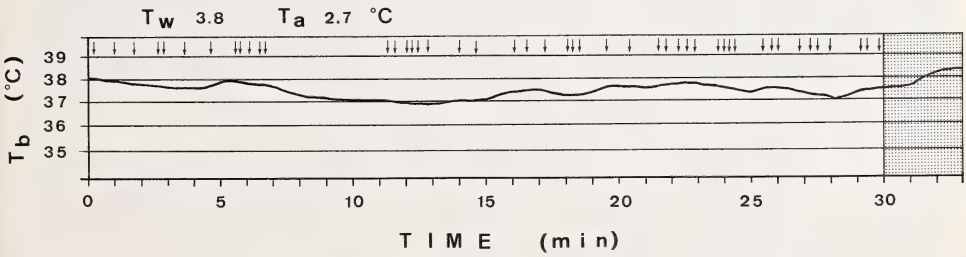

Fig. 3. Body temperature of *N. fodiens* during 30 minutes of enforced water activity. Arrows: diving. Shaded part: increase of Tb after experiment

Table 1. **Body temperature (mean and SD) of *Neomys fodiens* during terrestrial activity and rest under different conditions**

Ta 21 °C concerns stable indoor conditions, the lower Ta are daily mean temperatures in outdoor conditions

Animal	Ta (°C)	Tb activity	n	Tb rest	n	Significance
Nr 1	21	37.3 ± 0.3	28	37.0 ± 0.2	27	$p<0.001$
Nr 1	5	37.6 ± 0.2	23	37.3 ± 0.2	48	$p<0.001$
Nr 1	0	37.3 ± 0.3	23	36.8 ± 0.3	66	$p<0.001$
Nr 2	21	37.7 ± 0.1	29	37.1 ± 0.3	63	$p<0.001$
Nr 2	4	37.7 ± 0.3	18	36.9 ± 0.2	31	$p<0.001$
Nr 2	−7	37.2 ± 0.7	27	36.9 ± 0.2	52	$p=0.058$
Global mean		37.5 ± 0.4	148	37.0 ± 0.3	287	$p<0.001$

animals is only small and not significant. Therefore, as reference, we can use the global means: a Tb rest of 37.0 °C and a Tb activity of 37.5 °C.

To avoid handling of the animals before the experiment, they were caught with a Longworth trap impregnated with the odour of another shrew. The disturbance of springing the trap and of the succeeding capture (stress) led to an increase in Tb, to a mean of 38.5 °C ± 0.4 (n = 9). It is important to realize that all experiments started with a raised Tb.

Studying the effect of social stress, we put Nr. 2 in the same enclosure as another female and observed them for 30 minutes. Although little direct antagonistic behaviour occurred, mean Tb increased to 39.4 °C and an extreme value of 40.1 °C was observed.

Body temperature in aquatic habitats

In the first type of experiment, the shrews were obliged to swim or dive for 6 min in the standard swimming pool without any support (n = 6). The first trial was done with the animals taken from laboratory conditions. In one of the two animals (Nr. 1), at a Tw of 2.5 °C, Tb dropped linearly by 1.1 °C per minute (Fig. 2a) and continued even after the end of the experience down to 28 °C. The fur of this shrew was as wet as that of the shrew in Fig. 4a.

After improving the maintenance conditions by keeping the shrews outdoors in terrariums on wet soil, and allowing the animals to adapt for some days, Tb dropped only slowly and the fur of the experimental shrews was wet only on the surface (Fig. 4c), or, as in Nr. 2, remained completely dry (Fig. 4 d–f) and the Tb remained above 37 °C (Fig. 2b).

The second experiment, involving forced water activity of 30 min duration, was conducted only once with Nr. 2 (Tw 3.8 °C, Ta 2.7 °C). During this experiment the shrew was observed to dive over 40 times and ate four *Gammarus*. The minimal Tb, recorded after 13 min, was 36.9 °C, and Tb after 30 min was 37.6 °C (Fig. 3).

In the third type of experiment, executed with Nr. 2 in the special diving aquarium, the shrew was blocked under water for 10 minutes. In the first run, with a Tw of 8.5 °C, the shrew found the exit after 12 min and had a Tb of 37.3 °C. In the second run, at Tw of 1 °C, and after 10 minutes of total immersion, the Tb was 36.6 °.

If only the trials with dry or nearly dry fur are considered from all nine experiments and the Tb is taken after 6 min swimming activity (n = 6, mean Tw = 2.6 °C), Tb decreases only 0.2 °C per minute and a mean Tb of 37.4 °C ± 0.4 is observed. This Tb is roughly the same as the normal activity Tb in the terrestrial habitat.

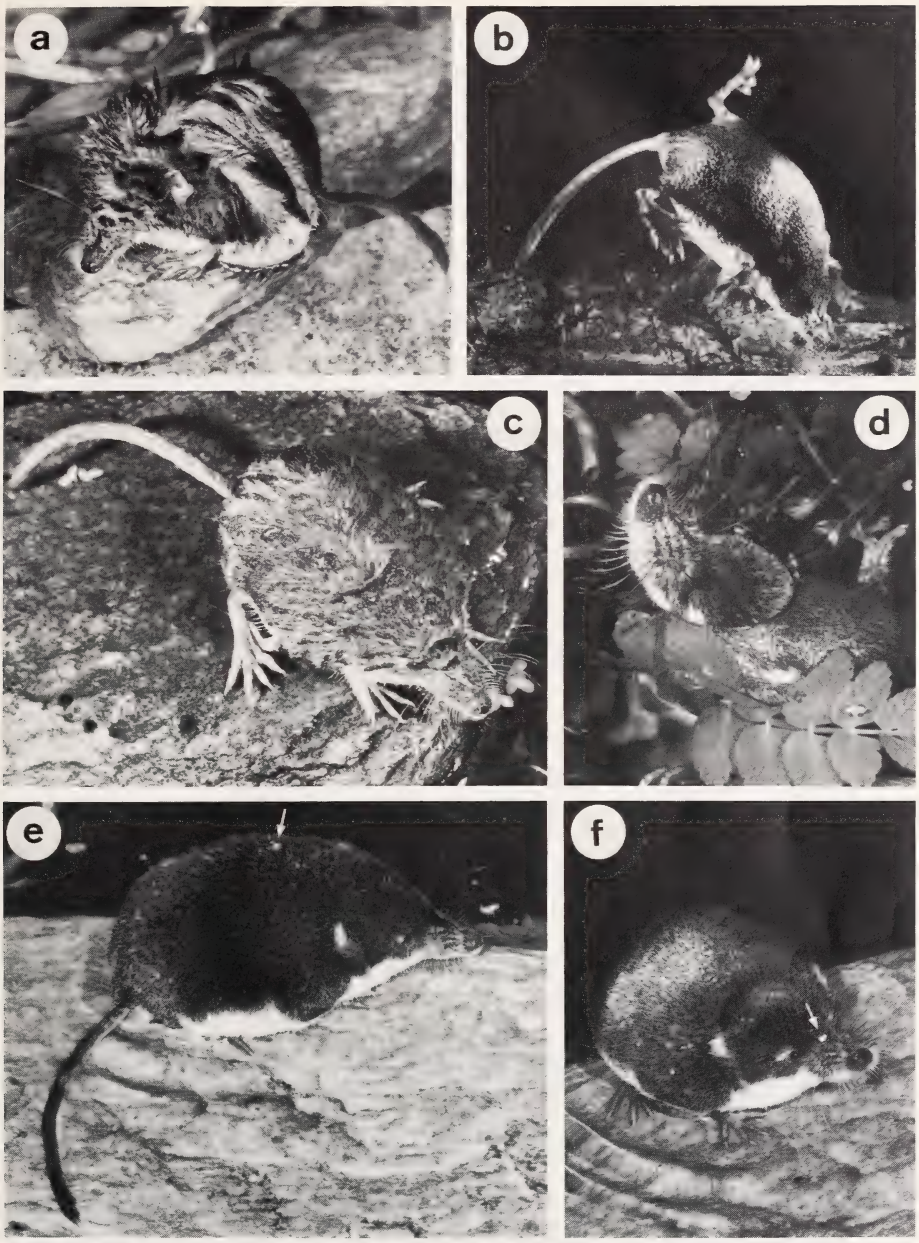

Fig. 4. Neomys fodiens during activity in water: *a.* shrew with wet fur; *b.* diving shrew with air layer in the fur; *c.* shrew with wet hairtips; *d.* the water retracts from dry fur of shrew slowly emerging with olfactive control; *e.* and *f.* dry shrew after diving. Arrow: water droplets adhering on dry fur

Discussion

After Gebczynski (1977), the mean body temperature of *N. fodiens* in terrestrial habitats is between 38.3 and 38.7 °C, depending on the season (range 37.4–39.6). These values are 1–1.5 °C above our mean Tb measured during activity with transmitters in undisturbed shrews and could be explained by handling of the shrews and insertion of a rectal thermocouple. This handling stress obviously does have thermogenetic consequences and caused hyperthermia. It could also explain the high Tb of our shrews after capture and, more importantly, the high temperatures observed during social stress.

Our mean value of Tb during activity (37.5 °C) agrees with the mean rectal temperature (37.3 °C) published by Nagel (1985). The measurements of this author were taken after 1 hour in a respirometric chamber with a rectal thermocouple of rapid reaction. The mean value measured by Lardet (1987) at the onset of his experiments (Tb = 36.1 °C) is about 2 °C lower than our values (Tb stress of 38.5 °C). The rectal probe in his experiments was inserted 15 mm, not deep enough to get a correct Tb. The intercept of his regression lines should be corrected by this amount.

Species of the genus *Sorex* are characterized by the highest Tb known amongst shrews (Frey 1979). However, a Tb of 39.9 °C measured by Calder (1969) for *S. palustris* is more than 1 °C higher compared to the mean Tb of the European *S. araneus* published by Nagel (1985). Here too, the stress induced by fixing the rectal probe on the tail may explain the difference.

Our results on the Tb in swimming water shrews differ strongly from those obtained by other authors in similar conditions. Calder (1969) observed in *S. palustris,* at Tw of 10–12 °C, that Tb drops by 2 °C per minute (Calder 1969). Lardet (1987) observed in *N. fodiens* under similar conditions (Tw = 5 °C) a decrease of 0.8 °C per minute. The decrease of Tb in our experiments is almost negligible although the water temperature was lower. This contrast can be explained by the difference of fur quality. Therefore, the important decrease of Tb observed by other authors, should be interpreted as an artefact of captivity conditions and it would be astonishing if the high conductance measured by Calder (1969) on dead immersed shrews is representative of living water-shrews.

The fur of the water-shrew is a highly specialized and very sensitive system which can lose its water-repellent property even as a result of the stress of capture in nature. This explains why the shrews kept by Kahmann (1955), Crowcroft (1957), Köhler (1984, p. 179 and Figs. 1; 5; 10) and Ruthardt and Schröpfer (1985) got wet fur. However, Lorenz (1952), Zimmermann (1959, in Köhler 1984) and Hutterer and Hürter (1981) stated in agreement with our observations, that the fur of a fit water-shrew remains dry even after extended water activity.

Captivity conditions play an essential role in fur quality. In our department, a study on diving behaviour of *N. fodiens* failed because the shrews didn't show any swimming activity in the confinement of the classical indoor animal room. On the contrary, the pelts of shrews caged under outside conditions in big containers with a deep humid soil, maintain the waterproof property.

Our own observations of other swimming semiaquatic mammals has shown that their fur gets wet on the surface: *Ornithorhynchus, Castor, Ondathra, Myocastor, Lutra, Galemys* and *Micropotamogale.* The latter has over-hairs with an enlarged apical part (Vogel 1983), a structure, which was also reported for *Potamogale, Desmana, Galemys* and *Ornithorhynchus* by Toldt (1935). Under water these hairs may protect the under fur from wetting.

The water-repellent property of the fur of the water-shrew is based on another principle. The particular structure of the terminal segment of the guard hairs revealed by scanning electron microscopy (Vogel and Koepchen 1978; Vogel and Besançon 1979) have been considered by Appelt (1973) and Hutterer and Hürter (1981) to be

responsible for air retention in the fur (Fig. 4b). If this structure really has the supposed significance, it can fulfill this function only together with other factors. Hair position (tonus of Musculi arrectores pilorum) and skin gland secretion may present such factors.

Shrews are the smallest semiaquatic mammals. Visibly they have developed a particular fur which allows them to keep a normal body temperature even in the coldest water. In fact, SCHLOETH (1980) observed in a mountain river, shrews diving at a Ta of −10 to −15 °C. This suggests a low conductance in water and high maximum heat production, factors which should be studied in adequate conditions.

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Zusammenfassung

Körpertemperatur und Fellqualität tauchender Wasserspitzmäuse, Neomys fodiens (Mammalia, Insectivora)

Die Körpertemperatur der Europäischen Wasserspitzmaus *Neomys fodiens* wurden mittels intraperitoneal implantierter Radiosender untersucht. Zwei unter Außenbedingungen gehaltene Tiere wurden im Februar und März getestet. Die mittlere Körpertemperatur (Tb) in Ruhe betrug 37,0 °C, in Aktivität 37,5 °C. Im Fangstreß stieg Tb auf 38,5 °C, während einer sozialen Konfrontation auf 39,4 °C.

Während erzwungenem Schwimmen nahm die Körpertemperatur bei einem Tier mit nassem Fell um 1,1 °C pro min ab. Wurden die Tiere unter guten Bedingungen gehalten, blieb das Fell trocken und sie konnten ihre Tb in den meisten überprüften Situationen bei 37 °C halten. In Wasser von 2,6 °C betrug die mittlere Tb nach 6 min erzwungenem Schwimmen oder Tauchen 37,4 °C, also praktisch gleich wie bei terrestrischer Aktivität. Der Pelz dieser Tiere wurde auch oberflächlich nicht naß und hat offenbar wasserabstoßende Eigenschaften, die unter semiaquatischen Säugern einmalig sein.

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Diet, food availability and foraging behaviour of badgers (*Meles meles* L.) in southern England

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Abstract

During a four-year study in the south of England the diet of badgers was investigated by analysis of faeces contents; availability of earthworms was assessed by formalin-sampling and by calculation of number of "worm nights" using meteorological data; and the foraging behaviour and habitat use of badgers was recorded from direct observation of radio-collared animals. The main foods of badgers were earthworms, insects, fruit and wheat, and grass was also ingested in substantial quantities. Earthworms appeared in the diet most frequently but wheat was almost as important a food overall in terms of percentage volume. Earthworm intake was correlated with worm biomass as measured by formalin-sampling, but not with number of "worm nights". There was a significant correlation between the amount of time radio-collared badgers spent foraging in a particular part of their territory and earthworm biomass at that location. Percentage time spent in different habitat types (pasture, scrub and arable fields) showed marked seasonal variation but absolute amount of time spent in pasture and scrub was constant over much of the year. We suggest that earthworm consumption, like that of other foods, is dictated primarily by availability.

Introduction

Badgers *(Meles meles)* are often described as omnivores (e. g. Neal 1977, 1986; Long and Killingley 1983). While the latter term may be questioned on the grounds that no animal eats everything, badgers do consume a remarkably wide range of animal and plant material. Their diet includes small mammals (e. g. mice, voles, shrews, lagomorphs and hedgehogs); various birds and their eggs; carrion; reptiles and amphibians; soft-bodied invertebrates such as slugs, snails and worms; insects including adults and larvae of beetles, flies, wasps and bees; honey; wild roots, tubers, fruits, berries and nuts; garden fruits and vegetables (e. g. apples, pears, plums, cherries, strawberries, raspberries, carrots, potatoes, peas and beans); and commercial crops such as cereals (oats, barley, wheat and maize), pulses and grapes (for references see Neal 1977, 1986; Stocker and Lüps 1984; Lüps and Wandeler in press). To give an example of the variety of more specific food types that can be consumed within just one general category, Andersen (1954) lists no fewer than 121 genera of insects eaten by badgers in Denmark, and in a single badger stomach he found insects from 35 genera as well as worms, toads and frogs. Thus badgers not only consume a wide variety of foods over a range of different geographical regions; they also eat many different food species within a single area and even in a single night (Lüps et al. 1987).

The simplest and most obvious hypothesis concerning food choice in badgers is that an individual eats whatever it happens to come across (e. g. Andersen 1954, p. 19). According to this view different foods are consumed independently of one another and would be expected to feature in the diet in proportion to their availability. However more recently Kruuk and his collaborators (e. g. Kruuk 1978, 1986; Kruuk and Parish 1981) have argued that badgers are "earthworm specialists", on the grounds that a. earthworms account for the bulk of the diet and are eaten year-round, whereas other foods are only eaten in relatively small amounts and at particular times of the year; b. badgers prefer

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earthworms, such that other foods are only eaten when earthworms are not available; and c. when earthworms are scarce badgers intensify their worm-hunting effort, whereas all other foods are eaten in direct proportion to availability.

There are, however, at least two problems with a universal description of badgers as "earthworm specialists". Firstly, it is now clear that in some parts of the badger's range earthworms form only a very minor part of its diet (e. g. Ibañez and Ibañez 1980; Kruuk and De Kock 1981; Ciampalini and Lovari 1985; Martín-Franquelo and Delibes 1985; Pigozzi 1988). Secondly, even in Kruuk's own study area in Scotland the importance of earthworms in the diet has diminished somewhat during the last few years, with cereals becoming increasingly important as an alternative food (Kruuk and Parish 1987). Thus the extreme preponderance of earthworms in the diet of badgers, which obtained in Kruuk's original study, may not be a general phenomenon.

In this paper we present data on diet, food availability and foraging behaviour of badgers in the south of England, from an area subjected to fairly intensive cereal farming. Our results differ in various respects from those of Kruuk and his collaborators, and we discuss these differences (and some similarities) in the context of the "worm specialisation" hypothesis.

Material and methods

Study area

The study, which lasted from September 1983 to October 1986, was conducted on private farmland in the South Downs near Lewes, East Sussex (for further details see Roper et al. 1986; Shepherdson 1986). The landscape consisted of chalk hills separated by steep valleys, the hilltops and valley bottoms being mostly arable and the hillsides left as permanent pasture grazed periodically by sheep and cattle. These areas of permanent pasture consisted of long tussocky grass (up to 25 cm in height) and a variety of herbs. Arable fields consisted of winter wheat *(Triticum aestivum)* except that in 1984 one field was planted with rape *(Brassica rapifera)*, in 1985 one contained peas *(Pisum sativum)* and in 1986 two contained barley *(Hordeum vulgare)*. On the south edge of the study area were two small vineyards. Scattered throughout the area, within pasture fields and on the edges of arable fields, were small irregular patches of scrub up to 1 ha in area, dominated by hawthorn *(Crataegus monogyna)*. Overall the area consisted of 65 % arable land, 28 % pasture and 7 % scrub.

Observations (see below) were conducted in the territories of four neighbouring badger groups which were surrounded by other occupied territories. The mean nearest-neighbour distance for 20 setts in the area was 520 m (sd 140 m) giving a density of about 2 setts/km^2.

Determination of diet

Diet was determined from faecal remains in two different ways. First, we conducted a monthly survey of the study area from September 1983 to August 1984, visually examining all faeces found. Second, we carried out a more detailed laboratory analysis on a smaller number of faecal samples collected over a two-year period in order to determine diet more precisely.

The monthly survey was conducted by walking around the study area on a prescribed route looking for defecation sites (Roper et al. 1986). Whenever a dungpit containing fresh faeces was found the contents were spread out on the ground with a trowel and their main constituents (i. e. any prey type judged to contribute more than 20 % to the total volume of faeces) noted after inspection with the naked eye. Wheat, insects, fruit and grass were readily identifiable from obvious remains, while faeces containing earthworm remains was identifiable from its earthy homogenous appearance and its characteristic smell (Skoog 1970). Since deposition of faeces by badgers at latrines is subject to seasonal variation (Roper et al. 1986) there was some variation in the number of faeces available for inspection each month (mean 35, range 21 to 48).

During 1984 and 1985 eight faecal deposits per month were collected from within the territory of a single social group and were frozen in plastic bags for subsequent detailed laboratory analysis. The method of analysis was based on those described by Kruuk and Parish (1981), Ashby and Elliot (1983) and Wroot (1985). Each sample was first defrosted, oven dried at 55 °C and weighed. Analysis for earthworm remains was conducted by taking 0.5-g subsamples of faeces, to each of which 5 drops of picric acid solution were added. Each sample was then "washed" by twice diluting it in 500 ml of water, allowing it to settle for 10 min and then withdrawing the sediment with a pipette. The final

sediment was examined under a 35× binocular microscope and the number of earthworm chaetae (stained yellow) was counted. Number of worms per unit weight of dry faeces was calculated on the assumption that one worm yields 1200 chaetae (Wroot 1985).

Analysis for contents other than earthworms involved weighing the remainder of each faecal sample, rehydrating it and washing it in a 1 mm sieve. The remaining solid material was then examined under the microscope in a shallow white dish. Number of insects was estimated from remains such as beetle elytra and skins of leatherjackets, and was converted to volume by multiplying up by the approximate bulk of the prey item in question (Kruuk and Parish 1981). Total volume of cereals was estimated from the number of husks and partly digested grains in the faeces, and volume of grass was measured directly on the assumption that none of the ingested grass had been digested. Volume of fruits (blackberries and grapes) was estimated from the number of seeds. All volumes were then expressed as a percentage of the total.

Earthworm availability

Earthworm availability was assessed in two ways: by formalin-sampling to determine earthworm biomass and by calculating the frequency of occurrence of "worm nights" (Kruuk and Parish 1981; MacDonald 1983) using meteorological data.

Formalin-sampling was carried out systematically at five sites each month during 1985, three sites being pasture fields and two arable fields planted with winter wheat. The method was based on that described by Raw (1959) and Satchell (1967). At each site four 50 cm × 50 cm quadrats were placed on the ground at random locations and each quadrat was treated with two applications consisting of 3 l of 0.6 % formalin, separated by an interval of 15 min. Any earthworms coming to the surface within 30 min of the first application of formalin were collected and returned to the laboratory for counting and weighing. At sites consisting of ungrazed pasture worms were difficult to see on the surface and so the top 5 cm of turf was removed in each quadrat prior to treatment with formalin. This layer of turf was hand-sorted and any earthworms within it were collected.

Formalin-sampling was also carried out periodically at places where radio-collared animals (see below) had been observed to forage during the month in question. A map of the study area was divided into 50 m × 50 m grid squares and during 1984 and 1985 formalin-sampling was carried out in a total of 27 squares where badgers had been observed to forage, some squares being sampled in both years so as to yield 42 sampling occasions in all. On each occasion six quadrats were sampled using the method already described, the purpose being to correlate earthworm biomass within a particular grid square with the amount of time that radio-collared badgers spent foraging in that square in the year in question.

Following Kruuk and Parish (1981) "worm nights" were defined as nights when the temperature remained above 0 °C and when at least 2 mm of rain had fallen within the last 72 h. Under these conditions earthworms (especially *Lumbricus terrestris*) appear on the surface of the ground, thus making them readily available to badgers. Number of "worm nights" was calculated for each month during 1984 and 1985, using meteorological data supplied by the Southern Water Authority and collected at a weather station 16 km west of the study area.

Radio tracking

Between January 1984 and October 1986 observations were made on 25 badgers (16 male and 9 female) from four adjacent social groups. The animals were trapped at their home setts, anaesthetised with ketamine hydrochloride and fitted with radio-collars and luminous green "betalights" (for details of trapping procedure and equipment see Cheeseman and Mallinson 1979; Shepherdson 1986). The maximum number of animals with functioning transmitters at any one time was 8 and the minimum 3.

On any one night a particular animal, designated in advance as the "focal animal", was followed on foot by an observer and watched through 7 × 50 binoculars fitted with a red-filtered 15-W tungsten-halogen spotlight. The animals rapidly habituated to the presence of observers and it was possible to stay within close range of a focal animal for several hours at a time. Observations (locating of the animal, its behaviour and the presence and behaviour of any other visible animals) were spoken into a pocket dictaphone, transcribed into note and map form the following day, and transferred onto computer for subsequent analysis. In addition, every 15 min "fixes" were taken on any other animals that were within radio range and if possible their precise locations were determined by triangulation. Observation sessions were scheduled to cover, as equally as possible, all the available animal for their whole nocturnal activity period. The total number of observation hours during the whole period (including only time when useful data were being collected) was 1205 h, with a minimum of 15 h and a maximum of 182 h in any one month. Usually an observer worked alone, but sometimes two observers worked simultaneously, either watching different animals within the same group or concentrating on different groups.

Results

Diet

The major constituents of the diet, as determined from visual inspection of all fresh faeces found during monthly surveys of the study area, were earthworms, insects, wheat, fruit and grass (see Fig. 1). All these items were subject to marked seasonal variation in their frequency of occurrence, with earthworms being the most frequently eaten food overall. Earthworms were an important constituent of virtually all samples from September to April; wheat occurred in a majority of samples from June to September; insects appeared to a substantial extent only in June; while fruit (blackberries or, in a few instances, grapes) occurred with fairly high frequency in August and September. Grass appeared with roughly the same seasonal pattern as earthworms, but with a lower frequency. The results suggest a diet dominated by earthworms in winter and spring and by vegetable matter (cereals and fruits) in summer and autumn.

Detailed laboratory analysis of faecal samples collected during 1984 and 1985 again revealed the presence of substantial amounts of earthworms, insects, wheat, fruit and grass (see Fig. 2). Insects were mainly dipteran larvae (e. g. one sample contained remains of 14 nematoceran larvae) and dung beetles (e. g. *Geotrupes* spp.), while fruits were mainly blackberries or, in a few samples, grapes. In addition a variety of other foods occurred occasionally in the diet including snails, rabbits (both young and adults, the latter probably eaten as carrion), partridge eggs, sugar beet, peas and cattle cake.

As judged from the frequency of occurrence of different prey classes (Fig. 2a), earthworms and grass were eaten most often from November to April, wheat during

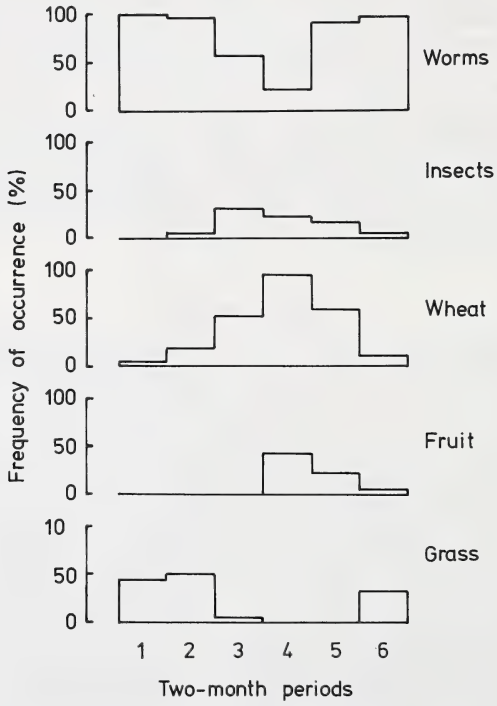

Fig. 1. Frequency of occurrence of different foods in badger faeces during two-month periods in a single year, as determined from gross inspection of faeces in the field

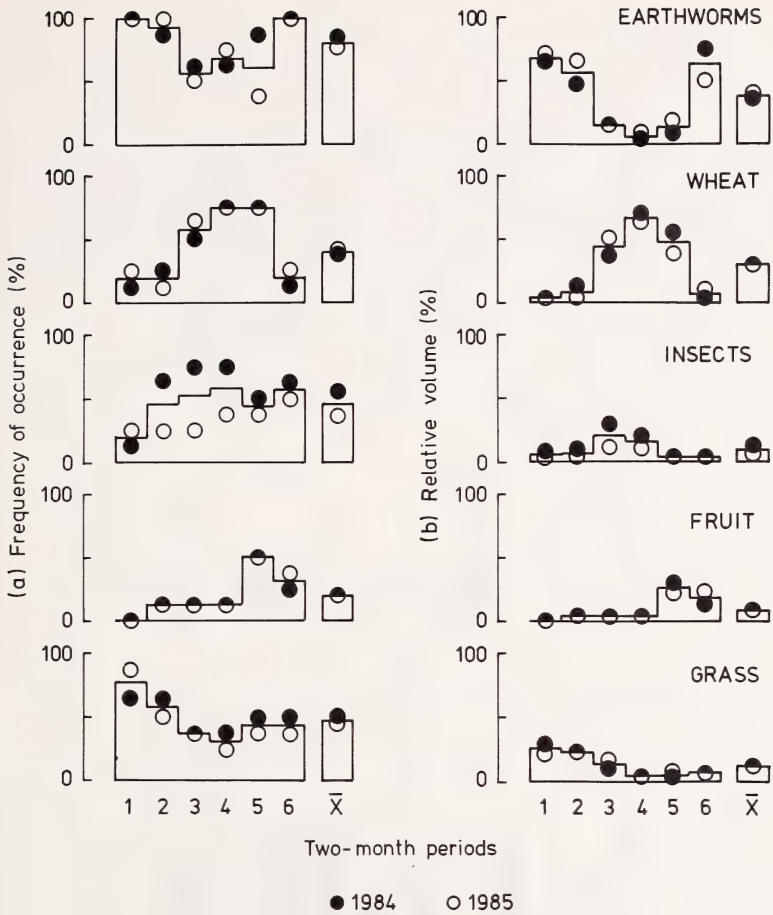

Fig. 2. a: Frequency of occurrence of different foods in badger faeces; b: estimated relative volume of different foods, during two-month periods in each of two years. Data were derived from laboratory analysis of faecal samples. Filled circles: 1984. Open circles: 1985

summer, fruit during late summer and autumn; and insects at any time of year. There was reasonable agreement between 1984 and 1985 except in the case of insects, which were eaten with high frequency during the hot, dry summer of 1984 but were less conspicuous in the diet during the cold, wet summer of 1985. Overall, earthworms were by far the most frequent category of prey. In terms of percent volume (Fig. 2b) the same general pattern emerged, except that averaged over the whole two-year period earthworms and wheat were of roughly equal importance (35 % and 30 % by volume respectively).

Earthworm availability

Formalin-sampling data from pasture and wheat fields in 1985 showed worm biomass to be on average higher in pasture (see Fig. 3a). However two-way analysis of variance showed that this difference was not statistically significant (main effect due to habitat type, $F_{1,3} = 3.99$). In both pasture and arable fields there was marked and significant seasonal variation

in worm biomass, with minimum biomass in mid-summer (main effect due to season, $F_{5,11} = 8.95$, $p < 0.001$).

Calculation of percentage of "worm nights" in each two-month period throughout the two years of the study (Fig. 3b) showed a markedly different pattern between the two years: in 1984 "worm nights" were most frequent in the winter whereas in 1985 they were most frequent in the summer. This difference between 1984 and 1985 was caused primarily by differences in rainfall, the summer being hot and dry in 1984 and cool and wet in 1985. Statistical comparison of the two years showed a significant difference ($X^2 = 55.1$, $p < 0.001$). Despite this difference in the seasonal pattern of "worm nights" between the two years there was no major corresponding difference in worm intake (compare Fig. 2. with Fig. 3b).

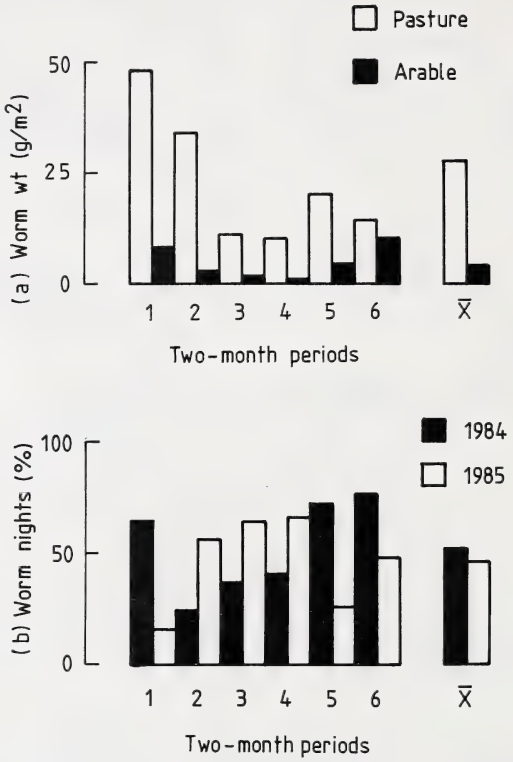

Fig. 3. a: Weight of worms extracted by formalin-sampling in pasture and arable fields, for successive two-month periods during 1985; b: Number of "worm nights" as calculated from meteorological data, for two-month periods in each of two years

In order to compare different measures of worm availability with worm consumption in a more systematic manner, the relevant data on availability were correlated with the percentage of worms by volume in the diet across two-month periods within each year for which data were available. Spearman tests on the ranked data showed no significant correlation between percentage of worms in the diet and percentage of worm nights, either in 1984 ($r = 0.31$, $N = 6$) or in 1985 ($r = -0.7$); nor was there a significant correlation between worm consumption and worm biomass in arable fields in 1985 ($r = 0.70$). However, a significant correlation did emerge between worm consumption and worm biomass in pasture in 1985 ($r = 0.94$, $p < 0.01$). (No data on worm biomass were available

for 1984). Thus of the various measures of worm availability taken in the study, the only significant predictor of worm consumption was the biomass of worms in pasture, as revealed by formalin-sampling.

Habitat use and foraging behaviour

Fig. 4 shows seasonal changes in the use of four main habitat types by radio-collared animals. (These habitats together accounted for 97 % of the total observation time; during the remaining 3 % of observation time animals foraged mainly around farm buildings.) Percentage of observation time spent in each habitat type (Fig. 4a) was calculated by summing data over all the animals that had been watched in a given two-month period, dividing by total observation time for those animals, and expressing the results as a percentage. Data were analysed separately for each of the three years of the study. Absolute time (Fig. 4b) was estimated by multiplying percentage time by the average number of hours per night for which animals were active during each two-month period.

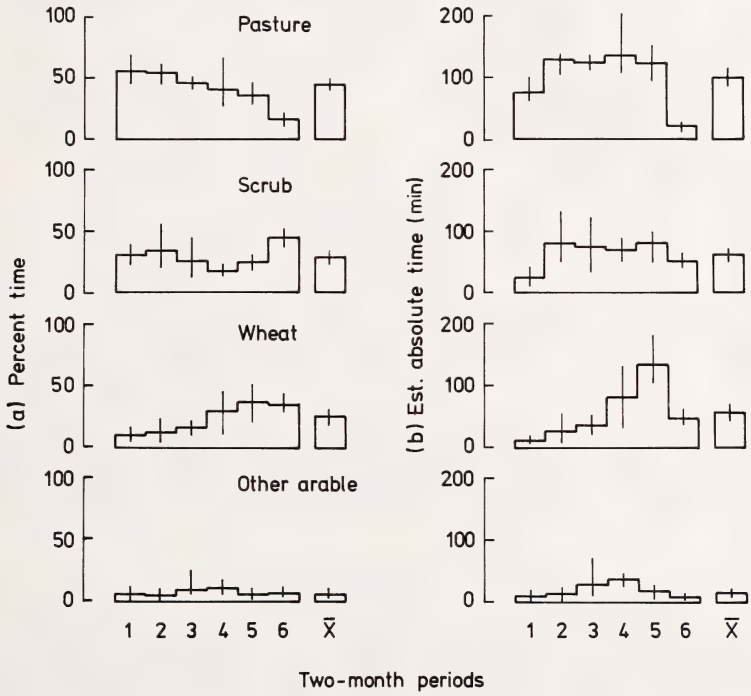

Fig. 4. a: Percent observation time spent by radio-collared badgers in four different habitat types, for two-month periods (mean and range over three successive years, 1984–1986); b: Estimated absolute time spent in each of four main habitat types

All four main habitat types were used throughout the year but there were seasonal differences in the proportion of time allocated to different habitats. Thus, a large proportion of time was spent in pasture and scrub in the winter and spring, with a shift to wheat and other arable crops in the summer and autumn. Absolute time spent in each habitat varied in a rather different manner, with more time being spent in all habitats from spring to autumn (March to October) than in winter (November to February). This was simply a consequence of the activity period being relatively short in winter, when the

animals only emerged for a few hours per night. A more interesting finding ist that the absolute time spent in pasture and scrub was relatively constant from March to October, by comparison with strong seasonal variation in time spent in wheat and other arable crops.

No correlation was found between percentage of time spent in any one habitat type and percentage by volume of any one food category in the diet ($r < 0.65$ in all cases). However such correlations would only be expected if there were a one-to-one relationship between habitat and prey, and observations showed that this was not the case. From July to August radio-collared badgers visited wheat fields primarily to feed on the growing crop, but they also occasionally foraged for worms in wheat fields throughout the year. The same was true of other arable crops. Pasture and scrub were visited primarily to obtain worms, but also yielded insects and (in the case of scrub) blackberries.

Two distinct methods of capturing worms were observed. On most occasions a badger would meander slowly around in a circumscribed area, nose to the ground, snuffling in the grass or earth. Every few minutes the animal would halt and thrust its nose into the surface, grubbing vigorously for prey. Usually grubbing with the snout was accompanied by digging with one or both forepaws, which often persisted for a minute or more and could result in a hole up to 12 cm deep being made in the earth. In the case of pasture, large lumps of turf (up to 20 cm × 20 cm) were often torn up in such digging operations. On several occasions we chased a badger off while it was digging a large hole and found one or more earthworms lying in the bottom of the hole. In the second method of worm-hunting the animal moved slowly and more or less linearly over the substrate with its nose close to the ground, picking earthworms straight off the surface and swallowing them with a backwards jerk of the head. We observed this behaviour only 12 times during the whole three-year period of the study, always in stubble fields from which wheat had been harvested.

Between mid-June and early September wheat was eaten by knocking down the growing crop. An animal would either jump up, seize an ear of wheat and bring it down to the ground in its jaws or, more usually, it would knock down a number of stalks with one fore-leg and then stand on the stalks while eating the ears. Much more wheat was trampled down than was actually eaten. Each year consumption of standing wheat began within a day or two of the ears emerging from their surrounding sheath of leaves. After the harvest, leftover grains of wheat were scavenged directly off the surface of the ground, and throughout the winter badgers continued to find small amounts of wheat around the edges of fields and in barns where straw was stored.

Foraging behaviour and earthworm biomass

Fig. 5 illustrates typical foraging patterns, showing the use of space by four radio-collared males (M1 to M4) during a single representative month. All four males belonged to the same social group, centred on sett 1. The maps were constructed by dividing the study area into 0.25-ha grid squares and logging the total amount of foraging time spent by each animal in each square during any one month. Grid squares were then ranked in order of importance, enabling heavily used squares to be distinguished from those that were used less frequently or not at all. In Fig. 5 the most heavily used squares, which together account for 70 % of an animal's foraging time in that month, are denoted by large filled circles; less heavily used squares that together account for a further 20 % of foraging time are denoted by intermediate-sized circles; and the least heavily used squares, accounting for the remaining 10 % of foraging time, are denoted by small circles. Thus the squares containing large circles together constitute a "core foraging range" for a particular animal, where it spent most (i.e. 70 %) of its foraging time during that month.

It is clear from Fig. 5 that use of space by each animal was "patchy" in the sense that

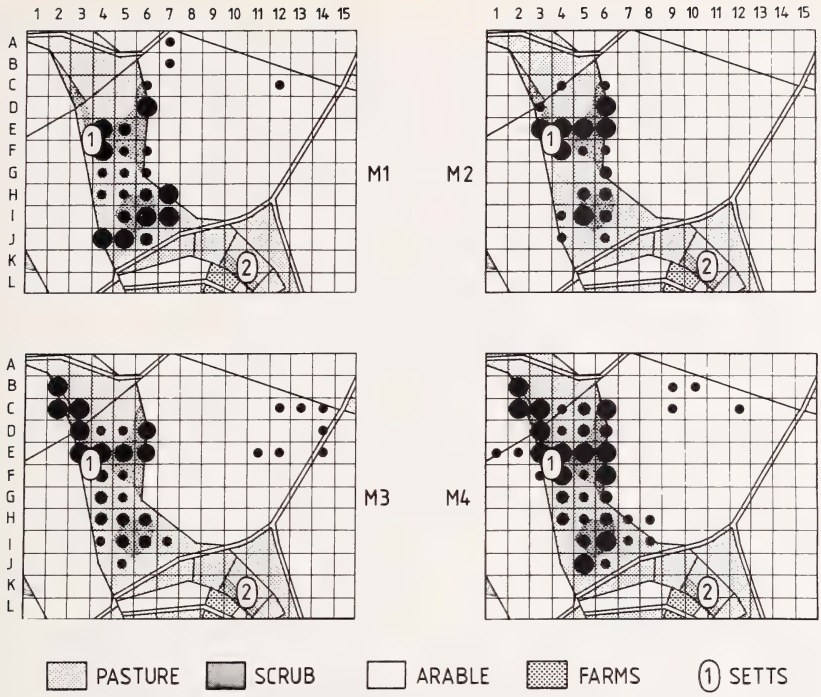

Fig. 5. Maps of part of the study area showing locations used for foraging by four males from sett 1, in May 1986. Each grid square is 0.25 ha. Single lines represent fences and double lines show roads. Filled circles show which grid squares were used for foraging by each animal (for further explanation see text). The territory of group 1 covered the whole area to the NW of the road running diagonally from square L4 to square B15

some locations were used more heavily for foraging purposes than others, while much of the home range was not used at all. Furthermore, different individuals had different favourite foraging locations. Similar individual differences in use of space were evident in other months, and other social groups.

In order to determine whether this "patchy" use of space was related to earthworm biomass we plotted earthworm biomass (as determined by formalin-sampling) against foraging time (i.e. total foraging time for all radio-collared animals in a given social group during the year in question) for 42 individual grid squares. Because not all grid squares were formalin-sampled at the same time of year it was necessary to correct for seasonal changes in worm biomass, and this was done using mean values for worm biomass in successive two-month periods (as shown in Fig. 3a). Thus, the data from each sampling occasion were expressed as the weight of worms that would be expected had sampling been carried out in the Jan-Feb period. The results (see Fig. 6) show a significant positive correlation between the two variables ($r = 0.64$, $N = 42$, $p < 0.001$). Thus badgers were sensitive to local differences in worm biomass (which could be considerable even in adjacent grid squares covering the same habitat type), and they spent more time foraging where worm biomass was greater.

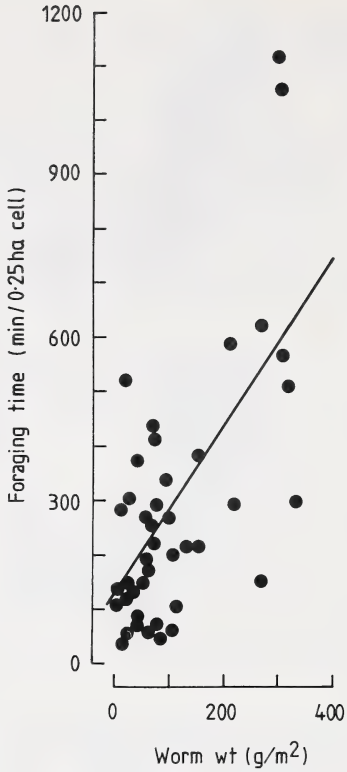

Fig. 6. Correlation between the amount of time that radio-collared badgers spent foraging in a particular 0.25 ha grid square in a given year, and the weight of worms extracted by formalin-sampling

Discussion

The results show that earthworms are an important year-round food for badgers in the south of England, and in this respect they are consistent with the majority of previous studies of badger diet in the British Isles (Fairley 1967; Paget and Middleton 1974; Kruuk 1978; Kruuk and Parish 1981; Ashby and Elliot 1983; Neal 1986) and elsewhere in N. Europe (Andersen 1954; Skoog 1970; Stocker and Lüps 1984). On the other hand there are a number of differences between our results and those of at least some previous studies. First, in our study wheat was a major food, eaten year-round, accounting for almost as large a proportion of the overall diet by volume as did earthworms. Previous studies have reported consumption of cereals (e.g. Andersen 1954; Skoog 1970; Lüps et al. 1987: Kruuk and Parish 1985) but not on such a large scale. Second, in our results both the frequency of occurrence of earthworms in the diet and the percentage volume were subject to marked seasonal variation, whereas the same measures of worm intake in a Scottish population of badgers remained comparatively constant throughout the year (Kruuk and Parish 1981, Fig. 5). Third, in our study area worm biomass as revealed by formalin-sampling was the best predictor of worm intake, whereas Kruuk and Macdonald have suggested that worm availability for predators like the badger depends more on local climatic conditions (number of "worm nights") than on biomass (e.g. Kruuk et al. 1979; Kruuk and Parish 1981; Macdonald 1980, 1983). Fourth, and probably related to the previous point, in our study badgers obtained worms mainly by actively grubbing and digging in long-grass pasture and arable fields whereas others have described them picking

worms straight off the surface of short-grass pasture (e.g. Kruuk et al. 1979; Macdonald 1980).

What are the implications of these results for the concept of badgers as worm specialists (Kruuk 1978, 1986; Kruuk and Parish 1981)? Two reasons for employing the latter term are that badgers do eat a lot of earthworms in some parts of their geographical range, and that they adopt special methods of hunting for worms. But by these criteria one could with equal justification say that badgers are olive specialists or beetle specialists in Italy (Kruuk and De Kock 1981; Ciampalini and Lovari 1985); fruit, insect or rabbit specialists in Spain (Ibañez and Ibañez 1980; Martín-Franquelo and Delibes 1985); toad specialists in France (Henry 1984); wasp specialists in Switzerland (Schmid and Lüps 1988) or wheat specialists in the south of England (the present study). An attempt to rescue the idea of badgers as food specialists could be made by saying that they specialise on different things in different places (Kruuk and De Kock 1981), but there are other environments in which the diet is not dominated by any single food category (e.g. Harris 1984; Pigozzi 1988).

An additional reason for referring to badgers as "worm specialists" is the suggestion that badgers change their foraging effort to compensate for fluctuations in earthworm availability (Kruuk and Parish 1981). This suggestion derives from the fact that in Scotland the percentage by volume of worms in the diet was found to remain fairly constant throughout the year (Kruuk and Parish 1981, Fig. 5). This finding, however, was not replicated in the present study; and other studies have also reported substantial seasonal variation in worm intake (Andersen 1954; Mouchès 1981; Harris 1982; Ashby and Elliot 1983; Henry 1984). Our results suggest that during most of the year badgers spend about the same absolute amount of time foraging for earthworms regardless of changes in earthworm availability, with the result that earthworm intake is correlated with availability. Perhaps then the lack of marked seasonal variation in relative worm intake in Kruuk's study reflects a relative lack of seasonal variation in the availability of worms and other foods in that particular study area, and is not a general phenomenon.

In conclusion, we suggest that badgers may be better described as opportunistic than as specialist feeders: that is, badgers eat whatever is most readily available in a particular place at a particular time of year. When the availability of earthworms outstrips that of any other suitable food (as it will do in moist northern European habitats dominated by well-fertilised short-grass pasture) then earthworms will be the dominant food; but in our view there is little evidence that the principles governing earthworm intake are qualitatively different from those governing intake of other foods.

Acknowledgements

D. J. Shepherdson was supported by a SERC studentship; P. Lüps thanks the Burgergemeinde Bern for allowing him sabbatical leave at Sussex University. We thank Robinson Farms, Iford, Ltd for allowing us to work on their land, and Mr D. Cripps for introducing us to the local badger population.

Zusammenfassung

Nahrungsangebot, Nahrungssuche und Nahrungsaufnahme von Dachsen (Meles meles L.) in Südengland

Zur Ermittlung der Nahrungsstrategie des Dachses in einem landwirtschaftlich genutzten Hügelgebiet (South Downs) im Süden Englands (East Sussex) wurden von 1983–1985 verschiedene Methoden kombiniert angewandt: 1. Kotanalyse (Vorkommenshäufigkeit und Volumenanteile pro Monat), 2. Analyse von Klimadaten zum Erkennen von „Wurm-Nächten" Temp. > 0 °C, ≥ 2 mm Regen innerhalb 72 h), 3. Bodenproben zur Erfassung der vorhandenen Regenwurm-Biomasse und 4. Radiotelemetrie (total 14 Tiere) um die Habitatnutzung festzustellen und die Technik des Nahrungserwerbs zu beobachten.

Über das ganze Jahr betrachtet am häufigsten erbeutet und mit dem höchsten Volumenanteil verzehrt werden Regenwürmer (Lumbricidae) mit 35 %, gefolgt von Weizen (*Triticum* sp.) mit 30 %.

Regenwürmer bildeten von November bis April, Weizen von Juni bis September die Hauptnahrung. Häufig, aber mit geringen Volumenanteilen, wurden Insekten (v. a. im trockenen Sommer 1984) und Gras gefressen. Auf Früchte (Brombeeren und Weintrauben) konzentrierten sich die Dachse vor allem im August und September. Für die Aufnahme von Regenwürmern ist weniger die Häufigkeit von „Wurm-Nächten" als ihr Vorhandensein in den obersten Bodenschichten (v. a. im Weideland) im Jahresverlauf maßgebend. Die verschiedenen Habitat-Typen werden im Verlauf des Jahres unterschiedlich stark genutzt. Die im Gebüsch und Weideland verbrachte Zeit blieb über weite Teile des Jahres annähernd konstant. Die in den Sommermonaten durch längere Aktivitätsphasen resultierende zusätzliche Zeit für die Nahrungssuche verbrachten die Dachse häufig in Weizenfeldern.

Es hat sich gezeigt, daß Dachse Regenwürmer in erster Linie entsprechend ihrer Verfügbarkeit im Boden als Nahrung nutzen. Von einer echten Spezialisierung auf dieses Beutetier kann daher kaum gesprochen werden.

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Crossarchus ansorgei nigricolor, a new subspecies of Ansorge's cusimanse (Carnivora, Viverridae) from south-central Zaire

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Abstract

Described a new subspecies of Ansorge's cusimanse. Recent observations of the little-known *Crossarchus ansorgei* were made in the rain forest of the south-central Zaire basin. Close to a hundred specimens were collected from the bush-meat markets in three localities. We studied the new material as well as the holotype and the museum collections. The result of this analysis shows that the ca 30 skins originating from the Zaire basin are characterized by the stability of their pigmentation as well as by a colour pattern differing from the holotype collected in Angola. According to these new morphological and biogeographical data, a new subspecies is described.

Introduction

Until 1984 known only from two skulls and skins, Ansorge's cusimanse, described from a relic forest in northern Angola, was also found in the forests on the left bank of the Zaire/Lualaba River.

The holotype of *Crossarchus ansorgei* Thomas, 1910, whose type locality is Ndalatando (09° 15′ S, 14° 52′ E), is the only specimen collected in Angola. It is held in the British Museum (Nat. Hist.) No. 10.4.8.7, together with a second specimen (No. 11.10.19.10) for the first time mentioned by Coetzee (1977) and originating from Baringa (00° 45′ N, 20° 52′ E), a small village on the Maringa River in the Equator region of Zaire. Both skulls and skins are complete and in good condition.

Recent observations were made in Zaire in the Lomami/Lualaba forests by Colyn (1984) who collected 21 specimens in the region between the Kitcho-ya-tembo and Lusa Rivers on the Kisangani-Ubundu road. The field studies have been continued in this region, and altogether close to a hundred specimens were obtained from "bushmeat markets" (Colyn et al. 1988). *Crossarchus alexandri* and *C. ansorgei*, sympatric species, are very common in the above-mentioned region and take an important place in the dietary protein supply of the native human population.

From the locality situated on the Kisangani-Ubundu road (00° 04′ S, 25° 17′ E) as well as from the Yaenero Plantation (00° 12′ N, 24° 47′ E), 23 skins and a number of skulls have been obtained from the villagers. Furthermore four skins were collected in Kodoro (01° 16′ N, 20° 06′ E), situated in the basin of the Lopori/Maringa Rivers, and one skin originating from Ikela (01° 11′ S, 23° 16′ E) was discovered, while examining the *C. alexandri* collection in the Koninklijk Museum voor Midden-Afrika (KMMA).

The authors have compared the whole of this new material with the two specimens in the BMNH, and in particular with the holotype. It appears that all the skins originating from Zaire present a colouration with relative stable and identical characteristics, differing from that of the holotype from Angola.

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Results

Genus *Crossarchus* F. Cuvier, 1825

Crossarchus F. Cuvier, 1825. Geoffroy Saint-Hilaire and F. Cuvier, Hist. Nat. Mamm., 47:3.

Crossarchus ansorgei Thomas, 1910

Crossarchus ansorgei Thomas, 1910. Ann. Mag. Nat. Hist., (8)5:195 Holotype from Ndalatando, 800 m ASL, Angola; adult female; skin and skull (BMNH No. 10.4.8.7.).

Crossarchus ansorgei nigricolor subsp. nov.

Diagnosis

Same size as the nominal subspecies but of a very dark general colouration. The limbs, underparts, and tail completely black. A light-coloured stripe on the side of the head differentiates it from the holotype from Angola.

Holotype

Adult female: skin and skull in good condition, deposited in the KMMA, Tervuren, Belgium, No. "Vert. Sect. 88-14-M-1".

Type Locality

Amadjabe (00° 04′ S, 25° 17′ E), between the Lusa and Kitcho-ya-tembo Rivers, Zaire.

Paratypes

From Amadjabe we selected 20 skins and 50 skulls. As the specimens were collected over a period of ca 18 months and as these skins and skulls were obtained from different villagers, we consider this a series of 70 different specimens (KMMA Nos. "Vert. Sect. 88-14-M-2 to 71").

Description

The new subspecies is a small mongoose showing the same form and external measurements as *C. a. ansorgei* with which it has the nuchal crest in common. The general colouration is sepia black. The back, flanks, neck, and head are speckled with hairs annulated with white or yellow ochre. A darker dorsal medial line extends from the nuchal crest to the base of the tail. The underparts, tail, and limbs are completely blackish. Chin and muzzle are dirty white. A white to yellow-ochreous stripe extends from the corner of the mouth under the external ear to the side of the neck (Fig. 1). A whitish tuft decorates the internal base of the ear.

After comparison of the museum specimens and also of the male and female kept in captivity (Colyn 1984), it appears that the tail of the male is more bushy than that of the female.

Skull measurements

The skull of *C. a. nigricolor* is similar in all measurements to that of *C. a. ansorgei* (Table 1).

Etymology

The name *nigricolor* is the Latin adjective for "coloured black" and refers to the dark overall colour distinguishing it from the nominal subspecies.

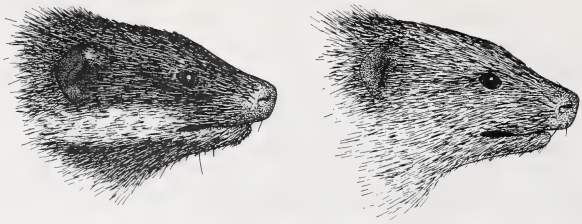

Fig. 1. Left: *Crossarchus ansorgei nigricolor* – Right: *Crossarchus ansorgei ansorgei*

Table 1. **Skull measurements (in mm)**

Variables	*C. a. ansorgei* holotype BMNH 10.4.8.7	*C. a. nigricolor* holotype KMMA 88-14-M-1	*C. a. nigricolor* Baringa, Zaire BMNH 11.10.19.10	*C. a. nigricolor* 50 paratypes		
				Min.	Max.	$\overline{X}$
GSL	63.2	65.9	64.3	60.3	66.9	64.1
CBL	62.5	63.5	63.1	59.4	65.9	62.6
ROL	20.6	20.4	19.9	18.1	21.0	19.7
PAL	29.4	29.8	27.5	26.0	30.9	28.9
MAX	20.5	21.2	20.8	19.7	22.9	21.4
TYM	13.1	13.6	–	12.4	14.3	13.2
CAN	11.5	12.4	12.2	10.8	12.7	11.6
ROB	15.6	15.4	15.5	14.1	16.6	15.2
IOB	12.6	13.0	12.8	11.1	13.7	12.4
PAB	19.3	19.5	19.2	17.5	20.8	19.1
ZYG	32.9	34.7	33.4	31.2	35.2	33.4
BRB	24.6	26.4	25.0	23.8	26.5	25.3
MAS	26.2	28.6	27.3	25.1	28.7	27.0
BRH	20.7	21.7	20.4	19.5	22.3	21.0
MAL	42.6	43.2	42.6	39.3	45.0	42.5
MAN	24.0	23.8	23.0	22.1	25.0	23.7
CMH	17.8	15.7	16.8	14.1	18.1	16.5

GSL: greatest skull length, from the anterior edge of I1 to posterior edge of occipital bone; CBL: condylobasal length of the skull, from anterior edge of I1 alveolus to posterior edge of occipital condyle; ROL: length of rostrum, from lateral base of hamular process of lacrimal to most anterior edge of premaxillae; PAL: length of palate, from posterior edge of I1 alveolus to posterior edge of palatine; MAX: greatest crown length of maxillary toothrow; TYM: greatest length of tympanic bulla, not along longitudinal axis of skull; CAN: breadth of canines, distance between labial crown edges of C1–C1; ROB: breadth of rostrum, distance between lateral base of hamular process of lacrimals; IOB: least interorbital breadth; PAB: breadth of palate, distance between labial crown edges of M1–M1; ZYG: greatest zygomatic breadth; BRB: breadth of braincase, greatest breadth of braincase at the right angle to longitudinal axis of skull; MAS: mastoid breadth; BRH: height of braincase, distance from occipital bone between bullae to parietal, excluding sagittal crest; MAL: mandible length from anterior edge of I1 alveolus to posterior surface of mandibular condyle; MAN: greatest crown length of mandibular toothrow; CMH: mandible height, perpendicular distance from dorsal edge of coronoid process to line from angular process to ramus.

Distribution

C. a. nigricolor is actually known from two localities of the Lomami/Lualaba forest. Moreover, one specimen of the KMMA (No. 17217) originated from Ikela on the other bank of the Lomami River and we have collected four skins from Kodoro in the Lopori-Yekokoro fluvial system. The only other known skin originated from Baringa and is mentioned in the introduction (Fig. 2).

The distribution of *C. a. nigricolor* is probably limited to the forest blocks between the Zaire/Lualaba and Kasai Rivers. Colyn (1984) found its supposed distribution to "central Kivu, west of Lake Kivu" (Coetzee 1977) highly improbable in view of the numerous faunal surveys in this region, which never resulted in an observation or collection of a specimen.

The distribution pattern of the two subspecies, *C. a. ansorgei* and *C. a. nigricolor*, in which the Kasai River seems to act (or have acted) as a barrier, is also typical for other mammalian species: this is, among others, the case for numerous primate species as

Fig. 2. Distribution of *Crossarchus ansorgei*. Type locality of *C. a. ansorgei* (triangle) and of *C. a. nigricolor* (square). Hatched parts indicate non-forest regions

Cercopithecus mitis, C. ascanius, C. wolfi, Cercocebus aterrimus . . . which are represented by different subspecies on both sides of the Kasai River.

More to the south, *C. a. ansorgei* inhabits the forests and forest patches north of the Cuanza River, Angola (Goldman 1984). *Crossarchus ansorgei*, including the populations of the Angolan relic forests, is typically endemic for the biogeographical "south-central" region as defined by Grubb (1982).

Affinities

The stable colouration of the 29 specimens of *C. a. nigricolor* has incited us to differentiate the populations inhabiting the forests north of the Kasai River from those of Angola, of which, unfortunately, only one specimen, the holotype of *C. a. ansorgei* is known. The latter has a reddish-brown general colour and all the hairs annulated. It has no facial stripe, and only the forearms, toes of the hind feet, nuchal crest, and distal part of the tail are blackish. About its general colouration some confusion exists: Hill and Carter (1941:132) also described the colour "near Mars Brown, both above and below"; this in contrast with the original description: "the general colour above and below coarsely grizzled blackish, as in *C. obscurus*, but with a strong tawny suffusion" (Thomas 1910:195). The measurements (in mm) of both the subspecies are comparable: head and body: 342 and 320, tail: 208 and 212, hind foot: 70 and 60, for a male *C. a. nigricolor* and the female *C. a. ansorgei* respectively.

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Zusammenfassung

Crossarchus ansorgei nigricolor, eine neue Unterart der Angola-Kusimanse (Carnivora, Viverridae) aus dem südlichen Zentral-Zaire

Von der bisher wenig bekannten Angola-Kusimanse *(Crossarchus ansorgei)* wurden nahezu 100 Exemplare (Felle oder Schädel) auf Märkten von drei verschiedenen Orten im südlichen Zentral-Zaire erworben. Die ungefähr 30 Felle aus Zaire sind durchweg dunkler als das Typus-Exemplar aus Angola. Für sie wird eine neue Unterart, *Crossarchus ansorgei nigricolor*, beschrieben.

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Cytogenetics of Vesper mice, *Calomys* (Rodentia; Cricetidae): Robertsonian variation between *Calomys callidus* and *Calomys venustus*

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Abstract

Investigated karyotype relationships between *Calomys callidus* and *Calomys venustus* to determine the chromosomal repatternings involved in karyological differentiation. Chromosomal analysis was performed in seven specimens of *C. venustus* from San Luis and Córdoba provinces, Argentina. A 2n = 56 (NF = 69) karyotype similar to that previously reported for specimens from the type locality was found. G-band comparisons showed that *C. venustus* and *C. callidus* (2n = 48, NF = 69) karyotypes were interrelated by means of four Robertsonian rearrangements which accounted both for numerical and structural changes. These data, together with those previously reported for other species of the genus, support the existence of three karyological groups within *Calomys*: group I, karyotypes with higher chromosomal numbers (2n = 64–60), mostly telocentric; group II, asymmetrical karyotypes (2n = 56–48) interrelated by fusion-fission processes; and group III, karyotypes with lower diploid numbers (2n = 38–36) representing highly rearranged states from an all-telocentric ancestral condition (2n = 70).

Introduction

Systematics of the South American genus *Calomys* (Cricetidae, Sigmodontinae) is still not completely clear. Both the number of species and their relationships are poorly understood, as reflected in the variability of classifications recognized by different authors (Thomas 1916; Tate 1932; Ellerman 1941; Cabrera 1961; Hershkovitz 1962; Honacki et al. 1982; Reig 1984a). Recently, however, cytogenetic data have been accumulated, proving a useful tool to clarify species distinction in these rodents (Reig 1984b; Vitullo et al. 1984).

It is generally assumed that the species belonging to the genus *Calomys*, on the basis of their larger or smaller size, are to be classified in two distinct groups. Nevertheless, there are no conclusive studies to elucidate whether this distinction is a morphological convergence or a cladistic divergence (Corti et al. 1987). Hershkovitz (1962) has proposed that all the large *Calomys* with sharp interorbital edges belong to the same species, including them under the name *C. callosus* (Rengger 1830). The cytogenetic study of specimens referred to as *C. callosus* in Argentina, according to Hershkovitz' classification, has shown gross chromosomal differences to those from the type locality of *C. callosus* in Paraguay (Hurtado de Catalfo and Wainberg 1974; Lisanti et al. 1976; Pearson and Patton 1976; Gardenal et al. 1977). In the light of these differences, the revalidation of *C. venustus* (Thomas 1894) was proposed for the large *Calomys* distributed in Argentina (Forcone et al. 1980; Reig 1984b).

In this paper we analyse the chromosomal relationships between *C. venustus* and *C. callidus*, showing that both species together with *C. fecundus* from Bolivia make up a distinctive group of species within the genus, according to their karyotype features. In addition, cytogenetics is reviewed in order to evaluate the karyotype evolution of the genus *Calomys*.

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Material and methods

Chromosomal analysis was performed in 7 *C. venustus* from Donovan, San Luis province (4 males), and Cosquín, Córdoba province (1 male, 2 females) from Argentina. Voucher specimens were preserved at the Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina.

Chromosomes were obtained from bone marrow. Briefly, the animals were injected with colchicine (1 μg/g body weight), and killed 2 to 3 hours later by an overdose of ether anesthesia. Hypotonic treatment was performed in 0.075 M KCl for 20 min at 37 °C. Cells were fixed in cold 3:1 methanol:acetic acid. Chromosomal spreads were air-dried and Giemsa stained. G-bands were induced by Trypsin digestion according to Seabright (1971). Chromosomes were classified according to Levan et al. (1964), and arranged and numbered by decreasing size. Fundamental numbers are referred to as NF, autosomal arms plus XY arms, or NF_a, autosomal arms only.

G-banded karyotypes of both *C. venustus* and *C. callidus* were arm-to-arm compared, and chromosomal similarities were established by equivalent banding patterns and sizes. The data corresponding to *C. callidus* were reanalysed from the material reported in a previous paper (Vitullo et al. 1984).

Interspecific crosses between *C. callidus* females and *C. venustus* males were established in monogamous pairs under laboratory conditions previously standardized for *C. callidus* (Hodara et al. 1984; Merani et al. 1988).

Results and discussion

The 7 specimens of *C. venustus* analysed showed an identical 2n = 56 (NF = 69) karyotype (Fig. 1). The first five pairs of autosomes were metacentric chromosomes decreasing in size. The remaining autosomal pairs were made up by telocentric chromosomes grading in size, with the exception of pair 19 which comprised small metacentric chromosomes. Sex chromosomes were XY with a submetacentric X, and a small subtelocentric Y chromosome (Table 1). This karyotype was similar to a previously reported one from the type locality, Cosquín (Gardenal et al. 1977). No differences in diploid number, chromosome morphology, and G-banding pattern were found in specimens from San Luis province.

C. callidus showed a 2n = 48 (NF = 69) karyotype with nine large distinctive metacentric pairs (Fig. 1) (Vitullo et al. 1984). Arm-to-arm comparisons of G-banded karyotypes showed identical *C. venustus* and *C. callidus* chromosomal complements, as well as the existence of four Robertsonian repatternings which accounted both for numerical and structural changes (Fig. 2).

Back in 1894, specimens from Cosquín, Córdoba were named *C. venustus* by Thomas. Cytogenetic studies on these animals from Córdoba and Tucumán provinces have shown 2n = 56 and 2n = 54 karyotypes, respectively (Hurtado de Catalfo and Wainberg 1974; Lisanti et al. 1976; Gardenal et al. 1977). However, in both reports the animals were referred to as *C. callosus* (Rengger, 1830) according to Hershkovitz (1962) who considered *C. venustus* as a synonym of *C. callosus*. Forcone et al. (1980) and Reig (1984b) have proposed the revalidation of *C. venustus* as a full species in the light of the finding of a 2n = 36 karyotype in specimens of *C. callosus* from the type locality, Paraguay (Pearson and Patton 1976). Furthermore, Thomas (1916) distinguished two subspecies of *C. venustus*: *C. v. venustus* distributed from Córdoba province to the northwest Argentina, and *C. v. callidus* restricted to the Mesopotamian region. Cytogenetic studies in *C. v. callidus* showed a 2n = 48 karyotype (Vitullo et al. 1984). It was then proposed that chromosomal variation was so striking that it must be taken as an indication of the establishment of a natural reproductive barrier; thus, it was suggested that *C. callidus* must be considered as a full species (Vitullo et al. 1984). 4 out of 9 interspecific crosses between *C. callidus* females and *C. venustus* males delivered at least once. F_1 hybrids showed a 2n = 52 (NF = 69) karyotype with 4 heteromorphic pairs. Although interspecific gestation proceeded to term, it was found that the F_1-males were sterile (Vitullo, unpubl. results). This reinforces our early hypothesis that *C. callidus* is reproductively isolated from *C. venustus* (Vitullo et al. 1984).

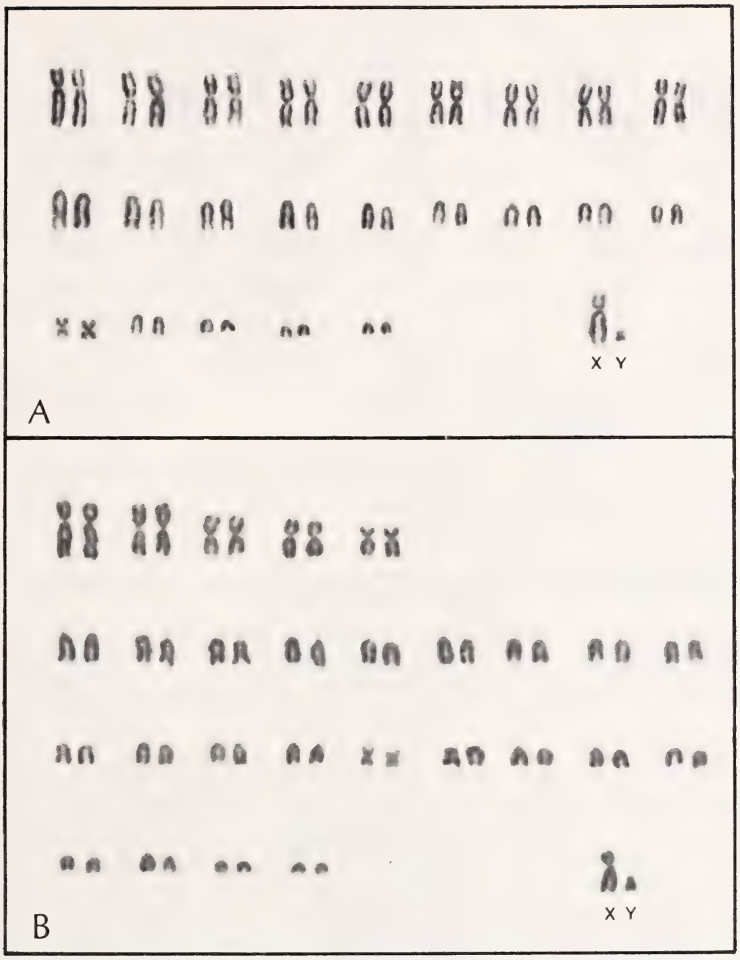

Fig. 1. Giemsa-stained karyotypes of: A – *Calomys callidus* (2n = 48, NF = 69); B – *Calomys venustus* (2n = 56, NF = 69)

Hershkovitz (1962) has argued that all the large *Calomys* with sharp interorbital edges belong to one species, namely *C. callosus*. According to this criterion, *C. venustus* and *C. callidus* from Argentina, and *C. fecundus* from Bolivia were synonymized with *C. callosus*. However, chromosomal data here presented suggest that species distinction made by Thomas is more consistent than Hershkovitz' reclassification.

Pearson and Patton (1976) have proposed that *Calomys* species can be divided into two distinctive groups, *C. laucha-C. sorellus* and *C. lepidus-C. musculinus-C. callosus*, according to their chromosomal relationships. In addition, these authors proposed a somewhat intermediate position for *C. fecundus* between the above mentioned groups, to which *C. venustus* and *C. callidus* could be added. These three species show intermediate diploid numbers at the range displayed by the genus (2n = 64 to 2n = 36), forming a Robertsonian series from 2n = 56 to 2n = 48. Although banding patterns are not available for *C. fecundus*, its karyotype (2n = 50, NF = 69 with eight large distinctive biarmed autosomes) (Pearson and Patton 1976) and chromosomal lengths support the inclusion

Fig. 2. Comparison of G-banded karyotypes from *Calomys callidus* and *Calomys venustus*. Underlined numbers indicate the *C. venustus* haploid set

Table 1. **Chromosomal lengths of *Calomys callidus* and *Calomys venustus* expressed as percentage of the female haploid set**

Chromosome	*C. callidus* X ± SD	*C. venustus* X ± SD
1	7.24 ± 0.62 (1.61)*	7.70 ± 0.45 (1.64)
2	6.47 ± 0.46 (1.17)	7.36 ± 0.36 (1.00)
3	6.32 ± 0.36 (1.24)	6.00 ± 0.52 (1.09)
4	6.03 ± 0.40 (1.25)	5.37 ± 0.41 (1.16)
5	5.80 ± 0.26 (1.23)	4.36 ± 0.53 (1.43)
6	5.61 ± 0.28 (1.20)	4.10 ± 0.19
7	5.30 ± 0.20 (1.19)	3.89 ± 0.28
8	5.04 ± 0.38 (1.25)	3.59 ± 0.17
9	4.72 ± 0.31 (1.29)	3.55 ± 0.16
10	4.17 ± 0.28	3.47 ± 0.23
11	3.91 ± 0.22	3.38 ± 0.33
12	3.73 ± 0.22	3.26 ± 0.32
13	3.54 ± 0.24	3.09 ± 0.20
14	3.36 ± 0.30	3.00 ± 0.22
15	3.21 ± 0.25	2.83 ± 0.11
16	3.02 ± 0.26	2.83 ± 0.11
17	2.88 ± 0.22	2.83 ± 0.12
18	2.75 ± 0.19	2.70 ± 0.21
19	2.66 ± 0.28 (1.09)	2.73 ± 0.35 (1.19)
20	2.52 ± 0.26	2.62 ± 0.27
21	1.92 ± 0.40	2.54 ± 0.25
22	1.72 ± 0.30	2.45 ± 0.22
23	1.52 ± 0.36	2.41 ± 0.22
24		2.37 ± 0.17
25		2.16 ± 0.15
26		1.77 ± 0.26
27		1.56 ± 0.14
X	6.64 ± 1.27 (1.81)	6.02 ± 0.43 (1.75)
Y	2.26 ± 0.29	2.29 ± 0.55

* Numbers in parenthesis indicate the centromeric index (long arm/small arm) of biarmed chromosomes.

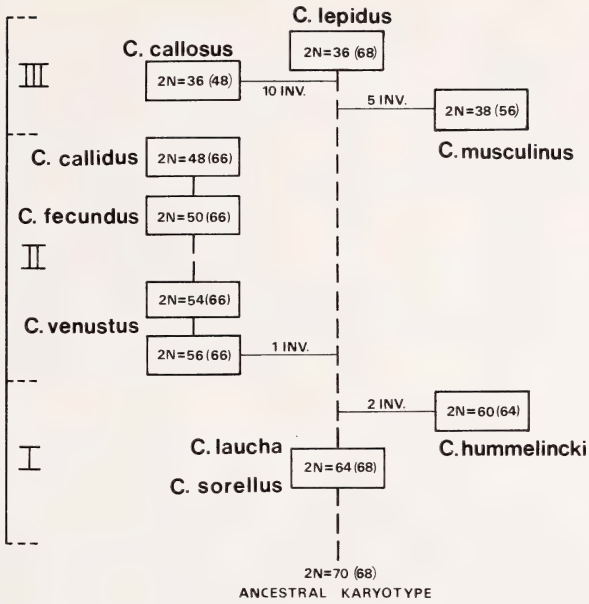

Fig. 3. Interpreted pathway of chromosomal changes within *Calomys*. Each vertical line indicates a Robertsonian fusion, and horizontal lines indicate superimposed pericentric inversions. Number in paranthesis are NF_a. Roman numbers refer to species grouping according to karyotype features and the degree of transformation from the ancestral condition (see text)

of this species in the Robertsonian series. In support, *C. venustus, C. callidus* and *C. fecundus* are more closely related to one another than *C. callosus* which shows a 2n = 36 (NF_a = 48) karyotype with 7 pairs of large biarmed chromosomes, a small-sized metacentric, and 10 pairs of subtelocentrics and telocentrics (Pearson and Patton 1976), suggesting that other rearrangements are superimposed on Robertsonian ones.

A basic pattern of chromosomal evolution by decrease in diploid numbers through Robertsonian reduction has been independently proposed for several major Neotropical Cricetidae: Sigmodontini (Zimmerman 1970), Akodontini (Bianchi et al. 1971; Vitullo et al. 1986), Oryzomyini (Gardner and Patton 1976), and Phyllotini (Pearson and Patton 1976). A karyotype of 68 telocentric autosomes (2n = 70, NF_a = 68) has been interpreted as the ancestral condition for the genus *Phyllotis* and the phyllotini group in general. This all-telocentric karyotype appears to have given rise to those represented in *Calomys* species through a basic series of 17 fusions leading to the all-metacentric karyotype (2n = 36, NF_a = 68) displayed by *C. lepidus* (Fig. 3). Throughout such a basic trend in chromosomal evolution, *Calomys* species may have developed in progressive steps involving a minimum of chromosome changes. Thus, it is possible to discern three groups of species in *Calomys* according to karyotype features (Table 2).

Group I includes karyotypes with higher chromosomal numbers (2n = 64–60) within the genus, closely related to the ancestral condition (2n = 70). These karyotypes, mostly telocentric, may be derived from a few Robertsonian repatternings. *C. laucha* from Argentina, *C. sorellus* from Perú, and *C. hummelincki* from Venezuela belong to this group (Fig. 3).

Group II comprises karyotypes ranging from 2n = 56 to 2n = 48 and forming a Robertsonian series at an intermediate position in the basic pathway of transformation from the ancestral type (Fig. 3). These karyotypes are clearly asymmetrical showing a

Table 2. **Grouping of *Calomys* species according to karyotype features**

Karyological Group	Species	2n	NF_a*	Reference
	C. laucha	64	68	Gardenal et al. 1977
I	*C. sorellus*	64	68	Pearson and Patton 1976
	C. hummelincki	60	64	Pérez-Zapata et al. 1987
	C. venustus	56	66	Lisanti et al. 1976
II		54	66	Hurtado and Wainberg 1974
	C. fecundus	50	66	Pearson and Patton 1976
	C. callidus	48	66	Vitullo et al. 1984
	C. musculinus	38	56	Forcone et al. 1980
III	*C. callosus*	36	48	Pearson and Patton 1976
	C. lepidus	36	68	Pearson and Patton 1976

* NF_a: number of autosomal arms.

variable number of large distinctive biarmed chromosomes. *C. venustus* and *C. callidus* from Argentina, and *C. fecundus* from Bolivia are included here.

Group III shows a greater heterogeneity when compared with the other two groups, as reflected in NF_a variability (Fig. 3). It contains karyotypes quite distant from the ancestral condition, which display a high degree of transformation by means of pericentric inversions. These karyotypes are mainly made up by metacentric, submetacentric and subtelocentric chromosomes. Except for *C. lepidus* which exhibits an all-metacentric karyotype, the other species included in this group, i.e. *C. musculinus* and *C. callosus*, show a variable number of subtelocentric chromosomes requiring up to 10 inversions superimposed on Robertsonian repatternings, to explain their appearance (Fig. 3).

The working hypothesis developed here on the basis of available chromosomal data may find support in a progressive knowledge of other species of *Calomys*, especially those distributed in Bolivia and Brazil, for which cytogenetics is still incipient.

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Zusammenfassung

Cytogenetik an Vespermäusen, Calomys (Rodentia, Cricetidae): Robertson'sche Variation zwischen Calomys callidus und Calomys venustus

Die Beziehungen zwischen Karyotypen von *Calomys callidus* und *Calomys venustus* wurden untersucht, um weitere Daten zur karyologischen Differenzierung in diesem Genus zu gewinnen. 7 Individuen von *C. venustus* aus den argentinischen Provinzen San Luis und Córdoba zeigten den gleichen Karyotypen (2n = 56, NF = 69) wie vorher für Tiere der Typenlokalität beschrieben. Vergleiche von G-Bandenmustern ergaben ferner, daß die Karyotypen von *C. venustus* und *C. callidus* durch 4 Robertson'sche Abstände voneinander getrennt sind. Diese und bereits bekannte Daten von anderen *Calomys*-Arten führen zu einer Annahme von folgenden 3 karyologischen Gruppen innerhalb des Genus: Gruppe I: Karyotypen mit größeren Chromosomenzahlen (2n = 64–60), zumeist telozentrisch; Gruppe II: asymmetrische Karyotypen (2n = 56–48), durch Fusionen und Fissionen entstanden; Gruppe III: Karyotypen mit geringen Chromosomenzahlen (2n = 38–36). Diese repräsentieren stark reorganisierte Stadien, die von einem telocentrischen ancestralen Zustand mit hoher Anzahl (2n = 70) entstanden sein mögen.

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Zur Nahrungsökologie von *Microtus arvalis* (Pallas, 1779) auf Dauergrünland

I. Allgemeine Nahrungspräferenzen

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Abstract

Nutrition ecology of Microtus arvalis (Pallas, 1779) on permanent meadow
I. General food preferences

Investigated were the food preferences of a population of the common European vole *Microtus arvalis* (Rodentia, Microtidae) inhabiting permanent meadow. The stomach contents of 363 individuals (186 ♀♀, 177 ♂♂) caught in 1984–7 with baited snap traps were microscopically analyzed. Plant species were determined using a new reference catalogue of photomicrographs taken from the epidermal structures of the 48 plant species of the volus' territory.

Species composition of the diet of the voles was not correlated to species composition of the vegetation, i.e. voles fed selectively on various plant species. The results indicate that the 48 available species may be divided into four categories, according to their importance as diet components:

1. Major food species (taken very frequently and at high volume percentage): 8 species,
2. minor food species (taken frequently, but only with low to medium volume percentage): 12 species,
3. casual diet (taken rarely and with low volume percentage): 20 further species, and
4. species totally avoided: 8 species.

Taraxacum officinale and *Trifolium pratense* were by far the most important food species concerning the frequency of occurrence as well as the volume percentage.

Einleitung

Die europäische Feldmaus *Microtus arvalis* (Pallas 1779) bewohnt in Mitteleuropa vorwiegend landwirtschaftlich genutzte Flächen und kann deshalb – zumal bei hoher Populationsdichte – durch den Verzehr von Feldfrüchten zum Schädling landwirtschaftlicher Kulturen werden. Der Einfluß ihrer Nahrungsaufnahme auf Kulturpflanzen ist demzufolge bereits des öfteren untersucht worden (Babinska-Werka 1979; Holišová 1975; Kokeš 1976; Rýszkowski et al. 1973; Tertil 1977; Truszkowski 1982).

In Monokulturen wie Getreide-, Rüben- oder Luzernefeldern sind die Wahlmöglichkeiten bezüglich der aufzunehmenden Pflanzennahrung naturgemäß äußerst beschränkt. Auf Dauergrünland siedelnden *Microtus-arvalis*-Populationen steht hingegen eine große Zahl von Pflanzenarten als potentielle Nahrung zur Verfügung. Dieses vielfältige Angebot wirft die Frage auf, ob die Anteile der einzelnen Pflanzenarten an der Nahrung der Feldmaus ihrem Anteil an der Vegetation entsprechen, oder ob *Microtus arvalis* bei der Nahrungsaufnahme selektiv vorgeht. Yu et al. (1980) konnten an einer französischen Population zeigen, daß der Anteil einer Pflanzenart am Nahrungsspektrum der Feldmaus nicht mir ihrem Anteil an der pflanzlichen Biomasse korrespondiert, und auch die Ergebnisse der in der Schweiz durchgeführten Untersuchung von Leutert (1983) weisen tendenziell in diese Richtung.

Aus dem deutschsprachigen Raum fehlen allerdings bisher quantitative Erkenntnisse darüber, welche Pflanzen auf Dauergrünland ansässige Feldmauspopulationen trotz eines

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geringen Anteils an Nahrungsangebot besonders bevorzugen, und welche sie – trotz eventuell leichterer Verfügbarkeit – nur in geringem Umfang aufnehmen oder sogar gänzlich meiden. Ziel der vorliegenden Untersuchung ist es deshalb, quantitative Zusammenhänge zwischen dem prozentualen Anteil der verfügbaren Pflanzenarten an der Vegetation und ihrem Anteil am Nahrungsspektrum von *Microtus arvalis* zu beschreiben.

Material und Methode

Als Untersuchungsgebiet dienten fünf landwirtschaftlich genutzte Dauergrünlandflächen von je ca. 0,5 Hektar in der Gemarkung von Pohlheim-Holzheim in der nördlichen Wetterau (Hessen).

Auf diesen Flächen wurden im Zeitraum von Oktober 1984 bis Mai 1987 insgesamt 363 Individuen (186 ♀♀ und 177 ♂♂ aller Altersstufen ab dem Zeitpunkt der Entwöhnung) der europäischen Feldmaus *Microtus arvalis* (Rodentia, Microtidae) mit Schlagfallen gefangen, wobei als Köder hauptsächlich Rosinen Verwendung fanden. Die Tiere wurden bis zur Präparation bei −20°C aufbewahrt.

Nach dem Auftauen wurde der Magen entnommen und der Inhalt mikroskopisch untersucht. Die Artbestimmung aufgefundener Pflanzenteile erfolgte anhand eines Kataloges von über 600 Referenzaufnahmen, die vorher von den Epidermisstrukturen aller oberirdischen Teile der im Untersuchungsgebiet festgestellten 48 Pflanzenarten angefertigt worden waren. Zusätzlich zur Artbestimmung wurde der Volumenanteil jeder Art am Gesamtinhalt des Magens aufgrund der auf dem Objektträger eingenommenen Fläche geschätzt.

Als Maß für die Verfügbarkeit einer Pflanzenart dient ihr Anteil an der Bodenvegetation in Prozent. Dieser Wert wurde aus je fünf im Mai und August durchgeführten Aufnahmen ermittelt.

Um die Präferenz, mit der verschiedene Pflanzenarten von *Microtus arvalis* aufgenommen werden, feststellen und miteinander vergleichen zu können, ist eine Maßzahl erforderlich, die die unterschiedlichen Anteile der Arten an der Vegetation berücksichtigt. Als Präferenzindex, der diese Bedingung erfüllt, dient hier, dem Vorschlag von Reichman (1975) sowie von Burton und Black (1978) folgend, der Quotient aus Nachweishäufigkeit bzw. Volumenanteil am Mageninhalt einerseits und prozentualem Anteil an der Bodenvegetation andererseits. Präferenzindices über 1,00 zeigen Bevorzugung, solche unter 1,00 Ablehnung an (Reichman 1975).

Ergebnisse

Nachweishäufigkeit der Nahrungspflanzen

Zunächst soll untersucht werden, ob die Häufigkeit, mit der eine Pflanzenart von *Microtus arvalis* als Nahrung aufgenommen wird, mit dem Anteil dieser Art an der Bodenvegetation in Einklang steht. Dazu sind in Tabelle 1 die im Untersuchungsgebiet vorkommenden 48 Pflanzenarten (Spalte 1) in der durch ihren prozentualen Anteil an der Vegetation (Spalte 2) gegebenen Reihenfolge aufgeführt. Diesem Wert ist in der dritten Spalte die Prozentzahl derjenigen Tiere gegenübergestellt, deren Magen Teile der betreffenden Pflanze enthielt (Nachweishäufigkeit in Prozent). In der vierten Spalte schließlich findet sich für jede Pflanzenart als Präferenzindex der Quotient aus Nachweishäufigkeit und Prozentanteil an der Bodendeckung.

Aus der Tabelle geht hervor, daß das Nahrungswahlverhalten von *Microtus arvalis* von der Verfügbarkeit einzelner Arten offenbar nur in geringem Umfang beeinflußt wird: *Arrhenatherum elatius, Alopecurus pratensis* und *Dactylis glomerata* – drei Gramineen-Arten also, die zu etwa gleich großen Anteilen in der Vegetation vertreten waren – traten in ca. einem Drittel, einem Viertel bzw. in unter fünf Prozent der untersuchten Mägen auf, während beispielsweise *Poa annua* und *Taraxacum officinale* – mit Anteilen von je unter einem Prozent am Aufbau der Pflanzendecke beteiligt – sich in etwa einem Viertel bzw. fast der Hälfte aller Mägen fanden.

Nach ihrem Präferenzindex (PI) lassen sich nun die Pflanzenarten des Untersuchungsgebietes bezüglich der Präferenz, die ihnen *Microtus arvalis* als Nahrungsobjekt entgegenbringt, den folgenden sechs Kategorien zuordnen:

Tabelle 1. **Anteil der Pflanzenarten des Untersuchungsgebietes an der Bodenvegetation, Häufigkeit ihres Auftretens in den untersuchten Mägen und Präferenzindex nach Häufigkeit, Volumenanteil am Gesamtnahrungsvolumen aller untersuchten Tiere und Präferenzindex nach Volumen**

Art	Anteil an der Bodenvegetation (%)	Nachweishäufigkeit (%)	Präferenzindex nach Häufigkeit	Anteil am Gesamtnahrungsvolumen (%)	Präferenzindex nach Volumen
Arrhenatherum elatius	13.50	32.51	2.41	5.15	0.38
Alopecurus pratensis	12.97	24.52	1.89	4.75	0.37
Dactylis glomerata	11.41	4.68	0.41	0.44	0.04
Trisetum flavescens	7.24	15.43	2.13	2.25	0.31
Poa pratensis	6.68	41.32	6.19	5.91	0.88
Holcus lanatus	5.07	5.51	1.09	1.31	0.26
Lolium perenne	3.09	26.72	8.65	3.35	1.08
Achillea millefolium	3.01	14.33	4.76	3.27	1.09
Galium mollugo	2.53	6.61	2.61	1.31	0.52
Bromus mollis	2.12	18.46	8.71	1.92	0.91
Poa trivialis	2.06	33.06	16.05	4.90	2.38
Ranunculus acris	2.00	1.38	0.69	0.07	0.04
Anthriscus sylvestris	1.89	15.15	8.02	3.22	1.70
Geranium pratense	1.89	1.10	0.58	0.41	0.22
Festuca pratensis	1.81	0.28	0.15	0.01	0.01
Heracleum sphondylium	1.59	5.79	3.64	1.39	0.87
Vicia sepium	1.48	8.82	5.96	2.86	1.93
Cerastium holosteoides	1.39	4.13	2.97	0.46	0.33
Trifolium pratense	1.36	8.82	6.49	2.03	1.49
Phleum pratense	1.25	10.19	8.15	1.42	1.14
Plantago lanceolata	1.17	5.79	4.95	0.96	0.82
Bellis perennis	1.03	–	–	–	–
Anthoxanthum odoratum	0.97	4.96	5.11	0.23	0.24
Lotus corniculatus	0.86	0.28	0.33	0.01	0.01
Poa annua	0.83	23.42	28.22	4.60	5.54
Taraxacum officinale	0.83	47.93	57.75	23.95	28.86
Glechoma hederacea	0.78	–	–	–	–
Leucanthemum ircutianum	0.75	2.75	3.67	0.14	0.19
Lolium multiflorum	0.75	3.03	4.04	0.23	0.31
Trifolium repens	0.67	39.39	58.79	18.60	27.76
Ajuga reptans	0.67	0.83	1.24	0.01	0.04
Centaurea jacea	0.64	2.75	4.30	0.42	0.66
Cirsium arvense	0.53	–	–	–	–
Vicia angustifolia	0.50	3.03	6.06	0.74	1.48
Veronica arvensis	0.50	6.89	13.78	1.83	3.66
Daucus carota	0.50	–	–	–	–
Ranunculus repens	0.47	1.10	2.34	0.26	0.55
Plantago media	0.45	0.28	0.62	0.03	0.07
Campanula rotundifolia	0.42	0.55	1.31	0.01	0.02
Rumex obtusifolius	0.31	1.10	3.55	0.51	1.65
Medicago varia	0.31	0.55	1.77	0.12	0.31
Myosotis arvensis	0.31	0.28	0.90	0.01	0.03
Crepis biennis	0.31	–	–	–	–
Lamium album	0.28	0.28	1.00	0.01	0.04
Trifolium dubium	0.28	–	–	–	–
Rumex crispus	0.19	4.41	23.21	0.77	4.05
Cynosurus cristatus	0.19	–	–	–	–
Urtica dioica	0.17	–	–	–	–

1. Arten mit sehr starker Präferenz (PI ≥ 10):
   Trifolium repens, Taraxacum officinale, Poa annua, Rumex crispus, Poa trivialis, Veronica arvensis (6 Arten, die zusammen 5,08 % der Pflanzendecke ausmachen).
2. Arten mit starker Präferenz (10 > PI ≥ 5):
   Bromus mollis, Lolium perenne, Phleum pratense, Anthriscus sylvestris, Trifolium pratense, Poa pratensis, Vicia angustifolia, Vicia sepium, Anthoxanthum odoratum (9 Arten, zusammen 19,34 %).
3. Arten mit weniger starker Präferenz (5 > PI ≥ 2):
   Plantago lanceolata, Achillea millefolium, Centaurea jacea, Lolium multiflorum, Leucanthemum ircutianum, Heracleum sphondylium, Rumex obtusifolius, Cerastium holosteoides, Galium mollugo, Arrhenatherum elatius, Ranunculus repens, Trisetum flavescens (12 Arten, zusammen 33,35 %).
4. Arten mit minderer Präferenz (2 > PI ≥ 1):
   Alopecurus pratensis, Medicago varia, Campanula rotundifolia, Ajuga reptans, Holcus lanatus, Lamium album (6 Arten, zusammen 19,72 %).
5. Arten mit negativer Präferenz (1 > PI ≥ 0):
   Myosotis arvensis, Ranunculus acris, Plantago media, Geranium pratense, Dactylis glomerata, Lotus corniculatus, Festuca pratensis (7 Arten, zusammen 18,73 %).
6. Vollständig abgelehnte Arten (PI = 0):
   Urtica dioica, Cynosurus cristatus, Trifolium dubium, Crepis biennis, Daucus carota, Cirsium arvense, Glechoma hederacea, Bellis perennis (8 Arten, zusammen 3,79 %).

Insgesamt werden also 15 Arten, die zusammen ca. ein Viertel der Vegetation des Untersuchungsgebiets stellen, stark oder sehr stark bevorzugt, 15 weitere Arten, die zusammen etwas mehr als ein Fünftel der Pflanzendecke bilden, werden abgelehnt oder völlig gemieden.

Volumenanteil der Nahrungspflanzen

Das im vorigen Abschnitt angewandte Verfahren zur Beurteilung der Bedeutung verschiedener Pflanzenarten als Nahrungsgrundlage von *Microtus arvalis* birgt die Gefahr, daß die Wichtigkeit häufig, aber immer nur in geringer Menge aufgenommener Arten regelmäßig überschätzt wird. Deshalb soll in diesem Abschnitt überprüft werden, ob sich andere Ergebnisse einstellen, wenn der Beurteilung nicht die Häufigkeit des Auftretens einer Pflanzenart, sondern ihr Volumenanteil an der Füllmenge der einzelnen Mägen zugrundegelegt wird.

Dazu dienen die beiden letzten Spalten von Tabelle 1. In Spalte 5 findet sich der prozentuale Anteil jeder Art am Gesamtinhalt aller Mägen und schließlich in der sechsten Spalte als Präferenzindex nach Volumen der Quotient aus den Werten der Spalten 5 und 2.

Offensichtlich wird die Bevorzugung einzelner Arten noch prägnanter, wenn das Volumen als Beurteilungskriterium dient. Die 15 Gramineenarten, immerhin mit fast 70 % an der Biomasse der Pflanzendecke beteiligt, stellen nur knapp 37 % des Nahrungsvolumens, die 33 Dicotyledonenarten hingegen zwar nur ca. 30 % der Biomasse, aber über 60 % der aufgenommenen Nahrungsmenge. Besonders auffällig ist dabei, daß zwei Arten, die zusammen nur 1,5 % der Vegetation repräsentieren, nämlich *Taraxacum officinale* und *Trifolium repens*, insgesamt mit weit über 40 % am Gesamtvolumen der Nahrung beteiligt sind.

Im einzelnen ergibt sich durch Einteilung in Kategorien nach Präferenzindices folgendes Bild:

1. Arten mit außerordentlich starker Präferenz (PI ≥ 10):
   Taraxacum officinale, Trifolium repens (2 Arten, zusammen 1,5 % der Vegetation).
2. Arten mit starker Präferenz (10 > PI ≥ 5):
   Poa annua (1 Art, 0,86 %).

3. Arten mit weniger starker Präferenz (5 > PI ⩾ 2):
Rumex crispus, Veronica arvensis, Poa trivialis (3 Arten, zusammen 2,75 %).
4. Arten mit minderer Präferenz (2 > PI ⩾ 1):
Vicia sepium, Anthriscus sylvestris, Rumex obtusifolius, Trifolium pratense, Vicia angustifolia, Phleum pratense, Achillea millefolium, Lolium perenne (8 Arten, zusammen 12,89 %).
5. Arten mit negativer Präferenz (1 > PI > 0):
Bromus mollis, Poa pratensis, Heracleum sphondylium, Plantago lanceolata, Centaurea jacea, Ranunculus repens, Galium, mollugo, Arrhenatherum elatius, Alopecurus pratensis, Cerastium holosteoides, Trisetum flavescens, Lolium multiflorum, Medicago varia, Holcus lanatus, Anthoxanthum odoratum, Geranium pratense, Leucanthemum ircutianum, Plantago media, Dactylis glomerata, Ranunculus acris, Ajuga reptans, Lamium album, Myosotis arvensis, Campanula rotundifolia, Lotus corniculatus, Festuca pratensis (26 Arten, zusammen 78,25 %).
6. Vollständig abgelehnte Arten (PI = 0):
Urtica dioica, Cynosurus cristatus, Trifolium dubium, Crepis biennis, Daucus carota, Cirsium arvense, Glechoma hederacea, Bellis perennis (8 Arten, zusammen 3,79 %).

Die 14 Arten der ersten vier Kategorien, deren Anteil am Nahrungsaufkommen höher liegt als ihr Anteil an der Vegetation, machen zusammen nur 18 % der Pflanzendecke aus. Die übrigen 34 Arten stellen über 80 % der Bodenvegetation, werden aber durchweg in Mengen aufgenommen, die unter ihrem Anteil an der Biomasse liegen.

Bemerkenswert ist, daß sich in der durch die präferenzindices gegebenen Reihenfolge kaum gravierende Unterschiede zwischen der Bewertung nach Nachweishäufigkeit und derjenigen nach Volumen ergeben. Insoweit könnten beide Verfahren als gleichwertig gelten. Andererseits macht der Vergleich der Ergebnisse der beiden Bewertungssysteme aber auch deutlich, daß die Aufstellung einer Rangfolge allein nur ein verzerrtes Bild von der Wichtigkeit einzelner Arten im Nahrungsspektrum von *Microtus arvalis* liefern kann: Nur durch die Betrachtung der Volumenanteile zeigt sich, daß sich die Feldmaus hauptsächlich von einigen wenigen Arten ernährt, während das Gros der verfügbaren Arten lediglich als Nebenbestandteil des Nahrungsspektrums oder sogar nur als Beikost aufzufassen ist.

Zusammensetzung des Nahrungsspektrums von *Microtus arvalis* auf Dauergrünland

Die bisher dargelegten Ergebnisse lassen den Schluß zu, daß eine Bewertung der Wichtigkeit verschiedener Pflanzenarten als Nahrungskomponenten von *Microtus arvalis* sowohl auf der Häufigkeit der Aufnahme als auch auf dem jeweils aufgenommenen Volumen basieren muß.

Ausgehend von dieser Überlegung und gestützt auf die Ergebnisse der beiden vorigen Abschnitte, können die 40 Pflanzenarten, die in den untersuchten Mägen nachgewiesen wurden, in ihrer Bedeutung als Bestandteile des Nahrungsspektrums von *Microtus arvalis* folgendermaßen charakterisiert werden:

1. Hauptbestandteile des Nahrungsspektrums:
1.1. Sehr häufig und mit sehr hohen Volumenanteilen aufgenommene Arten: *Taraxacum officinale, Trifolium repens.*
1.2. Sehr häufig und mit hohen Volumenanteilen aufgenommene Arten: *Arrhenatherum elatius, Poa pratensis.*
1.3. Sehr häufig, aber nur mit geringeren Volumenanteilen aufgenommene Arten: *Alopecurus pratensis, Lolium perenne, Poa trivialis, Poa annua.*
2. Nebenbestandteile des Nahrungsspektrums:
2.1. Häufig, aber nur mit mäßigen Volumenanteilen aufgenommene Arten: *Trisetum flavescens, Achillea millefolium, Anthriscus sylvestris.*

2.2. Häufig, aber immer nur mit geringen Volumenanteilen oder weniger häufig, aber mit höheren Volumenanteilen aufgenommene Arten: *Bromus mollis, Phleum pratense, Vicia sepium, Trifolium pratense.*

2.3. Weniger häufig und mit geringen Volumenanteilen aufgenommene Arten: *Holcus lanatus, Galium mollugo, Heracleum sphondylium, Plantago lanceolata, Veronica arvensis.*

3. Beikost (selten und nur mit geringen bis sehr geringen Volumenanteilen aufgenommene Arten): *Dactylis glomerata, Ranunculus acris, R. repens, Geranium pratense, Festuca pratensis, Cerastium holosteoides, Anthoxanthum odoratum, Lotus corniculatus, Leucanthemum ircutianum, Lolium multiflorum, Ajuga reptans, Centaurea jacea, Vicia angustifolia, Plantago media, Campanula rotundifolia, Rumex crispus, R. obtusifolius, Medicago varia, Myosotis arvensis, Lamium album.*

Insgesamt sind also 8 der genutzten Arten als Hauptbestandteile und 12 als Nebenbestandteile des Nahrungsspektrums zu betrachten, während die übrigen 20 Arten nur als Beikost konsumiert werden.

Diskussion

Seit der grundlegenden Arbeit von Summerhayes (1941) hat eine große Zahl von Bearbeitern zur Kenntnis der Nahrungsökologie von *Microtus*-Arten beigetragen. Dennoch ist das Bild noch lückenhaft und uneinheitlich. Das liegt zum einen am Artenreichtum der Gattung – in Mittel- und Osteuropa ist vorwiegend *M. arvalis,* in Skandinavien und Großbritannien meist *M. agrestis* und in Nordamerika hauptsächlich *M. pennsylvanicus* Gegenstand diesbezüglicher Untersuchungen –, zum anderen an Unterschieden in der jeweils gewählten Methode (Analyse des Mageninhaltes oder der Faeces bzw. Futterwahlversuche), nicht zuletzt aber auch an der Tatsache, daß sich Nahrungspräferenzen naturgemäß nur innerhalb der Grenzen des verfügbaren Nahrungsangebots manifestieren können. Dieses Angebot variiert aber nicht nur von Habitat zu Habitat, sondern auch von Population zu Population, was den Vergleich der Ergebnisse verschiedener Untersuchungen ungemein erschwert.

Als gesichert kann immerhin die auch hier dokumentierte Erkenntnis gelten, daß das Nahrungswahlverhalten von *Microtus arvalis* zumindest in Wiesenhabitaten, also bei vielfältigem Nahrungsangebot, nur zum Teil von der Verfügbarkeit der einzelnen Nahrungskomponenten, zum größeren Teil aber von ausgeprägten Präferenzen bestimmt wird (Yu et al. 1980; Leutert 1983). Keine nachweisbaren Präferenzen fand hingegen Holišová (1975) in suboptimalen Biotopen in Gewässernähe.

Sofern Präferenzen festgestellt wurden, liegen bezüglich einzelner Arten sowohl Übereinstimmungen als auch Diskrepanzen zu den hier dargelegten Ergebnissen vor. Auch für die von Yu et al. (1980) untersuchte Population war nämlich *Taraxacum officinale* die wichtigste Nahrungspflanze, gefolgt allerdings von *Festuca ovina, Medicago lupulina, Cynosurus cristatus, Anthoxanthum odoratum* und *Bromus erectus*; die letztgenannten fünf Gattungen (teilweise jedoch mit anderen Arten) spielten im Nahrungsspektrum der hier untersuchten Population nur eine untergeordnete Rolle. Weitere wichtige Nahrungsressourcen waren *Arrhenatherum elatius, Holcus lanatus, Trifolium repens* (allerdings erst an neunter Stelle der Rangliste), *Lolium perenne* und *Phleum pratense,* was mit den hier erhobenen Befunden weitgehend übereinstimmt, ebenso wie der geringe Nutzungsgrad von *Daucus carota* (Yu et al. 1980). Im Gegensatz zu den hier ermittelten Präferenzen wurden aber *Trifolium pratense, Poa annua, Poa prantensis, Achillea millefolium* und *Plantago lanceolata* nur in geringen Mengen aufgenommen (Yu et al. 1980).

Leutert (1983) untersuchte den Einfluß von Feldmauspopulationen auf die Artenzusammensetzung verschiedener Wiesenbiotope und stellte fest, daß die Anteile von *Dactylis glomerata, Festuca pratensis, Myosotis arvensis, Glechoma hederacea, Poa pratensis* und

Archillea millefolium nach Neubesiedlung einer Fläche zunahmen, die Deckungsgrade von *Arrhenatherum elatius* und besonders von *Taraxacum officinale* dagegen zurückgingen und *Trisetum flavescens, Plantago lanceolata* und *Plantago media* im Bestand ungefähr gleichblieben. Da eine Zunahme des Deckungsgrades mit Ablehnung, ein Rückgang hingegen mit starker Nutzung als Nahrungsressource durch die Feldmäuse gleichbedeutend ist, ergibt sich hier für alle genannten Arten mit Ausnahme von *Poa pratensis* und *Achillea millefolium* Übereinstimmung der Präferenz.

Bei einigen anderen *Microtus*-Arten wurden ebenfalls Präferenzen festgestellt, so z. B. von Bangs (1984), von Bélanger und Bergeron (1987), von Lindroth und Batzli (1984a), von Thompson (1965) sowie von Zimmerman (1965) bei *M. pennsylvanicus,* von Batzli und Jung (1980) bei *M. oeconomus,* von Gill (1977) und von Batzli und Pitelka (1970; 1971) bei *M. californicus,* von Ferns (1976) bei *M. agrestis* und von Fleharty und Olson (1969), von Cole und Batzli (1979) sowie von Zimmerman (1965) bei *M. ochrogaster.*

Andere Ergebnisse erhielten dagegen Bergeron und Juillet (1979) an *M. pennsylvanicus,* Godfrey (1953) an *M. agrestis* – hier wurde allerdings nur der Anteil verschiedener Grasarten festgestellt – und Spencer (1984) an *M. longicaudus* aus einem montanen Biotop.

Über die Ursachen der dargelegten Präferenzen ist bisher wenig bekannt, doch sind mehrere Ansätze erkennbar, hierüber Aufschluß zu gewinnen.

Partridge (1981) untersuchte den Einfluß experimentell erzeugter Nahrungsgewohnheiten an vier Kleinsäugerarten, darunter *M. agrestis,* und fand eine persistierende Bevorzugung der zunächst allein angebotenen Nahrung auch nach dem Zeitpunkt, zu dem den Tieren wieder ein vielfältigeres Angebot zur Verfügung stand. Sie erklärt dies mit einer gesteigerten Effektivität des Verdauungstraktes gegenüber regelmäßig konsumierten Nahrungsstoffen.

Stenseth et al. (1977) entwickelten ein mathematisches Modell zur Überprüfung der Hypothese, daß das Nahrungswahlverhalten herbivorer Microtiden von dem Bestreben gesteuert wird, die Relation von Energieverlust durch Nahrungssuche einerseits und Energiegewinn durch Nahrungsaufnahme andererseits zu optimieren. Dieses Modell war mit ihren Beobachtungen zum Nahrungswahlverhalten von *M. agrestis* vereinbar.

In jüngster Zeit schließlich wurde mehrfach der Versuch unternommen, die Bevorzugung oder strikte Ablehnung bestimmter Pflanzen mit deren artspezifischen Inhaltsstoffen in einen kausalen Zusammenhang zu bringen (Lindroth und Batzli 1984b; Jean und Bergeron 1986; Bélanger und Bergeron 1987; Bergeron et al. 1987). Teilweise zielen diese Untersuchungen auf die pathogene oder attraktivitätsmindernde Wirkung sekundärer Inhaltsstoffe, teilweise auf den Zusammenhang zwischen Nährwertgehalt und Attraktivität.

Da indessen keine dieser Untersuchungen an *Microtus arvalis* durchgeführt wurde, kann bis auf weiteres nicht entschieden werden, ob eine dieser Ursachen – und gegebenenfalls welche – das Nahrungswahlverhalten der Feldmaus bestimmt.

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Zusammenfassung

Zur Untersuchung der Nahrungspräferenz einer auf Dauergrünland siedelnden Population der europäischen Feldmaus *Microtus arvalis* (Rodentia, Microtidae) wurden in den Jahren 1984 bis 1987 unter Verwendung beköderter Schlagfallen 363 Tiere (186 ♀♀, 177 ♂♂) gefangen. Der Mageninhalt wurde mikroskopisch untersucht, aufgefundene Pflanzenfragmente wurden anhand eines eigens hergestellten Kataloges von Referenzaufnahmen der Epidermisstrukturen aller im Aktionsraum der Tiere vorkommenden Pflanzenarten bestimmt.

Die Zusammensetzung des Nahrungsspektrums stimmt weder nach der Häufigkeit der Aufnahme einzelner Arten noch nach der jeweils konsumierten Menge mit der Zusammensetzung der Pflanzendecke überein, die Tiere gehen also bei der Nahrungswahl selektiv vor.

Anhand der Ergebnisse lassen sich die 48 Pflanzenarten des Untersuchungsgebietes nach ihrer Bedeutung für die Ernährung der Feldmaus in die folgenden vier Gruppen einordnen:

1. Hauptbestandteile des Nahrungsspektrums (sehr häufig und mit meist hohen Volumenanteilen aufgenommene Arten): 8 Arten,
2. Nebenbestandteile des Nahrungsspektrums (häufig, aber nur mit mäßigen Volumenanteilen aufgenommene Arten): 12 Arten,
3. Beikost (selten und nur in geringen bis sehr geringen Mengen aufgenommene Arten): weitere 20 Arten, und
4. vollständig abgelehnte Arten: weitere 8 Arten.

Taraxacum officinale und *Trifolium repens* sind sowohl nach der Häufigkeit der Nutzung als auch nach dem jeweils aufgenommenen Volumen die weitaus wichtigsten Nahrungspflanzen der untersuchten *Microtus-arvalis*-Population.

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Banding pattern comparisons between *Akodon iniscatus*, and *Akodon puer* (Rodentia, Cricetidae)

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Abstract

Described the chromosomes of *Akodon iniscatus* (2n = 33–34, FN = 42) and compared with the karyotypes of *A. puer* (2n = 34, FN = 40). 37 specimens of *A. iniscatus* and 11 of *A. puer* were studied on their C, G and fluorescent (Q and CMA) banding patterns. Whole chromosomes and chromosome arms were shared between both species, 38 arms showed the same G-banding pattern in both species. *A. iniscatus* contains mainly wide-spread centromeric heterochromatin that is absent in *A. puer* and rare in other akodonts. Chromomycin banding revealed that centromeric heterocromatin was homogeneous and GC poor in all chromosomes, whereas the telomeric heterochromatin was GC rich. The present results support the hypothesis of close relationship between *A. iniscatus* and *A. puer* and that the former probably derived from an *Akodon* stock originally differentiated in the low-lands of northeastern Argentina. Therefore, *A. iniscatus* is related with the varying 2n = 40 akodont chromosome group.

Introduction

Akodon is a highly speciose genus of South American cricetids that is the most widely and better known of the genera of sigmodontine mice in its cytogenetics. Of the 38 recognized species of *Akodon* (Reig 1987), 29 are known in their karyotype and 17 have also been analysed in their banding patterns (Bianchi and Merani 1980; Bianchi and Merani 1984; Bianchi et al. 1976; Gallardo 1982; Lobato et al. 1982; Rodriguez et al. 1983; Vitullo et al. 1986; Yonenaga et al. 1975, 1976; Yonenaga-Yassuda 1979).

Akodon iniscatus Thomas is one of the few species of the genus for which the chromosomal complement has not been described. Several specimens from Collón Curá, Neuquén Province, Argentina were karyotyped some time ago by two of the present authors (O. A. R. and L. G.), but these determinations remained unpublished. More recently, *A. iniscatus* was found to be the most common cricetid in the coastal region of Chubut Province, Argentina where its presence had not been reported previously. *A. iniscatus* karyotype was very similar to that of *Akodon puer* Thomas, (Barquez et al. 1980; Kajon et al. 1984; Vitullo et al. 1986). Cytogenetic results on *A. iniscatus* and their comparison with new results from specimens of *A. puer* are presented here.

Material and methods

Cytogenetic analysis was performed on 37 specimens of *A. iniscatus* from Chubut and Neuquén Provinces and on 11 specimens of *A. puer* from Jujuy Province, Argentina. Localities for *A. iniscatus* were: 5 km S Pto. Madryn, Chubut (13 females and 18 males); Punta Lomas, 20 km S Pto. Madryn, Chubut (2 males), and Collón Curá, Neuquén (2 females and 2 males). *A. puer* was collected from León, Jujuy (7 females and 4 males). These specimens are deposited as skin and skull museum specimens in the Museo Municipal de Ciencias Naturales "Lorenzo Scaglia" of Mar del Plata,

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Argentina (MMP), and in the Collection of Mammals of the Centro Nacional Patagónico (CNP), in Puerto Madryn, Argentina.

Additional specimens have been studied for taxonomic comparisons and identification. These include the type specimen of *A. nucus* at the British Museum of Natural History (BMNH 26.10.11-42, male from Chos Malal, Neuquén), the type of *A. iniscatus* (BMNH 3.7.9.64, female from Valle del Lago Blanco, Chubut), a topotypical series of *A. iniscatus*, and 4 specimens from 20 km S of Leleque, Chushamen, Chubut.

For taxonomic studies, cranial and molar tooth morphology were examined with a Wild M-5 stereomicroscope. Skull and teeth were measured with a digital caliper and/or with an eye-piece reticule of the stereomicroscope to the nearest 0.1 mm following standard conventions.

Metaphase chromosome preparations were obtained from bone marrow (Barros and Patton 1985) of animals injected with yeast 24 hs prior to sacrifice (Lee and Elder 1980). C-bands were obtained following the procedure described in Barros and Patton (1985). Seabright's (1971) procedure was followed for G-bands. Chromomycin A_3/methyl green (CMA) bands were done according to Hack and Lawce (1980). Quinacrine/actinomycin D (Q) banding was done according to Hack and Lawce (1980). All fluorescent bands were photographed with Kodak Tri-X film exposed at ASA 800.

Diploid number and chromosome morphology were determined for all specimens, chromosomes were classified according to Levan et al. (1964). Reig and Kiblisky's (1969) size proposal convention was followed. Fundamental number is defined as the number of autosomal arms.

Results

Taxonomy

The type specimens of *A. iniscatus* Thomas, 1919 and of *A. nucus* Thomas, 1926 were found in Valle del Lago Blanco, SW of Chubut and Chos Malal, N of Neuquén, respectively. The two localities are separated by nearly 935 km in the mountainous region of the southern Andean slopes of Argentina (Fig. 1). The type specimens show that the two taxa are very similar in external, skull and tooth features, though they differ markedly in size, *A. nucus* being noticeably larger than *A. iniscatus*. *A. nucus* also differs from *A. iniscatus* in having nasals longer than frontals, parietals comparatively longer, the anterior border of the zygomatic plate in an upward position, and the M3 relatively smaller (Fig. 2).

Judging from the holotypes and additional topotypical or referred specimens in the British Museum of Natural History, the differences found seem to justify full species

Fig. 1. Map showing localities of *A. iniscatus* and *A. nucus*. 1. Chos Malal (type locality for *A. iniscatus*); 2. Collón Curá; 3. El Maitén; 4. Leleque; 5. Lago Blanco (Type locality for *A. nucus*); 6. Puerto Madryn

distinction, as proposed by one of us (Reig 1987). However, Cabrera (1961) considered that *A. nucus* is merely a subspecies of *A. iniscatus*, a course implicitly followed by Honacki et al. (1982), who did not list *A. nucus* as a separate species.

Our specimens from Collón Curá, a locality for which Thomas (1927) cited *A. nucus*, are fairly similar to the holotype of this species, and share all its distinctive characters. Our small available series from Leleque, which comes from 42 km S of Maitén, the type locality of the local form *A. iniscatus collinus* Thomas, 1919, is almost undistinguishable from *A. iniscatus*, thus confirming the distinction of the two (Table 1).

However, our sample from localities near Puerto Madryn, a region where no *Akodon* of this group has been found previously, is quite intermediate between *A. nucus* and *A. iniscatus* in size and morphology (Table 1). Additionally, the karyotype of specimens from these localities are similar to those from Collón Curá reported in this paper. Thus, the intermediacy of the Puerto Madryn *Akodon* as regards typical *A. iniscatus* and *A. nucus*, sheds doubts on the species status of *A. nucus*. We are probably dealing with a geographically variable group of populations which are better considered, at the present state of knowledge, as a single polytypic species. It would support Cabrera's proposal of treating *A. nucus* as a subspecies of *A. iniscatus*. However, this issue is a tentative one, and must be tested by further morphological and cytogenetic studies. But at present, we prefer to allocate provisionally all our chromosomally studied specimens to *Akodon iniscatus* without further refinement.

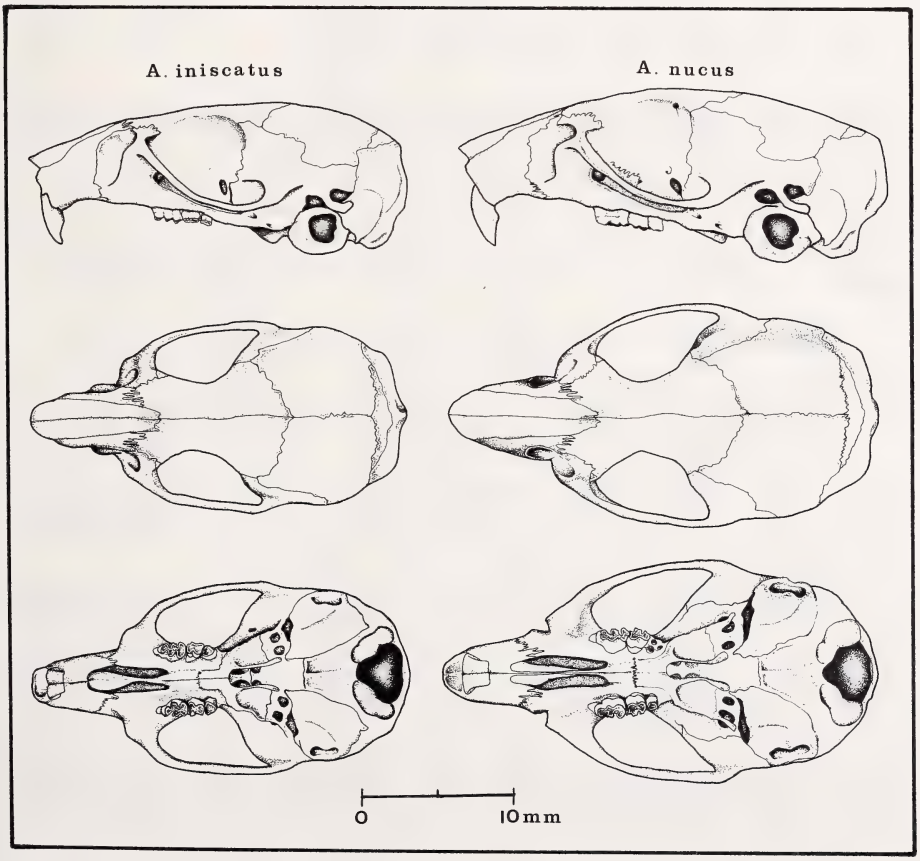

Fig. 2. Skull in lateral, dorsal, and ventral views of the holotypes of *A. iniscatus* and *A. nucus*

Table 1. **Measurements (mm) of *A. iniscatus* (AI) and *A. nucus* (AN) holotypes, and samples from Leleque, Puerto Madryn, and Collón Curá. N: sample size; X: mean; SD: standard deviation**

Variable	AI	AN	Leleque sample			PTO. Madryn sample			Collón Curá sample		
	Type	Type	N	X	SD	N	X	SD	N	X	SD
Total length	145.0	181.0	4	140.0	6.4	11	153.0	8.3	4	173.0	8.6
Tail length	53.0	77.0	4	55.8	2.2	11	60.2	6.0	4	65.9	3.9
Hind foot	19.0	23.0	4	18.9	0.6	12	20.6	0.9	4	22.6	1.0
Ear	11.0	14.0	4	11.8	0.2	12	12.5	0.7	4	12.8	1.5
Skull total length	23.7	26.8	4	23.0	0.6	13	24.5	0.9	4	25.8	0.2
Condylo basal	21.7	25.2	4	20.8	0.5	13	22.6	0.9	4	24.0	0.1
I-M3	11.1	12.4	4	10.5	0.3	13	11.1	0.4	4	12.0	0.3
Diastema	5.6	6.7	4	5.5	0.3	13	6.0	0.3	4	6.4	0.2
Zygomatic breadth	12.4	14.7	4	11.7	0.3	13	12.8	0.4	4	13.3	0.1
Mastoid breadth	11.3	12.1	4	11.1	0.1	13	11.5	0.1	4	11.3	0.2
Inteorb. constrict.	4.0	4.4	4	4.4	0.2	13	4.3	0.1	4	4.2	0.1
Nasal length	8.4	10.3	4	7.8	0.7	13	8.7	0.4	4	9.6	0.2
Frontal length	9.1	9.7	4	9.1	0.2	13	9.0	0.3	4	9.4	0.5
Parietal length	5.1	6.4	4	4.4	0.2	13	5.0	0.4	4	5.2	0.2
Incisor foramina	5.5	6.4	4	5.3	0.3	13	5.6	0.3	4	6.1	0.3
M1M3 alveolar	3.5	4.3	4	4.0	0.1	12	4.1	0.2	4	4.4	0.1
m1m3 alveolar	3.8	4.5	4	4.1	0.1	13	4.2	0.2	4	4.5	0.3

Chromosomal analysis

35 specimens of *A. iniscatus* have a chromosome complement of 2n = 34, FN = 42 (Fig. 3). These include 29 specimens from the Puerto Madryn area, 2 from Punta Lomas, and 4 from Collón Curá. Specimens from all three localities show the same karyotype. The first four pairs are large biarmed chromosomes distinguished from the remaining autosomes by a sharp size gap. Pair 1 is submetacentric, whereas pairs 2 to 4 are metacentric. Pairs 5 to 15 are telocentric. As in most akodontines, the last autosomal pair, (16), is a small metacentric. Pair 5 is medium-sized and pairs 6 to 16 are small autosomes gradually decreasing in size. The X and Y are small telocentrics, representing 5.12 % and 2.46 % of the complement respectively.

A male and a female from Puerto Madryn, which presented a heteromorphic Robertsonian variant of 2n = 33, FN = 42 were found. The decrease of 2n = 34 to 33 results from the presence of a metacentric chromosome whose G-band pattern matches the combined banding patterns of telocentric autosomes 9 and 11 of the 2n = 34 karyotype (Fig. 3D).

C and G banding results refer only to the Puerto Madryn sample. Well-developed pericentromeric C-bands (Fig. 3B) are present on nearly all autosomes of *A. iniscatus,* in striking contrast to other species of the genus, which are usually C poor. Additionally pair 16 shows a band in the telomeric region of both arms, and pair 5 shows a small interstitial band. G-bands are illustrated in Fig. 3C.

A. puer has a karyotype of 2n = 34, FN = 40 (Fig. 3). The first three pairs are large biarmed chromosomes, differing sharply from the remaining autosomes in size. Pair 1 is submetacentric and pairs 2 and 3 are metacentric. Pair 4 is medium-sized telocentric, and pairs 5 to 15 are small telocentrics. Pair 16 is a small metacentric one. The X chromosome is a medium-sized (6.87 %) subtelocentric and the Y is a small (2.20 %) telocentric chromosome.

C-bands (Fig. 3B) show that heterochromatin is found only in the short arm of the X and in the centromeric region of the Y. G-bands of *A. puer* are presented in Fig. 3C.

Fig. 4 shows the G-band correspondence between *A. puer* and *A. iniscatus.* This comparison reveals that 38 arms are shared by both species. Of the 38 shared arms, 28 belong to 24 whole chromosomes, two of which are biarmed. The remaining 10 shared

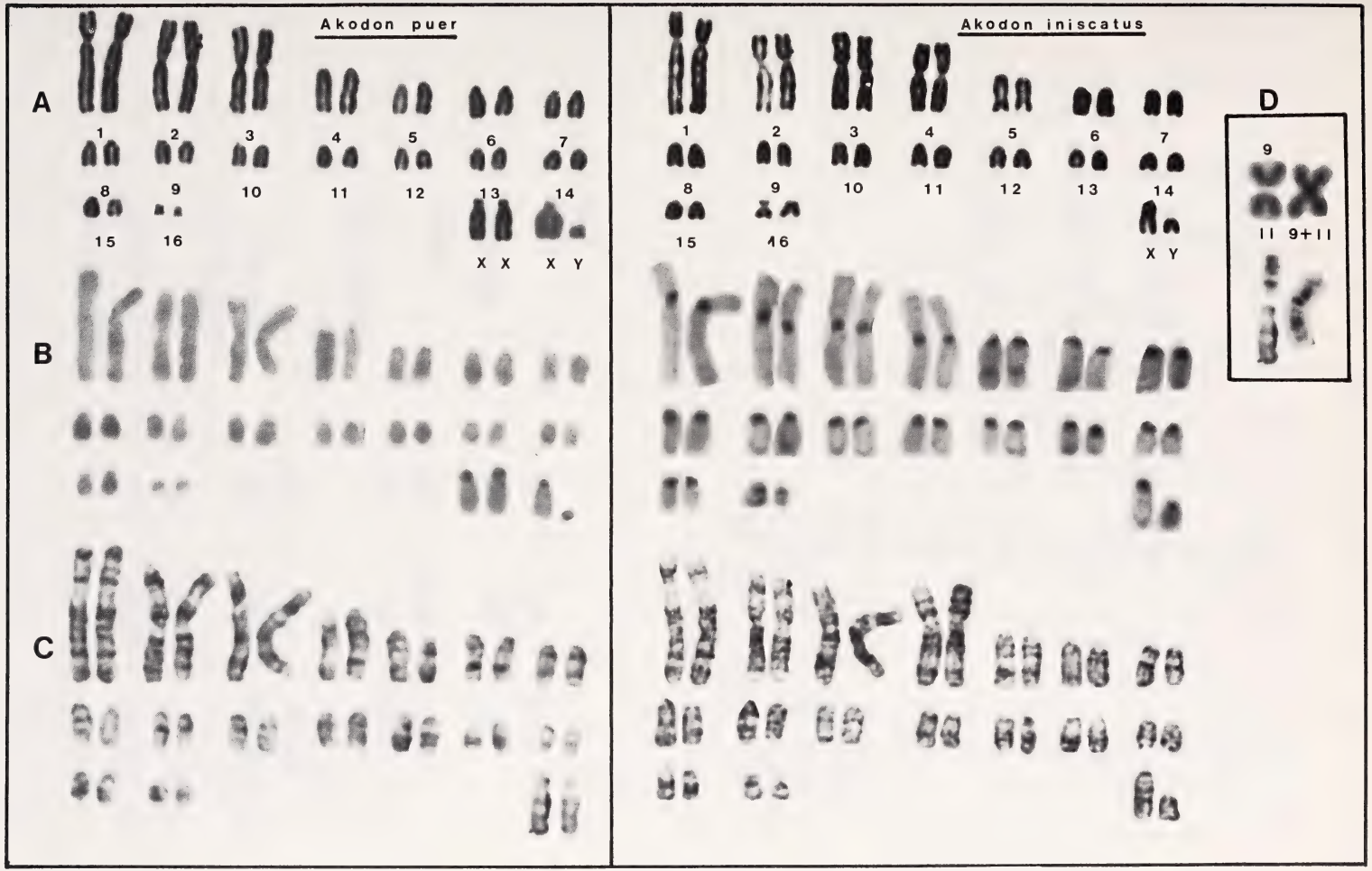

Fig. 3. Akodon puer and *A. iniscatus* giemsa stained karyotypes (A), C-bands (B), and G-bands (C). *A. iniscatus* heteromorphic pair of 2n = 33 morph (D)

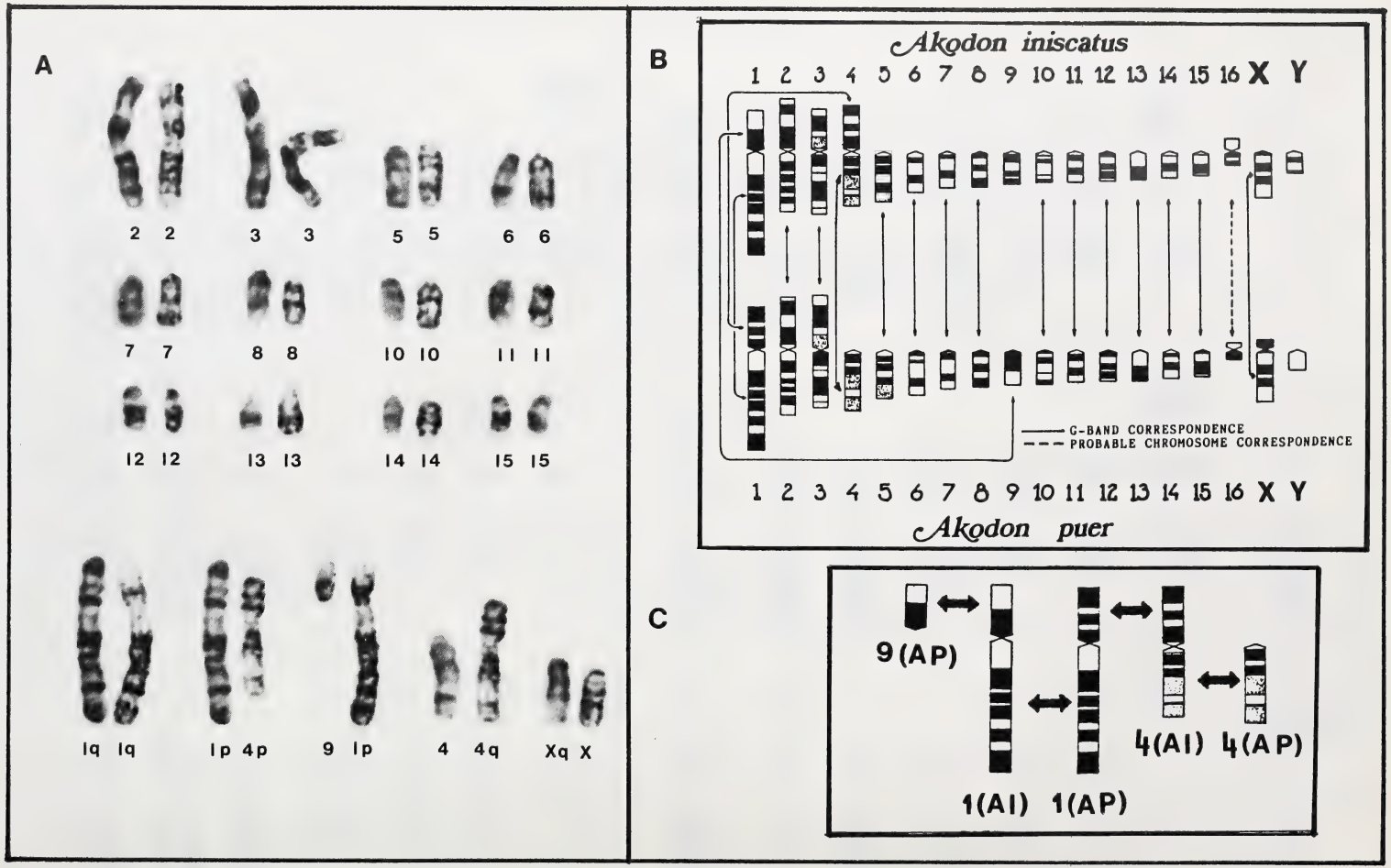

Fig. 4. G-banding pattern comparison between *A. puer* (left) and *A. iniscatus* (right). Pair numbers correspond to their position in each species' karyotype (A). G-banded idiogram comparison between both species (B). Diagram showing arms involved in monobrachial homology (AI = *A. indiscatus* and AP = *A. puer*) (C)

arms do not correspond to whole chromosomes in both species. Pair 9 of *A. iniscatus* and the short arm of the X of *A. puer* are unique elements to these species. Low G-band resolution of pair 16 did not clarify if this pair is shared between both species. Since the microchromosomal pair is present in most *Akodon* species, we conventionally take it as a shared pair. Although, the size difference between pair 16 of *A. iniscatus* and *A. puer* suggests an addition of heterochromatin in the former.

In order to analyze the shared chromosomes between both species we nominate *A. puer* as "*AI*" and *A. iniscatus* as "*AI*"; short arm as "p" and long arm as "q". Arm 1q and pairs 2 and 3 are shared by both species. The 1p of *AP* is shared with the 4p of *AI*. Chromosome 4 of *AP* is shared with 4q of *AI*. Chromosome 9 of *AP* is shared with 1p of *AI*. Pairs 5, 6, 7, 8, 10, 11, 12, 13, 14, and 15 are shared by both species. Thus, two biarmed autosomes of both species can be postulated as shared chromosomes. The remaining biarmed chromosomes (pairs 1 of both species and pair 4 of *AI*) result from Robertsonian rearrangements of different arms showing monobrachial homology (Fig. 4C) (Baker and Bickham 1986; Capanna et al. 1985; Corti et al. 1986).

Fluorescent bands are illustrated in Fig. 5. In the *A. iniscatus* karyotype (Fig. 5C), most CMA-positive bands occur within the euchromatin and in the telomeric heterochromatic region of pair 16. The remaining heterochromatic regions are CMA-negative. All CMA-positive bands seem to correspond with G-negative bands, with the exception of pair 16. Fluorescent CMA-bands suggest heterochromatin similarity in base composition among centromeric regions, as well as heterochromatin heterogeneity between these regions and the telomeric region of pair 16. *A. iniscatus* Q-bands (Fig. 5D) show that fluorescent and quenched Q-bands seem to correspond with G-positive and G-negative bands respectively, although better banding resolution is found in G-bands. The Q banding pattern is opposite to that obtained with Chromomycin A_3, except in the centromeric regions that are CMA-negative and Q-negative. *A. puer* CMA-bands (Fig. 5A) reveal that CMA-positive bands are located within the euchromatin, in regions which were identified as G-negative.

Heterochromatin observed in the sex chromosomes is CMA-negative. *A. puer* Q-bands (Fig. 5B) show that the Q-band pattern, as in *A. iniscatus,* is opposite to that with Chromomycin A_3. The same correspondence between Q and G bands as in *A. iniscatus* was found.

Discussion

Several results indicate that akodontine rodents underwent an intensive chromosomal evolution. The high degree of cladogenesis exhibited by 11 genera and 66 species belonging to the tribe (Reig 1987), is correlated with a high number of chromosomal rearrangements. However, this correlation does not imply an overall causal link between evolutionary divergence and chromosomal changes in the Akodontini. Within *Akodon,* a high range of chromosomal numbers is found, from 2n = 14 in *A. arviculoides* (Yonenaga 1972) to 2n = 52 in *A. illuteus* (Liascovich et. al., 1989), *A. longipilis* (Spotorno and Fernandez 1976), *A. olivaceus* (Gallardo 1982), etc. Species of the genus *Akodon* can be divided into two assemblages according to their overall karyotype characteristics. Species of the first group have a varying karyotype of around 2n = 40 chromosomes which may be reduced by fusions, the second group comprises species with a uniform 2n = 52, FN = 56 karyotype. A good knowledge of the degree of whole chromosome and arm sharing among the species is required for this study.

The term "shared chromosomes" refers to whole chromosomes or chromosome arms which share banding patterns. G-banding was first employed to analyze chromosomal homology of akodontines in a study of *A. azarae, A. molinae,* and "*A.*" *obscurus* (Bianchi et al. 1976). Full chromosome arm homology of species sharing the 2n = 52 karyotype was

demonstrated in *A. longipilis, A. olivaceus* and *A. sanborni* (Gallardo 1982), *A. xanthorhinus* (Rodriguez et al. 1983), and *A. illuteus* (Liascovich et al. 1989). Bianchi and Merani (1984) studied the karyological relationships among several akodontine species of the varying karyotype group: *A. azarae, A. dolores, A. molinae, A. mollis, "A." obscurus,*

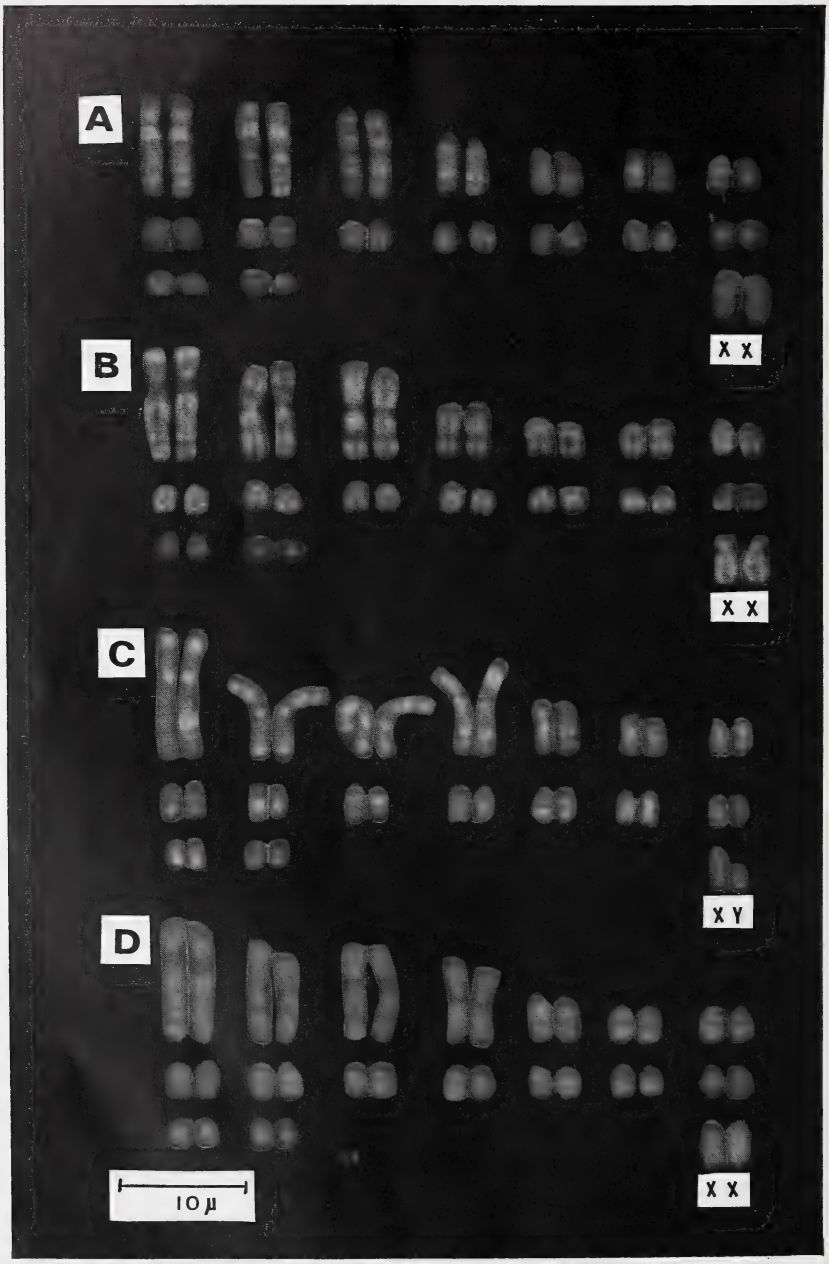

Fig. 5. Fluorescent banded karyotypes. *A. puer* CMA-bands (A), and Q-bands (BB); *A. iniscatus* CMA-bands (C), and Q-bands (D)

A. urichi, and *A. varius*. They demonstrated a high degree of arm sharing among species, which had mostly diverged by presumed Robertsonian processes. These studies are germane to the hypothesis suggested by Bianchi et al. (1971) that chromosome evolution within the akodontine rodents proceeds from low to high numbers by centromeric dissociations, or conversely from high to low numbers by centromeric fusions. One of the present authors (Reig 1987; Vitullo et al. 1986) claimed that the second alternative is the most plausible. Our present results show a high degree of chromosomal homology between *A. iniscatus* and *A. puer*, which suggests close phylogenetic relations between these species. The reductional process of chromosomal number in these two species involved metacentrics, resulting from the fusion of the same autosomes, and then give fully shared chromosomes, and of metacentrics derived from the fusion of different telocentrics which show merely monobrachial homology. Baker and Bickman (1986), Capanna et al. (1985), Corti et al. (1986), and Moritz (1986), have recently pointed out that monobrachial homology probably results in full hybrid sterility. The degree of meiotic breakdown depends on the number of fusions that are monobrachially homologous, and on the specific chromosomes involved. Generally, those studies are based on hybrids with monobrachial homology. The allopatric distribution presented by the species under study led us unable to find hybrids in nature. In order to evaluate the extent of monobrachial homology as a cause of hybrid sterility, studies on laboratory hybrids should be done.

The finding of a polymorphism for one Robertsonian rearrangement in two of the thirty seven studied specimens of *A. iniscatus* is in good keeping with the general occurrence of Robertsonian translocations in the group. In the Puerto Madryn population, this fusion polymorphism is not as extensive as it is in *A. dolores, A. molinae* (Bianchi and Merani 1980), and *A. simulator* (Liascovich et al. 1989). In view of the extensive arm homology found between *A. iniscatus* and *A. puer*, it was of interest to investigate if other chromosomal changes revealed by more refined techniques were involved in the differentiation of these related species.

As species of *Akodon* usually show very little heterochromatin, it was unusual to find a wide-spread occurrence of centromeric heterochromatin in the *A. iniscatus* complement. The few previously known cases of centromeric heterochromatin in *Akodon* were in *A. mollis* (Lobato et al. 1982), *A. arviculoides, A. aff. arviculoides* (Yonenaga et al. 1975; Yonenaga-Yassuda 1979; but see Honacki et al. 1982, and Liascovich and Reig 1989, for correct naming of these forms), *A. (Deltamys) kempi* (Sbalqueiro et al. 1984), and *A. (Hypsimys) budini* (Vitullo et al. 1986), in which modest amounts of heterochromatin have been described. Relevant to our study is the fact that C-positive bands are almost nonexistent in *A. puer* and *A. azarae* (Vitullo et al. 1986), both of which are considered to be closely related to *A. iniscatus* (Reig 1987).

In other groups of mammals, G-banding patterns appear to be quite stable, but extensive interspecific variation in constitutive heterochromatin has been reported (Arnason 1974; Elder and Lee 1985; Pathak et al. 1973; Stock 1981). We have no indication of the processes which were involved in the presence of the centromeric and telomeric heterochromatin, or of its function in *A. iniscatus*, but it is relevant to these problems to have found sequence diversity in the heterochromatin of *A. iniscatus*.

Some fluorescent antibiotic dyes exhibit a nucleotide specificity with helical DNA. A guanine and cytosine (GC) specificity was found for chromomycin A_3 (Sahar and Latt 1978, 1980), whereas a less clear adenine and thymine (AT) specificity has been proposed for quinacrine (Comings 1978). Despite the fact that the molecular mechanisms of interaction between these specific fluorescent dyes and DNA are not well known, they permit a cytological characterization of presumed heterogeneity of DNA sequences within the genome (Barros and Patton 1985).

Chromomycin A_3 has revealed heterogeneity between the heterochromatin of all chromosome pairs and the telomeric heterochromatin found in pair 16 of *A. iniscatus*

karyotype. The latter type of heterochromatin appears as predominantly GC rich, whereas the former is not. This telomeric heterochromatic region is not observed in *A. puer*'s pair 16. An increase/decrease of this GC rich region could be responsible for the size difference observed in pair 16 between the species analyzed.

John et al. (1985) present a review of the concept of equilocality, the similar location of C-bands found between non-homologous chromosomes within the complement. By comparative fluorescence studies on heterochromatin of acridid grasshoppers, these authors found that certain groups of chromosomes that presented a similar C-band distribution also showed a similar fluorescence behaviour with specific dyes, although heterochromatin heterogeneity was also found between similar sites which differ in size and structure. A form of equilocality is present in *A. iniscatus* where all chromosomes, except pair 16, carry a C-band at a centric location, which is CMA and Q negative, while a different heterochromatic site (telomeres of pair 16) respond differentially to CMA.

Although centromeric regions in *A. iniscatus* are heterochromatic, while those in *A. puer* are euchromatic, no fluorescent staining difference was found between them. Findings of CMA and Q negative fluorescence in centromeric heterochromatin could reflect an insufficient number of AT or GC clusters of DNA (Schweizer 1981; Sahar and Latt 1980). While DNA composition is an important determinant in fluorescence staining, the possible role of chromosomal proteins remains unknown (Comings 1978). Comparison of the centromeric regions of *A. iniscatus* and *A. puer* therefore needs to be defined by further sequence analysis. Coincidentally, no composition differences were found between the remaining complement of both species, except for pair 16, which also confirms the chromosome correspondence analysis based on G-bands.

In biarmed complements, equilocality has been explained in terms of a specific ordering of the chromosomes during metaphase (Schweizer and Ehrendorfer 1983), where a sequence transposition or convergence is assumed to occur between repeated sequences of chromosomes in proximity, but according to John et al. (1985) the initial production of C-bands could occur by sequence amplification. Although we don't know if a non-random chromosome distribution is present in *A. iniscatus*, chromosome interactions between centromeric heterochromatic areas have been found to occur between several chromosomes at metaphase (Fig. 6). Following John et al. (1985), an alternative basis for equilocal distribution of centric heterochromatin in *A. iniscatus* could be explained by concerted amplification of the centromeric C-bands between non-homologous chromosomes.

A peculiar result of this study is the finding of a reduced 2n = 34 karyotype of the varying 2n = 40 chromosome group in *A. iniscatus*, as this species inhabits an area where all the remaining akodontine mice show the constant 2n = 52 karyotype. The latter was found in *A. andinus, A. brachiotis, A. hershkovitzi, A. illuteus, A. longipilis, A. olivaceus, A. sanborni, A. xanthorhinus*, and in species of *Geoxus* and *Chelemys* (but see Reig 1987, and Liascovich et al. 1989), all of which inhabit the southern Andes and the Patagonian tableland. Reig (1984, 1986, 1987) recently postulated that the akodontine radiation took its origin in the Puna region during Miocene times from a 2n = 52 *A. andinus*-like *Akodon* ancestor. From this area of original differentiation a chromosomally conservative phylad dispersed to the southern Andes and to Patagonia, maintaining the original 2n = 52 karyotype unaltered in a cladogenetic process which involved species of the subgenera *Akodon* and *Abrothrix* and genera such as *Chelemys, Geoxus,* and *Notiomys*. Another main dispersing branch descended from the Puna to the southeastern lowlands, presumably from a 2n = 40 *A. boliviensis*-like species, giving rise to the different species in central and northern Argentina, Paraguay, Brazil, and Uruguay. Regarding the origin of *A. iniscatus* and the related (and now considered co-specific) Neuquenian form *A. nucus*. Two alternative hypothesis were postulated by Reig (1987): both forms may have derived from the southern Andean branch or from the southeastern lowland one. Reig inclined himself

Fig. 6. Chromosome interactions between centromeric heterochromatin in *A. iniscatus*

toward the second alternative in view of the greater morphological similarities of these forms with *A. puer* and *A. azarae*. The results presented here indicating a high chromosomal similarity between *A. iniscatus* and *A. puer* are consistent with the latter hypothesis.

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Resumen

Comparación de patrones de bandeo entre Akodon iniscatus y Akodon puer (Rodentia, Cricetidae)

Se describen los cromosomas de *Akodon iniscatus* (2n = 33–34, NF = 42) y se comparan con el cariotipo de *A. puer* (2n = 34, NF = 40). Se estudian los patrones de bandeo C, G y fluorescentes (Q y CMA) de 37 ejemplares de *A. iniscatus* y 11 de *A. puer*. *A. iniscatus* presenta heterocromatina localizada principalmente en la región centromérica, la cual está ausente en *A. puer* y es poco frecuente en otros akodontinos. Las bandas de cromomicina revelan que la heterocromatina de la región centromérica de todos los cromosomas es homogénea y pobre en GC, mientras que la heterocromatina telomérica es rica en GC. Ambas especies comparten brazos cromosómicos y cromosomas completos, siendo 38 los brazos en los que se encuentra el mismo patrón de bandas G. Estos resultados apoyan la hipótesis de una cercana relación entre *A. iniscatus* y *A. puer* y sugieren que la primera probablemente deriva de un stock akodontino que originalmente se diferenció en las tierras bajas del noreste de Argentina. Por lo tanto, *A. iniscatus* estaría relacionada con el grupo de especies de *Akodon* de alrededor de 40 cromosomas.

Zusammenfassung

Vergleiche von Bandenmustern zwischen Akodon iniscatus und Akodon puer (Rodentia, Cricetidae)

Der Karyotyp von *Akodon iniscatus* (2n = 33–34, FN = 42) wird erstmals beschrieben und mit dem von *A. puer* (2n = 34, FN = 40) verglichen. Dazu wurden die C-, G- und Fluoreszenzbandenmuster

(Q, CMA) von 37 *A. iniscatus* und 11 *A. puer* untersucht. Eine Reihe ganzer Chromosomen und 38 Chromosomenarme besitzen bei beiden Arten gleiche G-Bandenmuster. Im Gegensatz zu *A. puer* und den meisten *Akodon*-Arten besitzt *A. iniscatus* auffälliges Heterochromatin in der Zentromeren-Region. Die CMA-Färbung zeigt, daß das Heterochromatin der Zentromeren-Region arm an den Basen CG ist, wogegen das telomerische Heterochromatin deren viele enthält. Der Vergleich der Chromosomen spricht insgesamt für eine enge Verwandtschaft von *A. iniscatus* und *A. puer*. *A. iniscatus* hat sich wahrscheinlich in tiefgelegenen Gebieten im Nordwesten Argentiniens differenziert und ist innerhalb von *Akodon* der Artengruppe mit etwa 40 Chromosomen zuzuordnen.

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Female-female mounting in the European rabbit

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Abstract

Mounting behaviour between adult females (FFM) was observed in experimental groups of previously unfamiliar female rabbits, housed in outdoor enclosures. Observations covered two periods: 1. the 1st week, when social organization was gradually being established (Phase 1), and 2. the 2nd and 3rd weeks, when social structure and dominance hierarchy were fully settled. FFM was more frequent in Phase 1 than in Phase 2, and was positively correlated with aggression (AG) in both Phases. Although the more aggressive females were higher in rank than less aggressive ones, no link was found between FFM and rank. The correlation between FFM and AG might thus depend on the fact that more aggressive females participated more in all forms of social interactions, including FFM. Analysis of dyads in Phase 2 revealed that the mounting females were usually dominant over the mountees. The frequent occurrence of FFM in unfamiliar rabbits suggests that it plays some role in the organization of social structures, although it does not seem to contribute directly to the establishment of dominance hierarchy. In addition, results indicate that once the rabbits are familiar with each other, FFM influences the dominance/subordination relationship, possibly by contributing to its maintenance and consolidation. Finally, the performance of FFM seems to be affected by contingent social conditions rather than by individual tendencies.

Introduction

Mounting between conspecific females (female-female mounting: FFM) has been reported in several mammals (see Dagg 1984 for an extensive review). Similar to the mounting of males by females, FFM has mainly been observed during the breeding season (Japanese macaques in particular, Hanby and Brown 1974; Wolfe 1976; Fedigan and Gouzoules 1978; Gouzoules and Goy 1983), and in oestrous females (Dagg 1984; see also Young 1961 on several species; Fedigan and Gouzoules 1978 on Japanese macaques; Fulkerson et al. 1983 in cattle). However, FFM has also been reported in non-reproductive and, more specifically, non-sexual contexts. Mounting behaviour is known to occur in anoestrous females in rabbits (Yaschine et al. 1967), in dogs and some ungulates (Dagg 1984), and in rats (Beach and Rasquin 1942).

In oestrous females, FFM has generally been considered to be an aspect of female sexual behaviour (Fedigan and Gouzoules 1978), possibly due to "sexual excitement" (Hammond 1925, p. 70; Dagg 1984, p. 177). Unfortunately, this explanation sounds rather vague and says little about the causation and function of this behaviour.

Outside the sexual context, a link between FFM and aggression can be inferred from Bernstein and Mason's (1963) observations of the high rate of FFM and aggressive behaviours during the formation of a social group in Japanese macaques. FFM has also been reported to occasionally occur during aggressive interactions between unfamiliar rabbits (Mykytowycz and Hesterman 1973).

In primates (where FFM has probably been best studied) FFM has been suggested to favour the development of affinitive relationships between unrelated females (Gouzoules and Goy 1983). Indeed, Fairbanks et al. (1977), working on rhesus monkeys, found that pairs of reciprocally mounting females consistently formed aggressive alliances against other females.

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Still in primates, an apparent correlation between FFM and social dominance has been found repeatedly (Hinde and Rowell 1962; Poirier 1970; Doyle 1974; Poirier and Smith 1974; Seyfarth 1976; Stammbach 1978).

Obviously, the function of FFM and its proximate causes may differ widely from species to species. Nevertheless, although the information on FFM at hand is fragmentary and at times even contradictory, it does seem possible that this behaviour may affect the formation and nature of social relationships between females.

In order to explore this possibility, we recorded the occurrence of FFM in groups of female domestic rabbits. Groups were formed experimentally from initially unfamiliar females. We expected FFM to be more frequent during the gradual organization of social structure and the reciprocal familiarization of the animals than later, when stable social structure had been fully established.

The correlation between FFM and aggression was also investigated. Finally, since social organization in female rabbits is characterized by a uni-sexual dominance hierarchy (Myers and Poole 1961), the possible relationship between FFM and individual rank was studied.

Materials and methods

Experimental conditions

Forty four female domestic rabbits *(Oryctolagus cuniculus L.)* were used, which came from a non-inbred stock supplied by a local breeder. From birth to weaning, they had lived in cages with their mothers and litter-mates; at weaning, about 60 days after they were born, mothers and male litter-mates were removed. The study was started when the animals were approximately 100 days old; they were divided into 11 groups of four, including each unfamiliar subjects from four different litters, with similar body weight (mean weight 2.816 ± 307 g). Each group was housed in an outdoor enclosure (4 × 4 m) with food and water ad libitum.

Procedure

Preliminary observations had revealed that when unfamiliar female rabbits are put into an unfamiliar environment, a brief period (usually two to three days) of intense activity, characterized by frequent agonistic interactions, is followed by a long lasting phase of low activity and apparently relaxed social interactions. Accordingly, observations focused on two distinct phases of behavioural organization:

1. Phase 1 – an initial phase with unfamiliar animals (the females selected to form a group) newly introduced into an unfamiliar environment (the enclosure). Phase 1 observations began immediatly after the animals were introduced into the enclosure (day 1) and continued up to the fourth day, when social organization appeared fully established.
2. Phase 2 – the following phase, when the animals were fully familiar with their group-mates and environment. Phase 2 observations took place during the second and third week of the animal's stay in the enclosure (days 8–10 and 21–23), when social organization appeared mostly stable.

Observations were carried out at dawn and dusk, when rabbits are known to be most active (Mykytowycz and Rowley 1958). In Phase 1, each group was observed for about one hour a day (mean daily observation time per group 65.5 min.). In Phase 2, each group was observed for a shorter period (mean daily observation time per group 43.4 min.), but for a greater number of days.

Behavioural items

For the purposes of this paper, female-female mounting (FFM), aggression (AG) and social activity (SA) were taken into consideration.

FFM includes mounting (clinging to the back of a conspecific with the forelegs and performing a series of pelvic thrusts) and attempts to mount (any attempt at mounting, which ended in failure to clasp the conspecific, usually because it moved away). These behaviours have already been described in female rabbits by Hammond (1925), Brooks (1938), Beyer et al. (1964) and Palka and Sawyer (1966), and by "cinematographic analysis". They were indistinguishable from the equivalent male behaviours (Yaschine et al. 1967).

AG includes chasing, biting group-mates and hitting them with the hindlegs ("ripping" in Mykytowycz and Hesterman 1973; see also Grant and Mackintosh 1963; Farabollini 1987).

SA includes attending (orienting head, ears or whole body towards a conspecific); approaching

(moving towards a conspecific); nose-to-nose contact (touching the nose of a conspecific with nose); investigating (sniffing a conspecific's body); allo-grooming (grooming a conspecific); leaving (breaking contact with a conspecific by quietly moving away; see GRANT and MACKINTOSH 1963).

As the animals could be recognized individually by the colour patterns on their fur, both the subject and the object of behaviours were recorded.

Every occurrence of each behaviour (ALTMANN 1974) was recorded on an EPSON microcomputer. The durations of the behaviours here in concern were too short to allow reliable recording. Consequently, we used frequency measures for statistical analysis.

Dominance hierarchy

The dominance or subordination of each individual in the dyadic relationship with each of its groupmates was assessed by computing a "subordination index (I)". Given two females, A and B, the subordination index of A in her relationship to B is computed as follows:

$$I_{A,B} = FL_{A,B}/AP_{B,A} \qquad (1)$$

where $I_{A,B}$ is the subordination index of A in her relationship with B; $FL_{A,B}$ is the frequency of A's fleeing away from B; $AP_{B,A}$ is the frequency of B's approaching A. The higher the index, the higher the frequency with which A flees from B as B approaches. If the index of A is higher than that of B, then A is considered to be subordinate to B, and B is regarded as dominant over A (see for instance BERNSTEIN and SHARPE 1966).

The individual subordination index allowed us to assess the directionality of each dyadic dominance/subordination relationship between members of a given group. Hence, individuals could be ranked according to the number and identity of their subordinates, the top-ranking individual having the highest number of subordinates and the bottom-ranking individual none at all. To give an example, in group 4, Phase 1, female B was found to be dominant over females A, C and D; female D dominant over females A and C, female A over female C, and female C over none. The females were ranked accordingly in descending order B, D, A, C.

The linearity of dominance hierarchies was assessed using the Landau's index (h) for linearity (LEHNER 1979). Hereafter, whenever the females could be ranked in a linear order, they will be referred to as alpha (top-ranking female), beta (second), gamma (third) and omega (lowest in rank).

Dominance hierarchies were assessed separately for Phase 1 and Phase 2. They were also assessed a third time by further observations beginning seven days after Phase 2 had ended (ALBONETTI 1987). This third period of observation will be referred to as Phase 3. Its relevance for the purpose of this paper is solely concerned with the evaluation of concordance between hierarchies assessed at different times (see below).

Data analysis

Correlation between behaviours

The correlation between FFM, AG and SA in each Phase was assessed by computing the Spearman's correlation index (SIEGEL 1956).

Comparison between Phases

The frequencies of FFM, AG and SA respectively in Phase 1 and Phase 2 were compared by the two-tailed Wilcoxon matched-pairs signed rank test (SIEGEL 1956).

Concordance between dominance hierarchies

The concordance between hierarchies in Phase 1, 2 and 3 was evaluated as follows:

Step 1. The animals and ranks in each group were each assigned a number from 1 to 4 (animal A = 1, animal D = 4; alpha = 1, omega = 4) for all three Phases. Taking group 4, Phase 1, again as an example, this gives:

animal	rank
B (2)	alpha (1)
D (4)	beta (2)
A (1)	gamma (3)
C (3)	omega (4)

Step 2. For each group in each Phase, the Spearman correlation index was computed between the numbers assigned to the animals and the numbers assigned to rank, giving a series of 11 correlation indices for each Phase (one for each group).

Step 3. The Spearman correlation index was computed between the series of correlation indices for Phases 1 and 2, and those for Phases 2 and 3.

Comparison between ranks

The difference among behavioural frequencies recorded for individuals of different rank was evaluated by Friedman's non-parametric analysis of variance (Siegel 1956). This analysis was carried out separatedly for FFM and AG; for Phase 1 and Phase 2; for individuals who performed (i.e., who were subject of) the behaviours and individuals who received (i.e., who were object of) them. Whenever a significant difference was found, ranks were compared using the two-tailed Wilcoxon signed rank test.

Finally, hierarchial relationships between subjects and objects of FFM were analyzed in detail. The Chi-square and two-tailed Binomial test (Siegel 1956) were used.

Results

Total observation times for each group and Phase are given in Table 1.

Correlation between behavioural items

A significant correlation was found between FFM, AG and SA in both Phases 1 and 2 (see Table 2 for significances).

Table 1. **Observation time per group per phase**

Group	Observation time Phase 1	Phase 2
1	161 min.	263 min.
2	240 min.	376 min.
3	161 min.	264 min.
4	204 min.	252 min.
5	157 min.	258 min.
6	222 min.	374 min.
7	167 min.	245 min.
8	175 min.	258 min.
9	189 min.	279 min.
10	310 min.	353 min.
11	178 min.	261 min.
total	2.164 min.	3.183 min.

Table 2. **Correlation between female-female mounting (FFM), aggression (AG) and social activity (SA)**

		ϱ_s	P	N
Phase 1	FFM vs AG	.296	= .05	44
	FFM vs SA	.482	< .001	44
	AG vs SA	.535	< .001	44
Phase 2	FFM vs AG	.360	< .02	44
	FFM vs SA	.309	< .05	44
	AG vs SA	.298	< .05	44

Comparison between Phases

FFM, AG and SA resulted significantly more frequent in Phase 1 than in Phase 2 (FFM, P = .044; AG, P < .001; SA, P < .001; Table 3).

Table 3. **Female-female mounting (FFM), aggression (AG) and social activity (SA): comparison between Phases**

		mean frequency acts/hour (N = 44)	Wilcoxon T	N	P
FFM	Phase 1:	.579	115	28	= .044
	Phase 2:	.303			
AG	Phase 1:	2.086	94	37	< .001
	Phase 2:	.358			
SA	Phase 1:	16.062	216	44	< .001
	Phase 2:	12.246			

Dominance hierarchy

The mean Landau's index for linearity of dominance hierarchy (h) per group was .963 in Phase 1 and .927 in Phase 2. As the lowest linearity threshold is h = .900 (LEHNER 1979), the dominance hierarchies may be regarded as linear.

A significant correlation was found between the dominance hierarchies in Phase 1 and Phase 2 (ϱ_s = .695, N = 11, P < .05) and in Phase 2 and Phase 3 (ϱ_s = 0.88, N = 11, P < .01).

Comparison between ranks

Individuals of different rank performed and received FFM with similar frequencies in either Phase (Table 4 and Fig. 1)

Individuals of different rank performed and received AG with significantly different frequencies (.02 < P < .01 and P < .05 respectively) in Phase 1, but not in Phase 2 (Table 5 and Fig. 2).

In Phase 1, AG was performed significantly more often by alpha females than by gamma (.01 < P < .02) and omega (P < .01) females, and by beta females significantly more often than by omega females (P = .02). Conversely, alpha females were significantly less often the object of AG than gamma (P < .01) and omega (P < .01) females (Table 6).

Table 4. **Female-female mounting (FFM): comparison among ranks by Friedman analysis of variance**

		χ^2	df	P
Phase 1:	performed	.16	3	NS
	received	.30	3	NS
Phase 2:	performed	5.31	3	NS
	received	1.20	3	NS

The analysis of pairs involved in FFM showed that in Phase 1 the number of dyads with the dominant partner acting as the performer and the subordinate as the recipient was not significantly different from that of dyads with the subordinate as the performer. However, in Phase 2 the dominant-as-performer dyads were significantly more numerous than the other ones (P = .036; Table 7).

In both Phases 1 and 2 significantly fewer pairs were involved in reciprocal FFM (i.e., with both partners having the same probability of performing and receiving FFM) than in unidirectional FFM (with the same individual always playing the same role; Phase 1, P < .001; Phase 2, P = .008; Table 8).

Significantly fewer pairs were involved in FFM in both Phases (N = 6) than in one Phase only (N = 42; χ^2 = 27.00; df = 1; p < .001).

When dyads where the dominant partner mounted the subordinate were considered, in Phase 1 mountings resulted significantly fewer where the dominant individual ranked immediatly above the subordinate (e.g., alpha females with beta, or beta with gamma), than in other combinations (P < .001). In other words, mountings were significantly fewer between individuals of adjacent rank than between individuals less distant in hierarchy. The opposite result was obtained in Phase 2 (P = .020; Table 9).

Table 5. **Aggression (AG): comparison among ranks by Friedman analysis of variance**

		χ^2	df	P
Phase 1:	performed	10.80	3	.02 < P < .01
	received	7.98	3	P < .05
Phase 2:	performed	3.18	3	NS
	received	7.60	3	NS

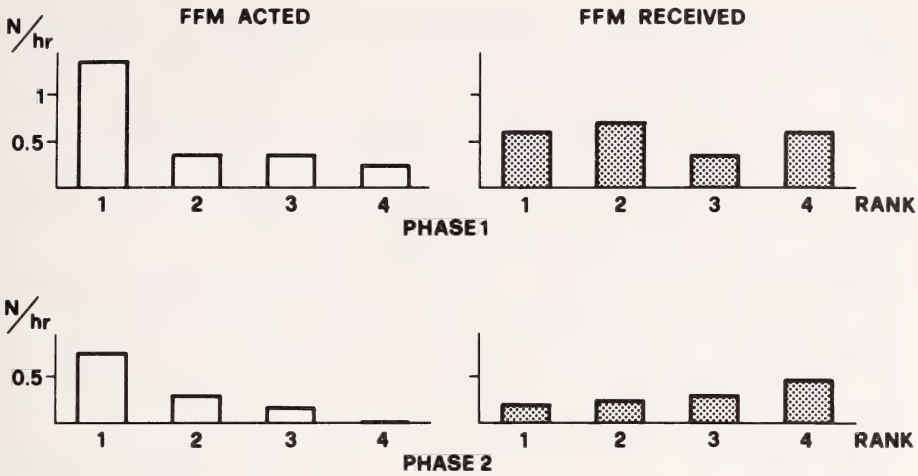

Fig. 1. Frequencies of performed and received female-female mounting (FFM) by females of different rank in Phase 1 and Phase 2 respectively.
N/h = number of acts per hour; rank 1 = alpha; rank 2 = beta; rank 3 = gamma; rank 4 = omega

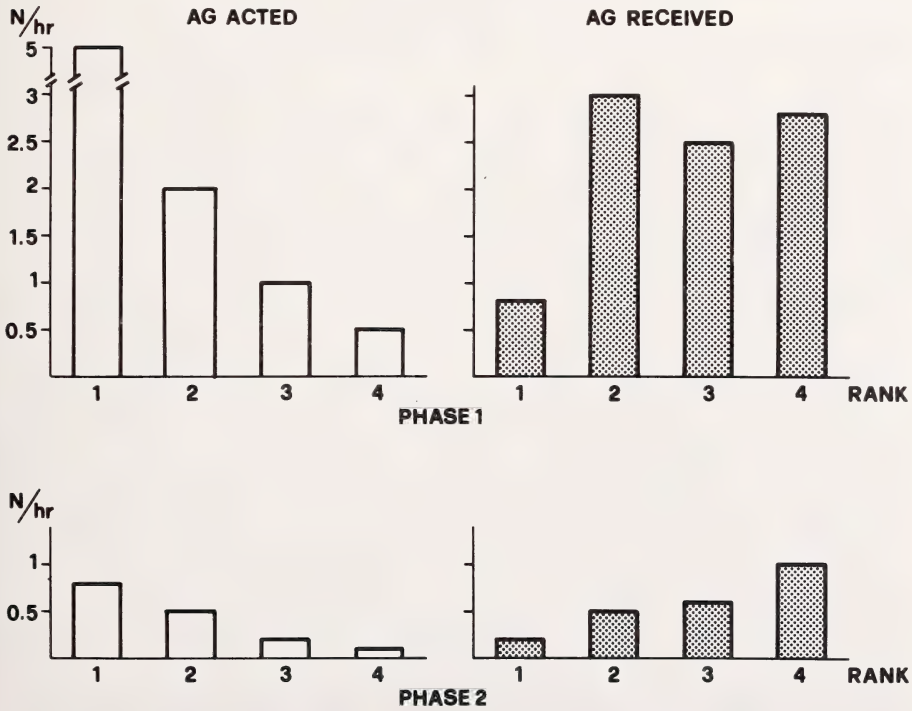

Fig. 2. Frequencies of performed and received aggression (AG) by females of different rank in Phase 1 and Phase 2 respectively. Further details as in Fig. 1

Finally, in Phase 1, 47.57 % of recorded FFMs was performed by the same individual (group 8 alpha female); 89.79 % of her mounting activity was directed towards the gamma female.

Table 6. **Phase 1, Aggression (AG): comparison between pairs of ranks**

pairs of ranks	Wilcoxon T	N	P	
		AG Performed		
alpha, beta	18	9	NS	
alpha, gamma	4	10	$.01 < P < .02$	alpha > gamma
alpha, omega	0	9	$< .01$	alpha > omega
beta, gamma	15	10	NS	
beta, omega	3	9	$= .02$	beta > omega
gamma, omega	17	11	NS	
		AG Received		
alpha, beta	10	9	NS	
alpha, gamma	0	9	$< .01$	alpha > gamma
alpha, omega	1	10	$< .01$	alpha > omega
beta, gamma	17	8	NS	
beta, omega	22	10	NS	
gamma, omega	11	10	NS	

Table 7. **Numbers of pairs with the dominant partner mounting the subordinate and vice versa**

	mounting partner: dominant	subordinate	
Phase 1	16	17	$\chi^2 = .03$ df = 1 NS
Phase 2	12	3	Binomial test, p = .036

Table 8. **Numbers of pairs involved in reciprocal and uni-directional female-female mountings (FFM)**

FFM:	reciprocal	uni-directional	
Phase 1	5	28	$\chi^2 = 16.03$ df = 1 $p < .001$
Phase 2	2	13	Binomial test, p = .008

Table 9. **Numbers of mountings directed by dominant individuals towards subordinate ones**

pairs of individuals with:	adjacent rank	non-adjacent rank	χ^2	df	
Phase 1	21	53	13.83	1	$p < .001$
Phase 2	39	21	5.40	1	$p = .020$

Discussion

The above findings provide new evidence on female-female mounting (FFM) occurring in the domestic rabbit even outside the breeding season. Under our experimental conditions, FFM was observed even though no males, or male cues of any kind, were present which could possibly favour the onset of reproductive activities (Bronson 1974; Cheal 1975).

A positive correlation was found between FFM and aggression (AG) during the establishment of social structure in groups of initially unfamiliar females (Phase 1) and under stable social conditions (Phase 2). This correlation was more stringent in Phase 2 than in Phase 1.

Both FFM and AG were more frequent in Phase 1 than in Phase 2; the dramatic fall in AG in Phase 2 is particularly evident (Table 3 and Fig. 1).

A significant correlation was found between the dominance hierarchies in Phases 1 and 2, and in Phases 2 and 3. As a higher correlation index resulted between Phases 2 and 3 than between Phases 1 and 2, hierarchies were in better agreement in Phases 2 and 3 than in Phases 1 and 2. This suggested that changes in rank occurred between Phase 1 and 2, but not (or only in a minority of cases) between Phase 2 and 3. Therefore, hierarchies in Phase 2 were regarded as definitive, and animals were ranked according to them.

In Phase 1, females of different rank performed FFM with similar frequencies. However, the females which succeded in gaining the top ranks performed AG more frequently than lower ranking individuals. This result cannot be a mere by-product of the methods used to assess dominance hierarchies, since behaviours other than aggression were taken into account for this purpose.

In Phase 2, neither the frequencies of FFM or AG were dependent upon rank.

The positive correlation between FFM and AG and the higher frequency of these behaviours in Phase 1 than in Phase 2 suggest that they must be linked by a relationship (causal, functional, or both). However, similarities between FFM and AG go no further: in Phase 1, only the distribution of AG is affected by rank, not that of FFM.

The higher frequencies of AG in high-ranking females suggest that AG plays a role in the acquisition of social dominance. The marked fall in AG once the dominance hierarchy has been firmly settled (Phase 2) supports this hypothesis.

Contrary to AG, FFM does not seem to play a role in dominance acquisition, as no obvious relationship appears to exist between FFM and dominance hierarchy. It should be noted, however, that the opposite is true for male rabbits (Farabollini 1987). In her study on four-male groups, the author reports frequent intra-sexual mountings by the dominant buck only.

Any possible connection between FFM and AG, suggested by their correlation and similar distribution in Phases 1 and 2, could simply depend on the fact that aggressive individuals generally tend to participate more in social interactions (agonistic and non-agonistic) than less aggressive ones (and vice versa). Indeed, FFM and AG were both highly correlated with social activity (SA), a large behavioural category including a number of different social, non-agonistic behaviours. In this respect, FFM could be seen as a social, presumably non-agonistic behaviour, whose correlation with AG depends on individuals being more or less interactive independently from the kind of social interaction itself. This hypothesis could also explain the different distribution of FFM in the two phases: its higher frequency in Phase 1 could depend on the fact that all social behaviours (including FFM and AG) are more frequent when the rabbits are familiarizing with each other and are building their social structures. Although FFM may not serve any specific function in the establishment of the dominance hierarchy, it can still provide information about conspecifics, e.g. through assessment of the reaction to approach and close physical contact, or detection of chemical signals, and thus act as a preliminary to more decisive interactions.

However, it would be premature at this stage to dismiss Bernstein and Mason's (1963) suggestion that FFM could simply be a behavioural consequence of "arousal due to novel situation" (p. 30), and that it serves no particular function in group formation.

If FFM does play a role in the familiarization with conspecifics, what possible function could it have in Phase 2, when the animals are fully familiar with each other? In other words, why is there no dramatic fall in FFM as there is in AG in Phase 2?

Since the establishment of rank order within the group did not seem to provide the

answer to the problem of the function of FFM, attention was focused on the partners involved in FFM, and the dominance/subordination relationship between them was investigated. The directionality of diadic dominance relationships did not appear to influence FFM in Phase 1, when the process of dominance acquisition in diadic relationships themselves was taking place. In Phase 2, however, once dominance was apparently fully established, the mounting female was usually dominant over the mountee. This suggests that, under stable social conditions, FFM could be aimed at confirming and consolidating dominance in diadic relationships. It must be stressed that FFM need not necessarily have the same functional significance, if any, during the development of social organization and under stable social conditions.

As an additional comment, one of the females (A8) performed FFM extremely frequently in Phase 1. This observation seems to support Hanby and Brown's (1974) suggestion that FFM can represent an individual peculiarity (see also Yaschine et al. 1967). In this instance, however, as A8 almost always mounted one and the same groupmate (C8), FFM seemed to be a characteristic of a given diadic relationship rather than of a given individual. In Phase 2, A8 did not show any behavioural peculiarity. This observation, together with the fact that the same individuals rarely performed FFM in both Phases 1 and 2, suggests that the tendency to engage in FFM is influenced more by the social context than by individual propensities.

Reciprocal FFM ist extremely rare, which indicates the uni-directional nature of this behaviour in female rabbits and supports the hypothesis of a link between FFM and dominance in diadic relationships. On the other hand, FFM never appears to have an affiliative function by strengthening social bonds between two reciprocally mounting females, as seems to be the case in some Primates (Fairbanks et al. 1977; Gouzoules and Goy 1983).

As a final point, since rabbits are reported to ovulate as a result of mounting and even in the absence of intromission (Hammond 1925; Fee and Parkes 1930), FFM might cause ovulation in the mounted female. Infertile ovulation is usually followed by pseudopregnancy (Hammond 1925) and consequently the mounted female could suffer prolonged delay in reproduction. FFM could thus decrease reproductive success in conspecific females, and be one of the possible determinants of differential reproductive success in female rabbits. Further investigation is needed to clarify the actual effectiveness of female mounting as a stimulus inducing ovulation, and to evaluate the neuro-endocrinal consequences of this behaviour in the mounting and the mounted female.

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Zusammenfassung

Aufreitversuche zwischen weiblichen europäischen Kaninchen

Die vorliegende Verhaltensstudie befaßt sich mit Aufreitversuchen zwischen weiblichen Kaninchen (female-female mounting = FFM). Zum Zweck unseres Experimentes wurden Versuchsgruppen von weiblichen, untereinander fremden Kaninchen in einem Freigelände eingesperrt und über zwei Zeiträume hin beobachtet: 1) während der ersten Woche nach der Einsperrung, als sich so langsam eine Sozialordnung herauskristallisierte (Phase 1) und 2) während der zweiten und dritten Woche, als die Sozialordnung und die Hierarchie feststanden. Während Phase 1 konnten mehr FFM beobachtet werden als in Phase 2, wobei FFM in beiden Phasen mit Aggression (AG) verbunden war. Vom hierarchischen Standpunkt her kann davon ausgegangen werden, daß die aggressiveren Weibchen die ranghöheren Positionen belegen. Allerdings konnte kein direkter Zusammenhang zwischen FFM und AG festgestellt werden. Die Verbindung von FFM und AG mag allenfalls darin liegen, daß die

aggressiveren Weibchen intensiver an jeder Art von sozialer Interaktion beteiligt sind, und demnach auch an FFM. In der zweiten Phase vorgenommene Paaranalysen haben ergeben, daß die aufreitenden Weibchen gewöhnlich über die aufgerittenen Weibchen dominieren. Das häufige Auftauchen von FFM bei untereinander fremden Weibchen mag darauf hinweisen, daß FFM eine Rolle bei der Organisation der Sozialstrukturen spielt, auch wenn es wahrscheinlich keinen direkten Einfluß auf die Festlegung der Hierarchie ausübt. Unsere Beobachtungen ergeben auch, daß FFM bei Kaninchen, die sich nicht mehr fremd sind, die Über- und Unterordnung beeinflußt und sich möglicherweise auf ihre Beibehaltung und Verstärkung auswirkt. Das Auftreten von FFM scheint eher von zufälligen sozialen Voraussetzungen beeinflußt zu sein als von individuellen Tendenzen.

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WISSENSCHAFTLICHE KURZMITTEILUNG

Gray's beaked whale *Mesoplodon grayi* in the South East Pacific

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Receipt of Ms. 19. 6. 1989

A beaked whale stranded still alive at Bahía de Paracas (13° 49′ S), Peru, on 23 March 1988. Personnel of the Reserva Nacional de Paracas took photographs of the animal just after death and reported the event to the author. Unfortunately when arriving at the location three days later, the whale was already in decomposition with the genital area damaged by sea birds.

The cetacean, a 467 cm female was identified as a Gray's beaked whale *Mesoplodon grayi* von Haast, 1876 by means of external characters and confirmed afterwards by examination of the cranial features as described by Sielfeld (1979). The complete skeleton, stomach contents, the right eye and the right ovary were collected and placed in the author's private cetacean collection (No. JCR-1342). The state of the carcass made still possible some external measurements (in mm, after Norris 1961): tip of snout to angle of mouth 47.0, tip of snout to center of eye 69.0, tip of snout to blowhole 67.0, tip of snout to external ear 77.5, tip of snout to tip of dorsal fin 321.0, tip of snout to unbilicus 218.0, tip of snout to anus 355.0, height of dorsal fin 22.0, anterior length of flipper 15.0, posterior length of flipper 34.5, maximum width of flipper 15.0, fluke width 106.0, girth at axillae 224.0. The beak was long and narrow, the throat grooves well developed. The dorsal fin was placed on the posterior third of the back. The flippers were rather pointed. The rear margin of the flukes showed a convexity on its center, lacking a central notch. From the photographs of the freshly dead whale some notes on the coloration can be given. The back and sides were brownish gray, being deeper on the flippers, flukes and around the eyes. The lower flanks had a mottled appearance due to the presence of gray patches. The gray belly shows whitish areas around the umbilicus and genital area, while the beak was pure white. Scars were not evident.

Selected skull measurements (in mm, after Ross 1984) are: Condylobasal length 883, length of rostrum 608, width of rostrum 174, breadth of skull across postorbital processes of squamosals 298, zygomatic width 293, greatest span of premaxillary crest 118, greatest width of premaxillae anterior to superior nares 116, greatest length of temporal fossa 103, greatest width of temporal fossa 61, greatest condylar length of mandibular ramus 767, greatest length of mandibular symphysis 305, greatest height of mandible at coronoid process 110, greatest length of right tooth 42, greatest antero-posterior width of right tooth 57, greatest breadth of right tooth 6. The pair of mandibular teeth were unerupted in the fresh head, but in the prepared skull they were observed being triangular in shape, emerging vertical 11 mm above the alveoli and placed 47 mm behind the posterior end of the mandibular symphysis. A row of 18 small teeth was present on each side of the upper jaw, a constant character of *M. grayi* (von Haast 1876; Boschma 1950; Robson 1975; Sielfeld 1979). Most of these maxillary teeth were worn, revealing that they were functional. The mesorostral canal was filled by the vomer in 25 % of its length. Proximally the vomer reached the level of the premaxillaries, decreasing towards the distal end. The

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pulp cavity of the teeth was completely occluded and the vertebral epiphyses fused to the centra. Both conditions indicate that the whale had reached physical maturity. The vertebral formula was C7, T10, L12, Ca19 = 48. Seven of the 10 pairs of ribs had capitular and tubercular attachments.

The right ovary weighed 10 g and did not bear any ovarian corpora; the left ovary was lost. The left uterine horn was dilated and its endometrium strongly vascularized, carrying a foetus of an estimated length of 50 cm. This foetus was already decomposed and only some bones, including the lower jaw with the corresponding tooth, were collected (JCR-1343). The stomach was empty except for the presence of four very digested squid beaks. No ectoparasites were observed. A cyst of the cestode *Phyllobothrium delphini* was found in the blubber around the anus.

Gray's beaked whale is considered to have a circumpolar distribution in the southern hemisphere between 30° S and 45° S (Ross 1984). This range includes the western south Pacific, western south Atlantic and the Indian ocean (Gaskin 1968; Leatherwood and Reeves 1983; Lichter 1986). The species has also been recorded as far south as Patagonia and Tierra del Fuego (Goodall 1978; Sielfeld 1979, 1980; Delhon et al. 1987). For the South East Pacific there are no consistent records. Mann (1957) cited the species for Chilean waters but he did not indicate either locality or specimen, although he probably referred to the account of Bini (1951) who reported a *Mesoplodon* sp. caught by fishermen off Iquique (20° 10′ S). The tentative identification of this specimen as *M. grayi* by Hershkovitz (1966) is unreliable, since all existing evidence are photographs of a young female. Females and juveniles of *Mesoplodon* are difficult to identify to species by external characters only. Another beaked whale stranded at Paracas in 1955 is probably a record of Andrew's beaked whale, *M. bowdoini.* The extensive scarring observed in the existing photographs placed this specimen in the complex *stejnegeri – carlhubbsi – bowdoini,* featuring relatively short beaks and massive teeth, characters which have been related to social behavior (Heyning 1984). Two sightings of an unidentified species of *Mesoplodon* off the northern Peruvian coast were reported by Pitman et al. (1987). These authors described the beak of the whales sighted as "moderately long, appearing similar in size to that of *M. densirostris*". Posteriorly Pitman (pers. communication) concluded that the whales he observed were not Gray's beaked whales.

From the foregoing review it is evident that the Peruvian specimen reported here is the first confirmed record of *Mesoplodon grayi* from the South East Pacific. The stranding location, Bahía de Paracas (13° 49′ S) is the northernmost known for the species in the southern hemisphere.

Acknowledgements

Julio Arenas and Carlos Obando (Reserva Nacional de Paracas) reported the stranding, provided the photographs and helped in many ways during the collection of the present specimen. Robert L. Pitman supplied information on his observations of beaked whales in the eastern tropical Pacific. James G. Mead and Koen Van Waerebeek made valuable suggestions on the manuscript. Moreover, J. G. Mead provided photographs of the beaked whale stranded in 1955.

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BUCHBESPRECHUNGEN

THENIUS, E.: **Zähne und Gebiß der Säugetiere.** Handbuch der Zoologie Bd. VIII Mammalia, Teilbd. 56. Berlin, New York: De Gruyter 1989. 513 pp., 830 Abb., 826,– DM. ISBN 3-11-010993-X

Die Zähne der Säugetiere haben durch ihre makromorphologische Ausprägung und durch die artkonstante Anzahl und Zuordnung im Gebiß als Merkmalskomplex u. a. traditionell eine große Bedeutung für systematische und taxonomische Fragestellungen und für Bewertungen von Homologien und Analogien. Bedingt durch die Fossilisierbarkeit dieser Hartsubstanzen werden über vergleichende Analysen Einsichten in den evolutiven Wandel und die radiative Entfaltung von fossilen zu rezenten Formen innerhalb von Stammesreihen besonders ermöglicht. Das vorliegende Werk, von dem ausgewiesenen Palaeontologen ERICH THENIUS verfaßt, stellt eine moderne Zusammenfassung über diese Thematik dar. Es ist in einen allgemeinen und einen speziellen Teil gegliedert. Zunächst werden behandelt: Allgemeine Morphologie, Benennung, Orientierung der Zähne; Gliederung des Gebisses, Zahnwechsel; Zahnkategorien der permanenten Dentition; lacteale Dentition; Höckerterminologie der Molaren; Gebiß als funktionelle Einheit, Abkauung; Theorien zur Zahnentstehung; Altersbestimmung; Geschlechtsunterschiede. Im weitaus umfangreicheren zweiten Teil wird auf die Situation zunächst bei Monotremen und mesozoischen Säugern eingegangen, dann auf die bei den Marsupialia inklusive der Fossilformen aus Nearctis und Neotropis. Schließlich werden die fossilen und rezenten placentalen Säugetiere in den verschiedenen Ordnungen (auch ausschließlich fossile) als einzelne Kapitel abgehandelt. Eine tabellarische Übersicht über die Zahnformeln der besprochenen Formen, ein Literaturverzeichnis mit 1305 Zitaten und ein Register beschließen den Band.

Insgesamt ist eine überaus große Fülle von Informationen zusammengefaßt und übersichtlich dargestellt. Die Formulierungen im Text sind, für den Autoren kennzeichnend, knapp und treffend sowie verständlich und flüssig. Ferner beeindrucken ungewöhnlich zahlreiche fotografische und zeichnerische Abbildungen. Es gibt in neuerer Zeit nur wenige derartig erschöpfend informierende und gelungene Zusammenstellungen von Einzelautoren über umfangreichere Stoffgebiete. Dieses Werk, dem sich der Autor seit 1982 gewidmet hat, ist eine dieser wenigen Ausnahmen. Es stellt eine umfassende und kompetente Bearbeitung der Thematik dar. Es ist für die Säugetierkunde von fundamentaler Bedeutung. Ohne Zweifel wird es für lange Zeit als Standardwerk und Bezugsquelle dienen.

D. KRUSKA, Kiel

TYNDALE-BISCOE, C. H.; JANSSENS, P. A. (eds.): **The Developing Marsupial.** Models for Biomedical Research. 1988. Berlin, Heidelberg: Springer Verlag. 102 figs., 245 pp. DM 198,–. ISBN 3-540-19047-3

This volume documents the exponential increase over the last two decades of investigations concerned with the embryology of marsupial pouch young, and emphasizes the scientific importance of these investigations for a general understanding of ontogenetic development in mammals. In addition, the value of marsupials for the experimental investigation of mammalian development is demonstrated, especially due to the increasing difficulties in organizing experiments with eutherians. Most of the developmental processes, which occur in eutherians in the uterus, can be investigated in pouch young.

The idea for this publication originated from a 1986 Australian conference on "Lactation and the physiological development of the young marsupial". The extensively revised contributions of this symposium make up the 15 chapters of this book, which include: 1) Introduction, 2) Structural adaptation of the newborn marsupial, 3) Patterns of growth, 4) The composition of marsupial milk, 5) Hormonal control of lactation, 6) Control of milk protein synthesis in *Macropus eugenii,* 7) Growth of the brain, 8) Differentiation of the neocortex, 9) Development of the primary visual pathway, 10) Development of the cardiorespiratory system, 11) Metabolism and development of endothermy, 12) Changes in nutritional metabolism during weaning, 13) Development of renal function, 14) Immunological development, 15) Sexual development in pouch young. The presented observations were principally taken from four species bred in self-sustaining colonies: the fat-tailed dunnart, *Sminthopsis crassicaudata;* the gray short-tailed opossum, *Monodelphis domestica;* the tammar wallaby, *Macropus eugenii;* and the red-necked wallaby, *Macropus rufogriseus.* Additional data originated from: Virginian opossum, *Didelphis virginiana;* short-nosed bandicoot, *Isoodon macrourus;* brush-tailed possum, *Trichosurus vulpecula;* and quokka, *Setonix brachyurus.*

In the Introduction the editors point out that the old concept of marsupial development, which stressed that longer gestation periods were not possible due to insufficiencies of the uterus, placenta and hormonal control, has been experimentally rejected. Marsupials do indeed possess the ability for extended periods of gestation, but as alternative have developed during phylogeny a highly elaborate process of lactation. It is differentiated into three phases each characterised by a different composition

of the milk appropriate to the development of the suckling: In certain species of kangaroo with two simultaneous offspring of different ages sucking at adjacent teats the composition of the milk secreted by each gland is different and is appropriate to the age of the young. The comprehensive discussion of the patterns of growth of pouch young, composition of the milk and the hormonal control of milk secretion and composition is one of the main highlights of this volume. Moreover, the discussion possesses a rich source of current and biologically important data. A further topic of interest is the development of the brain, especially of the neocortex and visual pathway. The physiological development of metabolism, endothermy and the function of the cardio-respiratory and excretory systems are well documented. The stimulating reading of the various contributions demonstrates the large number of unanswered questiions in this field of research which may well lead to future research programs and new investigations in an effort to solve certain of these problems. Moreover, it presents a new and differentiated view of mammalian ontogenetic development and the different phylogenetic strategies that have been followed by metatherians and eutherians.

This book is indispensable to all investigators of developmental problems in vertebrates, especially in homeotherms. 29 pages of reference make it a valuable source of literature. Unfortunately, the relative high price is one obstacle for its potential distribution. H.-R. Duncker, Gießen

Jerison, H. J.; Jerison, I. (eds.): **Intelligence and evolutionary biology.** Nato ASI Series Ecological Sciences G 17. Berlin – Heidelberg – New York – London – Paris – Tokyo – Hong Kong: Springer 1988. 481 pp., 103 figs. DM 198,–. ISBN 3-540-16085-X

Der vorliegende Sammelband enthält 24 Beiträge (26 Autoren) verschiedener Disziplinen von der Philosophie, Psychologie bis zur Neurobiologie, Morphologie und Ethologie. Das Unternehmen ist als Versuch gedacht, auf breitester Basis zur Frage der naturwissenschaftlichen Grundlagen der Intelligenz beizutragen. Die Lektüre des Bandes ist bei der Heterogenität der Beiträge mühsam, zumal die redaktionelle Anordnung kaum eine Gruppierung nach Sachproblemen erkennen läßt. Eine Definition, was ist Intelligenz, wird beispielsweise erst auf Seite 279 (Beitrag Poli) versucht. Es wäre zweifellos von Vorteil gewesen, wenn der klare und inhaltsreiche Beitrag von M. D. Poli über spezies-spezifisches Lernen als Einführung in die Problematik am Anfang stehen würde. Hier sei vor allem auf die wichtigen Beiträge von Plotkin und von Hodos verwiesen. Plotkin unterstreicht die Bedeutung mehrerer hierarchischer Prozesse (genetisch, epigenetisch, individuelles Lernen, soziokulturelle Prozesse, die bei einer Analyse der „Intelligenz" beachtet werden müssen), betont die Komplexität des Geschehens und die Tatsache, daß Kenntnisse mindestens aus drei Niveaus der Hierarchie gewonnen werden. Hodos stellt klar, daß Intelligenz keine quantifizierbare Einheit ist, und daß Intelligenz bei verschiedenen Organismenformen nicht identisch ist. Eine universale Intelligenz, als quantifizierbares Geschehen existiert nicht und ist als Begriff nicht definierbar. Es wäre zu wünschen, daß diese Einsicht Verbreitung fände.

Für den Säugetierforscher dürften die Beiträge, die sich mit quantitativen Änderungen des Gehirns bei der Evolution befassen, von großem Interesse sein. Die Komplexität, die sich aus der funktionellen und morphologischen Gliederung des Nervensystems in Systeme hierarchischer Ordnung ergeben (Durchdringungsstruktur, Funktionswandel) werden ausdrücklich hervorgehoben. Tierische Intelligenz umfaßt zahlreiche Komponenten wie 1. Lerngeschwindigkeit, 2. Langzeitgedächtnis und dessen Nutzung, 3. Entscheidungsfähigkeit, 4. Problemlösung, 5. jede Form von Kommunikation, 6. Zählen, 7. räumliche Deutung, 8. Konzeptbildung, 9. Werkzeuggebrauch, 10. Lernen von Regeln.

Kruska gibt eine Übersicht über die Ergebnisse der Forschungen zum Thema Hirngröße/Körpergröße und Domestikationseinflüsse auf das Gehirn. Ref. bedauert, daß in der historischen Betrachtung dieses Beitrages wesentliche Autoren nicht genannt wurden. Über die „Sprache bei Säugetieren" geben Schusterman und Gisiner ein umfangreiches, kritisches Referat. Eingehend werden die Untersuchungen an Delphinen und die vergleichbaren Leistungen bei *Eumetopias* besprochen und die kognitiven Fähigkeiten und das Lernvermögen gewürdigt. Entgegen verbreiteter Meinung wird die Fähigkeit zu sprachanalogem Verhalten (Linguistik, Syntax) verneint. Bedauerlich ist, daß die Vertreter so differenter Fächer nicht zu einer Verständigung über die Terminologie von Grundbegriffen gekommen sind, so beispielsweise die Bezeichnung „functional homology" (p. 158) für eine Erscheinung, die der vergleichende Morphologe als „Analogie" benennen würde. Auf S. 120/121 werden die Homologiekriterien von Remane in wörtlicher Übersetzung aus Remane 1956 als Definition zweier Amerikaner angegeben, obgleich das Buch von Remane im Schrifttumsverzeichnis genannt ist. D. Starck, Frankfurt/M.

KRSTIĆ, R. V.: **Die Gewebe des Menschen und der Säugetiere.** Ein Atlas zum Studium für Mediziner und Biologen. 2. Aufl. Berlin, Heidelberg, New York, London, Paris, Tokyo: Springer 1988. 399 S., 190 Abb., DM 95,–. ISBN 3-540-19007-4

Dieser bewährte Atlas, der seit der 1. Auflage 1978 in mehreren Sprachen erscheint und sich wohl weltweit bewährt hat, liegt nun in einer korrigierten und aktualisierten neuen Auflage vor. Die Konzeption wurde beibehalten. In den großen Abschnitten über Epithel-, Binde- und Stütz-, Muskel- sowie Nervengewebe werden die histologischen Besonderheiten der Strukturen und Bauelemente auf zellulärer Ebene gekennzeichnet, vornehmlich in Form von beeindruckenden elektronenoptischen Blockdiagrammen. Einer Darstellung auf jeweils den rechten Buchseiten steht jeweils eine entsprechende Beschreibung der Strukturelemente auf den linken Seiten gegenüber. Ferner sind Vergrößerungsmaßstab und weiterführende Literatur angegeben. Entsprechend dem erweiterten Wissensstand sind für diese Auflage mehrere Abbildungen neu gezeichnet.

Auch diese Neuauflage kann als anschauliche zusätzliche Informationsquelle zu histologischen Lehrbüchern sehr empfohlen werden. D. KRUSKA, Kiel

DRECHSLER, H.: **Altersentwicklung und Altersansprache beim Rotwild.** Gestalten, Gesichter, Gehabe, Geweihe, Gebisse. Hamburg und Berlin: Paul Parey 1988. 133 S., 221 Abb., DM 58,–. ISBN 3-490-26512-2

Das Buch wird seinem originellen Untertitel mit den fünf „G"s voll gerecht durch subtile Beschreibung altersabhängiger und individueller Merkmale des Rothirsches und durch die nicht weniger als 72 Farbfotos von „Hirschpersönlichkeiten" mit exakter Fundbeschreibung auf 6 Seiten. Die 20 Farbfotos von Gebissen und die 43 Federzeichnungen FRITZ LAUBE's von verschiedenen Gesichtern und Gestalten des Rothirsches runden die Bilddiagnosen als die Spezialität dieses für den Jagdbetrieb wichtigen Buches ab. Die Bildergalerie läßt in bezug auf die „Frauenquote" allerdings noch zu wünschen übrig, denn sie beinhaltet nur 14 Stück „Kahlwild" gegenüber 58 „Geweihten", aber diese haben eben „was auf" und Trophäen sind nun mal das vorrangige Ziel der Rotwildjagd.

Für die Wildbiologen bedeutsam ist der Umstand, daß die Altersdiagnosen hier erstmals nicht nach Schätzungen, sondern mit Hilfe der Wildmarkierung erstellt worden sind und somit exakte Folgerungen in populationsdynamischen Fragen ermöglichen.

Der Harz, in dem der Autor durch langjährige Tätigkeit im Jagd- und Forstbetrieb seine reichen Erfahrungen für das vorliegende Werk sammeln konnte, beherbergt die nach wildbiologischen Daten bestens erfaßte Rothirschpopulation der Welt. Aus diesem reichen Fundus schöpft HARALD DRECHSLER, und dem Verlag ist zu danken, daß er das Ergebnis in einem reichhaltig ausgestatteten, sehr ansprechenden Buch zu veröffentlichen bereit war.

Nach einer kurzen Beschreibung der Markierungs- und Erhebungsmethoden bildet die Altersansprache nach Gestalt, Verhalten und Geweih den Hauptteil des Buches. Die Ontogenese des Rothirsches hat in der Jagdpraxis eine, den Spezialausdrücken in der Viehzucht vergleichbare, reichhaltige Terminologie, wie z. B. „Junge", „Heranreifende", „Reife" oder „Alte" Hirsche. Geweih und Rosenstock, sowie Abnutzung, Ersatzdentin- und Zementzonenbildung der Zähne sind altersbedingt Weiser für die Abschußplanung und werden in diesem Buch ausführlich behandelt. Zuwachsformeln der Population, „Güte"-Klassen mit „Normvarianten" und „Minusvarianten" sowie Jagdziele runden das für Altersbestimmungen im Wald und im Labor gedachte Buch ab. Die Zucht von „Rekordtrophäen"-Trägern durch Wahlabschuß wird an einer Stelle des Buches (S. 69) mit Recht abgelehnt, an anderer Stelle jedoch toleriert (S. 71) und die Eugenik „abschußwürdiger" Hirsche (S. 127) macht deutlich, daß das wildbiologische Gedankengut zwar in vielfältiger Weise Eingang in die Jagdpraxis gefunden hat, überholte „hegerische" Zielvorstellungen vergangener Zeiten in ihrer Grundtendenz aber noch gegenwärtig sind. Zu bemängeln ist schließlich das Literaturverzeichnis mit Quellenangaben wie z. B. „NIEDS, M. L., 1986: NJ Nr. 15", die einem Kreuzworträtsel gleichkommen und darüber hinaus im Text gar nicht erscheinen. Aber das mindert nicht wesentlich den Wert dieses sehr nützlichen, praxisorientierten Rothirschbuches. A. FESTETICS, Göttingen

Die Nordsee – ihre Warnsignale frühzeitig erkennen, richtig deuten und Abhilfe schaffen!

Die Nordsee ist in Gefahr. Umgeben von dichtbesiedelten und hochindustrialisierten Ländern wird sie vielfältig genutzt und als natürliches Ökosystem durch die Aktivitäten des Menschen stark beeinträchtigt. Verschmutzung, Fischerei, Schiffahrt, Küstenschutzmaßnahmen, Häfen und Industriestandorte, die Förderung von Erdöl und Erdgas, Millionen von Erholungssuchenden an den Küsten sowie militärische Übungen in Teilregionen gehören ebenso zu den Belastungsfaktoren wie die Einleitung von Schadstoffen und Düngemitteln über die Flüsse durch die im Landesinneren gelegene Industrie und Landwirtschaft. So wird die Nordsee immer mehr zum Auffangbecken von oft hochgiftigen, schwer abbaubaren und zur Anreicherung neigenden Schadstoffen. Das sind Belastungen, die kein natürliches Ökosystem auf Dauer verkraften kann. Dieses Buch mit Beiträgen von über 50 Wissenschaftlern hilft, entsprechende Warnsignale zu erkennen und richtig zu deuten. Die Autoren haben Fakten zusammengetragen und die Veränderungen in der Pflanzen- und Tierwelt sowie in den physikalischen und chemischen Bedingungen der Nordsee ausgewertet und bieten damit die notwendigen Informationen und Anregungen zur Diskussion für einen großen Interessentenkreis. Zu beziehen durch jede Buchhandlung. ★ **Warnsignale aus der Nordsee.** Wissenschaftliche Fakten. Herausgegeben von José Lozán/Walter Lenz/Eike Rachor/Burkhard Watermann/Hein von Westernhagen. 1990. 428 Seiten mit 186 Abbildungen und 54 Tabellen. Kartoniert 39,– DM

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Z. Säugetierkunde 55 (1990) 2, 73–144

Gustav Rosenberger

Die klinische Untersuchung des Rindes

3., neubearbeitete und erweiterte Auflage

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Nach dem Tode Gustav Rosenbergers übernahmen die Mitarbeiter der zweiten Auflage die Vorbereitung der Neuauflage. Dabei ist die bewährte Einteilung des Buches beibehalten, sein Inhalt aber um einige bedeutende Abschnitte, Übersichten und Abbildungen erweitert worden. Dazu wurden die im klinischen Unterricht sowie in der täglichen Patientenbetreuung gesammelten Erfahrungen der Autoren ebenso verwertet wie Informationen aus dem einschlägigen Schrifttum. Bei den Literaturangaben wurden nur solche Veröffentlichungen erwähnt, die nicht schon in der zweiten Auflage genannt worden sind.
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The domiciles, reproduction, social organisation and sex ratios of the Banana Bat *Pipistrellus nanus* (Chiroptera, Vespertilionidae) in Malawi, Central Africa

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Abstract

Investigated were the domiciles, reproduction, social organisation and sex ratios of the Banana Bat, *Pipistrellus nanus*, in Malawi. The bats were taken from furled banana leaves at fortnightly or monthly intervals from September 1984 to June 1985. The furled leaves were ephemeral domiciles lasting one to three days. A surplus of domiciles was always available. Females were monoestrus with the birth of twins in November and lactation lasted about eight weeks. The testes in males were scrotal from April to October, and attained maximal size in May. During lactation adult males roosted singly, while females with their young roosted singly or in maternity groups. Post-lactating females roosted singly or with groups of subadults and/or other post-lactating females, and the adult males continued to roost singly. In April, by which time the testes of all males have become scrotal, all bats were assumed to have reached sexual maturity and they began to live in harems (one adult male with one or more females). An equal number of males and females were born, but females outnumbered males for at least seven months of the year. The data from Malawi are compared with data from Kenya (O'Shea 1980), South Africa (Laval and Laval 1977), and elsewhere. Geographical variation in domiciles and reproduction, and the relationships between different aspects of the biology of *P. nanus*, are discussed.

Introduction

The Banana Bat, *Pipistrellus nanus* (Peters, 1852) occurs throughout Africa south of the Sahara, except in the arid zones. Throughout its range, it commonly roosts in the ephemeral furled leaves of bananas and other musaceous plants (Brosset 1966; Kingdon 1974; Laval and Laval 1977; Rosevear 1965; Verschuren 1957). Less commonly, it has been found in permanent domiciles such as thatch (O'Shea 1980; Rosevear 1965). Reproductive strategies of two kinds have been observed: aseasonal polyoestry (Anciaux de Faveaux 1972; Verschuren 1966) and seasonal monoestry (Laval and Laval 1977; O'Shea 1980). *Pipistrellus nanus* has been found singly, in pairs, in small groups and in colonies of up to 150 individuals (Laval and Laval 1977). In many parts of the geographical range, males outnumber females (O'Shea 1980; Verschuren 1957, 1966, 1982) but in South Africa adult males and females occur in equal numbers (Laval and Laval 1977).

Although many authors have described various aspects of the biology of *P. nanus*, two recent studies have concentrated on domiciles, reproduction, social organisation and sex ratios, and the relationships between them. The first study (Laval and Laval 1977) dealt with a population roosting in ephemeral furled leaves in the temperate climate of South Africa. The second (O'Shea 1980) dealt with a population roosting in permanent sites in thatch in the equatorial climate of Kenya. The present study deals with a population roosting in furled leaves at Zomba, in the southern region of Malawi. This locality has a highland tropical climate, and lies midway between Kenya and South Africa. The data

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from Kenya, Malawi and South Africa (and elsewhere) are compared to show the extent of geographical variation in some of the characteristics of *P. nanus*, and to investigate the ways in which domiciles, reproduction, social organisation and sex ratios might be interrelated.

The Study area

Malawi is located in Central Africa, from 9° 50′ S to 17° 00′ S, and from 33° 00′ E to 36° 00′ E. It lies in the southern savanna biotic zone as defined by Davis (1962). A brief description of the physiographic features and vegetation of this country is given in Happold et al. (1987) and further details are given by Pike and Rimmington (1965) and Jackson (1969).

Malawi has a hot wet season from November to early April, a cool dry season from April to July, and a hot dry season from August to October. The duration of each season varies with latitude. The mean annual rainfall is 775–2164 mm, depending on locality, with most of the rain falling between November and March. Temperature regimes range from extremely hot in the Shire Valley to cool on the high plateaux. Further information about the climate of Malawi is given by Pike and Rimmington (1965), Torrance (1972) and Malawi Government (1982).

This study was carried out principally at Zomba (15° 23′ S, 35° 19′ E; 800–900 m). This small town at the base of Zomba Plateau, has traditional and European-style buildings interspersed in a mosaic of ornamental gardens, maize and vegetable gardens, groves of bananas, plantations of exotic *Eucalyptus*, riverine forest, and *Brachystegia* woodland. Climatic data for Zomba are given in Fig. 1. The bats were collected from groves of bananas in and near Malonje Village in Zomba, and from the ornamental gardens of several colonial-style houses in the older part of Zomba. Additional data were obtained from Liwonde National Park (15° 02′ S, 35° 15′ E; 500 m) in the Upper Shire Valley, Lengwe National Park (16° 13′ S, 34° 46′ E; 100 m) in the Lower Shire Valley, and six other localities (Happold et al. 1987).

Material and methods

Banana Bats were taken from furled banana leaves, and caught in mistnets (details in Happold et al. 1987). At Zomba, the bats were taken from furled leaves in one of two ways. From September to November, the bats were collected by Malawian boys who folded the leaves to block the exit, and then took the bats out by hand. The bats were then placed in one bag and brought in for examination. From 12 December onwards, the authors and two of the boys used a 2 m long "butterfly-net" on a long pole, which was placed over each furled leaf. In this way, it was usually possible to capture all occupants of each leaf, and group compositions were recorded.

Samples were collected fortnightly from October to January (while females were pregnant or rearing young), and monthly from February to mid-June. Sample sizes were 8–45 bats. Adults were usually weighed to nearest 0.1 g (dead) or to nearest 0.5 g (live), and measured to nearest 0.5 mm. Details and results are given in Happold et al. (1987). To enable comparison with *P. nanus* from Kenya (investigated by O'Shea 1980), 43 specimens (including both sexes) were examined for the presence of tail glands (paired oval glandular structures on either side of the tail on the anterior fourth of the interfemoral membrane). Reproductive condition was assessed by abdominal palpation and by examination of the nipples and external genitalia, or by autopsy.

Results

Domiciles of *P. nanus* in Malawi

Within Malawi, *P. nanus* has been found in furled banana leaves (this study), among the curled up leaves of *Uapaca kirkiana* (B. Morris unpubl.), and two were found, singly, in deserted nests of Weaver Birds (*Ploceus* sp.) by Tarwina Kapunda and Elwin M'banga (this study).

Pipistrellus nanus was found in furled banana leaves from 1 m to about 4 m above the ground. The diameter of the entrance to leaves was 3–24 cm, and the minimum diameter at the base was approximately 3 cm. The percentage occupancy of leaves having different entrance diameters was as follows:

Diameter 3– 6 cm (n = 9): none occupied
Diameter 7–12 cm (n = 32): 22 % occupied

Diameter 13–18 cm (n = 31): 42 % occupied
Diameter 19–24 cm (n = 42): 73 % occupied

Banana leaves unfurl rapidly and are therefore ephemeral domiciles. Rates of unfurling vary. In December, a sample of 17 leaves showed that seven were suitable for occupation for only one day, seven for two days, and three for three days. Furled banana leaves were available from August to June (this study), and are said to be available throughout the year. At no time during this study were all suitable leaves occupied. From December to March, 38–50 % of the suitable leaves examined were occupied by one or more bats. At the beginning of June, suitable leaves were less numerous and 90 % were occupied, but by mid-June they were more abundant, and only 50 % were occupied. No quantitative data are available for July to November. No other species of bats were found in the furled leaves at Zomba or elsewhere in Malawi, and no other vertebrates or invertebrates were found competing with *P. nanus* for furled leaves.

Torpor

At the end of December (mid wet season), some bats in furled leaves were torpid but others were not torpid. In June (cool dry season) all bats taken from furled leaves were torpid. Data are not available for other months. Daytime torpidity in *P. nanus* occurs in Kenya (O'Shea 1980), but not in Natal (Laval and Laval 1977). Since Kenya is tropical and hot, and Natal is temperate and cool, these observations are the opposite of what might be expected.

Litter-size

All pregnant females from Zomba (n = 23) had twin foetuses. Thirteen of these females were autopsied and each had one foetus (near end to term) in each uterine horn.

Male reproductive chronology at Zomba

Observations on the position and size of testés show that they descend in April, reach maximum size (5 × 3 mm) in May, start to decline in size in June, and become abdominal no later than mid-October (Figure and Table 1). Adult males did not roost with adult females from October to April, but were roosting with adult females by 1 June. This suggests that copulation occurs in May–June, but this has not been confirmed by other evidence. In all males, the testes reached maximum size and were scrotal by May indicating that males reach reproductive maturity when they are about six months old.

Female reproductive chronology at Zomba

Female *P. nanus* were conspicuously pregnant when this study began in early October; they gave birth during the first three weeks of November, and stopped lactating approximately eight weeks later during the first two weeks of January (Table 1). No females were pregnant between mid-November and mid-June when this study was curtailed, indicating that in Malawi, females are monoestrous. In mid-June, females which had lactated in November to January had nipples with a slightly raised rim, and could be distinguished from the seven-month old females which had not yet bred. In October, the difference in nipples was still apparent and distinguished primiparous females from those which had bred in the previous year(s). This indicates that females breed at least twice, but the longevity of the species is not known. Although it is assumed that copulation probably occurs in May–June (see above), the gestation period of *P. nanus* in Malawi cannot be determined without knowing if sperm storage in the uterus, or delayed implantation,

Table 1. **The reproductive condition of 302 male and female *Pipistrellus nanus* collected from Zomba, Malawi, October 1984 to June 1985**

Date	Sample Size (males, females)	Males			Females			
		Testes Abdominal	Testes Scrotal	Young Born November 1984	Pregnant	Lactating	Post-lactating	Young Born November 1984
6–9 Oct	6, 4	5	1	0	4	0	0	0
20 Oct	7, 7	7	0	0	7	0	0	0
31 Oct	6,12	6	0	0	12	0	0	0
16 Nov	16,15	16	0	+	7	8	0	+
25 Nov	5, 3	5	0	+	0	3	0	+
2 Dec	10,14	2	0	8	0	6	0	8
14 Dec	9, 9	6	0	3	0	2	0	7
21 Dec	0, 3	0	0	0	0	2	0	1
30 Dec	15,25	6	0	9	0	13	0	12
12 Jan	2,14	1	0	1	0	1	4	9
27 Jan	6,14	4	0	2	0	0	8	5
2 Mar	3,11	1	0	1	0	0	6	5
30 Mar	5,25	2	0	3	0	0	6	19
28 Apr	8,12	0	8[a]		0	0	7	5
1 Jun	6,15	0	6[a]		0	0	8	7
16 Jun	3,12	0	3[a]		0	0	9	3

+ = neonates present but not sexed; [a] includes young males born November 1984 which could no longer be distinguished from older males

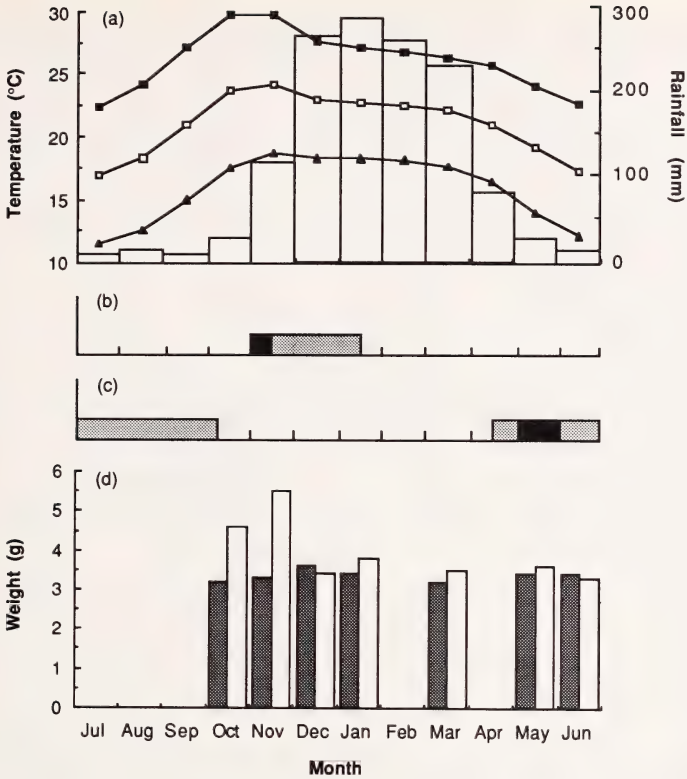
occur. Another possibility is that sperm produced in May is stored in the male epididymes until copulation occurs several months later (followed by the immediate onset of developmental gestation in the female), but the sudden change in roosting behaviour (see above) mitigates against this suggestion. Laval and Laval (1977) in Natal, and O'Shea (1980) in Kenya, were not able to resolve this problem, although O'Shea found that changing patterns of social behaviour suggested that copulation was occuring in May, well in advance of the period of developmental gestation.

In September and October, all females were pregnant showing that females attain reproductive maturity during their first year. One hundred percent pregnancy in large samples of females ($n > 20$) has also been recorded in Kenya (O'Shea 1980), Zimbabwe (Smithers and Wilson 1979) and Natal (Laval and Laval 1977).

Reproductive chronology is related to climate in Malawi: developmental gestation occurs during the dry season, and lactation coincides with the first half of the wet season when small flying insects (assessed qualitatively) are most abundant. Corroborative evidence that conditions are most favourable at this time comes from the monthly mean weights of adult males (see Fig.) which (although the differences were not significant [$F = 1.717$, $p < 0.25$]), were lowest at the end of the dry season, and increased during the first two months of the wet season. The monthly mean weights of adult females reached a peak in January, although the females were still lactating at the beginning of this month (Fig.).

Reproduction of *P. nanus* elsewhere in Malawi

The reproductive condition of 17 *P. nanus* from six other localities in Malawi (Happold et al. 1987), and the data recorded for five *P. nanus* in the literature (Kershaw 1922; Lawrence and Loveridge 1953) and for two specimens in the Museum of Malawi, Blantyre, are consistent with the data from Zomba. This indicates that throughout Malawi, in diverse habitats, *P. nanus* is monoestrous with the birth of twins at the beginning of the wet season.



The reproductive chronologies and mean weights of adult *Pipistrellus nanus* in relation to climate at Zomba, Malawi. (a) Climate: histogram = mean monthly rainfall; ■ = mean monthly maximum temperature; □ = mean monthly temperature; ▲ = mean monthly minimum temperature. (b) Reproductive chronology of females: black = births; stipple = lactation. (c) Reproductive chronology of males: stipple = testes scrotal; black = testes scrotal and at maximal size (see also Table 1). (d) Weights of adults: stipple = males; white = females. No samples in July to September, February, and April. Climatic data from Malawi Government (1982)

Social organisation

From December to June, 66 furled leaves were examined without any of the occupants escaping before they were counted: 38 % were occupied by single bats and 62 % were occupied by groups of 2–10 bats (Table 2). Seasonal changes in mean group size and the range of group sizes were apparent.

From December to June, 59 leaves were examined without any of the occupants escaping before they were aged and sexed (Table 3). These leaves were occupied by single adult females, single adult males, single young, or by groups whose compositions are given in Table 3. Seasonal changes in social organisation were conspicuous, and three distinct phases were observed during the study period. These can be referred to as the lactation phase, the post-lactation phase and the harem-formation phase.

During the lactation phase (30 December and 12 January) the adult males (n = 6) invariably roosted singly, 58 % of the lactating females (n = 12) roosted only with their own young, and 42 % roosted in maternity groups comprising one or two other lactating females and their young. The two single adult females observed on 12 December (Table 3) were post-lactating.

Table 2. **Group sizes of *Pipistrellus nanus* taken from 66 furled banana leaves at Zomba, Malawi, and their frequency of occurrence**

Date	Group Size										Mean Group Size
	1	2	3	4	5	6	7	8	9	10	
30 Dec 1984	8	4	3				1			1	2.5
12 Jan 1985	5	1		2			1				2.4
27 Jan 1985	6	4		1	1						2.1
2 Mar 1985	2		1	1		1					3.0
30 Mar 1985	3	1	2	1	1				1		3.2
1 Jun 1985	2	2	1	1		1		1			3.4
16 Jun 1985	1	2	1		1				1		3.7

Table 3. **Composition of groups of *Pipistrellus nanus* taken from 59 furled banana leaves at Zomba, Malawi, and their frequency of occurrence**

Date	Singles			Group Compositions				
	Single adult male	Single adult female	Single young[a]	One adult female with young	2–3 adult females with or without young	2 or more young	One adult male with one or more females	Two adult males with one or more females
30 Dec 1984	5	0	1	6	1	1	0	0
12 Jan 1985	1	2	2	1	1	0	0	0
27 Jan 1985	4	0	2	1	2	2	0	0
2 Mar 1985	1	1	0	0	2	0	0	0
30 Mar 1985	2	2	0	2	1	3	0	0
1 Jun 1985	0	1	0	0	1	0	4	1
16 Jun 1985	0	1	0	0	2	0	3	0

[a] From 30 Dec to 12 Jan, young = mostly unweaned juveniles; from 27 Jan to 30 Mar, young = subadults; from 1 Jun to 16 Jun, all bats were adults.

During the post-lactation phase (27 January to 31 March), adult males continued to roost singly. Post-lactating females (n = 16) roosted singly (19 %) or with groups of subadults and/or other post-lactating females (81 %). Subadults (n = 36) occasionally roosted singly (5 %), but usually roosted with other subadults and/or post-lactating females (95 %).

In April–May, the testes of all males descended, all bats were assumed to have reached reproductive maturity, and the harem-formation phase began. During this phase (1 June and 16 June), all of the males (n = 9) and 95 % of the females (n = 38) roosted in groups of 2–9 bats. Eleven intact groups were examined, and seven (64 %) of these were harems (one adult male with one or more females). One group comprised two males with two females, and three groups comprised only 2–3 females. O'Shea (1980) pointed out that the harems of *P. nanus* in Kenya, unlike those of many other species, were small and highly labile. The stability of the harems observed in Malawi was not investigated.

If data from the post-lactation and harem-formation phases are combined, some aspects of the social organisation of *P. nanus* in Malawi (this study), Kenya (O'Shea 1980) and South Africa (Laval and Laval 1977) can be compared. These phases are combined because O'Shea was not able to make observations during lactation. From 27 January to 16 June, 38 furled leaves at Zomba were examined without any of the occupants escaping before they were aged and sexed. Fourteen of the leaves contained single bats, one contained two newly weaned males, and 23 contained females in groups; of these, 14

(61 %) were harems, 8 (35 %) were females only, and one (4 %) was females with two adult males. The total number of bats examined was 106: 25 males and 81 females. Fourteen (13 %) were found singly and 92 (87 %) were found in groups. The 14 single bats comprised 7 (50 %) males and 7 (50 %) females. The 92 bats roosting in groups comprised 18 males (72 % of all males) and 74 females (91 % of all females). These data, and the equivalent data from South Africa and Kenya, are summarised in Table 5 (see Discussion).

Table 4. **Sex ratios in samples of *Pipistrellus nanus* from Zomba, Malawi**

Date	Sample	Total Males	Total Females	Ratio M:F
	Juveniles (unweaned)			
2 Dec	Week 5	8	8	1:1
Dec–Jan	Weeks 7–11	13	29	1:2.2
	Adults + Subadults			
Oct	Adults only	18	19	1:1
Nov	Adults only	22	23	1:1
Dec	Adults only	15	20	1:1.3
Jan	Adults only	5	14	1:3
Mar	Adults + Subadults	7	36	1:5
Apr	Adults + Subadults	8	12	1:1.5
Jun	Adults + Subadults	9	17	1:2
Total		84	141	1:1.7

Sex ratios

The ratios of males to females in the samples of *P. nanus* collected at Zomba (Table 4) show that although equal numbers of males and females are born, females outnumber males for at least seven months of the year.

Discussion

This study has dealt with the domiciles, reproduction, social organisation and sex ratios of *P. nanus* in Malawi. When the data from Malawi are compared with the data from Kenya (O'Shea 1980) and South Africa (Laval and Laval 1977), it can be seen that some aspects of the biology of *P. nanus* show geographical variation (Table 5). The differences help to elucidate some of the ways in which domiciles, reproduction, social organisation and sex ratios are interelated.

The furled-leaf domicile and its implications

Pipistrellus nanus commonly roosts in the furled terminal leaves of bananas and plantains *(Musa)*, strelitzias *(Strelitzia nicolai)* and other musaceous plants (Brosset 1966; Kingdon 1974; Laval and Laval 1977; Rosevear 1965; Verschuren 1957). Musaceous plants are abundant in moist habitats throughout most of Africa south in the Sahara, and *P. nanus* appears to be most abundant where musaceous plants are available. However it also exploits other domiciles such as the fruits and dead leaves of musaceous plants (Kingdon 1974; Rosevear 1965), palm leaves, thatch (O'Shea 1980; Rosevear 1965), holes and cracks in buildings, roofs, and road culverts (Rosevear 1965; Shortridge 1934). The domiciles are of two types, some being permanent and some being ephemeral. The use of both permanent and emphemeral domiciles has been recorded in diverse parts of the very extensive geographic range of *P. nanus*, and there is no evidence that the choice of domicile

Table 5. **A comparison of some characteristics of the domiciles, reproduction, social organisation, sex ratios, and related biology of *Pipistrellus nanus* from populations in Kenya (O'Shea 1980), Malawi (this study) and South Africa (Laval and Laval 1977)**

Characteristic	Kenya	Malawi	South Africa
Domicile	Permanent	Ephemeral	Ephemeral
Reproductive strategy	Seasonal monoestry	Seasonal monoestry	Seasonal monoestry
% twin births	100 %	100 %	Approx. 50 %
Mean group size ± SD (incl. solitary bats)	1.4 ± 0.9	2.8 ± 2.2	2.8*
Range group size	2–12	2–10	2–6*
% adults roosting in groups	49 %	87 %	28 %
% males roosting in groups	33 %	72 %	24 %
% females roosting in groups	79 %	91 %	34 %
% males of solitary bats	91 %	50 %	61 %
Roost site fidelity in males	High	Not possible	Not possible
Roost site fidelity in females	Low	Not possible	Not possible
Territoriality in males	High	nd, presumed absent	Absent
Competition for roosts by males	Present	nd, presumed absent	Absent
Group formation	Not random	nd	Random
Group composition	Labile	nd, presumed labile	Labile
Sex ratio in adults (M:F)	2:1	1:1.7	1:1
Sex ratio in juveniles (M:F)	1:1	1:1	1:2
Differential mortality	Greater in females	Greater in males	Greater in females
Daytime torpidity	Present	Present	Absent
Tail glands	Present	Absent	Absent

Data on social organisation excludes the period when females were giving birth and lactating, except where indicated by an asterisk. nd = no data

is related to climate. Throughout its range, the exploitation of permanent domiciles is uncommon. It might be relevant that 43 *P. nanus* from banana leaves in Malawi (this study), and *P. nanus* from banana leaves in Ivory Coast and some other parts of Africa (T. J. O'Shea, pers. comm.), did not have tail glands whereas those roosting in permanent domiciles in Kenya (O'Shea 1980) and Ivory Coast (T. J. O'Shea, pers. comm.) did have these glands. This discrepancy raises doubts about the taxonomic relationship between the leaf-roosting bats and those roosting in permanent domiciles (T. J. O'Shea pers. comm.).

Only two other species of bats in Africa are known to regularly exploit furled musaceous leaves for domiciles. *Myotis bocagei* (Vespertilionidae), which occurs in the rainforest and in some parts of the southern savanna, frequently roosts in the furled leaves of *Musa* and also in clusters of banana fruits and in dead banana leaves (Brosset 1966, 1976). The other species, *Myzopoda aurata* (Myzopodidae), is an extremely rare species found only on Madagascar (Hill and Smith 1984). One specimen of *Myotis welwitschii* from Livingstonia (Malawi) was found in a furled banana leaf by R. C. Wood (Ansell and Dowsett 1988) but this species is generally thought to hang from trees and low bushes.

Pipistrellus nanus has enlarged pads on the thumbs and soles which probably contribute to its ability to climb very easily over the slippery surfaces of banana leaves (Brosset 1966; Lang and Chapin 1917). Enlarged pads do not occur in *M. bocagei* or *M. welwitschii*, and therefore *P. nanus* is apparently the only species on the African mainland which is specialised, in both behaviour and anatomy, to roost in the furled leaves of musaceous plants. Therefore, although *P. nanus* may compete for food with syntopic species which are very similar in size and aspect ratio, it does not compete with these species for furled-leaf domiciles. This is probably one of the reasons why *P. nanus* has such a widespread distribution in Africa, and why it has been able to find an ecological niche in a wide variety of bat communities. On the mainland, competition for furled leaves might be expected

between *P. nanus* and *Myotis bocagei*, but has not apparently been documented. Furthermore, in Gabon (Brosset 1976), South Africa (Laval and Laval 1977) and Malawi (this study), where *M. bocagei* or *P. nanus* roosting in furled leaves have been studied in detail, only some of the available furled leaves have been occupied, suggesting that the availability of domiciles is not a limiting factor. Both *M. bocagei* and *P. nanus* feed mainly on Lepidoptera, Coleoptera and Diptera (Fenton and Thomas 1980; Whitaker and Mumford 1978), but *M. bocagei* is a larger species (FA = 39.3, WT = c. 7 g.; Happold et al. 1987) and can eat larger insects with harder integuments (D. C. D. Happold and M. Happold, unpubl.). Consequently, *M. bocagei* is unlikely to compete with *P. nanus* for the same species of insects.

Bananas and plantains *(Musa)* are not endemic to Africa. They originated in Malasia, and appear to have been introduced to Africa, via Madagascar, during the first 500 years A.D. (Simmonds 1962). Simmonds suggested that, in Africa, bananas spread up the Zambesi valley and the Great Rift Valleys and then across central Africa to West Africa. The present geographical range of *Musa* in Africa covers all but the most southern part of the range of *P. nanus*. The distribution and domiciles of *P. nanus* prior to the introduction of *Musa* to Africa are not known. Verschuren (1957) suggested that *P. nanus* may have roosted in ensete (*Ensete ventricosum* and other species), a banana-like plant sometimes called "wild banana" or "false banana". *Ensete* is endemic to Africa. It was utilised and/or cultivated in Ethiopia possibly as early as the Upper Pleistocene (Brandt 1984), and is distributed throughout most of the range of *P. nanus* in west, east, central and southern Africa and Madagascar (Simmonds 1962), Alternatively, *P. nanus* may have roosted in permanent domiciles before bananas became widespread.

In southern Africa *P. nanus* extends beyond the southern limit of the ranges of *Musa* and *Ensete*, into the range of *Strelitzia nicolai* which occurs mainly in the coastal forests of Natal and some parts of Cape Province. Where *Musa* and *Ensete* are absent, *P. nanus* roosts in furled *Strelitzia* leaves (Laval and Laval 1977). The distribution of *P. nanus* in southern Africa (Smithers 1983) appears to be restricted to habitats having either *Musa, Ensete* or *Strelitzia*. There is some evidence that *P. nanus* prefers *Musa* to both *Ensete* and *Strelitzia* (Laval and Laval 1977; Verschuren 1957). Laval and Laval concluded that *P. nanus* prefers *Musa* because they produce more leaves in closer proximity.

The furled leaves of musaceous plants are advantageous domiciles for *P. nanus* for at least three reasons. Firstly, they are available throughout the year although leaf production may fall off during colder periods (Simmonds 1959; this study). Secondly, the microclimate inside the furled leaf is undoubtedly very humid because of transpiration, and this would reduce the likelihood of bats becoming dehydrated during the day, and thirdly, there appears to be minimal competition for furled musaceous leaves on the African mainland.

The main disadvantage of furled musaceous leaves is that they unfurl rapidly, and are only suitable as domiciles for a few days. During the hot wet season, when leaves unfurl most rapidly, females have to carry non-volant young to a new domicile every 1–3 days, but they are aerodynamically well adapted to do this. The mean wing-loading in non-pregnant adult *P. nanus* is 0.05 g/cm^2 (derived from weights and aspect ratios given by Happold and Happold 1988), but when maximally loaded with two non-volant young, the wing-loading increases to 0.14 g/cm^2. Mean wing-loadings in non-pregnant adult bats of 33 other species from Malawi ranged from 0.05 to 0.22 g/cm^2, and 11 of these had wing-loadings above 0.1 g/cm^2 (Happold and Happold unpubl.).

Reproduction

The data currently available for *P. nanus* elsewhere in Africa can be summarised as follows:

1. South Africa, Natal, two localities at 28° 55′ S and 30° 24′ S, evergreen coastal forest,

rainfall unimodal with wet season October–April. Reproduction concluded to be monoestry with the birth of twins or (less often) singletons in November and early December (Laval and Laval 1977).

2. South-west Africa, Ovamboland, 17° 20′ S. "A female contained twin foetuses in October" (Shortridge 1934).
3. Zimbabwe, 16–20° S, southern savanna woodland, rainfall unimodal, wet season November–April. Females not pregnant in July (n = 17); some females pregnant in August; all females pregnant (with twins) in September (n = 26) (Smithers and Wilson 1979).
4. Kenya, Bushwhacker's Safari Camp, 2° 18′ S, dry thornscrub and bushland, rainfall bimodal with peaks during November–December and March–April, main dry season May–October. Reproduction was monoestry with the birth of twins (n = 16) in November. Mating assumed to occur from May to late August (O'Shea 1980).
5. East Africa, 5° N–12° S, rainforest and savanna, rainfall bimodal but varies with locality. "Breeding is apparently not seasonal as females with young have been collected at all times of the year" (Kingdon 1974).
6. Zaire, 5° N–5° S, rainforest and savanna, rainfall generally bimodal but varies with locality: no details available. "On rare occasions two young are born. We had at least one female in August with two embryos, though in December and January, single young were observed" (Lang and Chapin 1917).
7. Zaire, Parc National de la Garamba, 3° 40′ N–4° 40′ N, Guinea savanna, rainfall bimodal with peaks in April and November, main dry season December–February. Concluded to breed throughout the year (Verschuren 1957) but this was based on the limited observations that no females were pregnant or lactating in April and May, and that 44 specimens at the end of July included only two juveniles less than one month old. Verschuren also concluded that *P. culex* (now a synonym of *P. nanus* [see Hayman and Hill 1971]) gave birth in March because a colony of three females with seven non-volant young was found in mid-April.
8. Zaire, Parc National Albert, 1–2° N, rainforest and savanna, climate practically constant throughout year. Specimens were captured throughout the year (n = 362). Eighty-five were females of which only 10 were pregnant: one in February, one in May, four in July, three in August, and one at end of October. Only five juveniles were obtained: these were found in February, July, August and October. No cases of twin births were noted (Verschuren 1966).
9. Rwanda, 1–3° S. Details of habitat not available. Reproduction concluded to be aseasonal polyoestry (Anciaux de Faveaux 1972, quoted by Laval and Laval 1977).
10. Rwanda, Parc National de la Kagera, c. 1° 30′ S. Details of habitat not available. "No twin births were recorded" (Verschuren 1965 in Verschuren 1966).
11. Gabon, c. 1° N, rainforest, rainfall bimodal with peaks in February–June and September–December, and some rain in all months (Charles-Dominique 1971). Bats were collected from January–August 1965, November 1965 and January 1966. Pregnant females, and females with young of different ages were found in July–August, and in January–April. The number of young was one (n = 3) or two (n = 3). It was concluded that *P. nanus* in Gabon breeds throughout the year (Brosset 1966).
12. Rio Muni, c. 1–2° N, rainforest, rainfall bimodal with peaks March–May and September–December, main dry season June–August. Three specimens included a lactating female in August, and a male with scrotal testes 5 × 3 mm in November (Jones 1971).
13. Ghana, 6° 10′ N, rainforest, rainfall bimodal with peaks in May–June and September–October, dry season November–February. Lactating females with one and two young were obtained in March; no data for other months (Jeffrey 1975).
14. Liberia c. 4–8° N, rainforest, no climatic data given. Data for *Pipistrellus stampflii* (now a synonym of *P. nanus*, see Hayman and Hill 1971; Rosevear 1965). Females

were found with two embryos and with two young. It was concluded that twin births were more common in *P. stampflii* from Sierra Leone to Liberia, than in *P. nanus* from further east in West Africa (Kuhn 1962 in Rosevear 1965).

15. Senegal, Parc National du Niokolo-Koba, c. 11° N–12° 30′ N, Sudan savanna, rainfall unimodal, wet season May–September. Two females in late February were not lactating (Poché 1975).
16. Senegal, Parc National du Niokolo-Koba (see above) and Missira (no details available). Nine females in May were not pregnant (Verschuren 1982).

Several conclusions can be drawn from these data, but a comprehensive account of geographical variation in the reproduction of *P. nanus* must await further data. The data from Zimbabwe, Malawi and Kenya suggest that twinning is the norm throughout the southern savanna, in tropical and subtropical localities. The frequency of twin births in South Africa appeared to be approximately 50 %, but since this was based on counts of non-volant young, it was considered to be an underestimate. In marked contrast, no twin births were recorded in some parts of Zaire and Rwanda. The limited information from elsewhere indicates that both singleton and twin births occur in some parts of Zaire, Gabon, Ghana and Liberia, but the relative frequencies are not known.

The data from South Africa, South-west Africa and Zimbabwe, and from this study in Malawi, are consistant with the view that *P. nanus* in the southern half of the southern savanna biotic zone has an austral reproductive cycle characterised by monoestry and parturition in November at the beginning of the wet season. In the northern part of the southern savanna zone (Kenya), the austral cycle persists with parturition in November at the beginning of the first peak in the bimodal wet season. Births occur a little earlier in Kenya and Malawi than in Natal, but in all of these localities, developmental gestation occurs during the dry season, and lactation coincides with the early part of the wet season. Although Kenya and Malawi are tropical, and Natal is temperate, each has a prolonged dry season when conditions are least favourable with respect to the abundance of insects. In Kenya at 4° 15′ S, the abundance of insects increased about tenfold from October to December (McWilliam 1982, in Racey 1982), and an increase in the abundance of insects at the beginning of the wet season has been noted qualitatively in Malawi (this study), and South Africa (van der Merwe et al. 1986).

Data from localities in the northern savanna are very limited. Extrapolating from the southern savanna data, one would expect a boreal cycle characterised by monoestry and parturition in June at the beginning of the wet season. However, this does not seem to occur in Senegal, and it is clear that the reproductive chronology of *P. nanus* in northern savanna habitats needs investigating.

Aseasonal parturition occurs in some of the localities in or near the tropical rainforest zone (see sources 6, 7, 8 and 11), but it is not possible to tell if *P. nanus* is monoestrus with highly unsynchronised parturition, or polyoestrus. None of these sources record simultaneous pregnancy and lactation, and this mitigates against continuous polyoestry with a post-partum oestrus. In Parc National Albert, only 12 % of the 85 females captured throughout the year were pregnant which strongly suggests monoestry. In contrast, *P. nanus* in Rwanda appears to be polyoestrous and breeds continuously (Anciaux de Faveaux 1972, quoted by Laval and Laval 1977).

The combination of all these observations suggests that *P. nanus* exemplifies at least two reproductive strategies. First, it concentrates reproductive effort by having two young once per year in habitats where conditions fluctuate and are most favourable only once during the year. Second, it dilutes reproductive effort by usually having one young, but maybe more than one pregnancy per year, in habitats which are comparatively stable throughout the year.

Relationships between domiciles, reproduction, social organisation and sex ratios

Throughout its geographic range, *P. nanus* sometimes roosts singly, sometimes in small groups, and occasionally in large groups. Group size is obviously determined to some extent by the size of the domicile. In furled leaves, group sizes range from 2–6 (mean 2.8) in Natal (Laval and Laval 1977), 2–10 (mean 2.8) in Malawi (this study), 2–3 in Rwanda (Anciaux de Faveaux 1972), and 2–3 in Zaire (Verschuren 1957). O'Shea (1980) found groups of 2–12 (mean 1.4) roosting in the spaces (some very constricted) between leaflets of palm fronds in roofing thatch in Kenya. A very unusual record is that of a colony of 150 *P. nanus* in thatch in the Kruger National Park in Natal: this appeared to be a maternal colony (Laval and Laval 1977). Laval and Laval (1977) suggested that grouping may be more general in the tropics, and this is supported by the observations that the proportion of bats roosting in groups is only 28 % in South Africa, but 87 % in Malawi (both populations roosting in furled leaves) and 49 % in Kenya (population roosting in thatch) (Table 5).

The social organisation of *P. nanus* roosting in ephemeral furled leaves in Malawi (this study) appears to be very similar to that of *P. nanus* roosting in ephemeral furled leaves in South Africa (Laval and Laval 1977). Some minor differences (related to the lower incidence of group roosting in South Africa) are listed in Table 5, but in both places the social organisation is characterised by the following features: 1. the bats roost singly or in small groups, 2. roost-site fidelity is negligible, 3. lactating females roost alone with their young, or in small maternity groups, 4. adult males roost singly while females are rearing young, and 5. adult males almost never roost together. Other characteristics revealed by Laval and Laval (1977) but not investigated in the Malawian study are: 6. male territoriality does not occur, 7. group formation is random, and 8. group cohesion is negligible except between females and their unweaned young. The study by Laval and Laval (1977) on the South African bats did not reveal seasonal trends in group size or group composition, except for showing that mean group size was largest in November, when only maternity groups were encountered. In contrast, seasonal trends in group size and group composition were evident in Malawi, and two distinct phases (post-lactation and harem-formation) in social organisation were recognised in the five months following weaning of the young. The harem-formation phase was not seen in Malawi until June, but there is no data for May. In South Africa, the harem-formation phase was not recognised in May and there are no data for June, but it seems likely that this phase would have been observed in South Africa if data had been collected in June.

The social organisation of *P. nanus* roosting in permanent thatch in Kenya differs mainly because roost fidelity is possible. O'Shea (1980) found that males showed greater roost fidelity than females, and they defended their roost sites against invasion by other males. In contrast, the females gathered in small groups of labile composition attracted to the most vocal males. Males competed for the best roost sites and also for females, and the resulting mating system is one based on resource defence polygyny. O'Shea observed that females left the domiciles in his study area just prior to giving birth and he assumed they had gone elsewhere to establish a maternal colony. The main differences between the social behaviour of *P. nanus* in South Africa, Malawi and Kenya are summarised in Table 5, together with differences in other biological characteristics.

Some of the differences in social behaviour seem to be causally related to the differences in domiciles. When *P. nanus* roosts in ephemeral furled leafs, roost fidelity is almost negligible (Laval and Laval 1977; this study) but when *P. nanus* roosts in permanent thatch, roost fidelity is possible and is shown to a high degree by males (O'Shea 1980). There also appears to be a relationship between the evolution of male territoriality in *P. nanus* and the exploitation of permanent domiciles (O'Shea 1980): male territoriality occurs in the Kenya thatch-roosting population but not in the leaf-roosting population in South Africa. Furthermore, in the Kenya population, males compete for roost sites

(O'Shea 1980) whereas in both South Africa and Malawi, empty banana leaves were always available and competition for leaves was not observed.

Other differences in social behaviour are probably coincidental. When *P. nanus* exploits ephemeral domiciles, the formation of groups is random and group cohesion is not maintained except between females and their unweaned young (Laval and Laval 1977). When permanent domiciles are used, group formation is non-random and is influenced by several aspects of social behaviour: again group cohesion is not maintained (O'Shea 1980). However, as O'Shea (1980) pointed out, both non-random group formation, and maintenance of group cohesion, have been recorded in other leaf-roosting bats (e.g. *Myotis bocagei* [see Brosset 1976] and *Thyroptera tricolor* [see Findley and Wilson 1974]), and therefore, random group formation and the lack of group cohesion can not be consequences of roosting in ephemeral domiciles.

Brosset (1976) recorded a predominance of females in populations of *M. bocagei* roosting in furled leaves in Gabon. These bats formed harems and Brosset noted that harems seem to exist in species where adult females largely outnumber adult males. However, in *P. nanus,* harems (albeit small and labile) have been observed in populations exploiting both furled leaves and thatch, and in populations where males outnumber females, where females outnumber males and where the sex ratio is balanced (Table 5). In Malawi, females outnumbered males for at least seven months of the year (Table 4). In contrast, males outnumbered females in Senegal (Verschuren 1982), Parc National Albert in Zaire (3.2 males:1 female, n = 362) (Verschuren 1966), Parc National de la Garamba in Zaire (1.6:1) (Verschuren 1957), Burundi (Niort 1970 quoted by Laval and Laval 1977), and Kenya (2:1) (O'Shea 1980). In South Africa, Laval and Laval (1977) found equal numbers of adult males and females (n = 186), but the ratio was 0.5:1 (n = 54) in juveniles.

The apparent shift from the predominance of males in West Africa, East Africa and Zaire, to the predominance of females in Malawi and the balanced sex ratio in South Africa calls for further investigation, and one of the first objectives must be to ascertain the cause(s) of bias in each situation. Adult sex ratios can only be altered by differential maturation rates, unbalanced ratios at birth, or differential mortality (e.g. Wilson 1975). In both Kenya (O'Shea 1980) and Malawi (this study), the sexes mature at the same time, and in Malawi (and probably in Kenya), the sex ratio at birth was equal. This means that differential mortality is the most likely factor contributing to the biassed ratio in both Kenya (O'Shea 1980) and Malawi. Differential mortality also appears to contribute to the balanced sex ratio observed in adult *P. nanus* in South Africa because the ratio in juveniles (Laval and Laval 1977) is biassed in favour of females. O'Shea (1980) suggested that since females in the Kenya population roosted in groups more often than males roosted in groups, predation at roost sites (especially when bats were torpid) would result in a greater mortality of females. He also concluded that females were unlikely to experience a constant mortality factor imposed by the stress of birth and rearing of two young because, if this was so, it would lead to a greater frequency of singleton births. In support of this hypothesis, O'Shea outlined the differences between his observations and those of Laval and Laval (1977) in South Africa. In South Africa, females roosted socially 43 % of the time (as opposed to 79 % in Kenya), the predictability of roost site locations was minimal, and the bats did not enter torpor. Sex ratios were unbiassed, and the frequency of singleton births, based on post-partum counts of young, was about 50 % (as opposed to 0 % in Kenya). The data from Malawi, however, contrasts with that for South Africa in spite of the fact that ephemeral domiciles are exploited in both places. In Malawi, the proportion of females roosting socially (91 %) was even higher than in Kenya, the bats entered torpor, sex ratios were biassed in favour of females, and the frequency of singleton births was 0 %. These data (summarised in Table 5) suggest that there are no consistent relationships between sex ratios, domiciles, torpor, twinning, and roosting singly, with the exception

that the absence of torpor was associated with a reduced incidence of twinning and a reduced incidence of females roosting in groups. Since huddling is a means of conserving body heat, the absence of torpor is not likely to be causally related to the reduced incidence of roosting in groups. On the other hand, the absence of torpor might impose a level of stress on pregnant females which makes the bearing of twins less advantageous.

The overall conclusion from the comparison of data on *P. nanus* from diverse part of its range, is that the domiciles, reproduction, social behaviour, torpor, and sex ratios show considerable variation. While some of the differences appear to be causally interelated, others appear to vary independently. As a result, *P. nanus* has an unusual degree of flexibility which has undoubtedly contributed to its ability to exploit many diverse habitats, and to inhabit most of Africa south of the Sahara.

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Zusammenfassung

Aufenthaltsorte, Fortpflanzung, soziale Organisation und Geschlechterverhältnisse bei der Bananen-Zwergfledermaus Pipistrellus nanus (Chiroptera, Vespertilionidae) in Malawi, Zentralafrika

Es wurden Aufenthaltsorte, Fortpflanzung, soziale Organisation und Geschlechterverhältnisse der Bananen-Zwergfledermaus, *Pipistrellus nanus,* in Malawi untersucht. Die Fledermäuse wurden in der Zeit von September 1984 bis zum Juni 1985 alle vierzehn Tage oder monatlich aufgerollten Bananenblättern entnommen. Die aufgerollten Blätter stellten vorübergehende Aufenthaltsorte für ein bis zwei Tage dar. Es gab immer einen Überschuß an möglichen Aufenthaltsorten. Weibchen waren monöstrisch und warfen im November Zwillinge. Die Laktationszeit dauerte acht Wochen. Von April bis Oktober waren die Hoden der Männchen ins Skrotum descendiert. Sie erreichten ihre maximale Größe im Monat Mai. Während der Laktationszeit ruhten die Männchen alleine, die Weibchen mit ihren Jungen hingegen ruhten allein oder in Muttergruppen. Weibchen nach der Laktation ruhten alleine oder mit Gruppen subadulter Tiere und/oder anderen Weibchen, die nicht mehr laktierten. Die erwachsenen Männchen ruhten weiterhin allein. Es wurde angenommen, daß im April, in dem die Testes aller Männchen ins Skrotum descendiert waren, alle Fledermäuse ihre sexuelle Reife erreicht haben. Jeweils ein erwachsenes Männchen lebte mit einem oder mehreren Weibchen im Harem zusammen. Es wurden jeweils die gleiche Anzahl Männchen und Weibchen geboren, die Zahl der Weibchen übertraf aber die der Männchen in wenigstens sieben Monaten des Jahres.

Die Daten aus Malawi werden mit denen aus Kenia, Südafrika und anderen Lokalitäten verglichen. Die geographischen Unterschiede in den Aufenthaltsorten und in der Reproduktionsbiologie, wie auch die Beziehungen zwischen verschiedenen Aspekten der Biologie von *P. nanus* werden besprochen.

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Red squirrel (*Sciurus vulgaris* Linnaeus, 1758) population dynamics in different habitats

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Abstract

Between October 1984 and January 1988 the dynamics of two red squirrel (*Sciurus vulgaris* Linnaeus, 1758) populations in a coniferous and a deciduous woodland was studied. Squirrels were livetrapped and individually marked. Density fluctuated annually, with variation in food abundance and winter temperature. Annual survival was positively correlated with food abundance, and higher for adults than for subadults. The proportion of females entering oestrus and of oestrous females breeding successfully were density dependent. The number of young weaned per successful female was positively correlated with food abundance. Variation in the timing of immigration between males and females was related to differences in social behaviour. The emigration-rate in both populations increased at high density and decreased when density was low. Hence, density regulating processes seemed to be at work through density dependent reproduction and emigration.

Introduction

Many species of Holarctic tree squirrels have been, or still are, important game animals. They were hunted for their fur, for food or sport, and for wood management purposes. Biologists have made use of data on fur returns and of shot squirrels to study different aspects of their population ecology: reproductive activity and litter size (Ognev 1940; Brown and Yeager 1945; Smith 1968; Degn 1973; Tittensor 1977; Rusch and Reeder 1978), sex-ratios (Shorten 1954; Uhlig 1957; Lampio 1967; Kemp and Keith 1970; Farentinos 1972; Nixon et al. 1975), and the effect of variation in food abundance on density fluctuations (Mikheeva 1973; Lyubetskaja 1976; Kemp and Keith 1970; Nixon et al. 1975).

The counting of dreys has been used to estimate squirrel density in grey *Sciurus carolinensis* (Don 1985) and in red squirrels (*Sciurus vulgaris* Linnaeus, 1758) (Wauters and Dhondt 1988).

Where these studies provide information on population structure and density at a specific time, and give crude indices of year to year changes in numbers, they are unsuitable for discovering short-term density fluctuations or for examining the importance of different population processes.

Detailed studies, using live-trapping, on unexploited populations of pine squirrels *Tamiasciurus hudsonicus* (Kemp and Keith 1970; Rusch and Reeder 1978; Halvorson and Engeman 1983), tassel-eared *Sciurus aberti* (Farentinos 1972), grey (Thompson 1978; Kenward 1985; Gurnell 1987), fox *Sciurus niger* (Hansen and Nixon 1985) and red squirrels (Tittensor 1977; Tonkin 1983; Wauters and Dhondt 1985, 1986; Holm 1987), describe density changes over several years and investigate the effects of reproduction, survival and dispersal. Most of these studies have been relatively short-termed: in only two cases populations have been followed in detail for more than ten years now (Halvorson and Engeman 1983; Gurnell 1983, 1987).

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We have been studying a red squirrel population in a coniferous habitat from August 1983 onwards and a second population in a mainly deciduous habitat from October 1984 onwards. In this paper we use data until January 1988, and we (i) describe and compare density fluctuations in both populations, (ii) describe the sex-ratio and age structure of both populations, and (iii) examine the different population processes: survival, reproduction and dispersal.

Study areas

We used two study sites of 40.5 ha each. One in the "Merodese Bossen" at Herenthout (Province of Antwerpen, N. Belgium) is mainly coniferous woodland of 212 ha dominated by Scots pine, *Pinus sylvestris,* and Corsican pine, *Pinus nigra,* with some larch, *Larix decidua,* and a few plots with mature oak, *Quercus robur,* and beech, *Fagus sylvatica.* The south-side of the study-area is bordered by meadows and by a road, that were never crossed by resident squirrels. The west-side is bordered by farmland, meadows and less suitable patches of wood, that were only occasionally crossed by squirrels. Along the north and east-side suitable squirrel habitat continues.

The second study area lies in the Peerdsbos at Schoten (Province of Antwerpen, N. Belgium) a mixed mature wood of 150 ha dominated by oak, beech and birch, *Betula* sp., with some chestnut, *Castanea sativa,* and maple, *Acer pseudoplatanus.* A few plots are planted with Scots or Corsican pine and some spruce, *Picea abies.* The study area is bordered by houses and a road on the north-side and by meadows and a motorway along the south and west-side, that were never crossed by residents. On the east-side the forest continues.

Material and methods

Trapping squirrels

The coniferous population was first sampled in August 1983. During the first year trapping was carried out at any possible occasion, and trapping-intensity and trapping success varied over the year (Wauters and Dhondt 1986). From October 1984 onwards both populations were sampled very intensively. Two types of traps were used. Wooden box traps (60 × 17 × 17 cm) placed on the ground or on small tables at about 1 m height, and "British squirrel-traps" (J. Holm pers. comm.) that were hung up against the trunk of the tree at about 1 m height. Traps were baited with a handful of sunflower seeds, three hazelnuts and three peanuts. In the coniferous woodland traps were placed on a 75 m grid (about 1.5 traps/ha) while in the deciduous woodland they were randomly distributed at a density of 1.2 traps/ha. In both study-areas trapping sessions of four days pre-baiting followed by four days of trapping were performed every five weeks. This allowed us to tag all resident squirrels in both study-areas and to have a high percentage of recaptures in each session. Moreover squirrels entering the population through reproduction or immigration were also easily captured and marked. Hence, density was known at each moment. We examined two characteristics of trappability: 1) Trapping success (Ts), which was calculated using the following formula: Ts = (number of captures/ number of trap-days) × 100 %, with 30 traps set for four days equals 120 trap-days; and 2) the proportion of animals present on the study area that were recaptured in a trapping session.

Squirrels that were only trapped in edge-traps along those sides of the study-areas where suitable habitat continued (north and east-side in the coniferous, east-side in the deciduous woodland) were not regarded as belonging to the resident population. Hence they were not used in density-estimations.

Data on home range use (Wauters and Dhondt 1985; unpublished data) of radio-tagged animals also helped in determining which squirrels were residents in the study-area, and which only visited it occasionally.

Handling squirrels

Every squirrel was individually marked using small pieces of coloured wires inserted through the ear. At each recapture the squirrel was weighed, and its body measurements were taken (Wauters and Dhondt 1989a). Information about the age, sex and reproductive status of the squirrel was also recorded. Subadults are between four and ten months old, males having abdominal testes and a small scrotum; females having a small unperforated vulva. Adults are over ten months.

Estimating survival, reproduction and dispersal

Between October 1984 and October 1987 local survival was estimated from one trapping session to the next using the following formula: survival-rate from time t-1 to time t =[(number of tagged squirrels present at t-1 and at t) / (number of tagged squirrels present at time t-1)] × 100 %.

From January 1985 till October 1987 data were available for all reproductive periods. The number of females in oestrus, the percentage of oestrous females lactating and successfully lactating were estimated while examining the reproductive status of recaptured females. Not all juveniles were marked. However, trapping of weaned juveniles, marking of juveniles in the nest, and observations of lactating females and their young allowed estimates of the number of young per successful reproducing female (WATERS and DHONDT 1989b). That most juveniles were marked before, or soon after weaning, allowed us to distinguish them from immigrants.

Reliable data on dispersal of mammals are often hard to get, since it is not always possible to distinguish between emigration and mortality. However most immigrating squirrels could be trapped rather easily. When many new squirrels appeared in a trapping-sample, the number of days traps were set was increased, till no more unmarked immigrants were captured. In most trapping sessions however immigrants were captured during the first two days and there was no need to trap for more than four days.

Environmental factors

Mean monthly temperatures are derived from the nearest station of the Koninklijk Metereologisch Instituut at Geel (15 km to Herenthout).

Food abundance was estimated using counts of fallen seeds on one square meter plots (WAUTERS and DHONDT 1988).

Analysing data

Since analyses of both reproduction and dispersal involve several parameters that contribute to total gains or losses in the population, and are affected by different environmental factors, the data were transformed logarithmically. This allowed us to add up values of each parameter and hence calculate the total gains or losses from one generation to the next for both reproduction and dispersal. The method is analogues to a k-factor analysis (DEMPSTER 1975) with the difference that our analysis was performed separately for reproduction and dispersal, as the different parameters contributing to reproduction and dispersal were not completely separated in time. Table 1 describes the sequence of parameters included in the analyses.

In order to combine the data set from the coniferous area (4 years) and the deciduous area (3 years), we normalised our data (in a set of normalised data, x_i, $\bar{x} = 0$ and $s_x = 1$), when the effect of environmental factors and when density dependence was investigated.

Results

Trappability

In both study-areas trapping success differed significantly between three periods (November–February, April–July, August–October), based on seasonal differences in the availability of tree seeds as primary food-resource (WAUTERS and DHONDT 1987), (Kruskal-Wallis analysis of variance: coniferous area $H = 13.26$; d.f. = 2; $P < 0.01$; deciduous area $H = 10.70$; d.f. = 2; $P < 0.01$). When in April–July tree seeds are no longer available to squirrels, the highest trapping success was reached. It was lowest in winter, when high energy food is most abundant. Squirrels thus became more trap-addicted when natural food was rare, and more trap-shy when natural food was abundant.

The proportion of resident squirrels recaptured in a trapping session varied less being usually over 75 %. The proportion of squirrels recaptured differed significantly between the three periods described above (Kruskal-Wallis analysis of variance: coniferous area $H = 9.00$; d.f. = 2; $P < 0.02$; deciduous area $H = 9.89$; d.f. = 2; $P < 0.01$). It was highest in the April–July period, when food is less abundant.

Density fluctuations

Squirrel numbers fluctuated over the year and between years (fig. 1). Also the abundance of tree seeds fluctuated between years (table 2). The seed-crop in year t was significantly correlated to October-density the next year (t+1), ($r = 0.743$; $n = 8$; $P < 0.05$) (fig. 2). In both habitats the October-density of 1986 was lower than expected based on the size of the

Table 1. **The different parameters involved in calculating the total gains or losses from one generation to the next for both reproduction and dispersal, using logarithmics**

Reproduction

N_0 = potential n° young in spring litter (= n° adult females present in January × 3.2 embryos/female)
k_1 = losses due to females not entering oestrus
N_1 = potential n° young produced by oestrus females in spring
k_2 = losses due to breeding-failure of oestrus females
N_2 = potential n° young produced by successfully breeding females
k_3 = losses due to nestling mortality
N_3 = actual n° young weaned in May
k_4 = female mortality and/or emigration from first to second breeding season (difference between log N_0 and log N_4)
N_4 = potential n° young in summer litter (= n° adult females present in May × 3.2 embryos/female)
k_5 = losses due to females not entering oestrus
N_5 = potential n° young produced by oestrus females in summer
k_6 = losses due to breeding-failure of oestrus females
N_6 = potential n° young produced by successfully breeding females
k_7 = losses due to nestling mortality
N_7 = actual n° young weaned in September

Dispersal

k_0 = gains due to winter-spring immigration
N_0 = actual n° immigrants in winter-spring
k_1 = further population increase due to spring reproduction
N_1 = n° immigrants and weaned juveniles in spring
k_2 = losses due to summer emigration
N_2 = n° immigrants and spring juveniles still present in October
k_3 = gains due to autumn immigration
N_3 = actual n° immigrants entering the population in autumn
k_4 = further population increase due to summer reproduction
N_4 = n° immigrants and weaned juveniles in autumn
k_5 = losses due to autumn-winter emigration
N_5 = n° immigrants and juveniles recruited in winter population

seed-crop the previous winter. The 1985–86 winter was the coldest of the four winters (mean max. temperature over the November–February period: 3.4 °C, against 6.1 °C in 1983–84, 4.9 °C in 1984–85 and 4.4 °C in 1986–87). Furthermore squirrel numbers tended to increase after a year with low density, and to decrease after a year with high density. However, in a multiple linear regression model the partial effects of food abundance ($p = 0.013$) and of winter temperature ($P = 0.049$) were statistically significant, while that of density the previous year ($P = 0.255$) was not. Variation in food abundance (partial $r = 0.943$) and in winter temperature (partial $r = 0.920$), together explained 96.6 % of the variation in squirrel-density between years.

Sex-ratio

Over the three years juveniles were captured and marked in the nest or soon after weaning, 58 young (28 males, 30 females) were tagged in the coniferous and 46 (23 males, 23 females) in the deciduous habitat. In both habitats sex-ratios of juveniles did not differ from an even sex-ratio.

Changes in the sex-ratio of the whole population (adults, subadults and juveniles) with time (fig. 1), did not occur randomly (Runs-test; coniferous area: $r = 3$; $N = 34$; $P < 0.001$; deciduous area: $r = 2$; $N = 34$; $P < 0.001$).

In the coniferous woodland more males than females were present from October 1984 until August 1985 (fig. 1). In September the number of females increased suddenly, due to

large numbers of females immigrating. From September 1985 until March 1987, females outnumbered males (fig. 1). In the spring of 1987 a slightly male biased immigration resulted in an even sex-ratio. The ratio of males over females stayed approximately 1 : 1 for the rest of the year (fig. 1). No apparent relation existed between sex-ratio and density. In

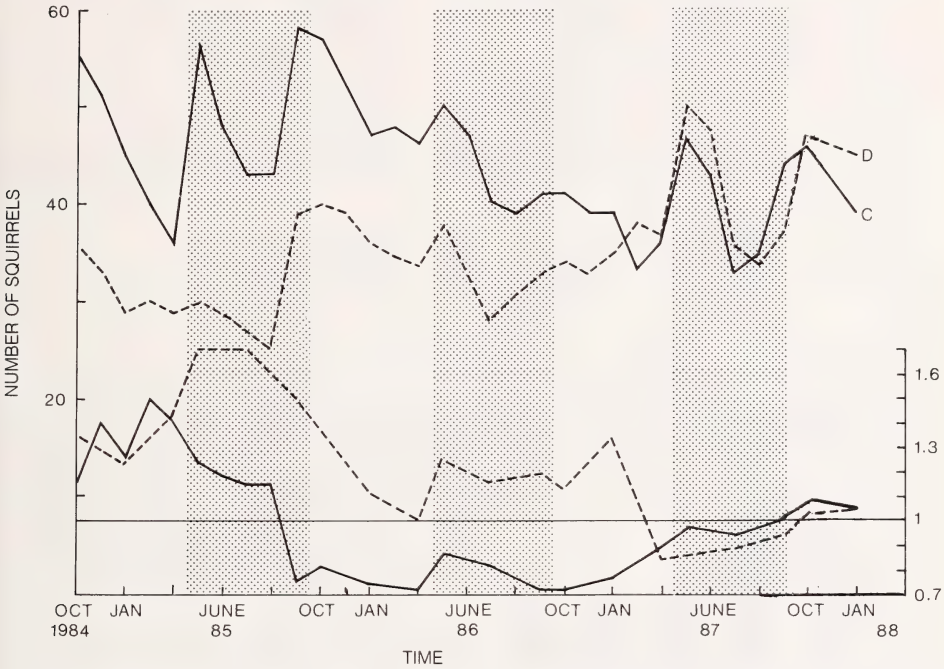

Fig. 1. Variation in squirrel numbers and in sex-ratio (males : females) between October 1984 and January 1988 in both habitats (coniferous = C, deciduous = D). Dotted area is the April-September period (spring and summer)

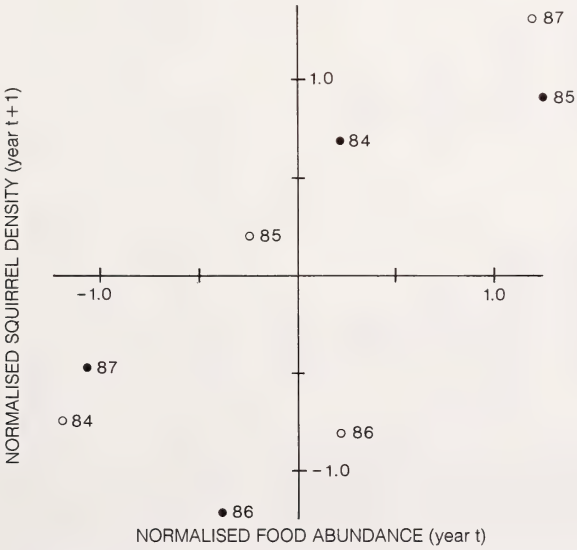

Fig. 2. Linear correlation between normalised food abundance and normalised squirrel density

Table 2. **Changes in food abundance, squirrel numbers, annual survival and annual recruitment of immigrants and juveniles, between October 1983 and October 1987**

Year (t)	Seed-crop in winter t t+1 (10^3 Kcal/ha)	N and (N/ha) in October year t	Survival (%) year t t+1 (adult surv.)	Number of immigrants and juveniles (recruited imm. + juv)
Coniferous woodland				
1983	152.5	43 (1.04)	54 % (76 %)	–
1984	184.9	55 (1.36)	53 % (62 %)	–
1985	135.0	57 (1.41)	44 % (53 %)	49 (21)
1986	112.0	41 (1.01)	46 % (50 %)	25 (10)
1987	–	46 (1.14)	–	39 (17)
Deciduous woodland				
1983	189.1	–	–	–
1984	742.6	35 (0.86)	47 % (65 %)	–
1985	1051.5	40 (0.99)	52 % (61 %)	30 (18)
1986	1607.5	34 (0.84)	53 % (61 %)	23 (13)
1987	–	47 (1.16)	–	44 (20)

the deciduous woodland more males than females were present from October 1984 until January 1987 (fig. 1). In February 1987 a lot of females immigrated into our study area and the sex-ratio became 1:1 (fig. 1). From February 1987 until January 1988, the sex-ratio varied between 0.85 and 1.05, hence close to a 1:1 ratio (fig. 1). In the deciduous woodland males outnumbered females when densities were low to moderate (October 1984, 1985, 1986). The sex-ratio was 1:1 when density was high (October 1987).

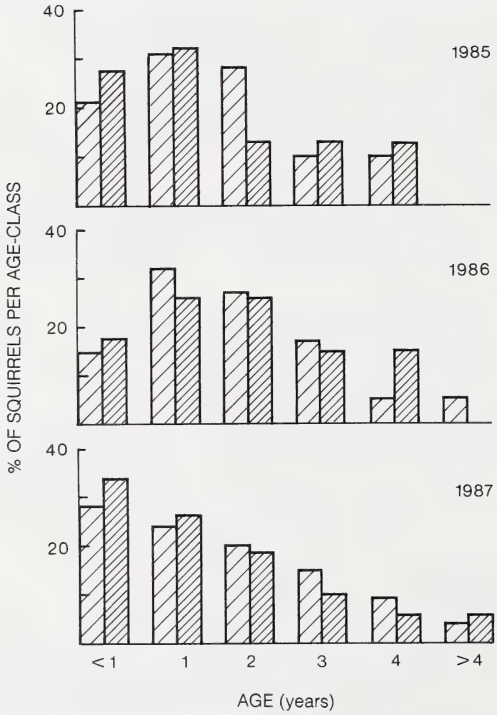

Fig. 3. Age structure of the squirrel population in both habitats in October of 1985, 1986 and 1987. Coniferous area ▨, deciduous area ▨. In the deciduous area no difference could be made between 2 year old and older squirrels in 1985, between 3 year old and older in 1986 and between 4 year old and older in 1987

Age-structure

The age-structure showed the same trend in both populations (fig. 3). The total number of three year old and older squirrels stayed rather constant over the years. In the coniferous woodland it varied from 11 in 1985 and 1986 to 13 in 1987, while in the deciduous woodland 10 squirrels were older than two in each year.

In all years and in both habitats the majority of the squirrels (71 %–81 %) were less than three years old, with yearlings and two year old squirrels as dominant age-categories (fig. 3). The percentage of subadults and yearlings was positively correlated with squirrel density (normalised data: $r = 0.864$; $n = 6$; $P < 0.05$). Thus when the proportion of immature squirrels in the population had increased, density was high, and when it had decreased density was low.

Table 3. **Differences in local survival in both habitats according to age and season and differences in annual survival according to sex, from October 1984 to October 1987**
Three-way G-statistics were used

Season	Coniferous area Adults	Coniferous area Subadults	G(age)	Deciduous area Adults	Deciduous area Subadults	G(age)
W 84–85	26/34 (76 %)	8/21 (38 %)	7.632 P<.05	17/20 (85 %)	8/15 (53 %)	7.772 P<.05
S 85	23/26 (88 %)	6/8 (75 %)		13/17 (76 %)	3/8 (38 %)	
G(season) = 3.017 N.S.				G(season) = 0.957 N.S.		
W 85–86	31/38 (82 %)	6/20 (30 %)	7.973 P<.02	22/28 (79 %)	7/12 (58 %)	1.765 N.S.
S 86	21/31 (68 %)	5/6 (83 %)		17/22 (77 %)	4/7 (57 %)	
G(season) = 0.046 N.S.				G(season) = 0.056 N.S.		
W 86–87	27/35 (77 %)	3/6 (50 %)	0.946 N.S.	24/25 (96 %)	3/9 (33 %)	11.17 P<.01
S 87	18/27 (67 %)	2/3 (67 %)		16/24 (67 %)	2/3 (67 %)	
G(season) = 0.248 N.S.				G(season) = 4.334 N.S.		

	Coniferous area Males	Coniferous area Females	Deciduous area Males	Deciduous area Females
84–85	16/31 (52 %)	13/24 (54 %)	8/19 (42 %)	8/16 (50 %)
G (sex) = 0.147 N.S. and G(area) = 0.103 N.S.				
85–86	11/27 (41 %)	15/31 (48 %)	11/22 (50 %)	10/18 (56 %)
G(sex) = 1.257 N.S. and G(area) = 1.577 N.S.				
86–87	9/18 (50 %)	11/23 (48 %)	9/18 (50 %)	9/16 (56 %)
G(sex) = 0.001 N.S. and G(area) = 0.261 N.S.				

S = April–Sept.; W = Oct.–March.

Local survival

Data on local survival according to half-year periods (autumn–winter period from October to March, spring–summer period from April to September), habitat type, age group and sex are summarised in table 3. Over the three years local survival was studied (October 1984–October 1987), no significant difference was found between years or areas (3-way G-test: factor year G = 0.019; d.f. = 4; N.S.; factor area G = 0.292; d.f. = 3; N.S.; 3-factor interaction G = 1.328; d.f. = 2; N.S.). Lampio (1967) suggested that due to changes in ranging behaviour and mobility, survival of male red squirrels differed from female survival. A 3-way G-test (factors sex, area, and survival) showed no differences in local survival according to sex or habitat type (table 3). In red squirrels body weight changes according to variation in food abundance and weather conditions (Wauters and Dhondt 1989a). Moreover a squirrels' chance of survival was correlated with its body weight (Wauters and Dhondt 1989b), so that older heavier squirrels survived better than younger squirrels of lower body weight. Therefore we tested for differences in local survival according to season and age using a 3-way G-test. Since no differences in survival were found between males and females, data on both sexes were combined. Separate analyses were made for each year survival was studied and for both areas. Seasonal differences in survival were statistically not significant (table 3), but differences between age-groups were significant in 1984–85 and 1985–86 in the coniferous and in 1984–85 and 1986–87 in the deciduous woodland (table 3). In all cases adults survived better than subadults.

The effect of winter-cold on survival was tested by correlating the mean monthly max. temperatures during the wintermonths (November–February) with monthly survival, combining the data of both habitats (fig. 4). Monthly survival during winter decreased significantly with temperature ($r = 0.784$; $n = 18$; $P < 0.001$).

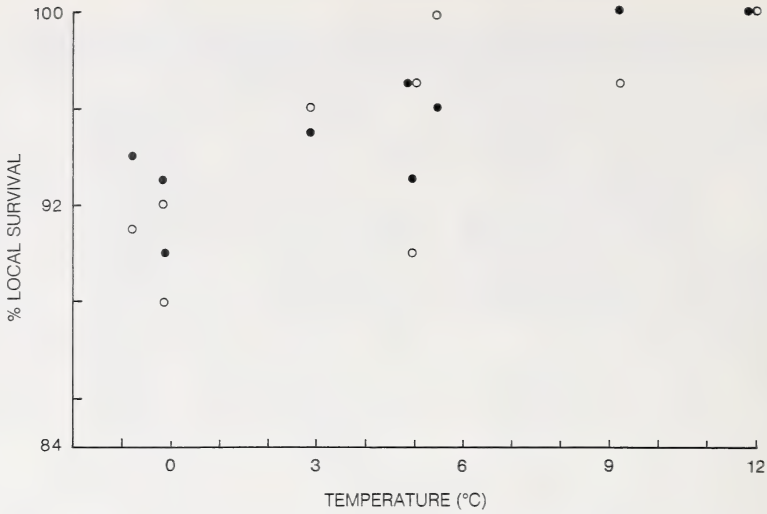

Fig. 4. Linear correlation of mean monthly maximum winter temperature with monthly survival (from November to February) over the three years of study, in both habitats. Coniferous area ○, deciduous area ●

Although changes between years in half-year survival-rate were small and statistically not significant, a positive correlation existed between food abundance in year t and annual survival (year t to t+1) ($r = 0.760$; $n = 7$; $P < 0.05$). No density dependent effect on survival was found.

Survival from year t to t+1 was not significantly correlated with density at year t+1 ($r = 0.668$; $n = 7$; $0.1 > P > 0.05$), although a tendency existed of higher densities after a year with a high survival-rate.

Reproduction

In order to invest in reproduction females must have a high body weight (Wauters and Dhondt 1989b). The percentage of females that came into oestrus varied between years (table 4) and between reproductive seasons (spring or summer reproduction).

The measurement of reproductive rate that can be compared between years is the number of juveniles weaned per adult female, which is the product of the proportion of adult females in oestrus, with the proportion of oestrus females that reproduced successfully and with the number of young weaned per successful female. The importance of each of these parameters was analysed as described in the methods and as shown in table 1.

Since the abundance of tree seeds and winter temperature both affect body weight in red squirrels (Wauters and Dhondt 1989a), and a minimum body weight is required to enter oestrus (Wauters and Dhondt 1989b), the effect of winter temperature and food abundance on k_1 and of food abundance on k_5 was tested. No significant relations were found however. The number of squirrels present at the start of the breeding season might also have an effect on the number of females entering oestrus. When density is high, intraspecific competition for food becomes more intense and many of the yearling females will decrease in weight and hence will not be able to enter oestrus. Normalised density at the onset of pre-oestrus (December or April) was positively correlated to k_1 or k_5 ($r = 0.698$; $n = 12$; $P < 0.02$).

Once a female is in oestrus and has mated she can still fail in raising young. Losses of young caused by breeding-failure (k_2 and k_6) added most strongly to total reproductive losses (K) and was positively correlated with it ($r = 0.964$; $n = 6$; $P < 0.01$), (fig. 5).

Table 4. **Annual reproduction in both habitats from 1985 to 1987**

Year	n	Oestrus (%)			Total	Successful breeding (%)			Mean n° young/SF	Mean n° young/AF
		0×	1×	2×		1×	2×	Total		
Coniferous area										
1985	15	1	4	10	14 (94)	1	6	13 (93)	2.00	1.73
1986	20	4	5	11	16 (80)	3	1	5 (31)	1.80	0.45
1987	17	0	5	12	17 (100)	6	3	12 (71)	1.75	1.24
Deciduous area										
1985	10	1	4	5	9 (90)	5	0	5 (56)	1.80	0.90
1986	15	2	3	10	13 (87)	6	0	6 (46)	1.83	0.73
1987	17	1	5	11	16 (94)	8	2	12 (75)	2.17	1.53

Adult females divided into three categories: not in oestrus (0×); one breeding season in oestrus (1×); both breeding seasons in oestrus (2×). Adult females = AF; successfully reproducing females = SF

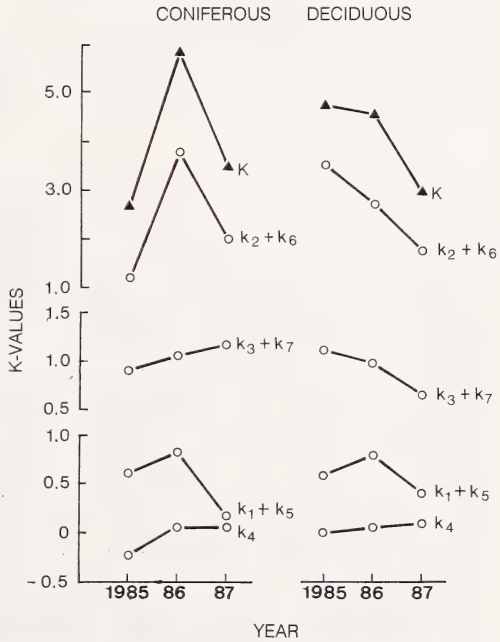

Fig. 5. The different k-values for reproduction as explained in Table 1, according to year and habitat

Breeding-failure can have two reasons: 1. an oestrus female does not have a sufficiently high body weight to cope with the increasing energy-costs of pregnancy, and the embryos are lost; 2. an oestrus females gives birth to a litter, but is not able to raise her young due to a strong drop in body weight while lactating, or due to nest-disturbance or nest-predation (Wauters and Dhondt 1989b). Since food abundance affects body weight and a high body weight is necessary to reproduce successfully (Wauters and Dhondt 1989b), the size of the seed-crop might influence breeding-success. Moreover successful breeding was only observed in dominant (rank I) females in the coniferous woodland, while in the deciduous woodland also a few lower ranked females (rank II) succeeded in raising young when food was very abundant. Related to their dominance position these rank-I females inhabit home ranges with intrasexual exclusive core-areas. Within these core-areas nests can be effectively defended, and interference from other squirrels minimalised (unpubl. data). When female density increases however, more subordinate females enter the population, and a lower proportion of females is able to establish a core-area than at low density. Hence the proportion of females successfully breeding is likely to fluctuate according to female-density. Therefore a multiple linear regression analysis of food abundance and female density at the onset of breeding on k_2 and k_6 was performed, for each habitat separately. In the coniferous area breeding-failure was strongly correlated with female density (partial $r = 0.959$; $n = 6$; $P < 0.01$), but not with food abundance (partial r =

−0.445; N.S.). In the deciduous habitat no relation was found.

Finally losses of young occur through mortality of sucklings between birth and weaning in litters of successfully breeding females ($k_3 + k_7$, fig. 5). Since a female's body weight must be sufficiently high while lactating, and body weight depends on food-availability (Wauters and Dhondt 1989b), the size of the seed-crop is likely to influence suckling mortality. Food abundance the previous winter was negatively correlated to $k_3 + k_7$ ($r = -0.884$; $n = 6$; $P < 0.02$). In addition the mean number of young weaned per successful female was higher following a winter with a large seed crop, than after a winter with a smaller seed-crop ($r = 0.976$; $n = 6$; $P < 0.001$).

Dispersal

Only a small proportion of squirrels that are born in a woodlot take up residence in the vicinity of their birth-place. Most juveniles disperse when about three months old (unpublished data). Adult squirrels, once they have established a home range, normally remain resident for the rest of their lives (Gurnell 1987; Wauters and Dhondt 1985). Hence dispersal does not take place the whole year round, but peaks in April–June and October–November, with some winter dispersal round January–February (fig. 6). A three-way analysis of variance was calculated to test the effects of area, sex and season on the number of immigrants. None of the three factors examined had a significant effect on the number of immigrants. The two-factor interaction between sex and season however was statistically significant ($F = 29.81$; d.f. = 1, 17; $P < 0.001$), while the others were not (2-factor interactions: area and sex $F = 2.217$; d.f. = 1, 17; N.S.; area and season $F = 0.55$; d.f. = 1, 17; N.S.). This suggested that there were differences in immigration rate between males and females according to the time of the year,

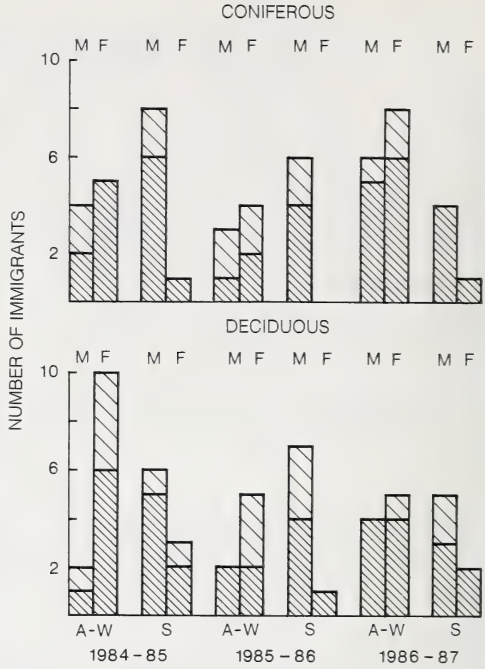

Fig. 6. Autumn-winter (A-W) and spring (S) immigration for males (M) and females (F) in both habitats between 1984 and 1987. Immigrants that did not settle in the study-area ▧, and recruited immigrants ▨

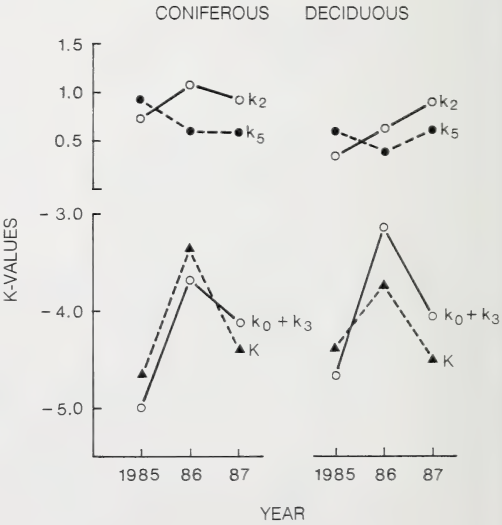

Fig. 7. The different k-values for dispersal as explained in Table 1, according to year and habitat

that were similar for both habitats. We therefore calculated a one-way ANOVA testing the effect of season on the number of immigrants, for each sex separately. Both in males ($F = 8.721$; d.f. = 1, 10; $P < 0.02$) and in females ($F = 21.788$; d.f. = 1, 10; $P = 0.001$), the number of squirrels immigrating differed according to the time of the year (fig. 6).

The number of squirrels that immigrated into the study areas differed between years. Table 1 shows how immigration and emigration rate were analysed. Total annual immigration rate ($k_0 + k_3$) showed the same pattern in both habitats (fig. 7). Since winter temperature fluctuates similarly in both habitats, and differences in winter temperature cause differential winter-survival of juveniles and subadults (which will immigrate in late winter or in the following spring), and because spring reproduction varies between years (spring-born juveniles immigrate next autumn), the effect of winter temperature on immigration rate the following year was tested. A positive correlation ($r = 0.931$; $n = 6$; $P < 0.01$) suggested that more squirrels immigrated after a relatively warm winter than after a cold winter.

Since both increased density and lower food abundance are likely to increase intraspecific competition, which on its turn might affect dispersal, a multiple linear regression analysis of density (spring and autumn) and food abundance on emigration rate in spring-summer (k_2) and in autumn-winter (k_5) was performed. Spring density was positively correlated with k_2 (partial $r = 0.888$; $n = 6$; $P < 0.02$), and autumn density with k_5 (partial $r = 0.879$; $n = 6$; $P < 0.02$). No correlations were found with food abundance. Thus emigration rate was higher at high density and decreased when squirrel numbers were low.

Discussion

Changes in numbers

Due to the fact that most squirrel studies have been relatively short-termed, evidence of density regulation, or the lack of it, is very scarce.

In our populations changes in density between years were not similar in both study-areas. Density fluctuations were positively correlated with food abundance and winter temperature, both factors explained together 96 % of the annual variation in density. Since these factors are density independent, they are not able to regulate red squirrel numbers. However the annual changes in density, from 1.01/ha to 1.41/ha, or 39 % in coniferous woodland, and from 0.84/ha to 1.16/ha, or 38 % in deciduous woodland, were small compared with the annual changes in food abundance (65 % in the coniferous, up to 750 % in the deciduous area, table 2). Thus, density fluctuations appear to be dampened. When density of the previous year was added to the regression model, its partial correlation coefficient ($r = -0.630$) was statistically not significant and it did not explain any additional variation in population density. It must be mentioned however that in the coniferous habitat no extreme shortate or abundance of food has been observed over the four year study-period, while in the deciduous habitat, as mentioned above, density varied little, despite extreme changes in the seed-crop of deciduous trees. Tonkin (1983) found similarly small changes in red squirrel numbers (0.5 to 0.8/ha) accompagnied by stronger changes in the acorn and hazelnut-crop in a British deciduous woodland.

If red squirrel populations are regulated to some extent, it is important to know where during the annual population-cycle density-regulating factors act, and on which processes (survival, reproduction, dispersal).

Survival

Local survival was not related to density in our two populations. On the other hand mean monthly temperature in the winter-months (November–February) was strongly correlated with monthly survival. The effect of temperature on survival, especially during periods of

stressing weather conditions, has also been demonstrated for other squirrel-species. In fox (Nixon and McClain 1969) and pine squirrels (Rusch and Reeder 1978) winter temperature was positively correlated with survival. In tassel-eared squirrels living in mountaneous areas with long periods of snow cover, the length of the period with a snow-depth of > 10 cm is strongly correlated with annual mortality (Stephenson and Brown 1980; Brown 1982). The size of the seed-crop positively influenced local survival in our study-areas. Tonkin (1983) also found a higher survival in a year following a good seed-crop and a poor survival when deciduous trees produced a small crop. Food abundance positively influenced survival also in pine squirrels (Kemp and Keith 1970; Rusch and Reeder 1978; Halvorson and Engeman 1983), tassel-eared squirrels (Keith 1965) and grey squirrels (Nixon et al. 1975; Gurnell 1987).

Although differences in survival between males and females are observed in pine (Rusch and Reeder 1978) as well as in red squirrels (Lampio 1967), we found no such differences in our study-areas. In pine squirrels males survived better than females, while in Scandinavian red squirrels the opposite was suggested based on sex-ratio data of shot animals. In both studies differential predation-pressure is used to explain these differences. The fact that important predators as marten, *Martes martes,* and goshawk, *Accipiter gentilis,* are absent in our study-areas, while others as fox, *Vulpes vulpes,* stoat, *Mustela erminea,* and buzzard, *Buteo buteo,* are rare, might be responsible for the equal survival-rates of both sexes, despite behavioural differences and differences in mobility (Wauters and Dhondt 1985, 1986). Year round survival of adult red squirrels (mean 61 %) was higher than that of subadults (mean 27 %). This is also the case in other squirrel-species, especially in winter (Barkalow et al. 1970; Kemp and Keith 1970; Nixon et al. 1975; Thompson 1978; Stephenson and Brown 1980; Halvorson and Engeman 1983; Tonkin 1983).

Reproduction

Reproductive rate, expressed as the number of young weaned per adult female, was investigated using transformed data (table 1). A first k-value referring to losses of young caused by infertility of adult females (not entering oestrus) was density dependent. While most of the females entered oestrus at lower densities, fewer females were in a good condition (> 300 g, Wauters and Dhondt 1989b) when density was high.

A significant effect of female density on breeding success was found in the coniferous woodland. As discussed above this was related to the social organisation of the population (ranging behaviour and dominance position) which differed according to habitat type. Since the k-values (k_2 and k_6) referring to losses of young due to breeding-failure were large and strongly correlated with total K, female density has a strong effect on the rate of reproductive increase in the squirrel population. Hence density fluctuations caused by reproduction are at least dampened due to density dependent effects.

The number of young weaned varied according to food abundance, with more young produced per successful female after a year with a heavy seed-crop. In pine squirrels, where mean litter size varied from 2.8 to 4.7, the date of onset of breeding was significantly correlated with mean yearly litter size over four years (Rusch and Reeder 1978). Onset of breeding on its term was influenced by the length of the period of snow-cover and by the size of the seed-crop.

Dispersal

In general the majority of dispersing squirrels are subadults and juveniles in search for an area to settle (Mosby 1969; Thompson 1978). In our red squirrel populations the total number of dispersing squirrels was not related to food-supply, nor was it density dependent. In contrast the proportion of immigrants and juveniles that settled ranged from 35 % in the coniferous and 43 % in the deciduous woodland when squirrel numbers were

high, up to 50 % and 64 % respectively at low density, and was strongly density dependent. Tonkin (1983) found only 33 % to 38 % of immigrants becoming residents in her study-area. Similar data are found in grey and fox squirrels, where juveniles and subadults are thought to be sensitive to changes in density, due to their low position in the social hierarchy (Nixon et al. 1975). When densities are high mortality and dispersal increase in these low ranked individuals. Thompson (1978) stated that in grey squirrels the dispersal of surplus young animals, caused by intraspecific agonistic behaviour of residents during autumn (when seeds are harvested and cached), is a major factor in the determination of winter density. The results of his study agree with the general idea of pre-saturation dispersal (Lidicker 1962). Also in territorial pine squirrels a similar mechanism is found. In autumn resident adults reaffirm their year-round territories in suitable habitat, while juveniles disperse and try to establish transient territories in less suitable (deciduous) habitat or become floaters with no territory (Kemp and Keith 1970; Rusch and Reeder 1978). Since they need a large midden of cached food (cones, nuts) to survive winter (Smith 1968), only pine squirrels that established a territory in suitable habitat will have a high survival, while many dispersing young animals will die.

Furthermore sex-ratios of immigrants were male biased in late spring and female biased in autumn-winter in both our study-areas. We suggest that these differences in immigration-rate and timing between the sexes are related to seasonal changes in the intensity of intraspecific competition that are triggered by changes in the food-supply and in home range use. The situation presented here is typical for the coniferous habitat, but might be applied to the deciduous habitat also if some minor changes are made. From September onwards, throughout winter adult females do no longer defend their young, which have become independent, and concentrate their activity in small areas of their home range where seed abundance is high. Dispersing females now have the chance to immigrate into suitable habitat between the core-areas of the adult females' ranges. There however intraspecific competition with other immigrants and with juveniles is high, and many of them, as well as many juveniles, are forced to emigrate. Only the more dominant, with the highest body weight (Wauters and Dhondt 1989b) are able to establish permanent home ranges. From March onwards until September adult females become very aggressive towards other squirrels, especially other females, while defending nesting-sites and possibly also patches of good foop-supplies scattered throughout their home range. No further immigration is possible at this time. In males, which use their home ranges more homogeneously and which show stronger overlap of ranges, competition for food is more intense as long as tree seeds are available (July to April). Therefore only few immigrants will enter the population during this period. In May and June however squirrels feed on food-resources that are overabundant, but only for a short time (Wauters and Dhondt 1987), and two or three squirrels sharing the same oak searching for flowers and insects are not a rare sight. Moreover in May adult males are occupied in several mating-chases and hence do not have the time to interact with immigrating subadults. Therefore immigration-rate of males is highest in the May–June period, while in July, when the new cone-crop is harvested (Wauters and Dhondt 1987), some will be forced to emigrate and others will establish residency.

We conclude that although red squirrel numbers clearly fluctuate in relation to changes in food-supply and weather conditions, these fluctuations are dampened by density dependent processes. Both in reproduction (% of adult females entering oestrus and number of females successfully breeding) but especially in dispersal (recruitment rate of immigrants and juveniles) regulating processes are at work, triggered by the intensity of intraspecific competition, which increases at high density and decreases at low density. More data, however, over a longer time period, on the relationship between social behaviour, spatial organisation, food-supply and population processes are needed to confirm our conclusions about density regulation in red squirrel populations.

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Zusammenfassung

Populationsdynamik von Eichhörnchen (Sciurus vulgaris Linnaeus, 1758) in verschiedenen Habitaten

Von Oktober 1984 bis Januar 1988 untersuchten wir die Populationsdynamik von Eichhörnchen *(Sciurus vulgaris)* in einem Nadel- und einem Mischwald. Dazu wurden die Hörnchen regelmäßig lebend gefangen und individuell farbig markiert. Ihre Dichte schwankte im Jahreslauf und wurde vom Nahrungsangebot und der Winterkälte beeinflußt. Die jährliche Überlebensrate war positiv mit dem Nahrungsangebot korreliert und bei Adulten höher als bei Jungtieren. Der Anteil von Weibchen, die in Östrus kamen und von solchen, die Junge aufzogen, war dichteabhängig. Die Zahl der in einem Wurf aufgezogenen Jungen war ebenfalls positiv mit der verfügbaren Nahrungsmenge verknüpft. Männchen und Weibchen wanderten in unterschiedlichen Jahreszeiten zu, was mit Unterschieden im Sozialverhalten erklärt werden konnte. Die Emigrationsrate war in beiden Populationen bei höherer Dichte größer als bei geringerer. Die Dichte wurde also offenbar über die Fortpflanzungs- und die Abwanderungsrate gesteuert.

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Comparison of the diets of two sympatric lagomorphs, *Lepus europaeus* (Pallas) and *Oryctolagus cuniculus* (L.) in an agroecosystem of the Ile-de-France

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Abstract

The diets of the European hare (*Lepus europaeus* Pallas) and wild rabbit (*Oryctolagus cuniculus* L.) in an agrosystem of Ile-de-France are compared. The results are based on analysis of faeces collected at least monthly at 4 sites over one or two annual cycles.

Hares and rabbits had very similar diets. Grasses made up the base of their diet (50 to 100 % of the fragments found in the faeces) of which wheat was the preferred food item throughout the year. Their diet was more varied in summer and fall, and included maize, inflorescences of grasses, and various dicotyledons, as well as *Equisetum arvense* for the hare. The difference between to two species' food choices are related to the behaviour of food selection: the proximity of food resources to the warrens for the rabbits and, on a larger scale, the repartition of fields for the hare.

These results show that the rabbit is a generalist compared with the hare which is more selective. Although feeding on the same plants in certain seasons, the two Lagomorphs exploit different areas, and are therefore unlikely to compete for food under these circumstances.

Introduction

The European hare *(Lepus europaeus)* and the gray partridge *(Perdix perdix)* are the main game species of the agroecosystems of Ile-de-France. In spite of this and the determining role of diet on the status and management of the hare population, its diet has not yet been studied in France. Our current knowledge is essentially based on the works of Matuszewski (1966), Brüll (1976), Steineck (1978), Homolka (1982, 1983, 1987a, 1987b), and of Frylestam (1986), which were carried out under different climatic conditions, particularly during winter snow cover.

Another lagomorph, the wild rabbit *(Oryctolagus cuniculus)* is equally associated to these agroecosystems, when uncultivated zones exist close enough to allow installation of warrens. Their diet in uncultivated areas has been the subject of numerous publications (Gillham 1955; Cooke 1974; Chapuis 1981; Bhadresa 1982), but few deal with their dietary preferences in cultivated areas (Turcek 1959; Chapuis 1981, 1982; Homolka 1987b, 1988).

On the other hand, following the drop in rabbit populations resulting from the introduction of the virus myxomatosis, Morel (1956), Moore (1956), Rothschild (1961), Rothschild and Marsh (1956, 1958) noted a general increase in hare populations. In 1960–1970, while rabbit populations were recovering (Trout et al. 1976; Arthur et al. 1980), a decrease in the number of hares was recorded (Broekhuizen 1975; Tapper and Pearson 1984). Different hypotheses were proposed to explain the nature of these interrelations: behaviour, parasitic and pathological interactions, food competition, intensification of farming (Moore 1956; Broekhuizen 1975; Broekhuizen and Kemmers 1976). Barnes and Tapper (1986) recently refuted some of these hypotheses, notably the

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food competition. On the contrary, in agrocenoses of Czechoslovakia, Homolka (1987b) states that "hares and rabbits are evident trophic competitors exploiting similar trophic supplies during the greatest part of the year".

In this paper I analyze the diet of these lagomorphs in an agroecosystem of Ile-de-France (Paris region), which is favorable to the hare, though the rabbit is also found locally here. Their utilization of trophic resources is compared in order to evaluate the possibility that they could compete for food.

Study area

Situated 18 km southeast of Paris (48°44′ N, 2°11′ E) the study area consists of 200 hectares of heavily cultivated land on siliceous-clay silt. The climate is oceanic with continental tendencies and some years it is marked by a 15 day period of light snow cover in January/February which does not, however, prevent access to the herb layer.

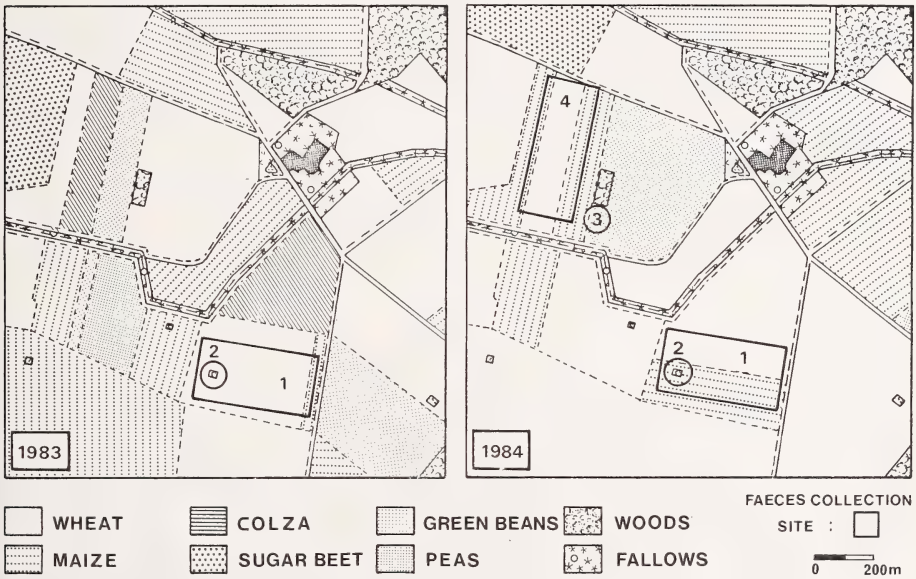

Fig. 1. Distribution of the cultivated plots in June 1983 and June 1984, and localization of faecal collection sites for the hare and rabbit

The study area (Fig. 1) consists of 3 to 15 hectares fields cultivating mainly winter wheat *(Triticum sativum)* (40 to 50 % of the study area depending on the year), maize *(Zea mays)* (30 %), peas *(Pisum sativum)* (10 %) and, less commonly, oilseed rape *(Brassica napus)* (up to 10 %), sugar beet *(Beta vulgaris)* (5 %) and green beans *(Phaseolus vulgaris)* (3 %). The uncultivated zones (isolated woods, access roads, fallows) cover only small surfaces. About 15 adventice species (*Solanum nigrum, Equisetum arvense, Polygonum* spp.) are well represented on the cultivated plots. Roadside vegetation is primarily graminaceous (*Lolium multiflorum, Phleum pratense, Poa* spp.) with a few dicotyledons *(Trifolium pratense, Achillea millefolium, Ranunculus repens).* In the fallows (banks of ditches), the herb layer is mainly composed of *Agropyrum repens, Phalaris arundinacea, Urtica dioica,* the shrub layer of *Salix* spp. and *Prunus spinosa.* A few fruit trees, *Pirus malus, Cerasus avium,* are also found. The wooded zones which offer protection to the warrens are dominated by trees, mainly *Fraxinus excelsior, Quercus pedunculata* and *Cerasus avium,* by *Sambucus nigra, Prunus spinosa, Ligustrum vulgare* and *Crataegus monogyna* for the shrub layer, and by *Urtica dioica, Rubus* sp., *Hedera helix* and *Galium aparine* for the herb layer.

Hares occupy the entire study area; the sites for faeces collection were therefore selected according to the localisation of rabbits (Fig. 1). In the first year, samples were taken from two sites (1, 2) in one zone; in the second year two others were added (3, 4) in another zone. Based on home ranges of

approximately 2 ha for the rabbit (from 1.2 to 2.7 ha in the same habitat: Arthur (1989) and 30 ha for the hare (from 16 to 38 ha according to the habitat: Pielowski 1972; Schneider 1978; Broekhuizen and Maaskamp 1982; Ricci 1983, Homolka 1985), cultivated species available per site were as follows: site 1 (hare): wheat and maize, to which were added oilseed rape, peas, and green beans in 1983; site 2 (rabbit): wheat, maize; site 3 (rabbit): peas, maize and wheat; site 4 (hare): wheat, maize, sugar beet, peas.

Material and methods

The hare's and rabbit's diets were analyzed by a previously tested method of microscopic identification of epidermal fragments in faeces (Chapuis 1980). The samples were collected on surfaces of 0.3 ha for the rabbit (sites 2 and 3) and 3 ha for the hare (sites 1 and 4). The collection periodicity varied from 15 days to one month depending on the season, from February 1983 to February 1985 at sites 1 and 2, and from January 1984 to January 1985 at sites 3 and 4. Each sample was comprised of 15 to 20 fecal pellets taken from a maximum number of pellet groups. I identified 350 to 400 fragments (from 0.25 to 2 mm in size) per sample, distributed among 100 microscopic fields (20 fields/slide). The results are expressed in percentage of relative abundance.

This method has been evaluated elsewhere (Westoby et al. 1976; Chapuis 1980; Holeckek et al. 1982). To minimize the problems of underestimation of certain food items, many authors (Stewart 1967; Barker 1986) recommend applying correction factors. As my aim was to compare the diets to two species having the same digestive mechanisms and to study the evolution of their food preferences over the seasons depending on food availability, I didn't consider it necessary to calculate and apply these correction factors.

Further observation of browsing traces showed that all species noted as having been consumed were also found in the faeces. This suggests that the method of fecal analysis did not lead to major biases here.

For comparisons I used the overlap index C of Zaret and Rand (1971) and the diversity index I of Shannon and Weaver (1949).

Results

Hare's feeding

At site 1 (Fig. 2), starting in October, the hare's most important food source was wheat germinated from winter crops. In June the leaves were left in favor of the ears which were ingested until August. If ploughing did not immediately follow harvesting, young shoots of grains left on the ground were consumed, before the appearance of the young shoots on neighboring fields resulting from the fall sowing. This was reflected by the predominance of this cereal in their diet during the two study years. In summer, feeding was more varied with consumption of maize during the first two months following germination (maximum 40 % in June 1983 and 30 % in August 1984) and consumption of *Equisetum arvense* (30 % maximum in July/August). Various dicotyledons (*Matricaria discoidea, Polygonum* spp.) and graminea (*Lolium multiflorum, Poa* spp.) were ingested in small amounts, especially in June and September–October, periods when the leaves of wheat had dried out or were unavailable. Even though the field was close to the site of faeces collection in 1983, pea plants were rarely consumed. A maximum of 8.6 % was recorded in May upon apparition of the young shoots and grain in October (5 %) upon germination of fallen grains. The green bean plant was ingested only in July (4.2 %) when the first leaves appeared.

The hare's diet at site 4 (Fig. 3) was very similar to that in site 1. The only differences were related to a lesser consumption of *Equisetum arvense,* and to a greater proportion of various graminea at the onset of summer, essentially *Lolium multiflorum* found along roads. The leaves and roots of beet were virtually not consumed (maximum 1 % in November).

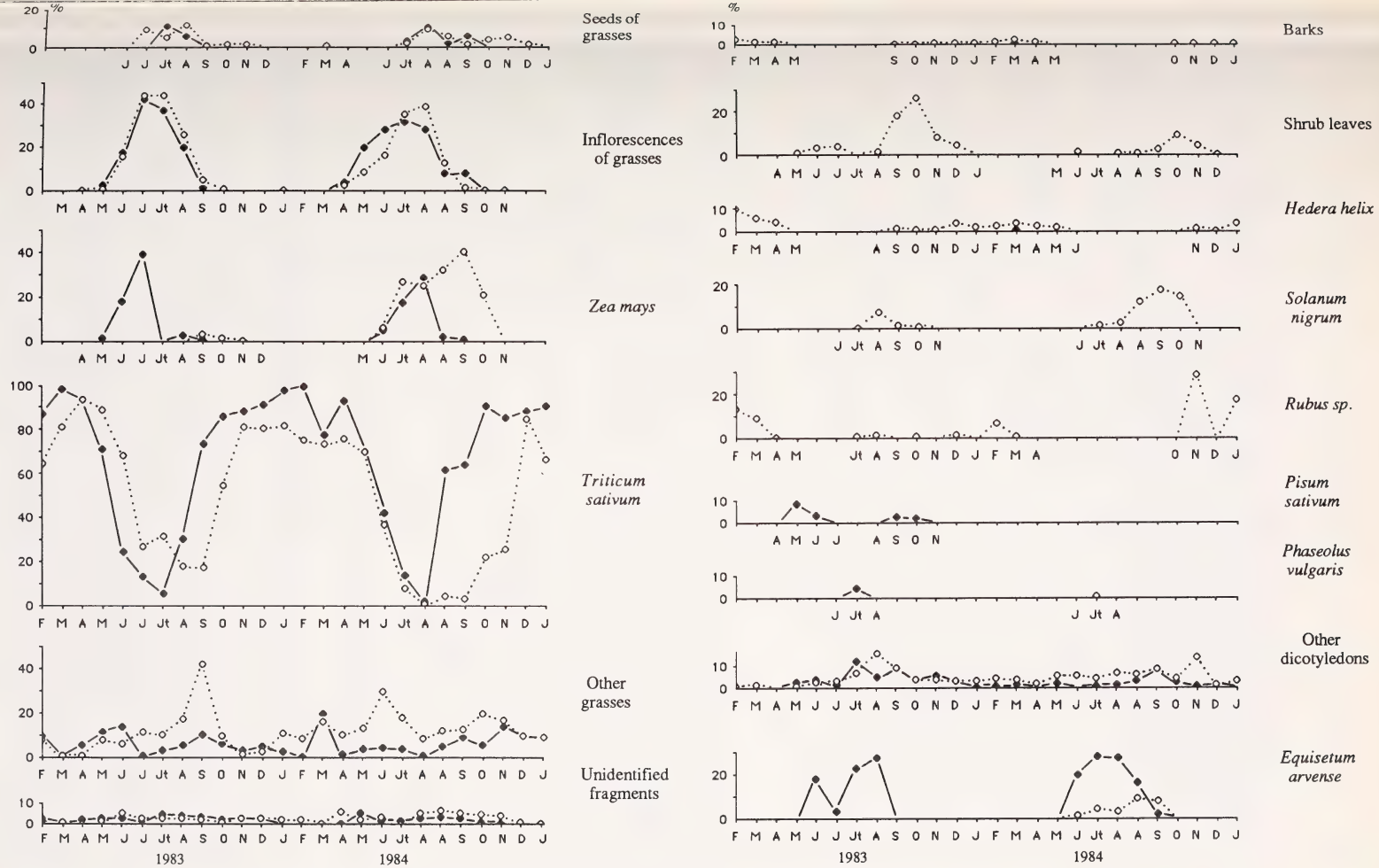

Fig. 2. Evolution of the diet of the European hare (solid symbols) and the wild rabbit (open symbols) from February 1983 to January 1985 at sites 1 and 2

Wild rabbit's feeding

The rabbit's diet at site 2 (Fig. 2) was very similar to that of the hare: wheat was preponderant in winter, spring and fall. In summer rabbits mainly fed on inflorescences of graminea (wheat) and leaves of maize, in different proportions according to the year. Maize and its adventice plant *Equisetum arvense*, were ingested in 1984 at a time when the field was in the immediate vicinity of the warrens, but were ignored by the rabbits in 1983 because of the field's distance (approx. 100 m from the warrens). The grain teguments

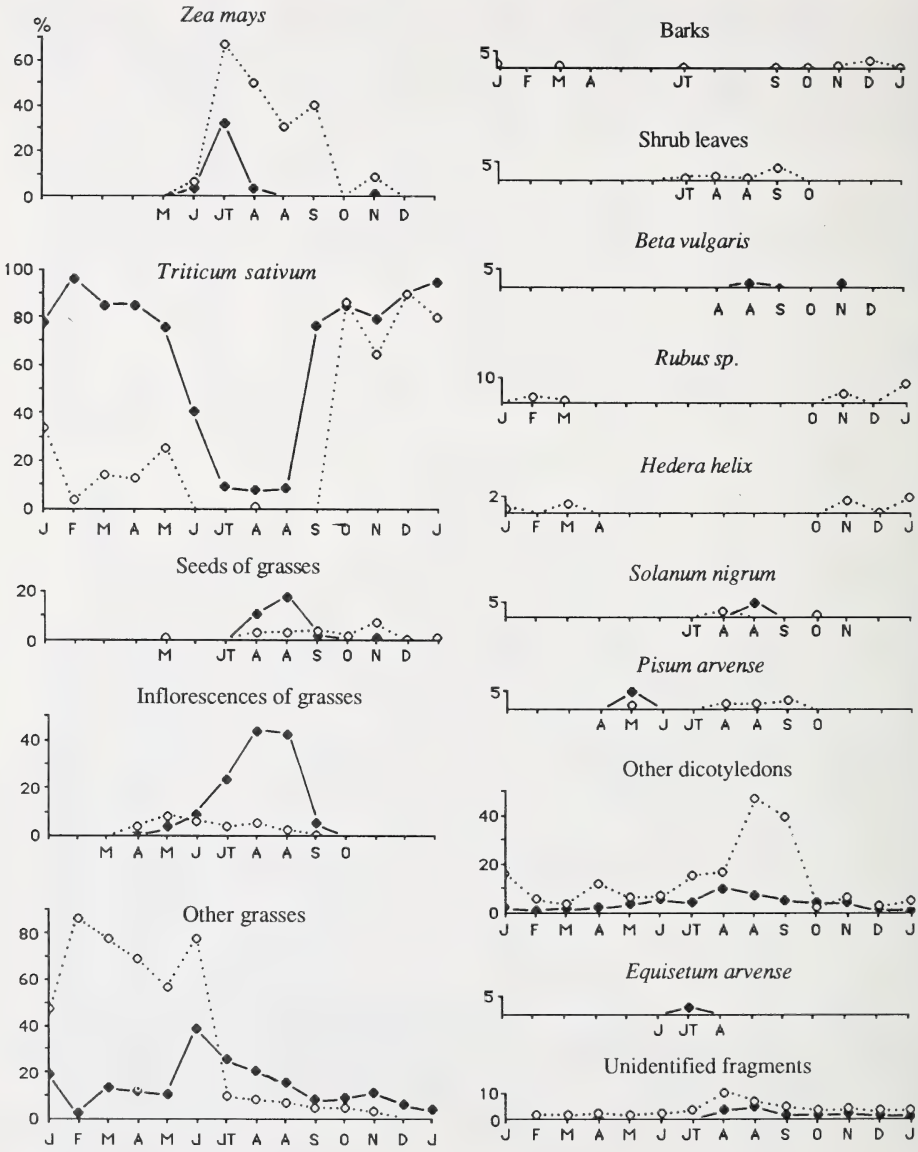

Fig. 3. Evolution of the diet of the European hare (solid symbols) and the wild rabbit (open symbols) from January 1984 to January 1985 at sites 3 and 4

present in the faeces collected from October to December 1984 correspond mainly to the consumption of maize issued from cut or fallen stalks and ears left over from harvesting. Because of the drying out of wheat leaves and before the appearance of new shoots, the rabbit's diet was more varied at the beginning and end of summer. It consisted mainly of maize, wheat ears, and various grasses *(Lolium multiflorum, Phleum pratense, Poa trivialis),* of *Solanum nigrum* (foliage, flowers and seeds) and of other various dicotyledons. Fall was marked by the consumption of shrub leaves *(Prunus spinosa, Cerasus avium, Crataegus monogyna),* and in winter other underwood species (*Hedera helix, Rubus* sp.) were ingested along with small proportions of shrub bark.

At site 3 (Fig. 3), the absence of wheat on fields next to the warrens explains the consumption from January to June of grasses found on the access road situated at more than 100 m from the warrens. Nevertheless the rabbits cross the abandoned ditches, dry for most of the year, to feed on wheat. From October on, when newly sown wheat replaces the peas, the rabbits fed almost exclusively on this cereal, and did so until the end of the study. During summer the rabbits fed on maize, from its germination in June until September. At this time, various adventice dicotyledons were also ingested, especially in August and September. Among the other available species, the rabbits ate peas plants from a field adjacent to the woods (maximum 2.4 % only, in September), and in fall-winter, underwood species (bramble, ivy, shrub leaves and bark). As for site 2, consumption of gramineae grains (maize) was noted from August 1984 to January 1985.

Interspecific comparison

The fact that every food item cannot be determined down to the species level implies that the indexes do not give an absolute quantification of the diversity and the competition level between the two species, in terms of resource allocation. Nevertheless, relative variations of these indexes indicate the seasonal variations of food habits and of the overlap of their diets. The diversity indexes of the hare and rabbit diets show similar evolution over the seasons for the four sites (Fig. 4). Low in winter, these indexes increase in spring until

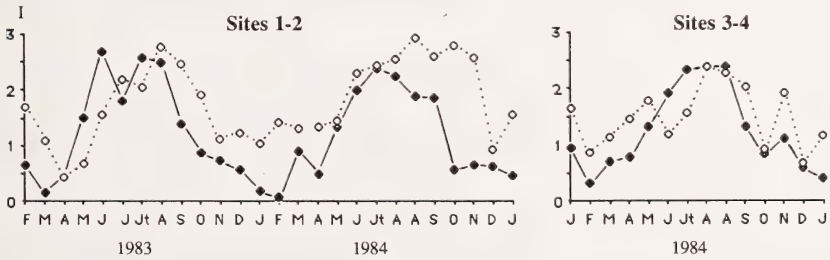

Fig. 4. Evolution of the diversity index I (Shannon and Weaver 1949) of the diets of the European hare (solid symbols) and the wild rabbit (open symbols) at sites 1–2 and 3–4

reaching a maximum in June–July for the hare and August–September for the rabbit. During fall-winter they decrease more rapidly for the hare than for the rabbit. The main differences between their diets are found during the seasons when the rabbits consume a greater variety of plants than do the hares. The differences recorded for the rabbit (site 1) from 1983 ro 1984 are linked to the availability of food in the vicinity of the warrens (presence of wheat in 1983 and maize in 1984).

The comparison of overlap index C (Fig. 5) shows that at site 1–2 the two species used the same food resources during winter and spring. The index decreased in summer and fall, notably in 1984 where $C < 0.6$ from August to November, indicating a very small overlap

of the diet (Brown and Lieberman 1973). At site 3–4 the index reveals the use of different resources from January to September, with nonetheless a great similarity of species consumed in June–July. From October to the end of this study, their diets were very similar (mainly wheat).

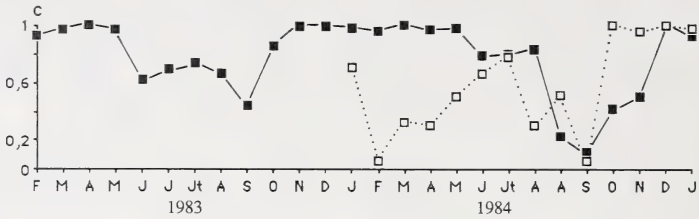

Fig. 5. Evolution of the overlap index C (Zaret and Rand 1971) of the diet of the European hare and the wild rabbit at sites 1–2 (solid symbols) and 3–4 (open symbols)

Discussion

In the study area, as in most other habitats, hares and rabbits fed essentially on grasses (50 to 100 % of the fragments found in the faeces). Among these, the leaves of wheat constituted the base of their diet from October to May. The rest of the year they consumed ears of wheat, leaves of maize, and various dicotyledons found in the fields and along the access roads. One adventice fern, *Equisetum arvense,* was particularly sought out by the hare.

Considering the availability of food resources, these results agree with the observations of other authors, particularly those of Homolka (1983) on the hare and of Chapuis (1982, 1986) and Homolka (1988) on the rabbit, in cultivated zones. However, Brüll (1976) and Frylestam (1986) noted a significant consumption of oilseed rape by the hare (15 to 39 % of the epidermis found in the stomachs collected in winter). Oilseed rape (variety "Bienvenu") occupied 10 % of our territory in 1983 and was completely ignored by the hare. This divergence of results could be due to difficulties in identifying rape leaf epidermes in faeces. More likely, it should be related to the presence of large surfaces of winter wheat, preferred to the crucifer. For the rabbit the oilseed rape was too far from the warrens and was therefore unaccessible. Even in other situations, this crucifer is usually ignored by the rabbit or ingested in small proportions (Chapuis 1982). On the other hand, contrary to observations in Eastern Europe (Turcek 1966; Kaluzinski 1976; Szukiel 1976; Homolka 1982), the hare did not use woods and thickets for feeding purposes in this study area. A constant winter snow cover in the East's more continental climate, which prevents access to the herbaceous layer explains this difference in diet.

At the study sites the monthly evolution of the diet of these two lagomorphs reveals some discrepancies at certain seasons, showing their different utilization of food resources. Since the morphological and physiological features of the two species are quite similar, the differences observed in their diet can be explained by their behaviour. For example at site 3 (Fig. 3) rabbits usually did not move further than 100 m to feed on wheat, which is still a preferred species (Chapuis 1982, 1986). In the same way, in August and September, they only ate the young wheat sprouts (from fallen grains after harvest) near their warrens. When wheat is no longer available, rabbits vary their diet. In summer, they fed on grasses and dicotyledons growing on access roads, on maize and, especially at site 1, on weeds such as *Solanum nigrum*. In fall, they ingested shrub leaves *(Prunus spinosa, Cerasus avium, Crataegus monogyna)* and in winter, underwood plants (*Rubus* sp., *Hedera helix*). In comparison, the hares cover larger areas and thus have a different diet at certains

seasons. They ate more wheat than rabbits, particulary in summer and fall, when young shoots were available. Maize was only consumed during June and July but *Equisetum arvense,* a scarce and localized species, was actively sought after from June to August (site 2). In fall, soon after wheat seedling time, hares fed almost exclusively on this crop until early summer. At this time, they discarded leaves and fed upon ears.

These results show that the two lagomorphs are selective herbivores, choosing precise foods, according to what is available in their feeding area. These choices are closely related to the phenological stage of plant species.

On the other hand, these results strengthen Westoby (1974) and Belovsky (1978) statement i.e. herbivores become "specialists" when food is abundant and "generalists" when food resources are limited. Because of the different behaviour of these two lagomorphs in the study area, this "specialist" tendency is more marked for the hare, whose foraging area is larger. This species also makes better use of the trophic potentialities of its habitat in adapting its foraging movements to the crops' phenology. Therefore, the hare can be more selective than the rabbit, whose feeding area is limited to the vicinity of its warren. This is why at certain seasons, the rabbit has to diversify its diet and, in that way, adopts a more "generalist" behaviour earlier than the hare (Fig. 2 and 3).

Although the results are close to those of Homolka (1987b), an interpretation leeds to the opposite conclusion: in the type of agroecosystem studied here, the two species do not compete for food. Even if their diets overlap at certain seasons, the plants eaten during these periods are in fact available in excess. Moreover, the two lagomorphs do not exploit the same surfaces.

These results clearly demonstrate that hares and rabbits have different trophic niches in this type of habitat. They also reinforce Barnes and Tapper (1986) assumption that the current decline of hares is not due to the increasing rabbit populations but to changes in farming practises. Moreover, the characteristics of new varieties of cultivated species could affect wild animal populations. For example, increasing cultivation of a new variety (00) of colza *(Brassica napus)* could be responsible for the mortality of the roe deer *(Capreolus capreolus)* in Austria (Onderscheka et al. 1987). Current studies in Europe are testing this assumption for the hare. However, preliminary results indicate that colza "00" does not seem to be directly responsible for the mortality of hares.

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Zusammenfassung

Vergleich der Nahrungsspektren von zwei sympatrischen Hasenartigen, Lepus europaeus (Pallas) und Oryctolagus cuniculus (L.) in einem Agrosystem der Ile-de-France

Die Nahrung des Feldhasen *(Lepus europaeus)* und des Wildkaninchens *(Oryctolagus cuniculus)* wird in Ackerland der Ile-de-France verglichen. Dazu wurden in monatlichem Abstand an vier Stellen Kotproben über 1–2 Jahre gesammelt und analysiert. Danach ist die Nahrung von Hase und Kaninchen sehr ähnlich. Gräser, und davon vor allem Weizen, bilden 50–100 % der Fragmente in den Faeces. Im Sommer war die Nahrung vielfältiger als im Winter und enthielt dann Mais, Grasblüten, verschiedene Kräuter und beim Hasen Ackerschachtelhalm *(Equisetum arvense).* Die Unterschiede in der Nahrung beruhen vor allem auf dem größeren Aktionsradius des Hasen und seinem Aufenthalt auf Feldern. Im Vergleich zum Kaninchen ist der Hase hier eher ein Nahrungsspezialist. Obwohl Hase und Kaninchen zu manchen Jahreszeiten dieselben Pflanzenarten fressen, besteht zwischen ihnen wahrscheinlich doch kaum Konkurrenz um Nahrung, weil sie diese unterschiedlichen Standorten entnehmen.

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Biochemical variation and differentiation in the Brown hare *(Lepus europaeus)* of Central Europe

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Abstract

Genetic variation in 127 brown hares *(Lepus europaeus)* from populations in Poland, Hungary and Austria was investigated by horizontal starch gel electrophoresis. 25 isoenzyme systems were examined in kidney and liver tissues. For comparison, data on Czechoslovakian brown hares screened by Hartl (1987) were also included in this study. From 39 loci scorable, 10 were polymorphic. Values of polymorphism (mean $\overline{P}$ = 0.163) and expected average heterozygosity (mean $\overline{H}$ = 0.048) were found to be similar to the corresponding mean values in mammals. Genetic differentiation between populations, however, is remarkably low, even over large geographic distances. These results are discussed with respect to genetic variability and differentiation in other lagomorphs, such as the wild rabbit and the pika.

Introduction

In contrast to other groups of mammals such as rodents, insectivores, seals and artiodactyles the amount and distribution of genetic variability in wild living populations of lagomorphs is only poorly known. Population genetic data obtained by electrophoretic multilocus investigations are available only for rabbits *(Oryctolagus cuniculus)* from Australia (Richardson 1980, 1981; Richardson et al. 1980; Daly 1981) and for pikas (*Ochotona princeps*– Glover et al. 1977; Tolliver et al. 1985) and cottontails (*Sylvilagus floridanus* – Scribner et al. 1983; van den Bussche et al. 1987) from North America.

Although the brown hare *(Lepus europaeus)* has been subjected to various biochemical-systematic investigations to evaluate the genetic distance from some close relatives (e.g. Schneider and Leipoldt 1983; Bonhomme et al. 1986; Hartl 1987), population genetic data are still lacking in this species. To get a first large scale impression on the amount and distribution of genetic variation in the brown hare we scored individuals from different sampling sites in Poland, Austria, Czechoslovakia and Hungary. The results are discussed with respect to the distribution of this species in Central Europe and to the population genetic data in other lagomorphs already studied, such as the wild rabbit and the pika.

Material and methods

A total of 127 brown hares was investigated in this study. The distribution of sampling sites in Poland, Austria and Hungary is shown in the map (Fig. 1). Tissue samples were collected either by local hunters or by members of the institutes mentioned in the list of authors' addresses. Liver and kidney were frozen immediately after death of the specimens and were stored either in liquid nitrogen or in a freezing box at −20 °C until electrophoresis. Preparation of tissue extracts, electrophoretic and staining procedures as well as the interpretation of electrophoretic band-patterns were performed according to routine methods (Hartl and Höger 1986; Hartl 1987).

The following 25 isoenzyme systems were screened (abbreviation and E.C. number are given in parentheses): α-glycerophosphate dehydrogenase (GDC, E.C. 1.1.1.8), sorbitol dehydrogenase (SDH, E.C. 1.1.1.14), lactate dehydrogenase (LDH, E.C. 1.1.1.27), malate dehydrogenase (MOR, E.C. 1.1.1.37), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), 6-phosphogluconate dehydrogenase (PGD, E.C. 1.1.1.44), glucose dehydrogenase (GDH, E.C. 1.1.1.47), glucose-6-phosphate dehy-

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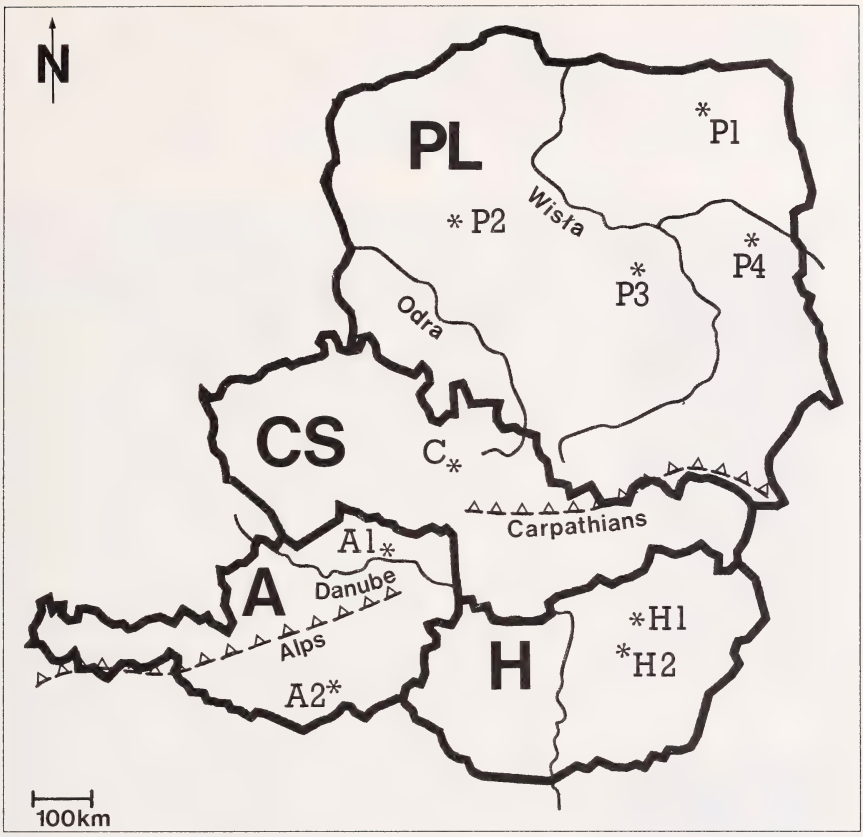


Fig. 1. Distribution of sampling sites in Poland (P1–P4), Hungary (H1, H2), Austria (A1, A2) and the origin of founder individuals of a brown hare breed at Litovel in Czechoslovakia (C)

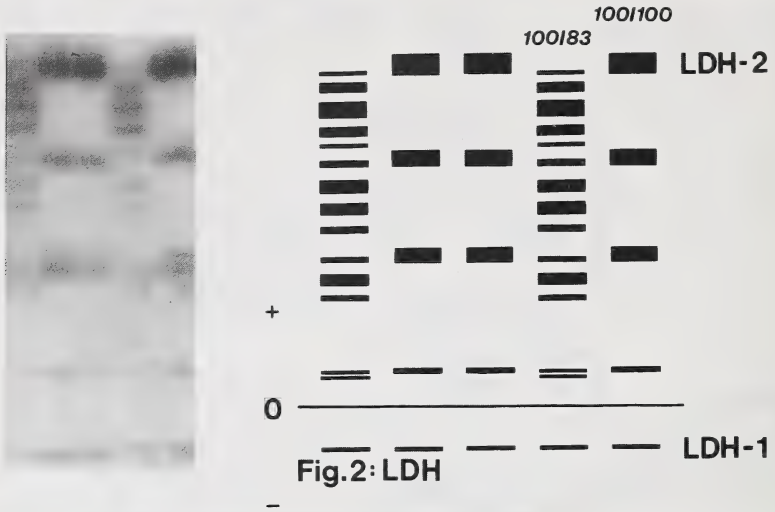
drogenase (GPD, E.C. 1.1.1.49), xanthine dehydrogenase (XDH, E.C. 1.2.3.2), glutamate dehydrogenase (GLUD, E.C. 1.4.1.3), catalase (CE, E.C. 1.11.1.6), superoxide dismutase (SOD, E.C. 1.15.1.1), glutamate oxaloacetate transaminase (GOT, E.C. 2.6.1.1), hexokinase (HK, E.C. 2.7.1.1), creatine kinase (CK, E.C. 2.7.3.2), adenylate kinase (AK, E.C. 2.7.4.3), phosphaglucomutase (PGM, E.C. 2.7.5.1), esterases (ES, E.C. 3.1.1.1), acid phosphatases (ACP, E.C. 3.1.3.2), peptidases (PEP, E.C. 3.4.11), aminoacylase-1 (ACY-1, E.C. 3.5.1.14), adenosine deaminase (ADA, E.C. 3.5.4.4), fumarate hydratase (FH, E.C. 4.2.1.2), mannosephosphate isomerase (MPI, E.C. 5.3.1.8) and glucosephosphate isomerase (GPI, E.C. 5.3.1.9).

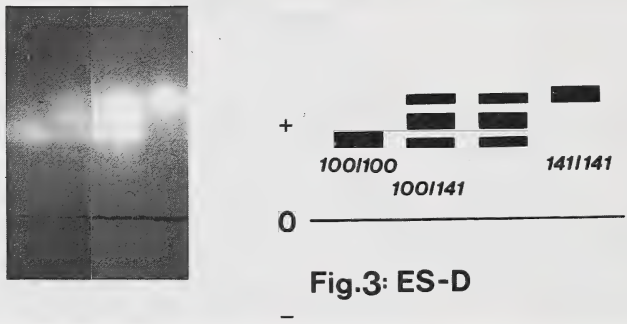
For comparison also the data on 25 brown hares from a breed at our institute (Hartl 1987) were included in the present study. ES-D was screened additionally in the same specimens, to make the data totally comparable. All these individuals are the offspring of a parent generation (24 animals) obtained from a breeding station at Litovel (ČSSR). This breed originates from wild living brown hares captured at the site shown in the map (Fig. 1, ČSSR).

Results

Screening of 25 enzyme systems representing 39 presumptive structural loci revealed polymorphism in 9 isoenzymes: LDH-2, MOR-2, IDH-2, PGD, ES-I, ES-D, PEP-2, ACY-1 and MPI. Additionally HK-2 is polymorphic in the Czechoslovakian hares screened by Hartl (1987). As an example, zymograms of the polymorphic isoenzymes

LDH-2 and ES-D as well as the genetic interpretation of band-patterns are shown in Figs. 2 and 3. Allele frequencies at the polymorphic enzyme loci are given in Table 1, values of polymorphism, heterozygosity and average heterozygosity are given in Table 2. The following isoenzymes were monomorphic in all specimens studied: GDC, SDH, LDH-1, MOR-1, IDH-1, GDH-2, GPD, XDH, GLUD, CE, SOD-1, -2, GOT-1, -2, HK-1, -3, CK-2, AK-2, -3, PGM-1, -2, ACP-1, -2, -3, PEP-1, ADA-1, FH, GPI-1 and -2.





Figs. 2–3. Electrophoretic and diagrammatic representation of some polymorphic isozenzymes in the brown hare

The total amount of genetic variation was analysed using Nei's (1975) measures of gene diversity. The average diversity among populations (D_{ST}) was 0.0028 and accounted for approximately 5.5 per cent (G_{ST} = 0.055) of the total gene diversity (H_T = 0.051).

Genetic relationships between populations were estimated using a number of different distance and cluster algorithms. The distance measures used were those compiled by Nei et al. (1983) and Rogers (1986). Dendrograms were constructed using the UPGMA as described by Nei (1975), Wagner networks according to Farris (1972). Furthermore, Fitch-Margoliash and Cavalli-Sforza – Edwards trees were constructed using the PHYLIP package of Felsenstein (1985). Nei's (1978) distances corrected for small sample sizes are given in Table 3. Fig. 4 shows a dendrogram which was constructed by means of

Table 1. **Allele frequencies at the polymorphic enzyme loci in the brown hare populations studied (99 % criterion)**
n = sample size of individuals

Population		H1	H2	P1	P2	P3	P4	C	A1	A2
n		17–30	25	16	5	10	12	19–25	12	17
Enzyme locus	allele	allele frequencies								
Ldh-2	*100*	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.91
	83	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.09
Mor-2	*100*	0.98	0.98	0.94	0.90	0.90	1.0	1.0	1.0	1.0
	121	0.02	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	79	0.0	0.02	0.06	0.10	0.10	0.0	0.0	0.0	0.0
Idh-2	*100*	0.98	0.96	1.0	1.0	1.0	1.0	0.98	1.0	0.94
	130	0.0	0.02	0.0	0.0	0.0	0.0	0.02	0.0	0.0
	83	0.02	0.02	0.0	0.0	0.0	0.0	0.0	0.0	0.06
Pgd	*100*	0.92	0.96	0.97	0.90	1.0	1.0	0.98	1.0	0.97
	170	0.07	0.02	0.0	0.10	0.0	0.0	0.0	0.0	0.0
	129	0.0	0.0	0.03	0.0	0.0	0.0	0.02	0.0	0.03
	117	0.01	0.02	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hk-2	*100*	1.0	1.0	1.0	1.0	1.0	1.0	0.95	1.0	1.0
	67	0.0	0.0	0.0	0.0	0.0	0.0	0.05	0.0	0.0
Es-I	*−100*	0.47	0.58	0.41	0.80	0.55	0.63	0.72	0.83	0.77
	−108	0.09	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	−75	0.32	0.42	0.59	0.20	0.45	0.33	0.28	0.17	0.23
	−42	0.12	0.0	0.0	0.0	0.0	0.04	0.0	0.0	0.0
Es-d	*100*	0.75	0.86	0.81	0.80	0.85	0.96	0.92	0.75	0.82
	141	0.25	0.14	0.19	0.20	0.15	0.04	0.08	0.25	0.18
Pep-2	*100*	0.77	0.72	0.81	0.90	0.85	0.63	0.74	0.77	0.71
	104	0.23	0.28	0.19	0.10	0.15	0.37	0.26	0.23	0.29
Acy-1	*100*	0.33	0.34	0.28	0.10	0.10	0.38	0.14	0.42	0.33
	81	0.40	0.42	0.66	0.60	0.70	0.37	0.74	0.33	0.38
	66	0.27	0.24	0.06	0.30	0.20	0.25	0.12	0.25	0.29
Mpi	*100*	0.98	1.0	0.81	0.90	1.0	1.0	1.0	0.96	1.0
	126	0.02	0.0	0.19	0.10	0.0	0.0	0.0	0.04	0.0

At each polymorphic isoenzyme locus the most common allele in population A 1 was designated arbitrarily *"100"*, variant alleles in the same or in other populations according to their relative mobility

the UPGMA using Nei's (1972) standard genetic distances. A comparison of the dendrograms based on different clustering algorithms and genetic dissimilarity measures displays the following relationships among the populations studied: The "eastern cluster" (H1, H2, P4), the "western cluster" (A1, A2) and the "northern cluster" (P2, P3, C) have been found in almost all cases, whereas the subclustering in the clusters consisting of three members changed frequently. To test the influence of sample size and the composition of genetic loci chosen the well known bootstrap and jackknife methods have been applied to automatically produce a range of comparable dendrograms. Constructed was a majority rule consensus tree (PHYLIP, Felsenstein 1985) for a hundred Nei (1972) distance/UPGMA trees, where the allele frequencies were simulated using multinomial distribution with the allele frequencies observed. The same procedure was followed, where for every tree distances were recalculated after randomly omitting 25 % of the genetic loci investigated. Whereas the jackknife consensus tree confirms the result by using all genetic loci

Table 2. **Genetic variability in the brown hare populations studied; the values are calculated over 39 loci**

Population	H1	H2	P1	P2	P3	P4	C	A1	A2
n	17–30	25	16	5	10	12	25	12	17
Enzyme locus	expected heterozygosity (H) / observed heterozygosity (H_o)								
Ldh-2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.161
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.177
Mor-2	0.033	0.039	0.118	0.180	0.180	0.0	0.0	0.0	0.0
	0.033	0.040	0.125	0.200	0.200	0.0	0.0	0.0	0.0
Idh-2	0.033	0.078	0.0	0.0	0.0	0.0	0.039	0.0	0.111
	0.033	0.080	0.0	0.0	0.0	0.0	0.040	0.0	0.118
Pgd	0.154	0.078	0.060	0.180	0.0	0.0	0.039	0.0	0.056
	0.167	0.080	0.062	0.200	0.0	0.0	0.040	0.0	0.059
Hk-2	0.0	0.0	0.0	0.0	0.0	0.0	0.100	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	0.105	0.0	0.0
Es-I	0.652	0.487	0.482	0.320	0.495	0.497	0.403	0.278	0.360
	0.529	0.360	0.437	0.400	0.300	0.500	0.240	0.333	0.353
Es-d	0.375	0.241	0.305	0.320	0.255	0.080	0.147	0.375	0.290
	0.367	0.280	0.250	0.400	0.300	0.083	0.160	0.167	0.235
Pep-2	0.360	0.403	0.305	0.180	0.255	0.469	0.384	0.351	0.415
	0.471	0.400	0.250	0.200	0.300	0.583	0.440	0.273	0.353
Acy-1	0.658	0.650	0.487	0.540	0.460	0.656	0.418	0.653	0.663
	0.700	0.640	0.500	0.800	0.500	0.583	0.440	0.417	0.765
Mpi	0.033	0.0	0.304	0.180	0.0	0.0	0.0	0.081	0.0
	0.033	0.0	0.187	0.200	0.0	0.0	0.0	0.083	0.0
$\overline{P}$	0.205	0.180	0.180	0.180	0.128	0.103	0.180	0.128	0.180
$\overline{H}$	0.060	0.051	0.053	0.049	0.042	0.044	0.039	0.045	0.053
$\overline{H}_o$	0.060	0.048	0.046	0.062	0.041	0.045	0.038	0.033	0.053

n = sample size of individuals, $\overline{P}$ = proportion of polymorphic loci, $\overline{H}$ = expected average heterozygosity, $\overline{H}_o$ = observed average heterozygosity

Table 3. **Genetic identities – above diagonal – and genetic distances – below diagonal – calculated according to Nei (1978)**

	H1	H2	P1	P2	P3	P4	C	A1	A2
H1	–	1.0000	0.9974	0.9991	0.9983	0.9991	0.9965	0.9988	0.9992
H2	0.0000	–	0.9981	0.9992	0.9991	1.0008	0.9981	0.9991	1.0001
P1	0.0026	0.0019	–	0.9976	0.9997	0.9961	0.9967	0.9940	0.9948
P2	0.0009	0.0008	0.0024	–	1.0014	0.9979	1.0005	1.0004	1.0002
P3	0.0017	0.0009	0.0003	−0.0014	–	0.9975	0.9999	0.9961	0.9974
P4	0.0009	−0.0008	0.0039	0.0021	0.0025	–	0.9980	0.9992	1.0004
C	0.0035	0.0019	0.0033	−0.0005	0.0001	0.0020	–	0.9967	0.9980
A1	0.0012	0.0009	0.0060	−0.0004	0.0039	0.0008	0.0033	–	1.0009
A2	0.0008	0.0000	0.0052	−0.0003	0.0026	−0.0004	0.0020	−0.0009	–

(Fig. 4), telling us that no single locus has an overwhelming influence on the topology of the tree, the bootstrap consensus tree exhibits a striking difference with respect to the position of P2 due to the small sample size (n=5) available from this population.

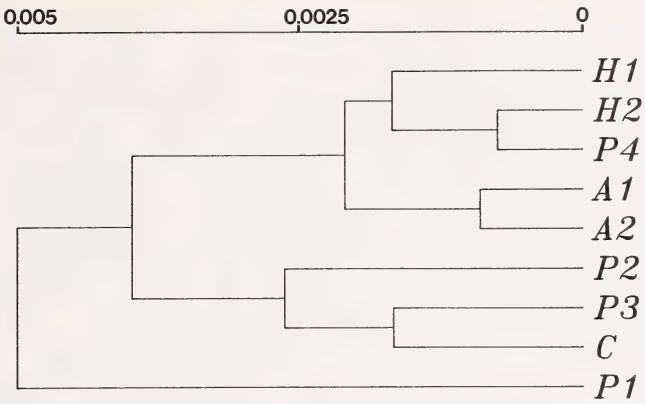


Fig. 4. Dendrogram constructed by means of the UPGMA using Nei's (1972) standard genetic distance

Discussion

The values of polymorphism (mean $\overline{P}$ = 0.163, sd. = 0.034) and expected average heterozygosity (mean $\overline{H}$ = 0.048, sd. = 0.007) detected in the present study on the brown hare are somewhat lower than those found by Bonhomme et al. (1986) in samples from Spain, possibly due to the larger number of rapidly evolving proteins examined by these authors (transferrin, several esterases). They are, however, closely similar to the mean values in mammals calculated over 184 species by Nevo et al. (1984). If genetic variation in brown hare populations (Table 2) is compared with population genetic data on other lagomorphs, quite similar values of polymorphism and heterozygosity have been found in a small sample of wild rabbits by Hartl (1987; $\overline{P}$ = 0.132; $\overline{H}$ = 0.042), where exactly the same set of genetic loci was examined. Similar results have also been obtained in an investigation of 26 loci in approximately 200 wild rabbits from England, France, Tasmania and mainland Australia ($\overline{P}$ = up to 0.192; $\overline{H}$ = 0.060) by Richardson et al. (1980). Whereas the extent of polymorphism and heterozygosity in populations of the brown hare and the wild rabbit seems to be rather equal, remarkably lower values of genetic variation, especially of average heterozygosity, were detected in a study on electrophoretic variation at 26 loci in 165 pikas from Colorado (USA; mean $\overline{P}$ = 0.115, sd. = 0.044; mean $\overline{H}$ = 0.005, sd. = 0.002; Glover et al. 1977). These results were confirmed by a later study on some more pika populations from Colorado carried out by Tolliver et al. (1985), where the low heterozygosity in the pika is explained as the result of founder effect and genetic drift occurring in the small isolated populations of this species during postglacial shifts in its range. However, since in a population from Montana (USA) a $\overline{P}$-value of 0.154 and a $\overline{H}$-value of 0.046 were detected by Glover et al. (1977), apart from the situation in Colorado, also the pika may have an extent of genetic variation similar to that in the brown hare and the wild rabbit.

Thus, as far as average values of polymorphism and heterozygosity are concerned, the ecological differences between the three species of lagomorphs do not seem to be reflected by substantial differences in the extent of biochemical genetic variation within populations. However, when the proportion of polymorphic loci is calculated for the whole species (by summing up all polymorphisms found in the different local populations instead of taking an average) the pika with 37 % (calculated from Tolliver et al. 1985) shows much the same value as the brown hare (38.5 %; present study), but the rabbit is different with

19.2 % (calculated from RICHARDSON et al. 1980). Furthermore, the proportion of polymorphisms shared by all populations studied is 40 % in the brown hare but only 10 % in the pika (TOLLIVER et al. 1985). These differences between species can be explained in various ways. The lower extent of polymorphism in the rabbit may either be an artefact because of different enzyme loci examined (other, possibly additional, polymorphisms were detected in Austrian rabbits by HARTL 1987) or the result of its history of distribution (see e. g. BARRETT and RICHARDSON 1986). The set of enzymes examined by GLOVER et al. (1977) and TOLLIVER et al. (1985) is rather similar to that investigated in the present study and the low percentage of polymorphisms shared by pika populations may be generally the result of its existence in so called „terrestrial islands" (GLOVER et al. 1977), which are of course more susceptible to losses of alleles by genetic drift than a more panmictic network of populations, occurring for instance in the European brown hare.

The data obtained in the present study suggest, that there is very low genetic differentiation not only between populations inhabiting continuous agricultural regions but also between populations occurring on different sides of broad rivers (Wisła, Danube) or mountain chains (Alps, Carpathians). In spite of the rather high genetic diversity within populations of the brown hare the genetic diversity between populations is comparatively low ($G_{ST} = 5.5$ %) and also genetic distances (calculated according to NEI 1978) are negligible in most cases. Since genetic distances are mainly influenced by the distribution of allele frequencies at the highly polymorphic loci, the high degree of genetic homogeneity between the populations studied may be caused to a certain extent by selective forces acting on these loci (see e. g. RICHARDSON 1980; PEMBERTON et al. 1988).

This hypothesis is supported by the data on Czechoslovakian animals. Although they were subjected to breeding for several generations, they are not very different in their allele frequencies from the other populations studied. Furthermore, their position in the various dendrograms is fitting quite well to the expectations derived from the geographical site of their origin. However, the selection hypothesis needs to be tested in more detailed investigations and the genetic similarity within the study area may simply be the result of a high amount of gene flow, which is possibly prevented by broad rivers, leading to the rather stable main clusters shown in Fig. 4.

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Zusammenfassung

Biochemische Variation und Differenzierung beim mitteleuropäischen Feldhasen (Lepus europaeus)

Die genetische Variabilität von 127 Feldhasen *(Lepus europaeus)* aus Populationen in Polen, Ungarn und Österreich wurde mit Hilfe der horizontalen Stärkegelelektrophorese ermittelt. Dazu wurden 25 Isoenzymsysteme aus Nieren- und Lebergewebsextrakten untersucht. Zum Vergleich mit Feldhasen aus der Tschechoslowakei wurden in der vorliegenden Arbeit auch von HARTL (1987) erhobene Daten herangezogen. Von 39 auswertbaren Genloci zeigten 10 einen Polymorphismus. Die gefundenen Polymorphie- (durchschnittl. $\bar{P} = 0.163$) und Heterozygotieraten (durchschnittl. $\bar{H} = 0.048$) liegen nahe dem generell für Säugetiere errechneten Mittelwert. Die genetische Differenzierung zwischen Populationen ist jedoch, auch über größere geographische Entfernungen hinweg, sehr gering. Diese Befunde werden unter Bezugnahme auf die genetische Variabilität und Differenzierung bei anderen Lagomorphen, wie etwa dem Wildkaninchen und dem Pfeifhasen, diskutiert.

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GTG-banded karyotype of *Gazella dama mhorr* Bennett, 1833

Cytogenetic relationship with other members of the subgenus *Nanger*

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Abstract

The GTG-banded karyotype of *Gazella dama mhorr* is described, showing an unusual sex-determining mechanism ♂ ($X_1X_2Y_1Y_2$), ♀ ($X_1X_1X_2X_2$) and two variants in the parameter 2n (42 individuals possess 2n = 38, and the rest, 13 individuals, 2n = 39, due to a structural heteromorphism in pair 1). The comparative study of the karyotypes of *G. dama mhorr, G. dama dama, G. granti* and *G. soemmeringi* reveals the relationship among these four members of the subgenus *Nanger*.

Introduction

The difficulties concerning a classification of the different species and subspecies of the genus *Gazella* (Groves 1969) stimulated karyotypical research in this genus (Nelson-Rees et al. 1967; Wurster 1972; Wahrman et al. 1973; Effron et al. 1976; Benirschke et al. 1984; Furley et al. 1988).

This paper presents a cytogenetic study of *Gazella dama mhorr*, a subspecies not studied in this respect to date. The sample analysed here is relatively large and of well-known and demonstrated origin, preconditions not given in similar studies on other *Gazella* species.

Material and methods

A total of 55 specimens (31 ♀♀ and 24 ♂♂) were examined, all of them belonging to a population developed in the Arid Zones Experimental Station in Almería (Spain) and deriving from 17 *G. dama mhorr* specimens (13 ♀♀ and 4 ♂♂) which had been trapped between 1971 and 1975 in the "Dora-El Gaada" region, in the northern part of the once Spanish colony of Western Sahara, bordering the South-Moroccan area, where the specimens studied by Bennett have been obtained (Cabrera 1932).

The classification of the specimens of the population under study is based on comparative analyses with *G. dama dama* and *G. dama ruficollis* (Cano 1984). On the other hand, specimens from this geographical area have been classified as *G. dama lozanoi* by Morales-Agacino (1949) and Eigener and Schliemann (1983).

For the analysis of metaphase plates, chromosome preparations were made from peripheral whole blood, 0,4 ml cultured in 7,5 ml RPMI-1640 medium supplemented by 15 % bovine fetal serum, L-glutamin, antibiotics and Pokeweed mitogen (Flow Laboratories).

The trypsin technique of revealing GTG bands was based on the procedure of Seabright (1972), with slight modifications (Arroyo and Murcia 1977).

Results

Chromosome analysis with conventional Giemsa staining showed that of the 55 animals analyzed, 42 (25 ♀♀ and 17 ♂♂) had a karyotype 2n = 38, and the remaining 13 (6 ♀♀ and 7 ♂♂) 2n = 39. By means of GTG banding technique, each pair was unequivocally identified. The chromosomes in the karyotypes were grouped morphologically: meta-

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submetacentric (1–10) and acrocentric (11–18). Within these groups the chromosomes were ordered according to their length and matched to their respective banding patterns.

The karyotypes with 2n = 38 (fig. 1: ♀♀, fig. 2: ♂♂) possess 34 chromosomes (10 meta-submetacentric and 7 acrocentric pairs) identical in both sexes with regard to morphology, relative lengths and banding patterns. The four remaining chromosomes (set off in frames in figs. 1 and 2) differentiate the karyotypes of male and females. In the female (fig. 1) the four chromosomes involved in sex differentiation are paired: two submetacentric ones of maximum length form the gonosomal pair (X_1X_1) and two acrocentric chromosomes form the autosomal pair 14 (X_2X_2). By contrast, in the male the four sex-differentiating chromosomes, (marked out at the end of the karyotype) result unpaired due to their lengths or different banding patterns. The longest of these is identical to the X_1 gonosome, while the acrocentric X_2 when applying the same criteria, appears homologous to the q-arm of the male Y_1 gonosome in the female, the other one is a long submetacentric chromosome, similar in length to that of pair 2, which has been identified as the male Y_1 gonosome. Finally, there are two smaller acrocentric chromosomes Y_2 and X_2, of similar length, but unpaired among themselves due to their different banding patterns. The Y_2, by its relative length and banding patterns, turns out to be homologous to the terminal half of the q-arm of the female X_1 gonosome (fig. 2b). Additionally it is identical to pair 14 (X_2) in the female (fig. 1b) in relative length and banding patterns.

The homoeologies of these two acrocentric and unpaired chromosomes support the assumption that the present morphology of the sex chromosomes X_1 and Y_1 are apomorphies originated by the respective translocations of ancestral X and Y gonosomes with two acrocentric autosomes (Y_2 and X_2) of different pairs. The translocation between the ancestral X and the autosomal Y_2 would be of the tandem type, by fusion of the telomeric region of the ancestral X with the paracentromeric region of the autosome. This chromosome would then inactivate or lose its centromere and incorporate its genetic material to the neo-X (X_1), thus lengthening its q-arm. On the other hand, the translocation between the ancestral Y, which is short and acrocentric, and the autosome X_2 would have to be Robertsonian – centric fusion – and generating the long submetacentric male Y_1 gonosome. Both gonosomes in their present morphology, thus possess two regions: one which corresponds to the ancestral sexual chromosomes – gonosomal region g – and another one corresponding to the translocated autosome – region a – (fig. 2b).

Thus, the actual karyotype, ♂ 2n = 38 ($X_1X_2Y_1Y_2$), ♀ 2n = 38 ($X_1X_1X_2X_2$) – according to the notation proposed by Fregda (1970) and Hsu (1979) – preserve the ancestral genetic material and are balanced as regards both sexes. In the females the autosomal designate Y_2 pair would be incorporated in the terminal segment of both X_1 gonosomes (double apomorphy), whereas the X_2 pair would make up pair 14 (X_2) (double plesiomorphy). In the males, however, the Y_2 pair would have a chromosome incorporated in the female gonosome (simple apomorphy) and the other Y_2 would be free and acrocentric (simple plesiomorphy). Pair 14 (X_2) would possess a chromosome from this pair, incorporated in the male Y_1 (male-specific sex chromosome) forming its q-arm (simple apomorphy), and the other acrocentric free X_2 (14) simple plesiomorphy. The Y_2 acrocentric free chromosome is present only in males.

The karyotypes with 2n = 39 only differ from the type with 38 chromosomes in the autosomal pair 1, which present structural heteromorphism – due to Robertsonian translocation (one submetacentric chromosome and two acrocentric chromosomes which are homologous to the arms p and q of the submetacentric) – (fig. 3). The rest of the pairs, including the gonosomal ones, are identical for both variants.

In the analyzed population no 2n = 40 specimens were identified. Theoretically these variants are likely to appear in offspring of inbreeding between 2n = 39 specimens.

Figs. 1 and 2. 1a: GTG banded female karyotype of *G. dama mhorr* 2n = 38 (animal n° 258). The four chromosomes involved in sex differentiation are framed out; *1b:* Detail of the sex-differentiating chromosomes from another metaphase. *2a:* Male karyotype of *G. dama mhorr* 2n = 38 (animal n° 370). At the end of the karyotype the four chromosomes involved in sex differentiation are framed out. The free acrocentric autosomes X_2 (14) and Y_2 are paired and aligned with the respective homologous segments in the neogonosomes Y_1 and X_1; *2b:* Detail of the male sex-differentiating chromosomes, marking the gonosomal region g and the autosomal region a

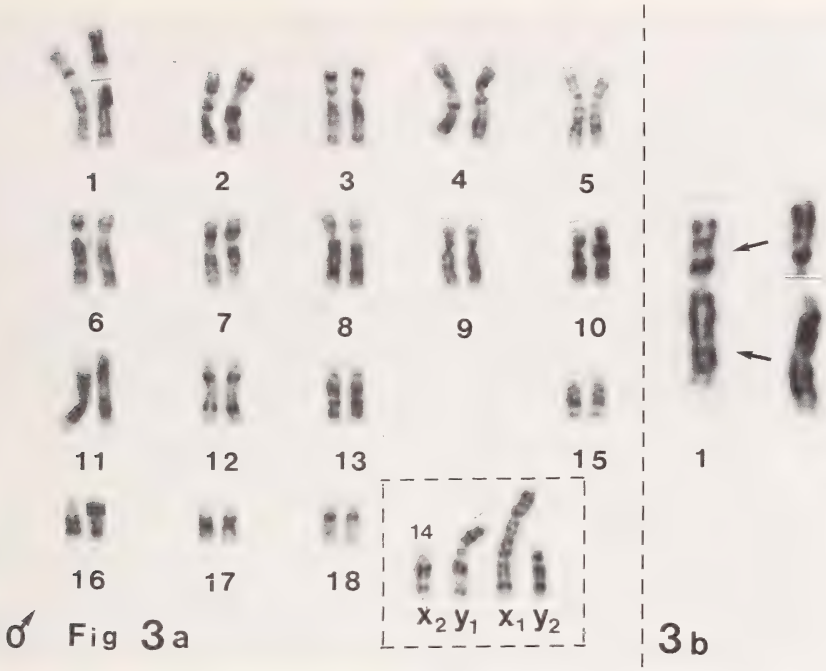

Fig. 3. a: Male karyotypes of the *G. dama mhorr* 2n = 39 (animal n° 284). Structural heteromorphism in pair 1: one submetacentric and two acrocentric chromosomes, these latter homologous with the p and q arm of the submetacentric; *b:* Detail of pair 1

Discussion

The comparison of the karyotypes of *G. dama mhorr* and *G. dama dama* Pallas, 1766, (Effron et al. 1976) allows the following conclusions:

1. Female karyotypes with 2n = 38 are identical in both subspecies (10 meta-submetacentric pairs, 8 acrocentric pairs plus 2 female gonosomes of maximum length with translocations between X and autosomal Y_2).
2. Male karyotypes in turn, are differentiated: a. by karyological parameter 2n (39 in *dama,* 38 in *mhorr,* disregarding at the moment the Robertsonian polymorphism of autosome 1); b. by the morphology and size of the male gonosome (small acrocentric Y_1 in *dama,* and long submetacentric Y_1 in *mhorr*) and c. by the presence of two free autosomes of pair 14 in *dama* and only one free autosome of this pair in *mhorr.*

These three features distinguish the male karyotypes of both subspecies, and are the results of one single chromosomal rearrangement (Robertsonian translocatión, centric fusion) between the short acrocentric Y_1 male specific sex chromosome and an autosome of pair 14 in *dama,* which would result in forming the long submetacentric Y_1 gonosome, leaving the other autosome of pair 14 (X_2) free, in subspecies *mhorr* and reducing the diploid set to 2n = 38. This rearrangement likewise determines the evolution of male 2n = 40 karyotypes in *dama* towards the 2n = 39 in *mhorr,* which presents structural heteromorphism in both subspecies (due to Robertsonian translocation) in pair 1 (fig. 3). One single evolutionary novelty, the submetacentric apomorphy of the Y_1 gonosome, differentiates the karyotypes of both subspecies.

The comparison of the karyotypes of *mhorr* with *G. soemmeringi* Cretzschmar, 1826, (Benirschke et al. 1984) permits to establish the following relationships:

1. Both gonosomes have the same morphology and banding pattern in both members of the *Nanger* subgenus (long submetacentric male gonosome with autosomal translocation Y/X_2 in *mhorr,* X/17 in *soemmeringi*), and the maximum length submetacentric female chromosome X/Y_2 in *mhorr,* X/14 in *soemmeringi.*
2. The meta-submetacentric autosomes (1–10) in *mhorr* are identical to the meta-submetacentric ones in *soemmeringi* (16/11; 1–9).
3. The acrocentric pairs (11–18) in *mhorr* correspond to the acrocentric pairs (10–20) in *soemmeringi* (the numbering is influenced by the inclusion of the Y_2 and X_2 autosomes), although some individuals of these species are affected by Robertsonian translocations, 13/12 and 18/10.

With regard to the sexual chromosomes of both species, we agree with Benirschke et al. (1984), in assigning the autosomal region of the female X gonosome to the terminal half of the q-arm. We are, however, in disagreement with these authors regarding the identification of the autosomal region of the male Y_1 gonosome. Whereas they assign it to the short arm in *soemmeringi,* we identify it with the long q-arm in *mhorr.*

Finally comparison between the karyotypes of *mhorr* and *G. granti* (Effron et al. 1976) allows the establishment of the following relationships:

1. The meta-submetacentric pairs in *mhorr* (1–10) are identical to pairs (3, 5, 4, 8, 10, 6, 9, 12, 13 and 14) in *granti.*
2. The acrocentric pairs (11–18) of *mhorr,* by means of four Robertsonian translocations, are incorporated in the submetacentric chromosomes 1, 2, 3 and 11 of *granti.*
3. The female sex chromosomes are identical in both species; the male gonosome, however, is small and acrocentric and hence identical to *dama,* both being different from the long submetacentric Y_1 in *mhorr.*

Table 1 provides a synthetic view of the homoeologies that are assumed to exist among the chromosomes of the karyotypes of *G. dama dama, G. granti, G. dama mhorr* and *G. soemmeringi,* preserving the nomenclature and numbering of the respective authors.

Based on the hypothesized homoeologies outlined in Table 1, assuming the ancestral nature of the acrocentric morphologies and selecting a minimum number of evolutionary steps (Camin and Sokal 1965), it is possible to establish a hypothetical evolutionary scheme or cladogram (fig. 4) which would relate the four *Nanger* members cytogenetically by means of Robertsonian translocations, (centric fusion). Assuming these criteria as a working hypothesis, the *G. dama* karyotype would then correspond to the ancestral type among the members of the *Nanger* subgenus. Two different branches could have derived from the *dama* karyotype: one which would preserve the morphology of the *dama* sex chromosomes and giving rise to *granti,* whereas the other, by means of morphological modification of the male gonosome could have developed to *mhorr* and *soemmeringi.*

In one of the branches *dama* and *granti* share the morphology of the sex chromosomes and the meta-submetacentric autosomes of *dama.* Four Robertsonian translocations of the acrocentric pairs 13-12, 17-11, 15-14 and 18-16 in *dama,* would yield four submetacentric apomorphies (1, 2, 8 and 11) in *granti.* The diploid set is thus reduced to 2n = 31 and all chromosomes are meta-submetacentric.

For the other branch, Robertsonian translocation between the Y (small acrocentric) and the autosome of pair 14 in *dama* would generate the submetacentric male Y_1 gonosome in *mhorr,* (the only evolutionary novelty which differentiates both subspecies) whereas they share the morphology and structure of the other chromosomes, and the diploid set in *mhorr* is reduced to 2n = 38. Finally and starting from the *mhorr* karyotype, two Robertsonian translocations involving pairs 13-12 and 17-11 would give rise to the *G. soemmeringi* karyotypes 2n = 34-39. With respect to *dama, mhorr* and *soemmeringi* as a common synapomorphy share the submetacentric neomorphism of the male gonosome.

In the light of the cytogenetic relationships described above and ignoring the possibilities of hybridization among the different members of subgenus *Nanger* it is legitimate

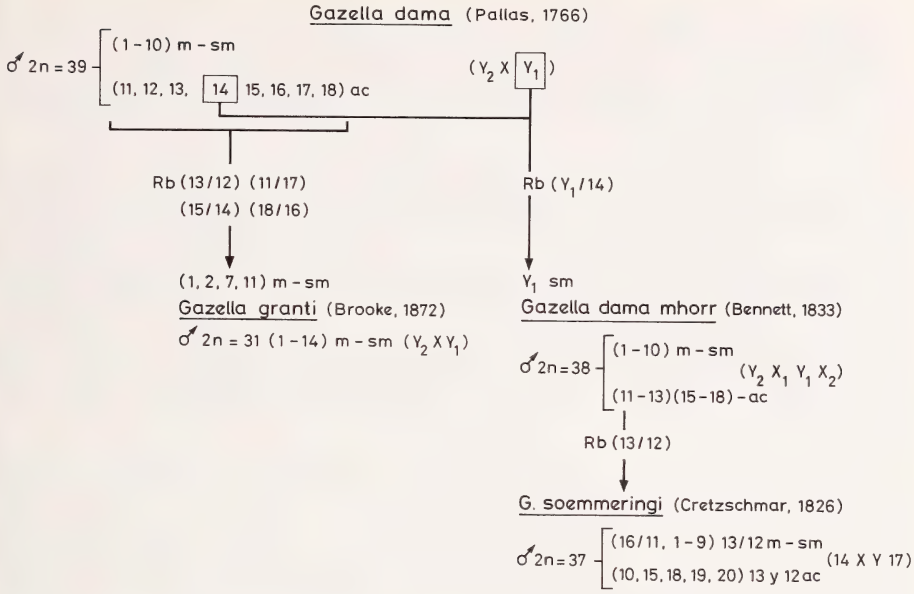

Fig. 4. Hypothetical evolutionary scheme

Table 1. **Presumptive chromosome homoeologies between *G. dama mhorr, G. dama, G. granti* and *G. soemmeringi***

G. granti (Effron et al. 1976) ♂ 2n=31 (Y_2 X Y_1)	*G. dama* (Effron et al. 1976) ♂ 2n=39 (Y_2 X Y_1)	*G. dama mhorr* (Arroyo et al. 1988) ♂ 2n=38 (Y_2 X_1 Y_1 X_2)	*G. soemmeringi* (Benirschke et al. 1984) ♂ 2n=37 (14 X Y 17)
3-sm	1-sm	1-sm	16/11-sm
5-sm	2-sm	2-sm	1-sm
4-sm	3-sm	3-sm	4-sm
8-sm	4-sm	4-sm	5-sm
10-sm	5-sm	5-sm	3-sm
6-sm	6-sm	6-sm	2-sm
9-m	7-m	7-m	7-m
12-sm	8-sm	8-sm	6-sm
13-sm	9-sm	9-sm	8-sm
14-sm	10-sm	10-sm	9-sm
2q-sm	11-ac	11-ac	10-ac
1q-m	12-ac	12-ac	12-ac 13/12-sm
1p-m	13-ac	13-ac	13-ac 13-12-a
7q-m	14-ac	X_2-ac(14 ♀)	17-ac
7p-m	15-ac	15-ac	19-ac
11q-m	16-ac	16-ac	15-ac
2p-sm	17-ac	17-ac	18-ac
11p-m	18-ac	18-ac	20-ac
Y_2-ac	Y_2-ac	Y_2-ac	14
X(X/Y_2)-sm	X(X/Y_2)-sm	X_1(X/Y_2)-sm	X(X/14)-sm
Y-ac	Y-ac	Y_1(Y/X_2)-sm	Y(Y/17)-sm

m = metacentric, sm = submetacentric, ac = acrocentric, p = short arm, q = long arm, Homoeology = partial or residual homology

to raise the question whether its four members actually are differentiated species or simply four karyotypic races of *G. dama*.

On the other hand, it would be interesting to know, whether the cytogenetically most closely related *Nanger* members occupy adjacent geographical areas. The lack of data about the geographical origin of the experimental animals, however, makes it impossible to correlate both variables.

The anomalies encountered in the sexual chromosomes of *G. dama mhorr*, especially in male specimens, with two free autosomes in different pairs homoeologous with the autosomal regions of both sex chromosomes, X_1Y_1, allow the assumption that a quadrivalent complex is generated during gametogenesis, consisting of four morphologically differentiated elements: the two sexual chromosomes and the autosomes X_2 and Y_2. This quadrivalent is likely to cause segregational problems during the first meiotic division with the consequential effects on fertility and the viability of descendants. As a matter of fact, the populations under study present reproduction problems together with considerable perinatal mortality. Hence a meiotic study would constitute a compulsory task for the future.

Mating has been performed randomly to date. Yet, since the karyotypes of the 55 experimental animals are now known, future matings will be guided, in order to match 38×38, 38×39 and 39×39. We are especially interested in inbreeding between hybrids with 2n = 39, i.e. with a heteromorphous pair 1, consisting of a submetacentric chromosome and two acrocentrics. The descendants thus inbred in theory could yield individuals with 2n = 40, e.i. specimens in which the submetacentric pair 1 of 2n = 38 individuals would be represented by two acrocentric pairs.

Zusammenfassung

GTG-Banden-Karyotyp von Gazella dama mhorr Bennett, 1833. Zytogenetische Beziehungen zu anderen Vertretern der Untergattung Nanger

Der GTG-Banden-Karyotyp von *G. dama mhorr* wird beschrieben. Er zeigt einen ungewöhnlichen geschlechtsbestimmenden Mechanismus (♂♂ = $X_1X_2Y_1Y_2$ und ♀♀ = $X_1X_1X_2X_2$) und zwei Varianten des Parameters 2n (42 Exemplare haben 2n = 38 und die übrigen 13 Tiere zeigen Heteromorphismus im Paar 1, also 2n = 39). Aus der vergleichenden Gegenüberstellung dieser Karyotypen mit denen von *G. dama dama, G. granti* und *G. soemmeringi* wird das zytogenetische Verhältnis abgeleitet, das für diese vier Vertreter der Untergattung *Nanger* besteht.

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Rudiments of the clavicle in the embryos of whales (Cetacea)

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Abstract

Investigated the existence of a clavicle in 64 embryos and fetuses of seven species of Odontoceti and four species of Mysticeti. Among the Odontoceti, a regular appearance of the clavicle as a temporary rudiment during embryogenesis has been established for *Stenella coeruleoalba, Stenella attenuata, Delphinus delphis* and *Phocoena phocoena*. In *Physeter macrocephalus* a minute rudiment of the clavicle was found in one developmental stage only. The reduction of the clavicle in this species has progressed further than in other Odontoceti. In the Mysticeti the clavicle does not appear at all during embryogenesis. Its reduction is complete. The potential existence of a clavicle in adult Odontoceti is discussed. The histogenesis of the clavicle is accomplished by pure desmal ossification. The histogenetic process confirms that the mammalian clavicle represents a desmal element of the exoskeleton without contribution of the chondral elements of the endoskeleton.

Introduction

It is generally believed that the clavicle (clavicula; collar bone) is absent in the shoulder girdle of whales (Cetacea). For a long time there had been no indications in the literature that would have referred to the existence of a clavicle; neither in toothed whales (Odontoceti) nor in whalebone whales (Mysticeti). This included adults and embryos as well. Therefore, as recent as 1976, Arvy had to summarize her critical remarks on the subject of the cetacean "girdles" as follows: "The flippers are . . . joined to the antero-lateral wall of the thorax. They are non-articulated, except where they articulate with the shoulder blades. There is never any trace of a collar bone: clearly the 'scapular girdle' does not exist." In 1978 a positive result concerning the existence of a clavicle in Odontoceti, that is in one embryo of the striped dolphin *Stenella coeruleoalba,* was reported for the first time (Klima 1978). Four years later a clavicle was also detected in adult Odontoceti, namely in three specimen of the killer whale *Orcinus orca* (Behrmann 1982).

This paper reconsiders the question of the existence of a clavicle in whales. The results of the investigation of 64 embryos and fetuses of seven species of the Odontoceti and of four species of the Mysticeti are summarized.

Material and methods

The material used in this investigation has been provided by the following collections: Frankfurt (Institute of Anatomy, Johann-Wolfgang-Goethe-University, Frankfurt/M., FRG), Seattle (National Marine Fisheries Service, Mammal Laboratory, Seattle, WA, USA), Tokyo (Department of Anatomy, Faculty of Medicine, University of Tokyo, Hongo, Tokyo, Japan) and Utrecht (Hubrecht Laboratory, International Embryological Institute, Utrecht, The Netherlands).

The embryos were sectioned into series of microscopical slides following customary histological methods, except for the large fetuses which were examined by macroscopical dissection. All information concerning the material is summarized in Table 1. Embryos No. 4 and No. 9 *(Stenella coeruleoalba)* and No. 62 and No. 63 *(Megaptera novaeangliae)* have already been inspected earlier

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Table 1. **Material and results: Occurrence or absence of the clavicle in the examined embryos and fetuses**

The size is given in millimeters for TL (total length from tip of snout to tip of tail) or for CR (crown-rump length). For details about the collection see text

No.	Size (mm) TL	CR	Labelling	Collection	Methods	Clavicle
Odontoceti						
Striped dolphin *Stenella coeruleoalba*						
1	7.0	–	–	Tokyo	slides	missing
2	11.0	–	–	Tokyo	slides	missing
3	12.0	–	–	Tokyo	slides	missing
4	17.0	–	–	Tokyo	slides	missing
5	25.0	–	2959.25	Seattle	slides	occurring
6	26.0	–	2959.26	Seattle	slides	occurring
7	26.0	–	2989.26	Seattle	slides	occurring
8	26.0	–	–	Tokyo	slides	missing
9	35.0	–	–	Tokyo	slides	occurring
10	35.0	–	2959.35	Seattle	slides	occurring
11	50.0	–	2989.50	Seattle	slides	occurring
Spotted dolphin *Stenella attenuata*						
12	21.0	7.5	K 13	Frankfurt	slides	missing
13	22.0	8.6	K 16	Frankfurt	slides	missing
14	25.0	9.2	K 12	Frankfurt	slides	missing
15	39.0	14.8	K 17	Frankfurt	slides	occurring
16	43.0	18.3	K 22	Frankfurt	slides	occurring
17	44.5	19.7	K 23	Frankfurt	slides	occurring
18	57.0	25.5	K 18	Frankfurt	slides	occurring
19	71.0	32.5	K 24	Frankfurt	slides	occurring
20	85.0	38.5	K 15	Frankfurt	slides	occurring
Common dolphin *Delphinus delphis*						
21	24.0	7.6	K 55	Frankfurt	slides	missing
22	39.5	13.0	K 56	Frankfurt	slides	missing
23	42.0	18.7	K 57	Frankfurt	slides	occurring
24	44.0	20.4	K 53	Frankfurt	slides	occurring
25	46.0	21.5	K 58	Frankfurt	slides	occurring
26	82.0	34.3	K 49	Frankfurt	slides	occurring
27	101.0	40.5	K 50	Frankfurt	slides	occurring
28	113.5	49.5	K 59	Frankfurt	slides	occurring
29	131.0	58.5	K 51	Frankfurt	slides	occurring
White-beaked dolphin *Lagenorhynchus albirostris*						
30	430.0	–	–	Frankfurt	dissection	missing
Common porpoise *Phocoena phocoena*						
31	(25.0)	10.0	MK 74	Frankfurt	slides	missing
32	(28.0)	11.0	MK 71	Frankfurt	slides	missing
33	39.0	14.0	MK 72	Frankfurt	slides	occurring
34	41.0	19.0	MK 73	Frankfurt	slides	occurring
35	42.0	18.0	MK 70	Frankfurt	slides	occurring
36	51.0	22.0	MK 67	Frankfurt	slides	occurring
37	60.0	24.0	MK 64	Frankfurt	slides	occurring
38	69.0	27.0	MK 75	Frankfurt	slides	occurring
39	70.0	29.0	MK 62	Frankfurt	slides	occurring
40	95.0	45.0	MK 61	Frankfurt	slides	occurring
41	107.0	46.0	MK 69	Frankfurt	slides	missing
42	125.0	55.0	MK 68	Frankfurt	slides	occurring
43	134.0	60.0	MK 76	Frankfurt	slides	missing
44	167.0	–	MK 48	Frankfurt	slides	missing
45	355.0	–	–	Frankfurt	dissection	missing

Table 1 (continued)

No.	Size (mm) TL	CR	Labelling	Collection	Methods	Clavicle
Narwhal *Monodon monoceros*						
46	137.0	–	–	Utrecht	slides	missing
Sperm whale *Physeter macrocephalus*						
47	19.0	10.0	MK 58	Frankfurt	slides	missing
48	37.0	14.0	MK 51	Frankfurt	slides	missing
49	75.0	–	PC	Frankfurt	slides	missing
50	97.0	45.0	MK 62A	Frankfurt	slides	occurring
51	102.0	47.0	MK 66	Frankfurt	slides	missing
52	170.0	73.0	MK 53	Frankfurt	slides	missing
53	315.0	–	PH 4	Frankfurt	dissection	missing
54	435.0	–	PH 3	Frankfurt	dissection	missing
55	455.0	–	PH 2	Frankfurt	dissection	missing
56	565.0	–	PH 1	Frankfurt	dissection	missing
Mysticeti						
Gray whale *Eschrichtius robustus*						
57	–	15.0	2956 F4	Seattle	slides	missing
58	–	65.0	2956 F3	Seattle	slides	missing
Minke whale *Balaenoptera acutorostrata*						
59	455.0	–	3119	Frankfurt	dissection	missing
Fin whale *Balaenoptera physalus*						
60	156.0	–	–	Utrecht	slides	missing
61	400.0	–	MK 65	Frankfurt	dissection	missing
Humpback whale *Megaptera novaeangliae*						
62	21.0	–	–	Tokyo	slides	missing
63	37.0	–	–	Tokyo	slides	missing
64	107.0	–	–	Utrecht	slides	missing

with respect to the existence of a clavicle (Klima 1978). All the others were investigated for the first time.

The scientific, english and german names used in this paper as well as the zoological system of the whales closely follow the publications of Fraser (1976), Nowak and Paradiso (1983) and Gewalt (1987). The terminology for the individual structures of the embryonic breast-shoulder apparatus is taken from Klima (1987).

Results

Appearance in Odontoceti

In the striped dolphin *Stenella coeruleoalba* the clavicle starts to develop in stages of about 25 mm TL and can still be recognized in stages of 50 mm TL. Later stages were not at disposal (Figs. 1 and 2).

In the spotted dolphin *Stenella attenuata* the first anlage of the clavicle appears in a 39 mm TL large stage and is conserved up to the largest stages of about 85 mm TL.

In the common dolphin *Delphinus delphis* the first anlage of a clavicle was detected in a 42 mm TL large stage and was observed continuously up to the largest of the available stages which measured 131 mm TL (Fig. 6).

No clavicle was detected in the only specimen of the white-beaked dolphin *Lagenorhynchus albirostris,* which had been investigated by us and measured 430 mm TL.

The largest sample of material that was at my disposal was from the common porpoise *Phocoena phocoena.* The first anlage of a clavicle was detected in a 39 mm TL large stage. It

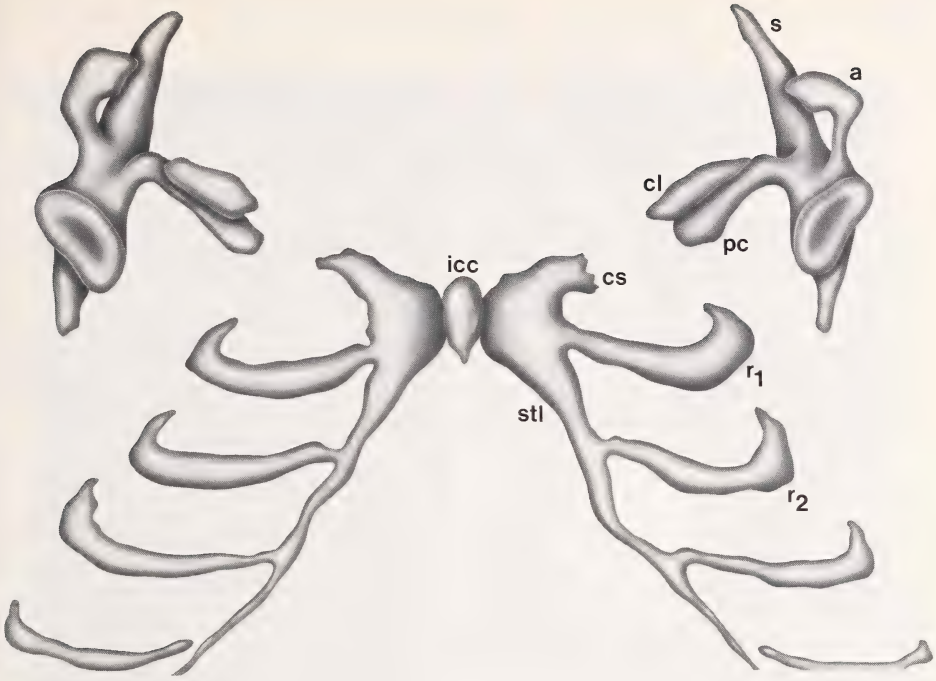

Fig. 1. Stenella coeruleoalba, embryo 25 mm TL (No. 5). Ventral view of the shoulder girdle and sternum. Abbreviations: a = acromion; cl = clavicle; cp = coracoid process; cs = coracoid-scapular plate; icc = unpaired sternal element; r1, r2 = ribs 1 and 2; s = scapula; stl = paired sternal band

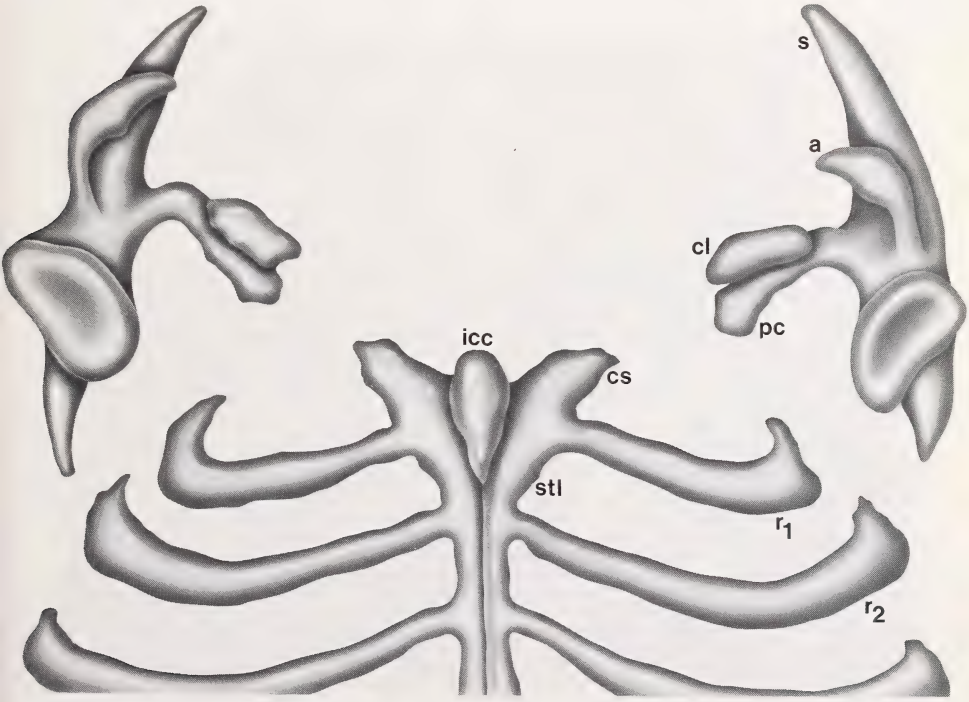

Fig. 2. Stenella coeruleoalba, embryo 35 mm TL (No. 10). Ventral view of the shoulder girdle and sternum. For abbreviations see Figure 1

is continuously present up to a stage of 95 mm TL. In one instance we found a very small clavicular rudiment in a 125 mm TL large stage. In stages of 134 mm TL to 355 mm TL a clavicle or clavicular rudiment is no longer detectable (Fig. 3).

In a specimen of the narwhal *Monodon monoceros* with a size of 137 mm TL no anlage of the clavicle was detected.

All in all, ten stages of the sperm whale *Physeter macrocephalus* measuring 19 mm TL to 565 mm TL had been at disposal. The clavicle was seen as a minute rudiment in a stage of 97 mm TL only (Figs. 4 and 5).

Appearance in Mysticeti

In the investigated Mysticeti, the gray whale *Eschrichtius robustus,* minke whale *Balaenoptera acutorostrata,* fin whale *Balaenoptera physalus* and humpback whale *Megaptera novaeangliae* none of the available stages showed any anlage of the clavicle.

Morphogenesis

In mammals that have a completely developed clavicle as adults as well it connects the craniolateral rim of the sternum with the acromion of the scapula. It attaches "joint-like" to both skeletal elements and, together with the sternum, forms the sterno-clavicular joint, with the scapula the acromio-clavicular joint, respectively. The lateral end of the clavicle comes close to the coracoid process of the scapula. With this skeletal element, however, it shares only a loose connection established by ligaments of the ligamentum coraco-claviculare.

A similar topographical position is displayed by the clavicular rudiments of whale embryos, whenever such rudiments are present at all. They are located precisely at the

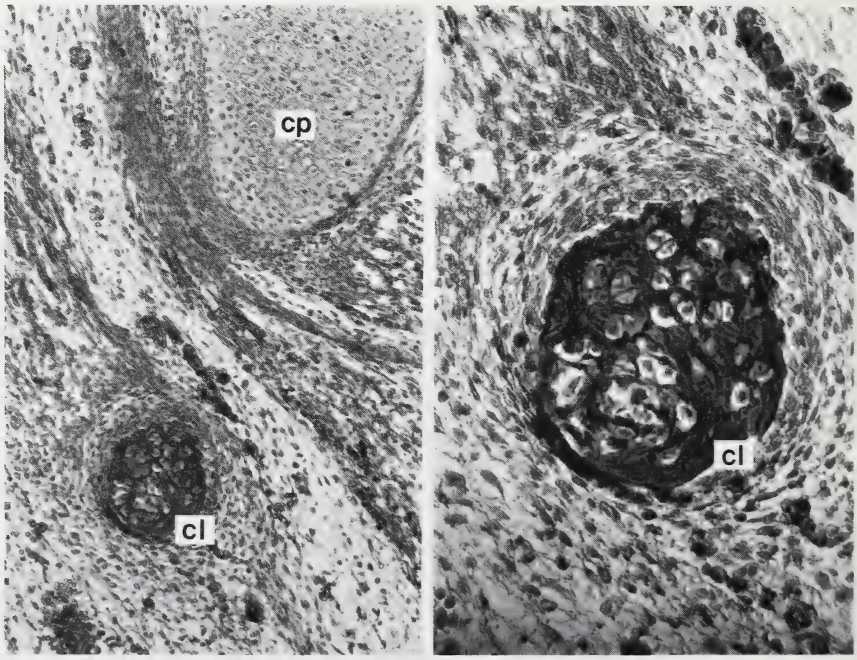

Fig. 3. Phocoena phocoena, embryo 70 mm TL (No. 39). A section of the clavicle (cl) and coracoid process (cp). *Left:* overall view; *right:* detail. For orientation see Figure 4

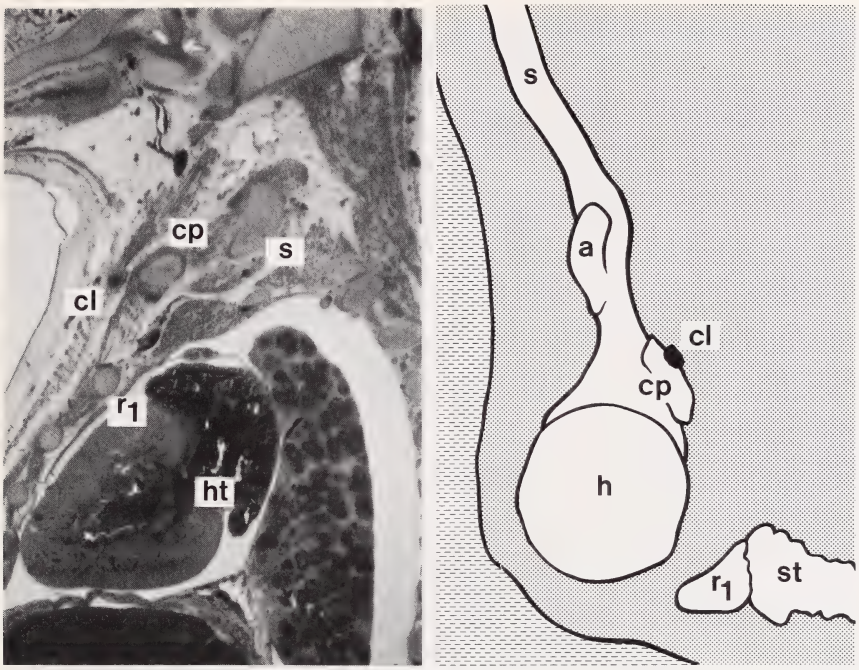

Fig. 4. Left: Position of the clavicle in embryos of *Phocoena phocoena,* 70 mm TL. Photograph of a longitudinal section of the thorax. *Right:* Position of the clavicle in embryo of *Physeter macrocephalus,* 97 mm TL. Diagrammatic drawing of the right shoulder viewed from the front. Abbreviations: a = acromion; cl = clavicle; cp = coracoid process; h = humerus; ht = heart; r1 = rib 1; s = scapula; st = sternum

interconnecting line between the anterior rim of the sternum and the tip of the acromion. However, they are very small in all phases of their development and therefore not able to bridge the relatively large distance between sternum and acromion. Consequently they remain at a substantial distance from both structures. Their closest position to any other skeletal element is towards the coracoid process. However, a direct connection between both structures does not exist.

The morphogenesis of the clavicle starts at a developmental stage when the paired anlagen of the breast-shoulder apparatus are still far apart in the lateral breast wall. Two processes are recognizable in the scapula anlage, the acromion and the coracoid process. The sternal anlage is visible in a small gap extending from the coracoid process towards ventromedial. It is composed of a part of the paired coracoid-scapular plates, the paired sternal bands and of an unpaired sternal element. In the course of further development all mentioned anlagen shift towards ventromedial and approach each other. The sternal anlagen fuse into a uniform piece of skeleton in the median plane. (For details see Klima 1978, 1987.)

During all these morphogenetic processes the clavicle's anlage remains in its position. It shows a close relation to the coracoid process. It is located, somewhat cranially shifted, ventromedially of the coracoid process, without establishing a direct connection with this element. Its longitudinal axis runs parallel with the coracoid processes' longitudinal axis. As the coracoid process shifts towards ventromedial the anlage of the clavicle displays the same movement. This topographic position as well as the mutual morphogenetic activities are recognizable from the depiction of two developmental stages of the soulder girdle and sternal apparatus of *Stenella coeruleoalba* (Figs. 1 and 2).

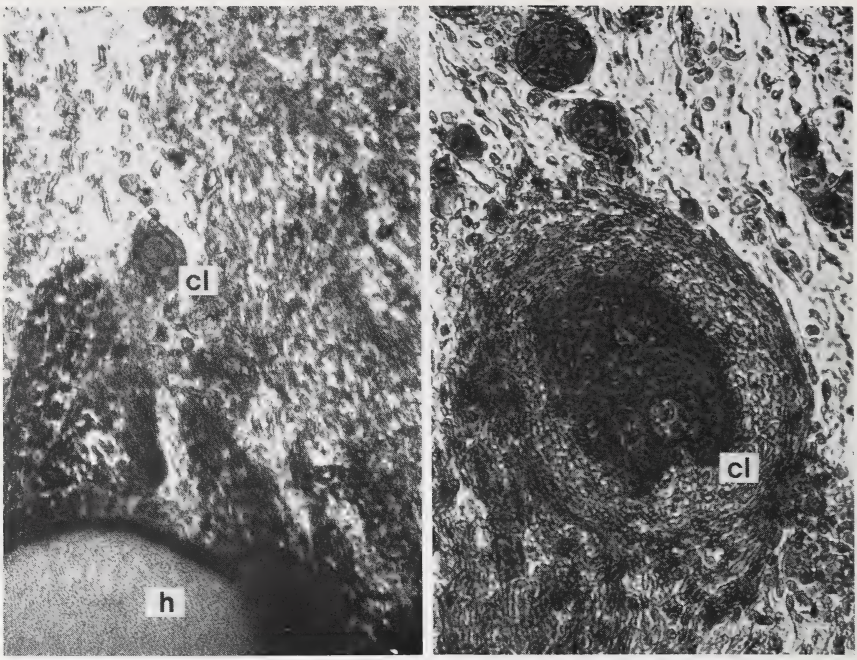

Fig. 5. Physeter macrocephalus, embryo 97 mm TL (No. 50). A section of the clavicle (cl) and humerus (h). *Left:* overall view; *right:* detail. For orientation see Figure 4

Histogenesis

As a part of the exoskeleton, the clavicle stems histogenetically from desmal ossification. First of all, the embryonic mesenchyme condenses at the location where the anlage of the clavicle comes into being (Fig. 6a). Singular mesenchyme cells become bone-forming osteoblasts and start with the secretion of the first osseous ground substance. In the further course of ossification (Fig. 6b) the peripheral zone appears more distinct. It is becoming bone-forming periost. In its inner layer numerous osteoblasts differentiate out of mesenchyme cells. Then the ground substance, the osteoid, is massively secreted into the inner portion and nearly fills the complete anlage (Fig. 3 *Phocoena phocoena*). Immured bone cells, the osteocytes, are located in its inside. Soon however, the bone substance is loosened up (Fig. 6c). Openings are penetrating from the outside and step by step the channel system of the primary bone marrow develops. In the further course of development decomposition processes are gradually taking over (Fig. 6d). They are initiated by an ever increasing number of osteoclasts. These giant multinuclear cells attack the inner wall of the bone from the primary marrow cavity and gradually dissolve it. Finally, the osteoclasts dissolve the last remnants of the bone and the anlage of the clavicle is completely decomposed.

Discussion

The whales (Cetacea) of both suborders, Odontoceti and Mysticeti, belong to mammalian forms that have reduced the clavicle completely (Slijper 1936; Bourdelle and Grassé 1955; Arvy 1976). There is no direct connection between the skeleton of the forelimb and

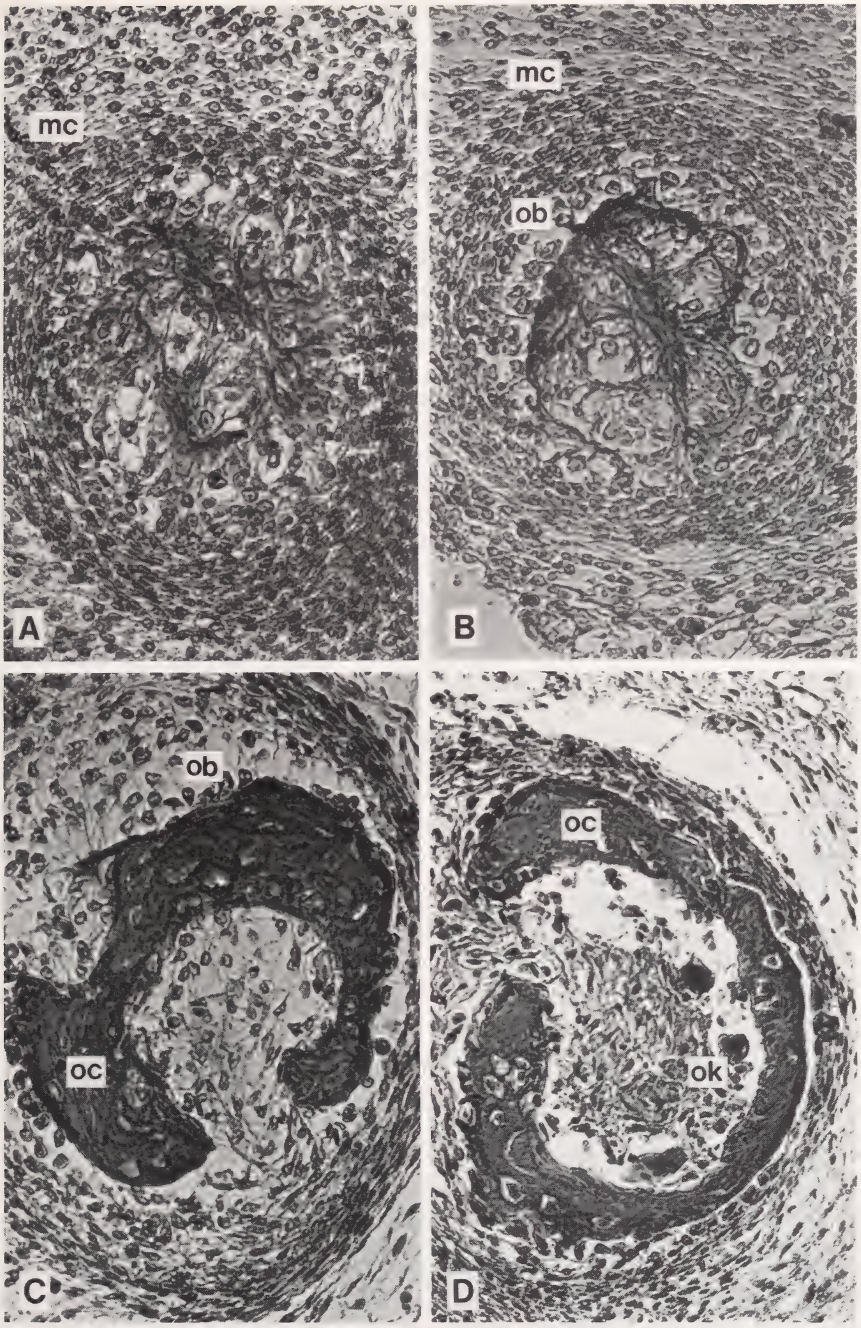

Fig. 6. Some selected stages of the ossification of the clavicle in *Delphinus delphis*. A = embryo 42 mm TL (No. 23); B = embryo 44 mm TL (No. 24); C = embryo 113 mm TL (No. 28); D = embryo 131 mm TL (No. 29). Abbreviations: mc = mesenchyme cells; ob = osteoblast; oc = osteocyte; ok = osteoclast. For details see text about histogenesis

the rump, except in the amazon dolphin *(Inia geoffrensis)* where the humerus supports itself to the sternum via a secondary joint (Klima et al. 1980).

The first positive result concerning a rudiment of the clavicle in whales (Klima 1978) leads to the following statement: "A rudimentary clavicle is also obvious in the Odontoceti during embryogenesis, as has been proved for *Stenella.* No rudimentary clavicle can be found in *Megaptera,* which, as I think, can be considered as a rule for all Mysticeti. This total reduction is in complete correspondence with the extensive reduction of the sternum." This opinion has generally been confirmed by the present investigation.

The investigations demonstrate a well developed rudimentary clavicle during embryogenesis in the following Odontoceti: striped dolphin *Stenella coeruleoalba,* spotted dolphin *Stenella attenuata,* common dolphin *Delphinus delphis* and common porpoise *Phocoena phocoena.* The clavicle starts to form in stages around 30 mm TL and is completely decomposed in stages measuring around 130 mm TL. During morphogenesis it is especially well developed at a time when the paired anlagen of the breast-shoulder apparatus interconnect in the median plane. The clavicle is located close to the coracoid process. It maintains a long distance to acromion and sternum. Histogenetically, the clavicle shows a typical desmal ossification.

Two additional representatives of the Odontoceti, the white-beaked dolphin *Lagenorhynchus albirostris* and the narwhal *Monodon monoceros* were investigated. However, in these cases I had only singular stages different from the above mentioned size-ranges. No rudiment of the clavicle was detected here.

The sperm whale *Physeter macrocephalus* takes a special position amongst the investigated Odontoceti with respect to the development of its clavicle. Despite the fact that extensive material in suitable size-ranges and developmental stages was at disposal, we found a minute rudiment of the clavicle only in one individual measuring 97 mm TL. Obviously, the reduction of the clavicle in the sperm whale, who displays many other special adaptations as well, has progressed further than in other Odontoceti.

No rudiment of the clavicle was detected in any representative of the investigated Mysticeti i.e. in the gray whale *Eschrichtius robustus,* minke whale *Balaenoptera acutorostrata,* fin whale *Balaenoptera physalus* and humpback whale *Megaptera novaeangliae.* The result supports the assumption that the reduction of the clavicle has progressed further in Mysticeti than in Odontoceti.

I consider it possible that a rudimentary clavicle may occasionally appear in adult Odontoceti. The necessary prerequisites are given by the regular appearance of the clavicle during embryogenesis. Exactly this requirement is not met in Mysticeti and therefore I trust that an occasional appearance of a rudimentary clavicle will never be demonstrated in Mysticeti.

In this sense I regard the reported existence of a clavicle in the adult killer whale *Orcinus orca* (Behrmann 1982) as a rare, occasional appearance. Apparently the clavicle may appear now and then in a few adult Odontoceti just as, for example the variable ossa suprasternalia (Ashley 1955; Klima 1968) or surplus cervical ribs (Hayek 1928; Töndury 1958) may sometimes come to existence in humans. A regular appearance seems to be unlikely. The opinion of Behrmann (1982) that the clavicles of the killer whale like those of the sea lion serve the function to support the animal on lands is incorrect. Sea lions like all Pinnipedia do not possess any clavicle at all.

Furthermore, I consider the position of the clavicle on the mounted skeleton of the killer whale (Behrmann 1979, 1982) to be incorrect. The sternal end should be positioned in front of the first rib's connection and the scapular end should run alongside the coracoid process towards the acromion. Afterwards however, the exact topographic positions can not easily be reconstructed. A direct connection to the acromion would not be essential as the presented results concerning embryos of Odontoceti clearly show. This absolutely reflects a statement made by Nauck (1938): "As a well developed acromion exists in nearly

all Cetacea despite a missing clavicle, acromion and clavicle are not causally dependent from each other . . ."

According to the histogenesis of the clavicle it should again be stressed that all our investigations revealed a pure desmal ossification. This finding is important because it contributes to the debate concerning the origin of the clavicle in mammals. There is an ongoing controversy whether the clavicle originates as a desmal or chondral or as a mixed element (Fuchs 1912; Fawcett 1913; Hanson 1920; Brandt 1935; Nauck 1938; Zawisch 1953; Koch 1960; Lessertisseur and Saban 1967; Oláh and Ludwig 1971; Starck 1979 and others). My results definitely confirm the opinion of Starck (1979) that the clavicle of mammals is a pure dermal skeletal element (membrane bone) independent from the special histogenetic mode of osteogenesis.

In many mammals chondral tissue additionally appears at both ends of the desmal anlage of the clavicle. The cartilage borders at the neighboring skeletal elements of the chondral breast-shoulder apparatus, that is medially at the sternum and laterally at the acromion but, it never joins them to form a singular unit. Some authors assume that the chondral parts of the clavicle represent certain elements of the chondral shoulder girdle. Thus, the medial chondral part is assumed to correspond to the original procoracoid which does not exist in placentals any more. However, more recent investigations of monotremes, marsupials and placentals (Klima 1973, 1987) have shown that the embryonic material of the procoracoid is either integrated into the manubrium sterni or forms the independent praeclavium. The same developmental mode is demonstrated in this investigation which has been conducted with the embryos of Odontoceti (see also Klima 1978). The anlage of the procoracoid becomes a part of the sternum. It becomes visible at the sternum at the same time when the isolated anlage of the clavicle which is located far away, develops as a pure desmal element (Figs. 1 and 2). Thus, the chondral parts cannot belong to the initial developmental pattern of the clavicle.

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Zusammenfassung

Rudimente des Schlüsselbeins bei den Embryonen von Waltieren (Cetacea)

Es wurde nach dem Vorkommen von Schlüsselbein (Clavicula) bei 64 Embryonen und Feten von sieben Arten von Zahnwalen (Odontoceti) und vier Arten von Bartenwalen (Mysticeti) gesucht. Unter den Odontoceti ist ein regelmäßiges Auftreten der Clavicula während der Embryogenese als ein vorübergehendes Rudiment bei Streifendelphin *Stenella coeruleoalba*, Fleckendelphin *Stenella attenuata,* Gewöhnlichem Delphin *Delphinus delphis* und Kleintümmler *Phocoena phocoena* nachgewiesen worden. Die untersuchten Stadien von Weißschnauzendelphin *Lagenorhynchus albirostris* und Narwal *Monodon monoceros* waren zu groß, um bei ihnen die Anlage einer Clavicula ebenfalls nachzuweisen. Bei Pottwal *Physeter macrocephalus* ist nur bei einem einzigen Stadium ein winziger Rest der Clavicula festgestellt worden. Die Rückbildung der Clavicula ist bei dieser Art weiter fortgeschritten als bei anderen Odontoceti. Von den Mysticeti sind folgende Arten untersucht worden: Grauwal *Eschrichtius robustus,* Zwergwal *Balaenoptera acutorostrata,* Finnwal *Balaenoptera physalus* und Buckelwal *Megaptera novaeangliae*. Bei den Mysticeti erscheint die Clavicula während der Embryogenese überhaupt nicht mehr. Ihre Rückbildung ist vollständig.

Das eventuelle Auftreten der Clavicula bei erwachsenen Odontoceti (Befund bei Schwertwal *Orcinus orca* von Behrmann 1982) wird diskutiert.

Die Histogenese der Clavicula erfolgt durch eine rein desmale Ossifikation. Dadurch wird bestätigt, daß die Clavicula der Säugetiere ein rein desmales Element des Exoskelettes darstellt, ohne Beteiligung der knorpeligen Elemente des Endoskelettes.

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BUCHBESPRECHUNGEN

VIGNE, J.-D.: **Les Mammifères Post-Glaciaires de Corse.** Étude Archéozoologique. XXVIe supplément à Gallia préhistoire. Paris: Editions du Centre National de la Recherche Scientifique 1988. 337 S., 102 Abb., 118 Tafeln. FF 330.00. ISBN 2-222-041309 ISSN 0072-0100

Über 42 000 Tierknochenfunde bilden die Grundlage, auf der eine Geschichte der Säugetiere der Insel vom 7. Jahrtausend v. Chr. bis zur frühen Neuzeit unter Einschluß der Haussäugetiere entworfen wird. Der Beitrag trägt den Untertitel „archäozoologische Untersuchungen", ein Zeichen dafür, daß Ergebnisse einer interdisziplinären Forschung vorgelegt werden, was auch im einleitenden Kapitel zum Ausdruck kommt, das geomorphologischen, paläoklimatischen, chronologischen, archäologischen, historischen, paläontologischen und zoologischen Aspekten Rechnung trägt. Das erste Kapitel geht in aller Breite auf methodische Fragen und Probleme ein, im zweiten werden die Faunen behandelt, wie sie sich in zeitlicher Abfolge darstellen. Das dritte und zugleich umfangreichste Kapitel stellt die einzelnen Tierarten unter Berücksichtigung ökologischer, biogeographischer und paläoethnographischer Gesichtspunkte vor, wobei zwei Themenkreise im Vordergrunde stehen: Die Anfänge der Haustierhaltung auf Korsika und ihre vieltausendjährige Entwicklung und die Besiedlung der Insel durch Säugetiere. Der Bedeutung der Haussäugetiere als der nahrungsökonomischen Basis der neolithischen und jüngeren Inselbewohner wird ein breiter Raum gewidmet. Die am Anfang der Entwicklung erkennbaren insularen Eigenheiten hinsichtlich der Haustiere verwischen sich in dem Maße, wie Kontakte zum Festland, vor allem während der Römerzeit, intensiviert werden. Die vier für Korsika nachgewiesenen endemischen Arten (*Episoriculus* cf. *corsicanus, Prolagus sardus, Rhagamys orthodon* und *Tyrrhenicola henseli*) sind spätestens seit der frühen Neuzeit verschwunden, durch den Menschen ausgerottet oder dem Konkurrenzdruck der eingeführten Arten unterlegen. Absichtlich (als Jagdtiere) oder unbewußt eingeführt und heute eingebürgert sind auf Korsika *E. europaeus, C. suaveolens, S. etruscus, M. martes, M. nivalis, L. capensis, O. cuniculus, G. glis, E. quercinus, A. sylvaticus, R. rattus, R. norvegicus* und *M. musculus*. Eingebürgert, inzwischen aber wieder ausgerottet sind *U. arctos* und *C. elaphus*. Zahlreiche bildliche und graphische Darstellungen runden die Ausführungen ab, die sich über weite Strecken auf morphometrische Befunde beziehen. In einem umfangreichen Tabellenanhang sind die Ergebnisse quantitativer Analysen niedergelegt (relative Artenhäufigkeit, Altersstruktur, Geschlechterverhältnis). Ein umfangreiches Schriftenverzeichnis und ein Index beschließen den Band. Das Studium des Beitrages wird allen jenen empfohlen, die sich besonders mit Fragen der Entstehung und Entwicklung von Haustieren und deren Bedeutung im Leben des vorgeschichtlichen Menschen befassen. Aber auch der tiergeographisch interessierte Leser wird das Buch mit Gewinn zur Hand nehmen. H. REICHSTEIN, Kiel

RAESFELD, F. VON; REULECKE, K.: **Das Rotwild.** Naturgeschichte, Hege, Jagdausübung. Hamburg und Berlin: Paul Parey 1988. 9. Auflage. 410 S., 510 Abb. DM 94,–. ISBN 3-490-40812-8

Die erste Auflage dieses Buches erschien 1899 und war eine Anleitung zur Jagd mit den damals hierfür notwendigen Kenntnissen über den Rothirsch. 90 Jahre danach hat die nun vorliegende 9. Auflage mit dem alten „RAESFELD" beinahe nur noch den Buchtitel gemeinsam. Die inhaltliche Wandlung des Werkes durch Mehrung der Kenntnisse und Wechsel der Bearbeiter tritt mit dieser Neubearbeitung durch K. REULECKE in die dritte Phase seiner Geschichte. Zunächst waren es also in rund 20 Jahren (1899–1920) 3 Auflagen, die noch FERDINAND VON RAESFELD selbst verfaßt hat. Seine dritte Auflage galt in den darauffolgenden 36 Jahren als der jagdliche Klassiker für Rothirschjäger des deutschen Sprachraumes. In diese Zeit fiel der große Umbruch im Jagdwesen durch neue Inhalte und Richtlinien der „Hege" mit allen positiven aber auch negativen Folgen des „Reichsjagdgesetzes". Auf eine Nachkriegspause von 12 Jahren folgte 1957–1978 die zweite Phase, durch die Federführung von FRIEDRICH VORREYER. Er hat in diesen 20 Jahren fünf weitere Auflagen herausgegeben und den Inhalt des Buches stufenweise dem neuen Kenntnisstand und jagdpolitischen Zeitgeist angepaßt. Nach einer Pause von 10 Jahren hat nun der dritte Bearbeiter, KURT REULECKE, den alten Jagdklassiker mit wildbiologischen Informationen für den Jäger beträchtlich erweitert.

Im ersten Teil (160 S.) liegt der Schwerpunkt auf der Schilderung der Lebensweise (42 S.) und der Geweihbildung (53 S.) des Rothirsches entsprechend der Faszination, die „Trophäen" auf Jäger ausüben. Taxonomie, anatomische Grundbegriffe, Pathologie, Zahnkunde und Jägersprache runden das Bild vom Rothirsch ab. Der zweite Teil (128 S.) ist der „Hege" gewidmet – ein Begriff, der sehr unterschiedlich definiert und interpretiert werden kann. Hier nehmen Waldgeschichte, forstliche Betriebsarten, Schäl- und Verbißschäden, ihre Verhütung, Biotopkultivierung im Interesse der Rothirschhege in der Gestalt von Äsungsgehölzen, Wildäckern, Walderschließung u. a. m. breiten Raum ein, aber auch die vielfach umstrittene Fütterung des Wildes. Es werden Futterschuppen,

Rübenbunker, Rauh-, Saft- und Kraftfutter beschrieben, die „Herbstmastsimulation" und das Fütterungsverbot im Konflikt zwischen Forst- und Naturschutzzielen auf der einen und den Hegezielen der Jägerei auf der anderen Seite diskutiert. Mehr als die Hälfte (71 S.) dieses „Hege"-Teils ist der Jagd unter dem Titel „Bewirtschaftung des Rotwildes" gewidmet. Revierbewertung, „tragbare" Wilddichten, Abschußplan, „Güteklassen", Geweihschauen u. a. m. werden hier neben Grundbegriffen der Genetik und Populationsökologie beschrieben. Der dritte Teil (106 S.) ist zur Gänze der Jagd (-ausübung) gewidmet, von der Bekleidung des Jägers, seiner Waffen, den historischen und gegenwärtig gebräuchlichen Jagdmethoden, bis hin zu Schußverletzungen an Hirschen, Wildbrethygiene und gipfelt in der „Trophäenbewertung" (19 S.) mit Geweihformeln und Ranglisten der „Rekord"hirsche und ihrer Erleger von Hermann Göring bis Ceausescu.

Insgesamt ist diese Neubearbeitung zu begrüßen, macht sie doch viele neue Erkenntnisse der Wildbiologie für die Jagdpraxis zugänglich, und auf der anderen Seite ermöglicht sie dem Nichtjäger einen guten Einblick in Ziele und Methoden des Waidwerks. Erfreulich fortschrittlich ist z. B. die Ablehnung der Verfütterung von Medikamenten an das Wild, die richtige Einordnung des Krankheitsgeschehens bei freilebenden Populationen, die Ablehnung der Hirschverfrachtungen zwecks „Blutauffrischung", das ausführliche Kapitel über Genetik und besonders die Aussagen über das Wald-Wild-Verhältnis aus forstlicher Sicht. Die gründliche Bearbeitung waldbaulicher Fragen in Zusammenhang mit dem schwierigen und komplizierten Problem der Erhaltung und Bewirtschaftung unserer Rothirschbestände ist besonders hervorzuheben. Das einmalige Datenmaterial über die Populationsdynamik des Rothirsches im Harz als des weltweit gründlichst erfaßten Bestandes dieser Wildart wurde naturgemäß ausführlich verwertet, waren doch beide Bearbeiter nach Raesfeld langjährige Geschäftsführer des „Rotwildringes Harz" – Vorreyer bis 1966 und Reulecke bis 1983. Hervorzuheben ist auch die reiche Bebilderung dieser 9. Auflage mit sehr informativen Fotos und den prächtigen Federzeichnungen Fritz Laubes, die in ihrer Detailfreudigkeit an Ridinger-Stiche erinnern.

Mit den gut aufbereiteten, modernen wildbiologischen Informationen vielfach im Widerspruch steht allerdings das an anderen Stellen des Buches geäußerte hegerisch-jagdpolitische Gedankengut. Der sich an Viehzuchtstrategien orientierende und vom biologischen Anpassungswert her gesehene kontraselektive Trophäenkult findet seinen Niederschlag in seitenlangen Tabellen mit Geweihbewertungsformeln und entbehrt in seiner „Punktierung" nicht einer gewissen unfreiwilligen Komik. Das gilt für „Reifealter" (S. 270), „Erntegeweihe" (S. 235) und „abschußnotwendige Geweihe" (S. 276), aber auch für die Bildunterschrift eines Gemäldes von einem Harzhirsch (S. 207). Dort heißt es „Lohn der Hege", als ob die Existenz dieses herrlichen Wildes allein in der Heranzüchtung von Ideal-Zuchttypen zu begreifen wäre, und hier wird die Sprache verräterisch. Auf die z. B. in Hessen sehr umstrittenen „Wildschutzgebiete" als überdimensionierte Jagdgatter wird nur in ein paar Zeilen ohne Problembewußtsein eingegangen, den Futtermitteln für Hirsche hingegen gleich 9 Seiten gewidmet. Bedenklich ist auch, wenn in Zusammenhang mit der Kraftfutter-Verabreichung die „Notzeit" für den Rothirsch (S. 220) von Oktober bis Juli (!) festgelegt wird und kritische Wildbiologen polemisch als „Fütterungsverweigerer" (S. 208) oder „Rotwildkritiker" (S. 206) abgetan werden. Kritisiert werden kann allenfalls der „Heger", aber nicht das „Rotwild"!

Eine merkwürdige Moral ist es auch, jenen Wilderer als „abartig" zu bezeichnen, der „nur töten" will (S. 227) und nicht „Fleisch-Wilddieb" ist, wenn man auf der anderen Seite für sich selbst – und das freilich durchaus legitim – in Anspruch nimmt, Freude an der Jagd um des Erlegens willen zu haben. Ähnlich subjektiv wird im Buch mit „wertvollen" und „wildernden" Hunden verfahren (S. 228). Einige Jagdausdrücke, wie z. B. „schweißiger Schleim" (S. 152) wirken ebenfalls etwas merkwürdig. Den Rothirsch als die „widerstandsfähigste" heimische Wildart zu bezeichnen (nach welchen Kriterien?) und Hasen fälschlicherweise zu den „Nagern" zu rechnen (S. 182) sollte in nächsten Auflagen vermieden werden. Naiv ist die Vorstellung im Buch, durch Vogelschutz das Rotwild von Rachenbremsen befreien zu können (S. 156), und veraltert ist die These, daß durch „Ausschaltung" von Luchs und Wolf der Rothirschbestand wesentlich ansteigen würde (S. 164). Unklar ist, weshalb Alterspyramiden beim Wild einen „erkenntnistheoretischen Nutzen" hätten (S. 268) und warum Spanien, Portugal, Korsika und Sardinien zum „außereuropäischen" Vorkommen des Rothirsches zählen (S. 25).

Der größte Mangel des Buches sind jedoch die unvollständigen, unbrauchbaren oder gar fehlenden Literaturhinweise in Text und Schriftverzeichnis. Eine Reihe von Autoren werden im Text – mal mit, mal ohne Jahreszahl – zitiert, erscheinen jedoch in der Literaturliste nicht. Andere wiederum nur dort und nicht im Text, und stehen somit völlig beziehungslos da. Es gibt aber auch solche, die mit vollständigem Zitat unnötigerweise gleich an beiden Stellen erscheinen.

Die vorliegende Neubearbeitung hätte es als wichtige Rothirschmonographie verdient, vor Drucklegung von einem Verlagslektor gelesen zu werden, um diesen ärgerlichen Umstand zu beseitigen. Für das Werk insgesamt ist – von der oben geäußerten Kritik abgesehen – dem Autor und Verlag jedoch zu danken, denn es ist eine wichtige Informationsquelle für jeden, der sich für den Rothirsch, dieses herrliche und größte wildlebende Säugetier unseres Landes, interessiert. Und das sind nicht wenige.

A. Festetics, Göttingen

TATTERSALL, J.; DELSON, E.; COUVERING, J. A. VAN (eds.): **Encyclopedia of Human Evolution and Prehistory.** New York: Garland Publ Inc. 1988. 603 pp. US $ 87.50. ISBN 0-8240-9375-5

Als Mitarbeiter dieser großformatigen und umfassenden Enzyklopädie zeichnen insgesamt 40, meist sehr bekannte Autoren. Der alphabetisch geordnete Stoff, der durch eine Übersichtsliste in der Einleitung ergänzt wird, reicht von der Anthropologie und Zoologie (Morphologie, Genetik, Ethologie, Evolution, Taxonomie etc.) über die Archäologie, Prähistorie und Paläontologie (Geräte, Industrien, fossile Primaten, Paläobiogeographie, Paläopathologie, Stratigraphie etc.) bis zur Geologie und Geophysik (Plattentektonik, Paläoklimatologie, Eiszeiten, Meeresspiegelschwankungen, Paläomagnetismus, Geochronometrie). So finden sich Stichworte wie „molecular clock" ebenso wie „Non-Darwinian evolution" und „extinctions" oder „cladistics" und „numerical taxonomy". Praktisch sämtliche Fundorte fossiler Menschen sind angeführt. Querverweise erleichtern die Suche nach bestimmten Begriffen. Eine Übersicht über das System der Primaten (mit allen rezenten und fossilen Gattungen) gibt den taxonomischen, Zeit- und Korrelationstabellen für das Tertiär (Känozoikum) und Quartär (mit Paläolithikum etc.) den zeitlichen Rahmen. Bei den ausführlich besprochenen Stichworten sind ergänzende Literaturhinweise vorhanden.

Menschenaffen und Menschen werden (wie bei Molekularbiologen meist üblich) als Hominidae mit den Unterfamilien Dryopithecinae (*Dryopithecus* etc.), Ponginae (*Pongo, Sivapithecus* einschließlich *Ramapithecus* etc.) mit Homininae (*Pan, Gorilla, Australopithecus* und *Homo*) klassifiziert! *Megaladapis* und *Lepilemur* werden als Angehörige einer eigenen Familie (Megaladapidae) bewertet. *Oreopithecus* als Vertreter einer eigenen Familie (Oreopithecidae) wird von (E. DELSON) als Angehöriger der Cercopithecoidea und nicht – wie besonders in jüngster Zeit wieder – als solcher der Hominoidea angesehen!

Von etlichen Wissenschaftlern, die sich um die obigen Themenbereiche Verdienste erworben haben, sind Kurzbiographien enthalten. Man vermißt allerdings Namen wie O. ABEL, E. LARTET, G. E. PILGRIM, M. SCHLOSSER (Fayum-Primaten) und D. STARCK, um nur einige zu nennen. Im Abschnitt Pliopithecidae ist im Text zwar H. ZAPFE erwähnt, seine Monographie über *Pliopithecus* (1961) jedoch nicht zitiert. Bei LAETOLI (Tansania) fehlt – wie meist – der Hinweis, daß die dortige Hominidenform erstmalig von H. WEINERT (1950) als *Meganthropus africanus* beschrieben wurde (ein Name, der in die Homonymie von *Australopithecus africanus* fällt).

Von dieser Kritik abgesehen, ist die hervorragend illustrierte Enzyklopädie jedem zu empfehlen, der sich rasch und umfassend über diesen Themenkreis informieren will und der keine Möglichkeit hat, die Originalliteratur zu konsultieren.

Insgesamt ein ausgezeichnetes und zugleich unentbehrliches Nachschlagewerk, das den neuesten Wissensstand berücksichtigt. E. THENIUS, Wien

BOCH, J.; SCHNEIDAWIND, H.: **Krankheiten des jagdbaren Wildes.** Hamburg und Berlin: Paul Parey 1988. 398 S., 250 Abb., 19 Tab. DM 98,–. ISBN 3-490-22812-X

Hauptanliegen der Autoren ist es, die Gesundheit bzw. Krankheiten heimischer Wildarten als „Ausdruck vielfältiger Wechselbeziehungen zwischen Landwirtschaft, Forstwirtschaft und Jagd" darzustellen, somit Krankheiten als Indikatoren für mögliche Umweltbelastungen kenntlich zu machen und weitsichtige Möglichkeiten zu deren Verminderung bzw. Vermeidung zu eröffnen.

Das Buch wurde für Praktiker, in erster Linie Jäger, geschrieben, denen Fachwissen für eine „möglichst frühzeitige Erkennung und wirksame Verhütung" von Wildtierkrankheiten (Parasitosen, bakterielle und virale Infektionen, Geschwülste, Mißbildungen und Regelwidrigkeiten) vermittelt werden soll. Weiter wird es als Orientierungshilfe für Forstleute, Wildbiologen und Tierärzte empfohlen, mit Hinweis auf das in der Regel umfangreiche Literaturverzeichnis nach jedem Kapitel, als Grundlage für weiterführende Arbeiten.

Wertvoll sind die vielen Freilanduntersuchungen und Praxisbeobachtungen sowie die Fülle neuerer Literatur aus den verschiedensten Wissensgebieten, begrüßenswert ist der stets deutliche Versuch, für die Krankheitsbilder einen Überblick aller beteiligten Zusammenhänge darzustellen. Auch die jedem Kapitel angefügten Untersuchungsergebnisse über die Schwermetallbelastung, Belastung mit chlorierten Kohlenwasserstoffen und mit Radionukliden des jeweiligen Wildprets sei lobend herausgestellt.

Dennoch wurde hier eine große Chance vertan: weder die Praktiker noch die anzusprechenden Wissenschaftler bzw. praktizierenden Tierärzte werden dieses Buch mit Gewinn bzw. ohne Ärgernis lesen können. Seine Schwäche liegt in dem Bemühen der Autoren, sich gleichzeitig an eine doch recht „heterogene" Leserschaft wenden zu wollen. So ist ein Buch voller „Brüche" entstanden, im Stil wie auch inhaltlich. Einer Einleitung, die mit einfachen Worten und bei Erklärung aller Fachtermini dem Laien sozusagen einen „Schnellkurs" durch die Pathologie und Mikrobiologie bereiten will, folgen, tierartlich gegliedert, Kapitel, die namentlich im Abschnitt der Parasitosen ein naturwissenschaftliches Studium voraussetzen. Wo einerseits der Begriff Parasit als „zusätzlicher Esser" erklärt wird, setzt

man kurz darauf voraus, daß „obligate Zwischenwirte“ etwa oder die Bedeutung von „Kutikula“ und „Alveole“ u.v.a. bekannt sind (auch wenn diese Begriffe eventuell in irgendeinem Kapitel erklärt werden, kann nicht vorausgesetzt werden, daß der Laie das gesamte Buch liest, um einen bestimmten Abschnitt verstehen zu können). Es ist weiter nicht einzusehen, wieso der Jäger die Systematik der Parasiten, deren lateinische Namen sowie ihren detaillierten Feinbau bis in den Bereich der Elektronenmikroskopie kennen sollte. Jeder Laie wird dabei sehr schnell das Interesse verlieren. Den Biologen (und den Tierarzt) werden die teilweise sehr schlicht geschriebenen Abschnitte stören und eventuell die sehr konsequent durchgehaltene „Jägersprache“ – in trautem Nebeneinander mit wissenschaftlichen Termini. Für mich jedenfalls ist es ein Stilbruch, wenn es etwa heißt: „die Bewegung des Stückes war beeinträchtigt“, wenn angeraten wird, „Losung“ an ein Veterinäruntersuchungsamt zu schicken, oder wenn Krankheiten der „Lichter“, „Spiegel“ usw. beschrieben werden – zusammen mit „nekrotischen Herden“ und z. B. „aviärem Erregertyp“.

Leider gibt es auch einige sachliche Fehler: beispielsweise wird einmal Meningitis mit Hirnentzündung übersetzt. Solche Nachlässigkeiten gibt es nicht im Bereich der für den Biologen/Tierarzt vorzüglich dargestellten Parasitosen. Diese nehmen jeweils den Hauptteil der Kapitel ein (beispielsweise für das Rotwild: 50 S. Parasitosen, 12 S. restliche Krankheiten), es wird jedoch eingangs darauf hingewiesen, daß Parasiten die häufigsten Krankheitserreger, zumindest beim Schalenwild, sind.

Dorit Feddersen-Petersen, Kiel

Fleming, Th. H.: **The Short-tailed Fruit Bat.** A Study in Plant-Animal Interaction. Chicago, London: The University of Chicago Press 1988. 365 pp. £ 39,95, US $ 57,50. ISBN 0-226-25328-7

Ökologie und Verhalten der neotropischen Fledermausart *Carollia perspicillata* (Phyllostomidae) werden monographisch dargestellt. Die Interaktionen zwischen diesen Fledermäusen und ihren Nahrungspflanzen dienen dabei als Modellsystem für die ökologische Bedeutung der früchteverzehrenden Fledermäuse in den tropischen Lebensräumen. In einem einleitenden Abschnitt werden erst die ernährungsbiologischen Besonderheiten der ganzen Familie und ihre Evolution dargestellt. *Carollia* nimmt dabei eine zentrale Stellung ein. Das Problem der Koevolution zwischen den Pflanzen und Fledermäusen wird behandelt. Die Untersuchungen an *Carollia* erfolgten in den Waldgebieten von Costa Rica. Hier dienen mindestens 37 Pflanzenarten als Nahrungsresourcen für Fledermäuse. Zu Beginn der Untersuchung steht eine demographische Erfassung der Populationen (Größen, Todes- und Geburtsraten, Strategien im Lebenszyklus, Ernährung und soziale Organisation). Den Schwerpunkt bilden die Untersuchungen über die Ernährung. Insgesamt dienen *Carollia* mehr als 50 verschiedene Arten von Früchten und etwa 11 Arten von Pollen und Nektar sowie einige Insektenarten als Nahrung. *Carollia* gilt in dieser Hinsicht als „Generalist“. Die Nahrungssuche dieser Fledermäuse konnte mit Hilfe von Radio-Telemetrie, aber auch durch Netzfänge dokumentiert werden. Die Fledermäuse suchen einzeln pro Nacht 2–4 Nahrungsplätze auf (weniger als 2 km vom Tagesquartier entfernt). In einem besonderen Abschnitt werden die energetischen Belange berechnet. Eingehend werden auch die Beziehungen zu den im gleichen Lebensraum vorkommenden Fledermausarten (Konkurrenz um Wohnung und Nahrung) behandelt. Es zeigte sich, daß der ökologische „Erfolg“ von *Carollia* vor allem auf den sehr allgemeinen Bedürfnissen, einer relativ geringen morphologischen Spezialisierung und der Fähigkeit, mit vielen verschiedenartigen Früchten auszukommen, beruht. Die abschließenden Kapitel sind der Beziehung zwischen dem Ernährungsverhalten der Fledermäuse und dem reproduktiven Erfolg der Nahrungspflanzen (Ausbreitung von Samen) gewidmet. Ein Vergleich der demographischen Daten zwischen Phyllostomiden und den Flughunden der Alten Welt zeigt, daß unterschiedliche Strategien eingeschlagen wurden, die wesentlich mit dem räumlich und zeitlich unterschiedlichen Angebot der Nahrung zusammenhängen.

Das Buch enthält 106 Abbildungen und 67 Tabellen. Es ist das Ergebnis von jahrelangen Beobachtungen und Experimenten im Freiland. Die Bindung der neotropischen Fledermäuse an ihren Lebensraum, aber auch ihre Bedeutung für diesen Naturraum, wird hier offenkundig.

E. Kulzer, Tübingen

Die Nordsee – ihre Warnsignale frühzeitig erkennen, richtig deuten und Abhilfe schaffen!

Die Nordsee ist in Gefahr. Umgeben von dichtbesiedelten und hochindustrialisierten Ländern wird sie vielfältig genutzt und als natürliches Ökosystem durch die Aktivitäten des Menschen stark beeinträchtigt. Verschmutzung, Fischerei, Schiffahrt, Küstenschutzmaßnahmen, Häfen und Industriestandorte, die Förderung von Erdöl und Erdgas, Millionen von Erholungssuchenden an den Küsten sowie militärische Übungen in Teilregionen gehören ebenso zu den Belastungsfaktoren wie die Einleitung von Schadstoffen und Düngemitteln über die Flüsse durch die im Landesinneren gelegene Industrie und Landwirtschaft. So wird die Nordsee immer mehr zum Auffangbecken von oft hochgiftigen, schwer abbaubaren und zur Anreicherung neigenden Schadstoffen. Das sind Belastungen, die kein natürliches Ökosystem auf Dauer verkraften kann. Dieses Buch mit Beiträgen von über 50 Wissenschaftlern hilft, entsprechende Warnsignale zu erkennen und richtig zu deuten. Die Autoren haben Fakten zusammengetragen und die Veränderungen in der Pflanzen- und Tierwelt sowie in den physikalischen und chemischen Bedingungen der Nordsee ausgewertet und bieten damit die notwendigen Informationen und Anregungen zur Diskussion für einen großen Interessentenkreis. Zu beziehen durch jede Buchhandlung. ★ **Warnsignale aus der Nordsee.** Wissenschaftliche Fakten. Herausgegeben von José Lozán/Walter Lenz/Eike Rachor/Burkhard Watermann/Hein von Westernhagen. 1990. 428 Seiten mit 186 Abbildungen und 54 Tabellen. Kartoniert 39,– DM

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Mit einer Beilage des Verlages Paul Parey

Walter Jaksch / Erich Glawischnig

Klinische Propädeutik der inneren Krankheiten und Hautkrankheiten der Haus- und Heimtiere

Pareys Studientexte, Nr. 5

3., neubearbeitete und erweiterte Auflage. Hrsg. von o. Univ.-Prof. Dr. E. Glawischnig, II. Medizinische Universitätsklinik für Klauentiere der Veterinärmedizinischen Universität Wien. Mit Beiträgen zahlreicher Wissenschaftler.

1990. 293 Seiten mit 102 Abbildungen und 25 Tabellen. Kartoniert DM 58,– ISBN 3-489-51516-1

In der dritten, neubearbeiteten und erweiterten Auflage vermittelt dieser Studientext Anleitungen und Kenntnisse sowohl für den Studierenden beim Erwerb diagnostischer Fähigkeiten und Fertigkeiten als auch für den praktizierenden Tierarzt bei der täglichen Arbeit am einzelnen Patienten und im landwirtschaftlichen Tierproduktionsbetrieb.
Die Neuauflage berücksichtigt auch die Heimtiere, da diese nunmehr einen erheblichen Anteil am Patientengut des praktischen Tierarztes ausmachen. Die Kapitel Blutuntersuchung und Nervensystem wurden völlig neu bearbeitet, die übrigen Abschnitte kritisch durchgesehen und den heutigen Anforderungen entsprechend ergänzt.
Die Untersuchung des Geflügels ist in einem separaten Kapitel zusammengefaßt. Für die Herdenuntersuchung bei Rind und Schwein wurden Checklisten neu erarbeitet bzw. auf einen praxisgerechten Stand gebracht.

Urteil über die 2. Auflage

»Jeder Untersuchungsvorgang ist straff gegliedert und schematisiert. Zusätzlich werden nach Möglichkeit für jedes Symptom zugleich auch die pathophysiologischen Grundlagen erörtert, um das Verständnis für das Krankheitsgeschehen zu fördern. Der klinischen Diagnostik beim Rind, bei den kleinen Wiederkäuern und beim Schwein, wird neben den bei Pferd und Hund anzuwendenden Verfahren breiter Raum gegeben. Naturgemäß werden auch Katze, Kaninchen, Geflügel, Stuben- und Ziervögel sowie die wichtigsten Pelztiere stark berücksichtigt. Erstmalig sind hier in einer klinischen Propädeutik bestimmte Untersuchungsschemata behandelt, die eigens für die Anforderungen der heute besonders für Geflügel und Schweine gebräuchlichen Intensivhaltung entwickelt sind, bei der Umweltverhältnisse besondere Aufmerksamkeit verdienen.
Ihre Beurteilung steht neben den diagnostischen Maßnahmen am Tier selbst im Mittelpunkt der Betrachtung der Massentierhaltung.
Das vorzüglich ausgestattete Buch beinhaltet für den Praktiker alles, was er in seiner täglichen Arbeit unmittelbar am Patienten sowie im landwirtschaftlichen Tier-Produktionsbetrieb benötigt.«

Die Kleintierpraxis

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Erratum

Zeitschrift für Säugetierkunde, Band 55, Heft 2, S. 106–114 (1990)

VERLAG PAUL PAREY

Durch ein bedauerliches Versehen sind bei der Drucklegung des Beitrags RINKE, „Zur Nahrungsökologie von *Microtus arvalis* (Pallas, 1779) auf Dauergrünland. Teil I" die Autorkorrekturen nicht ausgeführt worden, so daß der Beitrag einige Satzfehler enthält. Daraus ist leider auch ein sachlicher Fehler entstanden. Auf Seite 109 unter 5. muß es lauten:

5. Arten mit negativer Präferenz ($1 > PI > 0$)

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Rückstände von Chlorkohlenwasserstoff-Pestiziden in einer Wochenstube der Zwergfledermaus *(Pipistrellus pipistrellus)*

Von A. Nagel und J. Disser

AK Stoffwechselphysiologie am Zoologischen Institut der Johann-Wolfgang-Goethe-Universität Frankfurt/M., FRG

Eingang des Ms. 2. 2. 1989
Annahme des Ms. 7. 11. 1989

Abstract

Residues of organochlorine pesticides in a maternity group of the Common Pipistrelle (Pipistrellus pipistrellus)

A maternity colony of the Common Pipistrelle *(Pipistrellus pipistrellus)* was investigated with regard to the whole body concentration of the following chlorinated hydrocarbons: Aldrin, DDD, DDE, DDT, dieldrin, heptachlor, hexachlorbenzene, α-HCH, β-HCH, lindane, heptachlor-epoxide, pentachlorbenzene. Except for dieldrin, all chlorinated hydrocarbons could be found in the carcasses and different organs. DDT and its metabolites (DDD, DDE) together reached the highest concentrations of all pesticides analyzed (8.8 ± 5.8 mg/kg fat), followed by endrin (5.1 ± 4.7 mg/kg fat). The mean concentration of other substances analyzed was lower than 0.3 mg/kg fat. Adult females contained a lower concentration of organochlorine residues than their suckling young. Thus DDT and its metabolites were found in adult females at an average concentration of 4.5 ± 4.2 mg/kg fat. The corresponding value for the suckling young was 12.6 ± 4.7 mg/kg fat. It is likely that adult females transfer most of their accumulated residues across the placenta to the foetus during pregnancy and during lactation to the suckling young. The quantity of chlorinated hydrocarbons transferred to the young amounts to 83 % of the accumulated residues of total DDT in the adult females.

As males cannot get rid of their accumulated chlorinated hydrocarbons in the same way as females, they carry the highest pesticide burden. In 3 males from different parts of Hessen, the mean concentration of total DDT was 38.5 mg/kg fat. This value is almost ten-fold higher than in the adult females.

Einleitung

Der Bestand an einheimischen Fledermäusen hat in den letzten 30 Jahren einen drastischen Rückgang erfahren (Frank et al. 1980; Roer 1980/81). Er ist in manchen Winterquartieren auf 2–5 % des ursprünglichen Bestandes zurückgegangen. Einige Arten, z. B. die Kleine Hufeisennase *(Rhinolophus hipposideros)* oder die Mopsfledermaus *(Barbastella barbastellus)*, sind bereits in weiten Teilen der Bundesrepublik Deutschland ausgestorben, obwohl sie früher zu den häufigeren Arten gehörten (Nagel et al. 1987). Verschiedene Ursachen werden für diesen Rückgang verantwortlich gemacht. Änderungen und Intensivierungen der Landnutzung sind dafür verantwortlich, daß den Fledermäusen die notwendige Nahrungsbasis fehlt (Stebbings 1988). Die intensive forstwirtschaftliche Nutzung der Wälder und die Renovierungen von Gebäuden haben zu einem deutlichen Quartierverlust geführt. Eine weitere Ursache ist die Verwendung von Pflanzenschutzmitteln aus der Gruppe der persistenten Chlorkohlenwasserstoffe, die die Nahrungstiere der Fledermäuse vernichten, sich aber auch im Fett der Fledermäuse anreichern (Clark 1981b) und direkte Wirkungen haben können. Diese Substanzen werden entweder mit der Nahrung oder direkt über die Haut aufgenommen, wenn Körperkontakt mit behandeltem Holz in Dachstühlen besteht (Luckens und Davis 1965; Cockrum 1970; Jefferies 1972; Schmidt 1972). Die Auswirkungen dieser Substanzen können Änderungen des Verhaltens

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(Boyd 1987), des Energieverbrauchs (Braham und Neal 1974), der Fortpflanzungsfähigkeit (Clark 1978) und der direkten Überlebensfähigkeit sein (Clark 1981a).

Die Anwendung fast aller früher in der Land- und Forstwirtschaft verwendeten Chlorkohlenwasserstoffe ist heute verboten. Trotzdem scheinen Fledermäuse auch heute noch hochgradig damit belastet zu sein (Braun 1986). Deshalb wurden Tiere einer Wochenstube von Zwergfledermäusen *(Pipistrellus pipistrellus)* auf verschiedene Chlorkohlenwasserstoffe untersucht.

Material und Methode

Im Juni 1985 wurde uns eine Wochenstube von Zwergfledermäusen zum Teil schon tot übergeben, die restlichen Tiere gingen in den folgenden Tagen ein. Die Tiere waren bei einem Hausabbruch bei Darmstadt gefunden worden. Den toten Fledermäusen wurden verschiedene Organe entnommen, nachdem sie vermessen worden waren. Die gleichen Organe der adulten Weibchen und der Jungtiere wurden jeweils zu einer Probe zusammengefaßt. Jeder Restkörper wurde als eine Probe behandelt. Die Proben wurden bei 60 °C bis zur Gewichtskonstanz getrocknet und anschließend mit Seesand homogenisiert. Aus dem Homogenat wurde mit Petroleumbenzin in einer Soxhlet-Apparatur das Gesamtfett mit den darin gelösten Chlorkohlenwasserstoffen extrahiert. Dieser Fettextrakt wurde in zwei Schritten säulenchromatographisch gereinigt. 1) Eine Chromatographiesäule mit einem Durchmesser von 30 mm und einer Länge von 420 mm wurde mit 30 g Aluminiumoxid gefüllt; 250 ml Petroleumbenzin dienten als Elutionsmittel. 2) Eine Chromatographiesäule mit einem Durchmesser von 10 mm und einer Länge von 200 mm wurde mit 1 g Kieselgel gefüllt. Als Elutionsmittel diente ein Gemisch aus n-Hexan und Toluol (65 %/35 %), mit dem sowohl Pestizide als auch polychlorierte Biphenyle (Disser und Nagel 1989) gleichzeitig und mit guter Ausbeute extrahiert werden konnten. Beide Säulentypen wurden mit Natriumsulfat überschichtet. Die Proben wurden anschließend im Rotationsverdampfer (60 °C Badtemperatur) eingeengt und in iso-Oktan aufgenommen. Die Analyse erfolgte mit einem Gaschromatographen (Dani, Typ HR 3800), der mit einem EC-Detektor ausgerüstet war. Die Trennung der Chlorkohlenwasserstoffe erfolgte im Verlauf eines Temperaturprogrammes auf einer Kapillarsäule vom Typ „OV-101" (20 m Länge). Die Registrierung und Auswertung der Meßdaten wurde mit einem Computer (Apple II-Europlus) vorgenommen. Die quantitative Auswertung erfolgte über die Berechnung der Flächenintegrale der einzelnen Peaks. Mirex und ε-HCH wurden den Proben vor der Analyse als externe Standards zugefügt. Die Proben wurden auf die in Tab. 1 angegebenen Chlorkohlenwasserstoffe untersucht.

Tabelle 1. **Auflistung der 12 untersuchten Chlorkohlenwasserstoffpestizide, deren gebräuchliche Abkürzungen, die Nachweisgrenzen und die berechneten Durchschnittskonzentrationen aller untersuchten Tiere**

Substanz	Abkürzung	Nachweisgrenze [µg/l Lösung]	Weibchen und Jungtiere [mg/kg Fett]	(n)
Aldrin		30	0,02	(2)
Dichlordiphenyldichlorethan	DDD	90	3,05 ± 2,42	(23)
Dichlordiphenyldichlorethylen	DDE	30	4,64 ± 3,22	(23)
Dichlordiphenyltrichlorethan	DDT	90	1,09 ± 1,16	(14)
Dieldrin		30	–	
Heptachlor	HC	30	0,04 ± 0,07	(9)
Hexachlorbenzol	HCB	30	0,28 ± 0,28	(19)
alpha-Hexachlorcyclohexan	α-HCH	30	0,02 ± 0,04	(8)
beta-Hexachlorcyclohexan	β-HCH	30	0,05 ± 0,09	(6)
Lindan, gamma-Hexachlorcyclohexan		30	0,08 ± 0,09	(18)
Heptachlor-epoxid	HC-E	30	0,28 ± 0,16	(23)
Pentachlorbezol	PCHB	30	0,01	(1)

DDD und DDE sind Metabolite des DDT. HC-E ist ein Metabolit des HC. α-HCH und β-HCH sind Substanzen, die bei der Herstellung von Lindan entstehen. (n) ist die Anzahl von Proben in denen eine Substanz gefunden wurde. Nur Dieldrin konnte in keiner Probe nachgewiesen werden. Zu den regelmäßig gefundenen Substanzen gehören DDT, DDE und DDD, Lindan und HC-E.

Ergebnisse

Die Untersuchung der 23 Restkörper juveniler und adulter *Pipistrellus pipistrellus* zeigte, daß mit Ausnahme des Dieldrins alle Substanzen nachgewiesen werden konnten. Die durchschnittlichen Rückstandsmengen der meisten Substanzen lagen allerdings niedriger als 0,25 mg, bezogen auf 1 kg Fett (Tab. 1). DDT und seine Metaboliten erreichten zusammen die höchsten Konzentrationen aller untersuchten Insektizide (8,8 ± 5,8 mg/kg Fett). Die Häufigkeit der einzelnen Substanzen war ebenfalls unterschiedlich. Drei Substanzen (DDD, DDE, HC-E) konnten in allen Proben nachgewiesen werden. In mehr als der Hälfte aller Restkörper konnten zudem noch DDT, HCB und Lindan gefunden werden. Die anderen Substanzen waren weit weniger häufig. Vergleicht man die Chlorkohlenwasserstoffbelastung der Muttertiere mit der der fast erwachsenen Jungtiere, die noch niemals selbständig Nahrung zu sich genommen haben, so ist auffällig, daß die durchschnittlichen Konzentrationen von 7 Substanzen in den Jungtieren höher waren als in den adulten Weibchen (Aldrin, DDD, DDE, DDT, HCB, α-HCH, β-HCH). DDT und seine Metaboliten waren in einer Gesamtmenge von 4,5 ± 4,2 mg/kg Fett in den Restkörpern der Muttertiere (n = 12) nachweisbar (Tab. 2). Der entsprechende Wert der Jungtiere (n = 11) betrug 12,6 ± 4,7 mg/kg Fett.

Tabelle 2. **Vergleich der durchschnittlichen Konzentration in 12 Restkörpern adulter Weibchen und in 11 Restkörpern juveniler *Pipistrellus pipistrellus***
(n) ist die Anzahl von Proben in denen eine Substanz gefunden wurde. Die durchschnittlichen Konzentrationen von 7 Substanzen sind in den Jungtieren höher als in den adulten Weibchen

Substanz	Weibchen [mg/kg Fett]	(n)	Jungtiere [mg/kg Fett]	(n)
Aldrin	0,01	(1)	0,03	(1)
DDD	2,45 ± 2,77	(12)	3,71 ± 1,88	(11)
DDE	1,88 ± 1,43	(12)	7,66 ± 1,18	(11)
DDT	0,15	(3)	2,12 ± 0,75	(11)
HC	0,04	(3)	0,04 ± 0,05	(6)
HCB	0,21 ± 0,15	(9)	0,36 ± 0,36	(10)
α-HCH	0,02	(2)	0,03 ± 0,03	(6)
β-HCH	–		0,10 ± 0,10	(6)
Lindan	0,09 ± 0,12	(8)	0,07 ± 0,04	(10)
HC-E	0,35 ± 0,17	(12)	0,20 ± 0,11	(11)
PCHB	0,01	(1)	–	

Die Verteilung von DDT, DDD und DDE im Körper der Zwergfledermäuse ist in Abb. 1 dargestellt. Die höchsten Konzentrationen finden sich bei den adulten Weibchen im Gehirn, im Braunen Fett und in der Flugmuskulatur. In diesen stoffwechselaktiven Organen werden Konzentrationen erreicht, die um ein Vielfaches über denen des Restkörpers liegen. In den Jungtieren sind die Rückstände weitgehend gleichmäßig verteilt und erreichen keine derart hohen Maximalwerte. Die Darstellung einer Pestizidkontamination durch die Angabe der Konzentration im Fett ist jedoch problematisch, da der Fettgehalt je nach Ernährungszustand sehr stark schwanken kann. Aus diesem Grund ist es wichtiger, den Absolutgehalt einer Substanz in jeder Probe zu kennen. Wie aus Abb. 2 ersichtlich, finden sich nur in den Restkörpern und dem Braunen Fett sowie bei den adulten Weibchen in den Milchdrüsen nennenswerte Substanzmengen. Wird die Menge an Rückständen pro Tier berechnet, so ist ein adultes Weibchen mit 720 ng Gesamt-DDT und ein Jungtier mit 2424 ng belastet. Die großen Mengen an Rückständen in den Jungtieren lassen sich nur dadurch erklären, daß die Muttertiere während der Gravidität und der Laktation über Plazenta und Muttermilch einen Großteil ihrer angesammelten Rückstände an die Jungen

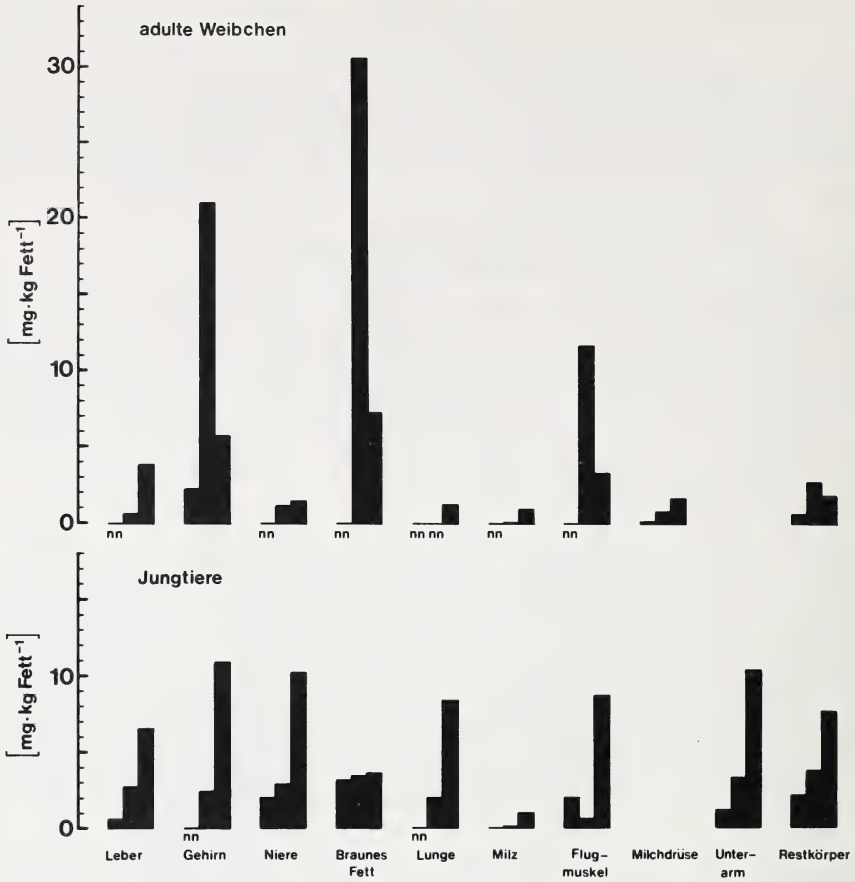

Abb. 1. Vergleich der Konzentrationen von DDT (1. Säule), DDD (2. Säule) und DDE (3. Säule) adulter Weibchen mit Jungtieren der Zwergfledermaus *Pipistrellus pipistrellus* in den Restkörpern und verschiedenen Organen. Während in den adulten Weibchen höchst unterschiedliche Konzentrationen auftreten, sind die Rückstände in den Jungtieren weitgehend gleichmäßig verteilt. Nicht nachweisbar = nn

abgegeben haben. Welche Menge an Rückständen war vor der Gravidität in den Muttertieren vorhanden? Da jedes Weibchen durchschnittlich 1,6 Junge aufgezogen hat, läßt sich eine mögliche Belastung vor der Gravidität aus der Pestizidbelastung der Jungtiere und dem Pestizidgehalt der Weibchen zum Zeitpunkt der Analyse näherungsweise berechnen.

$$\underset{\text{(W adult, vor Gravidität)}}{\text{Rückstandsmenge}} = \underset{\text{(Jungtier)}}{1{,}6 \times \text{Rückstandsmenge}} + \underset{\text{(W adult)}}{\text{Rückstandsmenge}}$$

Sowohl die Aufnahme und Ausscheidung von Pestiziden während der Gravidität und Laktation als auch eine mögliche Dezimierung der Jungtiere durch Aborte und postnatale Mortalität können in dieser Berechnung keine Berücksichtigung finden. Für Gesamt-DDT ergibt die Berechnung eine Menge von 4600 ng/Weibchen vor der Gravidität; gegen Ende der Laktation sind gerade noch 720 ng vorhanden. Dies bedeutet, daß 83 % der ursprünglichen Menge an Gesamt-DDT an die Jungen abgegeben wurde. Darauf, daß vor der Laktation in den adulten Weibchen sehr viel höhere Rückstandsmengen waren, deuten die

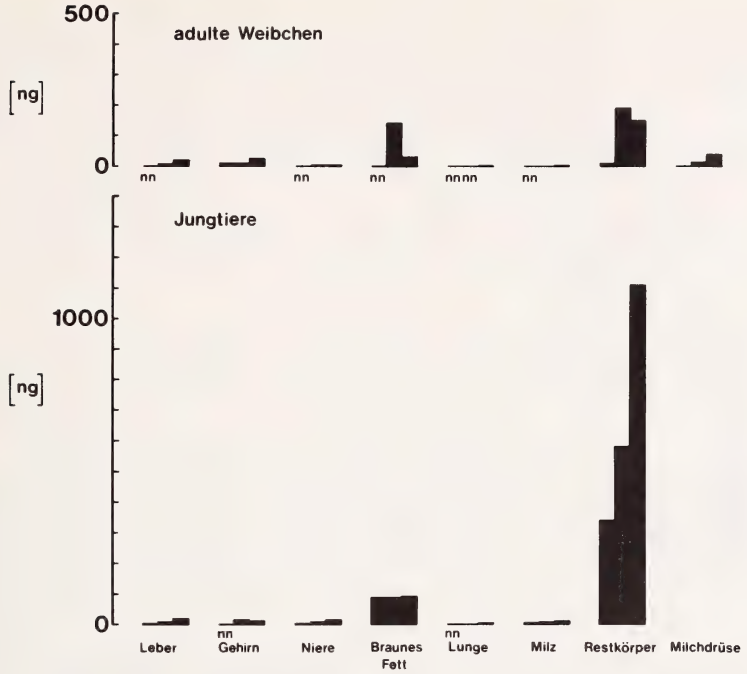

Abb. 2. Vergleich der Substanzmengen von DDT (1. Säule), DDD (2. Säule) und DDE (3. Säule) adulter Weibchen mit Jungtieren der Zwergfledermaus *Pipistrellus pipistrellus* in den Restkörpern und verschiedenen Organen. Nennenswerte Substanzmengen finden sich nur in den Restkörpern und dem Braunen Fett sowie bei den adulten Weibchen in den Milchdrüsen. An der Größe der geschwärzten Flächen ist unschwer erkennbar, daß die Rückstandsmengen in den Jungtieren wesentlich höher sind als in den adulten Weibchen. Nicht nachweisbar = nn

am Ende der Laktation immer noch sehr hohen Pestizidkonzentrationen im Gehirn hin, denn das Fett einschließlich der Pestizidrückstände dort wird offensichtlich selbst bei großem Energiebedarf nicht mobilisiert.

Diskussion

Die in dieser Untersuchung gefundenen Substanzen geben die ganze Vielfalt der einstmals verwendeten Pflanzenschutzmittel wieder. Obwohl heute nur noch Lindan verwendet werden darf (Pflanzenschutzmittel-Verzeichnis 1985), finden sich die anderen Chlorkohlenwasserstoffe zum Teil noch in erheblichen Konzentrationen in den Fledermäusen. Schon früh wurde die Giftigkeit des DDT für Fledermäuse entdeckt (Luckens und Davis 1964; Jefferies 1972; Clark 1981a). Heute werden hauptsächlich noch seine Metaboliten DDD und DDE nachgewiesen. Obwohl die Verwendung von DDT schon seit 1973 in der Bundesrepublik Deutschland verboten ist, machen sie einen Großteil der gefundenen Rückstände aus. Es konnten durchschnittliche Konzentrationen von 8,7 mg/kg Fett festgestellt werden. Die Konzentrationen der anderen Substanzen sind deutlich niedriger und erreichen kaum 0,3 mg/kg Fett. Dieldrin konnte als einzige Substanz in keiner Probe nachgewiesen werden. Diese Ergebnisse stimmen mit den Untersuchungen von Clark et al. (1975, 1978b, 1980, 1983a, b), Clark und Prouty (1976), Drescher-Kaden und Hutterer (1981), Müller (1985) und Braun (1986) weitgehend überein. Die Konzentra-

tionen sind vergleichsweise hoch und entsprechen denen von gefährdeten Greifvögeln (Conrad 1977). Allerdings sind in akut vergifteten Fledermäusen (Racey und Swift 1986; Leeuwangh und Voute 1985; Clark und Prouty 1977; Clark et al. 1978a) noch wesentlich stärkere Belastungen gemessen worden. Der Wirkort der Pestizide scheint das Zentralnervensystem zu sein, denn die Symptome bei akuten Vergiftungen lassen sich eher mit den Rückstandskonzentrationen im Gehirn korrelieren (Dale et al. 1963) als mit denen im Restkörper (Clark 1981a) oder in der Haut (Clark und Prouty 1984). Deshalb werden die Konzentrationen im Gehirn auch als die für das Tier relevanten Konzentrationen angesehen (Clark und Kroll 1977; Clark et al. 1978a; Clark und Stafford 1981). Neben diesen akuten Vergiftungserscheinungen gibt es vielfältige chronische Wirkungen der Chlorkohlenwasserstoffe.

DDT besitzt eine den Stoffwechsel steigernde Wirkung (Braham und Neal 1974). Dadurch wird bei winterschlafenden Fledermäusen mit großer DDT-Belastung der Fettvorrat schneller verbraucht, und die Tiere sterben dann an Energiemangel. Am Ende der Winterschlafzeit, in der ein Großteil des Fettvorrates verbraucht ist, sind die Pestizidkonzentrationen besonders hoch, denn die im Körper verbleibenden Chlorkohlenwasserstoffe sind in weniger Fett gelöst (Geluso et al. 1976; Clark und Krynitsky 1983).

Andere Wirkungen sind Änderungen im Verhalten der Fledermäuse (Boyd 1987) oder eine Zunahme von Aborten und Totgeburten (Clark und Lamont 1976a; Clark 1978; Clark und Krynitsky 1978). Die in dieser Untersuchung festgestellte Weitergabe von Chlorkohlenwasserstoffen der Muttertiere an die Jungtiere ist erheblich und beträgt zumindest 80 % der Menge, die in den Muttertieren vor der Gravidität und Laktation vorhanden war. Die Chlorkohlenwasserstoffe werden zu einem kleinen Teil bereits im Uterus, vornehmlich aber über die Muttermilch übertragen (Ottoboni und Ferguson 1969). Diese Weitergabe konnte für *Eptesicus fuscus* gezeigt werden (Clark und Lamont 1976b). Sie läßt sich auch für *Myotis myotis* aus den Daten von Gottschalk und Matthey (1975) erkennen. Diese hohe Transferrate bedingt von Geburt an eine außerordentlich hohe Belastung der Jungtiere mit Chlorkohlenwasserstoffen, die wesentlich höher ist als die von Vogeleiern (Disser 1987) oder von jungen Vögeln (Prinzinger und Prinzinger 1980). Die Weibchen selbst sind trotz dieser Weitergabe noch stark belastet, denn die Konzentrationen im Gehirn bleiben nach wie vor hoch (29 mg/kg Fett Gesamt-DDT). Für eine Population bedeutet das, daß die Chlorkohlenwasserstoff-Rückstände immer vom Muttertier auf die Jungtiere weitergegeben werden und somit nur durch den Tod von Männchen aus einer Population verschwinden können. Nur dadurch ist zu erklären, daß auch heute noch DDT und seine Metaboliten in so großen Mengen in Fledermäusen gefunden werden, obwohl DDT schon seit anderthalb Jahrzehnten nicht mehr angewendet werden darf. In diesem Umstand findet sich auch eine Erklärung für die aktuellen Häufigkeiten der Fledermäuse.

Gerade die Arten mit hoher Reproduktionsrate (2 Jungtiere pro Jahr), früh einsetzender Reproduktion (meist im folgenden Jahr) und geringer maximaler Lebenserwartung sind heute erfolgreich, wie zum Beispiel die Zwergfledermaus *(Pipistrellus pipistrellus)* (Nagel und Nagel 1989) und der Abendsegler *(Nyctalus noctula),* denn in deren Populationen werden die Chlorkohlenwasserstoff-Rückstände wahrscheinlich kein so großes Ausmaß erreichen können, weil die aufgenommenen Chlorkohlenwasserstoffe wieder schneller aus ihnen verschwinden. Im Gegensatz dazu scheinen Arten mit geringer Reproduktionsrate, spät einsetzender Reproduktion und hohem maximalen Lebensalter, wie zum Beispiel die Mopsfledermaus *(Barbastella barbastellus)* und die Kleine Hufeisennase *(Rhinolophus hipposideros),* heute besonders stark gefährdet. Nach diesen Befunden müssen die Männchen einer Population besonders durch Chlorkohlenwasserstoff-Rückstände belastet und gefährdet sein, denn sie besitzen keine Möglichkeit der Ausscheidung. Eine Untersuchung von drei Männchen aus verschiedenen Teilen Hessens bestätigt dies (Abb. 3). In diesen Männchen wurde eine durchschnittliche Konzentration von 38,5 mg/kg Fett Gesamt-

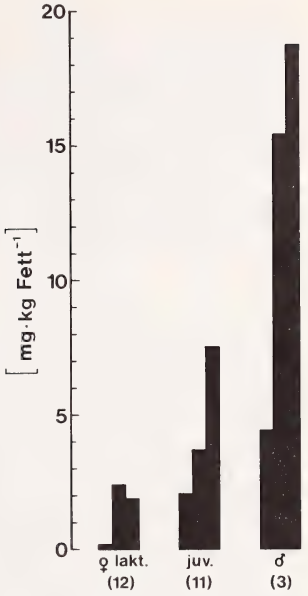

Abb. 3. Vergleich der Konzentrationen von DDT (1. Säule), DDD (2. Säule) und DDE (3. Säule) der Restkörper adulter Weibchen mit denen von Jungtieren und Männchen der Zwergfledermaus *Pipistrellus pipistrellus.* Die Konzentrationen von DDT, DDD und DDE der Männchen sind um ein Vielfaches höher als die der laktierenden Weibchen

DDT ermittelt; dieser Wert ist ungleich höher als der der laktierenden Weibchen und der Jungtiere. Das hat sicher Auswirkungen auf das Geschlechterverhältnis. Beträgt es bei Geburt meist 1 : 1, so finden sich immer mehr adulte Weibchen als adulte Männchen. Dies kann nicht nur in der besseren Auffindbarkeit der Weibchen begründet sein. Die weiteren Aussichten für die Fledermäuse können bis heute nicht abgeschätzt werden. Es ist zu hoffen, daß die hier untersuchten Chlorkohlenwasserstoff-Pestizide immer mehr aus Fledermaus-Populationen verschwinden. Anzeichen für eine Konsolidierung der Fledermausbestände gibt es bereits (Nagel und Nagel 1989). Allerdings muß eingewendet werden, daß eine andere Gruppe von Chlorkohlenwasserstoffen, die polychlorierten Biphenyle (PCB), in noch bedeutend größerem Umfang in Fledermäusen vorkommen (Nagel und Disser 1987; Disser und Nagel 1989) und die hier untersuchten Substanzen nicht die einzige Belastung der Fledermäuse darstellen. Ferner ist bis heute unklar, wie sich moderne Holzschutzmittel und Pflanzenschutzmittel langfristig auf die Fledermäuse auswirken. Allerdings scheinen erste Ansätze hierzu recht erfolgversprechend zu sein, denn es gibt bereits Holzschutzmittel, die ganz offensichtlich den Fledermäusen nicht schaden (Cymorek und Wegen 1983; Kulzer 1985).

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Zusammenfassung

Eine Wochenstube mit 23 Zwergfledermäusen *(Pipistrellus pipistrellus)* wurde auf folgende Chlorkohlenwasserstoffe untersucht: Aldrin, DDD, DDE, DDT, Dieldrin, Heptachlor, Hexachlorbenzol, α-HCH, β-HCH, Lindan, Heptachlor-epoxid, Pentachlorbenzol. Mit Ausnahme des Dieldrins konnten alle Substanzen nachgewiesen werden. DDT und seine Metaboliten (DDD, DDE) erreichten zusammen die höchsten Konzentrationen aller untersuchten Pestizide (8,8 mg/kg Fett). Die durch-

schnittlichen Konzentrationen der anderen untersuchten Substanzen sind niedriger als 0,3 mg/kg Fett. Die adulten Weibchen haben weit weniger an Chlorkohlenwasserstoff-Pestiziden als die Jungtiere. DDT und seine Metaboliten konnten in den adulten Weibchen in einer durchschnittlichen Konzentration von 4,5 ± 4,2 mg/kg Fett gefunden werden; bei Jungtieren waren es 12,6 ± 4,7 mg/kg Fett. Die höheren Pestizidkonzentrationen in den Jungtieren können nur dadurch erklärt werden, daß die Muttertiere während der Gravidität und der Laktation einen Großteil ihrer eigenen Rückstände an die Jungen abgegeben haben. Die Menge an Chlorkohlenwasserstoffen, die an die Jungtiere weitergegeben wurde, beträgt 83 % ihrer ursprünglich angesammelten Rückstände.

Da die Männchen nicht über diese Möglichkeit der Chlorkohlenwasserstoffabgabe verfügen, sind sie am meisten belastet. In drei Männchen aus Hessen wurde mit durchschnittlich 38,5 mg/kg Fett Gesamt-DDT fast zehnmal soviel wie bei adulten Weibchen gefunden.

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The occurrence of non-territorial adult and yearling males on the mating ground in the Pipistrelle bat *(Pipistrellus pipistrellus)*

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Abstract

Male pipistrelle bats set up individual territories at special mating grounds around their roosts. The occurrence of surplus males, non-territorials, indicates that the population density of males at the mating ground is limited by the number of roost sites and the territorial behaviour of the residents. The silence and sporadic appearence of the non-territorial males, and their response to high female densities, support the hypothesis that these males may try to steal matings from territory owners.

Immature male yearlings were excluded from the roosts of territorial males to the same degree as non-territorials. The high frequency by which yearling males return to the same roost makes them potential competitors for the territories. The relatively high percentage of returning male yearlings which become owners of a territory supports this hypothesis. The low recovery rate of non-territorials probably results from their failure to get established.

Introduction

In the pipistrelle bat (*Pipistrellus pipistrellus* Schreber, 1774), as in most temperate vespertilionids, there is a sex difference in dispersal after hibernation (Bradbury 1977). The sexes remain in unisexual units until late summer when mating groups are formed. In late spring, when fertilization by stored sperm takes place (Pagenstecher 1859), females aggregate at traditional roosts to form nursing colonies (e.g. Ryberg 1947; Hůrka 1966; Stebbings 1968; Grimmberger and Bork 1978; Swift 1980). At the same time, adult males arrive at the mating grounds. Here, mating grounds are defined as an area where males traditionally establish territories around their roost sites (in this case bat boxes). The males monopolize these roost sites until the end of the mating season. Following Kaufmann (1983), territory is defined as "space-related dominance" where the territory owner has priority of access to critical resources.

The young are born in mid June. After weaning at the end of July – earlier or later according to local climatic conditions – the mating period starts. Females attain sexual maturity in their first autumn (Racey 1974) and both adult and juvenile females aggregate at the mating ground, where they form harem groups. Mating activities decrease by the end of September. Pipistrelle males reach sexual maturity at an age of one year. The mating system of the pipistrelle bat has been described as a resource-defence polygyny, where the males control access to roost sites which are crucial for acquiring females (Gerell and Lundberg 1985; Lundberg and Gerell 1986).

Non-territorial adult and yearling males occasionally visit the mating grounds. In this paper the spatial and temporal distribution of non-territorial and yearling males in relation to that of territory holders is analysed.

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Material and methods

The pipistrelle population, which is the subject of this paper, has been studied since 1981 using bat boxes. The study area is a 150-ha pine plantation 30 km east of Lund in southernmost Sweden. The boxes (Gerell 1985) were grouped (2–4) at spatially separated stations, in all 22 during 1981–1983 and 33 during 1984–1987. The spacing between stations varied between 75 and several hundred metres. Each station functioned as the territory of a single male and contained a number of alternative roost sites (boxes). The boxes were checked throughout the season (March–November), but more regularly from April to the end of September. Captured pipistrelles were sexed, aged and banded. Body mass was determined to the nearest 0.25 g with a Pesola spring balance, while forearm length was measured to the nearest 0.1 mm with dial calipers. Ageing and assessment of reproductive status were done according to Racey (1974). Juveniles were recognized by the presence of unfused and translucent phalangeal epiphyses. Immature males were distinguished from adult males by their tunica vaginalis, which is densely pigmented and can be seen through the skin. A yearling is here defined as an animal that is born during the immediately preceeding breeding period. Hence, the category yearling includes juveniles, immatures and males undergoing puberty.

In order to be classified as non-territorial, a male had to be sexually mature and known not to have established a territory in the area. Male yearlings were about two months old when they left their natal area and first appeared at the mating ground. Male juveniles found in maternity colonies are excluded from the following analysis.

Ultrasonic detectors; QMC S 100 (QMC Instrument Ltd.) and a D-940 (Ahlén et al. 1984), were used for identifying the sounds of the bats.

Results

Time of occurrence and location of non-territorial and yearling males in relation to territory holders

A. Non-territorial males

The number of non-territorial males visiting the stations per season ranged from 6 to 19 ($\bar{x}$ = 10.3, S.D. = 4.7, n = 72). The visiting frequency peaked in June–Sept. (Table 1). No significant difference was found between the number of non-territorials found alone at a station and found at a station occupied by a territorial male (χ^2 = 2.26, p > 0.10, df = 1, Table 2). Most of the visiting non-territorial males, however, were caught at roost sites unoccupied by territorial males (χ^2 = 22.89, p < 0.001, df = 1). In 1984 when the number of non-territorial males was high, their occurrence was positively correlated with the density of females (r_s = 0.62, df = 10, p < 0.05).

Table 1. **Number of non-territorial males and male yearlings caught during the period March–November in bat boxes at Vombs Fure, southern Sweden, 1981–1987**

	Non-territorial males		Male yearlings	
	n	%	n	%
Mar	2	2.2	–	–
Apr	8	8.6	–	–
May	8	8.6	–	–
Jun	15	16.1	–	–
Jul	17	18.3	–	–
Aug	22	23.7	25	18.1
Sep	13	14.0	78	56.5
Oct	5	5.4	30	21.7
Nov	3	3.2	5	3.6
Total	93		138	

Table 2. **Number of non-territorial males (NT) and male yearlings (Y) captured at an unoccupied station, at the same station as a territory holder, and at the same roost as a territory holder**
Combined data from 1982–1987

	Unoccupied station		Station with territory holder		Same roost as a territory holder	
	NT	Y	NT	Y	NT	Y
Apr	2	–	1	–	5	–
May	4	–	1	–	3	–
Jun	11	–	3	–	0	–
Jul	11	–	5	–	1	–
Aug	9	12	7	9	1	2
Sep	9	34	2	28	2	16
Oct	4	17	0	2	0	0
Total	50	63	19	39	12	18

B. Male yearlings

The number of male yearlings banded per season ranged from 8 to 24 ($\bar{x}$ = 14.9, S.D. = 5.3, n = 104) and most of them were caught in September (Table 1). More than half of them (52 %) were captured at a station lacking a territorial male, 32 % at the same station as a territory holder, and 15 % at the same roost as a territorial male. Most of the yearlings, however, were found at unoccupied roosts (χ^2 = 33.50, $p < 0.001$, df = 1) (Table 2). Male yearlings did not appear more often than non-territorials at stations occupied by territorials (χ^2 = 2.16, df = 1, $p > 0.10$).

Recovery frequency

A. Non-territorial males

A total of 55 non-territorial pipistrelle males were banded during the period 1981–1986 (Table 3), of which only 6 were recaptured during consecutive years. One of them was recovered at the station where he was banded. In contrast, territorial males, showed a high rate of recapture and total roost-site fidelity.

Table 3. **Number of territorial, non-territorial and yearling males banded at Vombs Fure and recaptured in a succeeding year**
Combined data from 1981–87

	Number banded	Recaptures		
		n	%	at banding site (%)
Territorials	49	28	57.1	100.0
Non-territorials	55	6	10.9	16.7
Yearlings	80	24	30.0	66.7

In a particular season, the majority of non-territorial males were captured only once (Table 4). Data from the mating season only show the same pattern (76 % single captures).

B. Male yearlings

During the years 1981–1986 a total of 80 male yearlings were banded of which 24 returned to the study area during consecutive years (Table 3). Sixteen of these, now almost one-year old, were recaptured at the station where they were banded.

Table 4. **Number of times (%) non-territorial and yearling males were captured in the same season at Vombs Fure**
Combined data from 1981–87

	Capture frequency (times)		
	1	2	3
Non-territorials	50 (70.4)	18 (25.4)	3 (4.2)
Male yearlings	69 (71.9)	24 (25.0)	3 (3.1)

During a particular season most of the male yearlings were observed only once (Table 4). There was no difference in the number of times they were caught during the year of banding between those yearlings that returned the following season and those that did not ($\chi^2 = 1.50$, $p > 0.2$, df = 1).

Chance of becoming a territory holder

Only 4 % of the non-territorial banded during 1981–1986 later became territory holders in the study area, while the corresponding figure for the yearlings was 21 %. Of those that returned to the area no less than 71 % became owners of a territory compared with 33 % of the non-territorials.

Size and relative age of non-territorial males

A comparison of forearm length between territorial and non-territorial males showed that there was no significant difference in size between these two groups ($t = 0.93$, $p > 0.2$, df = 102). To determine whether territorial males were relatively heavier than non-territorials at the time of establishment, the ratio body mass : forearm length was compared between the two groups; the same comparison was also done for the mating season. During establishment no difference was found ($t = 0.19$, $p > 0.5$, df = 38), but during the mating period

Table 5. **Age distribution of captured non-territorial males (NT) and territorial males (T) during 1982–1986**

	Age class (years)					
	1		≥1		≥2	
	NT	T	NT	T	NT	T
1982	1	1	5	9	0	6
1983	0	2	8	10	2	5
1984	9	11	6	5	2	13
1985	4	3	3	4	0	9
1986	1	2	3	11	1	6
Total	15	19	25	39	5	39
χ^2	0.24		1.55		15.44	
p	>0.50		>0.20		<0.001	

non-territorial males were significantly heavier than territorial males ($t = 4.76$, $p < 0.001$, df = 80).

Comparison of the proportions of territorial and non-territorial males belonging to each of the age classes one year, and two years or older (Table 5), shows that territorials were significantly older than non-territorials ($\chi^2 = 10.79$, $p < 0.001$, df = 1).

Discussion

Most of the non-territorial males which visited the study area appeared on just a single occasion. Those that were caught more than once were never found at the same station twice. It may be interpreted that these males tried to get established in the area, but were prevented from occupying territories by the presence of residents. The very few occasions when a non-territorial male succeded in getting a territory occurred when a territory holder disappeared for some reason, or when excessive roost sites were provided (Lundberg and Gerell 1986). Thus, the density of the male population in the study area seems to be limited by the number of roosts and territorial behaviour.

The visiting frequency of non-territorials was highest in the period June–Sept. Spermatogenesis in pipistrelles is initiated in late spring (Racey and Tam 1974), and the males establish their territories in June. The relatively high number of non-territorial males recorded in the area before the females arrived (beginning of August) indicates that they compete for territories. Their still higher visiting frequency in August is probably related to the mating season. The search for females may result in an increased mobility of non-territorial males. The sound of advertising territorial males (Lundberg and Gerell 1986) may not only attract females but also non-territorial males.

In polygynous mating systems there is intense competition for mates, and the mating success varies between males. Most females are monopolized, and probably fertilized, by territory owners (Dewsbury 1982). Non-territorial or subordinate males often have developed alternative mating behaviours either as "satellites" (e.g. Hogan-Warburg 1966; Emlen 1976; Howard 1978; Perill et al. 1978; Wirtz 1982) or as "sneakers" (e.g. Le Boeuf 1974; Cluttonbrock et al. 1979; Gross 1982). The satellite tactic, where subordinates are associated with territory holders, does not apply to the pipistrelles studied. Non-territorial males were never observed to perform a song flight, the display by which territorial pipistrelle males attract females to their roost sites (Lundberg and Gerell 1986). Their silence, sporadic appearence, and response to high female densities suggest that non-territorial males try to make the best out of a bad situation functioning as sneakers, which (unnoticed) try to steal matings with the females of the territory holders.

There was no difference in size between non-territorial and territorial males. The dominance of the territory owners over non-territorial males is probably a result of both an age-related and an owner-intruder assymmetry. The lower body mass of territorial males during the mating period is caused by mating activities (Lundberg and Gerell 1986; Lundberg 1989). The relatively high body mass of non-territorial males during the mating season indicates that they really are non-territorial, and not just occasional visitors established elsewhere. It also shows that non-territorial males invest in survival rather than reproduction (Lundberg 1989).

In our pipistrelle bats, as in many mammals (Greenwood 1980), males tended to disperse while females remained mainly in their natal area. Both yearling females and males visited the study area during the mating period, but male yearlings appeared on average later (Gerell and Lundberg 1985). Studies on pipistrelle maternity colonies (Stebbings 1968; Rakhmatulina 1972; Swift 1980; Racey and Swift 1985) show no difference in development and time of leaving the colony between male and female yearlings. An explanation of the late arrival of the male yearlings to the mating ground could be the competition for unoccupied roost sites with non-territorial males.

Yearlings were excluded from territorial males' roosts to the same degree as the non-territorial males. Male yearlings cannot interfere with territorial males' chances to mate, so why do the latter bother to exclude these immature males? Yearling males may be prospecting for territories for future mating seasons. The high frequency by which yearlings return to the same roost, and their high success in getting territories, support this hypothesis. So, territory owners may make a future investment by excluding them.

The higher rate of recovery of yearlings compared with that of non-territorials may be explained by the difference in age. The probability of a yearling getting established is rather high compared with that of a non-territorial which has already failed. A better option for the latter is to visit other mating grounds, of which they already may have knowledge. Yearlings on the other hand return to the only area with which they are familiar.

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Zusammenfassung

Das Auftreten von nicht-territorialen erwachsenen und jungen Männchen im Fortpflanzungsrevier der Zwergfledermaus (Pipistrellus pipistrellus)

Männliche Zwergfledermäuse bauen individuelle Territorien in bestimmten Fortpflanzungsrevieren auf. Ihre Quartiere liegen innerhalb dieser Territorien. Das Auftreten von zusätzlichen, nicht-territorialen Männchen zeigt, daß die Populationsdichte der Männchen im Fortpflanzungsrevier durch die Anzahl der Quartiere und durch das Territorialverhalten der Revierinhaber begrenzt wird.

Die fehlenden Lautäußerungen und das sporadische Erscheinen nicht-territorialer Männchen und ihre Reaktion auf hohe Weibchendichte unterstützen die Hypothese, daß sich diese Männchen in schon besetzte Territorien einschleichen und sich dort vermutlich verpaaren.

Immature männliche Jungtiere wurden im selben Maß wie die nicht-territorialen Männchen aus den Quartieren der territorialen Männchen vertrieben. Da die Jungtiere sehr häufig zum selben Quartier zurückkehren, werden sie zu potentiellen Konkurrenten um die Territorien. Der relative hohe Prozentsatz zurückkehrender männlicher Jungtiere, die dann Inhaber eines Territoriums werden, unterstützt diese Annahme. Die geringe Wiederfangquote von nichtterritorialen Männchen ist wahrscheinlich dadurch bedingt, daß es ihnen im Gegensatz zu den männlichen Jungtieren nicht gelingt, sich zu etablieren.

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Short-term effects of the mass dying of Harbour seals in the Kattegat-Skagerrak area during 1988

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Abstract

Studied the effects of the recent mass dying of harbour seals, *Phoca vitulina,* in the Kattegat-Skagerrak area. Results from six aerial surveys in 1988 were compared to trajectories of the trend in the population during 1978–1986. The number of seals declined by 60 % compared to expected values for 1988 and by 47 % compared to 1987. The decline was evident in each of three different subareas indicating that the disease had similar effects in all subpopulations. By using the decline as an estimate of the overall mortality and applying this to the number of dead seals found, an estimate of the expected "true" population size in 1988 (i.e. excluding effects of the epizootic) was achieved. When this is compared to the extrapolated numbers of seals present on land about 77 % of the population is hauled out during the surveys.

Introduction

The development of the European seal stocks is closely linked to anthropogenic influence of which hunting was the most important during the first half of this century (Reijnders et al. 1981; Heide-Jørgensen and Härkönen 1988; Helle et al. 1976). Protective measures during the past decades resulted in increasing seal populations (Hansen 1986; Heidemann 1987; Stede 1987; Reijnders et al. 1981; Heide-Jørgensen and Härkönen 1988), although negative effects of pollutants were identified in some areas (Helle et al. 1976; Helle 1980; Reijnders 1986).

In the summer of 1988 an epizootic disease drastically altered the increasing trends for the harbour seal, *Phoca vitulina,* stocks in the North Sea area. The background for the virus infection and the mechanism behind the dispersal are still unsolved. It was the first well documented incident of mass mortality among free ranging harbour seals in European waters. Available data on the progress and dispersal of the disease and of earlier incidents of mass mortality in pinnipeds is compiled in Dietz et al. (1989).

This study aims to quantify the short-term effects of abortions and mass dying on the seal stocks in the Kattegat-Skagerrak.

Material and methods

Land based systematic observations and counts of seals have been carried out on Anholt (Fig. 1) since 1978. Sand dunes close to the seals were used as platforms for observations, and by using a powerful telescope (×15–25) the seals were counted twice on every occasion and the average numbers were reported. The observation effort was allocated to morning hours (0900) during the moulting season in August.

From 1979 to 1988 aerial surveys of all major haul-out sites in the Kattegat-Skagerrak area were carried out simultaneously in Denmark and Sweden. The aerial surveys were made late in the moulting season, at the end of August, and all haul-out sites were photographed obliquely for later enumeration

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of seals on the photos. Days with strong winds or rain were avoided for the surveys, as well as weekends with harassments from tourists. In 1982 and 1987 the surveys were considered unsuccessful in most areas and the results are rejected. In 1988 six aerial surveys were accomplished between 22 and 31 August to estimate the variance of the survey results.

Results from two aerial surveys in Subarea III (see Fig. 1), simultaneous with the surveys in the other subareas, were provided by Ebbe Bøgebjerg Hansen, Danish Game Biology Station.

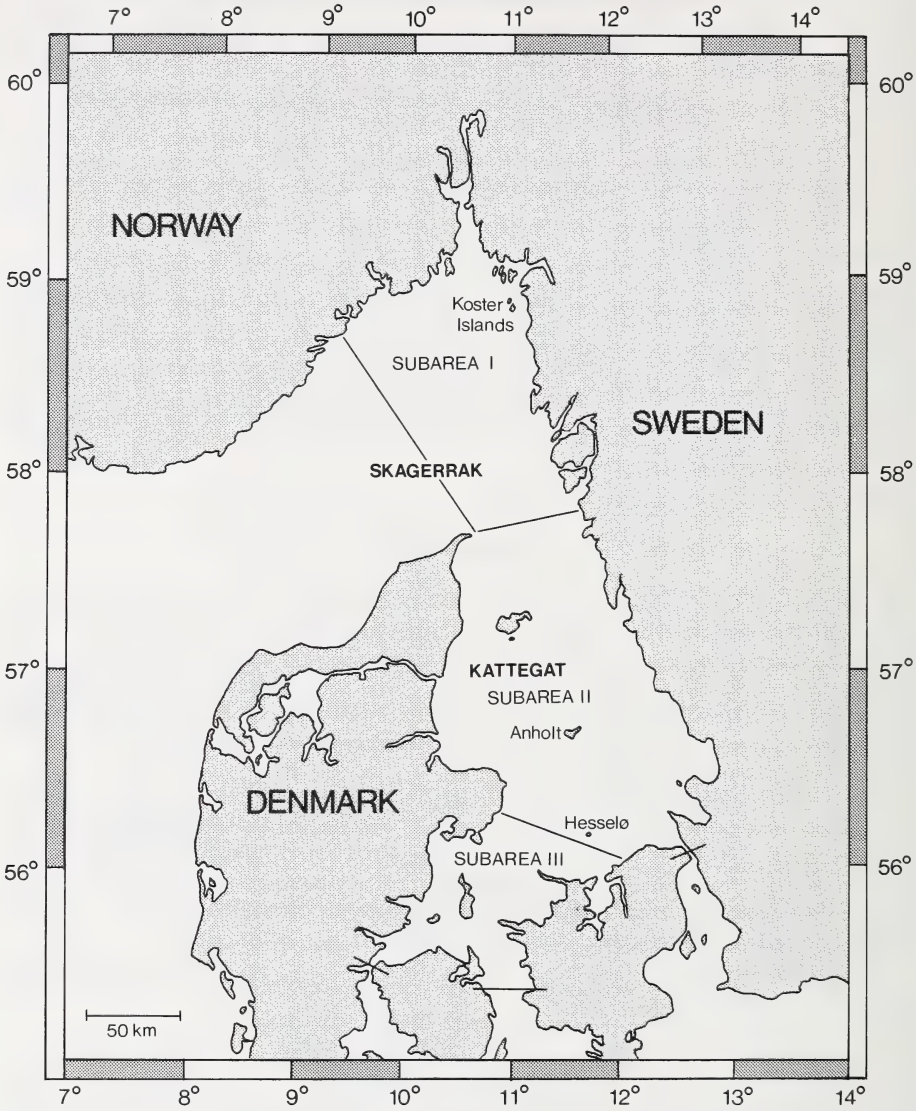

Fig. 1. Map of the area with localities and subareas mentioned in the text

The anticipated population size in 1987 and 1988 if the epizootic had not occurred, was calculated by trajectories of the population trend for the period 1979–1986 with matching confidence limits (see Heide-Jørgensen and Härkönen 1988).

Standard deviation of the log.-transformed data used in predictions for 1988 was calculated according to Sokal and Rohlf (1981, p. 473).

Data on number, age categories and sex classes of the dead seals were preliminarily compiled in Heide-Jørgensen and Härkönen (1989), where even the efficiency of the registration of dead seals is discussed.

Results

On Anholt changes in the coastline has rendered precise enumerations of seal herds more difficult in 1988 than in previous years. Nevertheless, a profound effect of the epizootic on the population at this locality is clearly perceptible from both maximum and mean numbers in August (Fig. 2; Table 1). The exponential rate of increase at Anholt was 0.10

Table 1. **Summary statistics for survey results and mortalities for different subareas**
Confidence limits (95 %) are given in brackets

Area	Anticipated number of seals in Aug. 1988 A[1]	Number of dead seals B[2]	Actual number of seals present during surveys in 1988 C[3]	Overall mortality rate D=(A–C)/A	Calculated population size in 1988 E=B/D	Fraction on land F=A/E
Anholt Max.	660 (542–800)	277	265	0.60	–	–
Anholt Mean	443 (341–574)	277	204 (186–222)	0.54	–	–
Subarea I	1666 (1418–1958)	1469	732 (684–779)	0.56	2623	0.64
Subarea II	4481 (4110–4885)	3164	1967 (1840–2093)	0.56	5650	0.80
Subarea III	806 (520–1249)	745	272 (178–365)	0.66	1129	0.71
Grand Total	7009 (996–7021)	5378	2901 (2497–3305)	0.59	9115	0.77

[1] Numbers are extrapolated from time series between 1978 and 1986 (1987 for Anholt). – [2] See Heide-Jørgensen and Härkönen 1989 for a detailed account of the registration of dead seals. – [3] Numbers were calculated as means of six aerial surveys in Subarea I and II, and three aerial surveys in Subarea III and Grand Total.

and 0.09 for maximum and mean numbers respectively during 1978–1987. Land based surveys on Anholt in 1988 showed that the maximum and mean numbers of seals in August were 265 and 204 respectively, compared to 525 and 341 in 1987 (Table 1). Assessment of the virtual decline on Anholt is subject to the proviso that conditions for precise countings have deteriorated in 1988.

In Subarea I and II six aerial surveys were accomplished in 1988, but in Subarea III only three surveys were carried out. Mean and confidence limits for the entire area is accordingly based on only three surveys. A mean of 2.901 seals with matching confidence limits (95 %) of less than 14 % was obtained for the entire area (Table 1C). In Subarea I and II confidence limits of less than 7 % were acquired. This low variance strengthens the conclusions of the present as well as past surveys.

The total number of harbour seals in the entire Kattegat-Skagerrak population diminished by approximately 60 % (Table 1D) from the anticipated (Table 1A) to the actual number present during aerial surveys in 1988 (Fig. 2; Table 1C). Comparison with expected values for 1987 revealed a decline of 47 %. The decline was of similar magnitude in three subareas, as well as on Anholt, indicating that the disease had a similar effect in all areas.

Assuming that the number of dead seals (Table 1B) represents the overall mortality of 0.59 (Table 1D) a hypothetical population size in 1988, in the case that the epizootic had not occurred, is calculated at 9115 seals (Table 1E). Applying this figure to the extrapolated number of seals present during aerial surveys (Table 1A) reveals a fraction of approximately 77 % of the seals hauled out during the surveys (Table 1F). If a similar fraction of the post-epizootic population of harbour seals in the Kattegat-Skagerrak was present on land during surveys in 1988 then the entire populations amounts to approximately 3768.

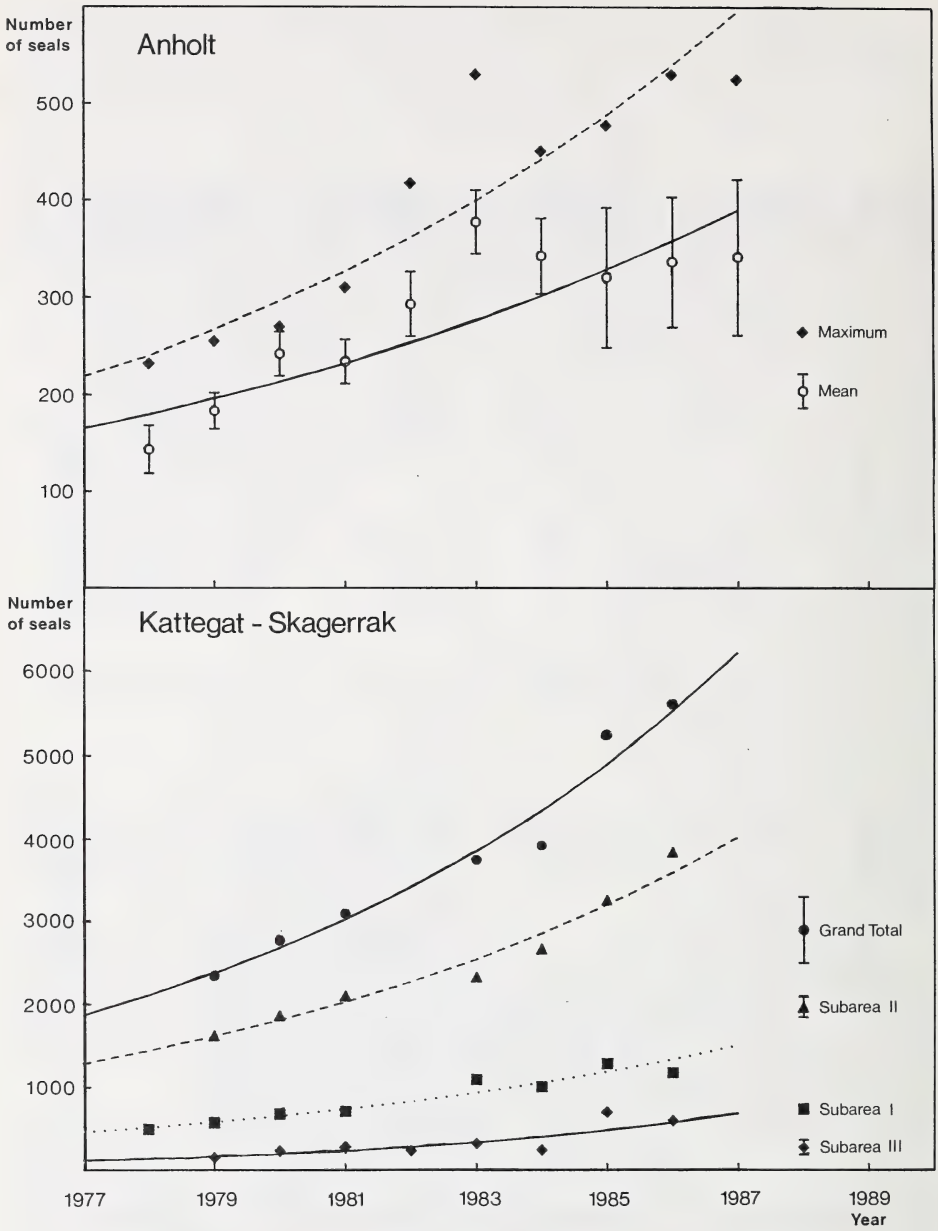

Fig. 2. Time series of surveys of seals on Anholt and in the entire area from 1978 to 1988

The variation between subareas of the fraction of seals on land (Table 1F) may reflect differences in the efficiency with which dead seals were recorded and the fact that corpses may have drifted between subareas. Hence, the estimate of the proportion of seals on land for the entire area must be considered the most reliable.

Discussion

The seal plague had its peak mortality during or shortly after the whelping season in the Kattegat-Skagerrak. Few pregnant females were found dead (n = 10) in the beginning of the epizootic and almost all pups from 1988 were hit by the disease either by being aborted, abandoned or infected (Heide-Jørgensen and Härkönen 1989). From this it appears that a full reproductive cycle has just been completed and the progeny wiped out prior to the surveys in late August. Thus, it is reasonable to compare censuses from 1988 with the anticipated (i.e. without the epizootic) number of seals in 1988.

Aerial surveys between 1978 and 1986 revealed an exponential rate of increase of 0.12 in the Kattegat-Skagerrak (Heide-Jørgensen and Härkönen 1988). Unfortunately no reliable surveys from 1987 are available except from Anholt, where the increase continued at 0.10 and 0.09 for maximum and mean numbers of seals, respectively. This is slightly less than the increase documented from aerial surveys of the entire area till 1986, hence trajectories from 1986 to 1988 will probably overestimate the actual number of seals, but the upward bias may well be negligible (Table 1A).

Among the various sources of errors inherent in these calculations the number of dead seals must be used particularly cautiously. The number of dead seals (Table 1B) does not include the autumn (1987) and winter mortality prior to the epizootic and consequently it underestimates the virtual number of seals that died between the surveys in 1987 and 1988. In addition, despite the collecting effort some dead seals were not registered. On the other hand pups that would have died from 'natural causes' during June through end of August are included, although the pregnant females that died during the epizootic reduces this error.

The epizootic killed 52 % (n = 821) males in the immature and mature (1+) segment of the population (Heide-Jørgensen and Härkönen 1989), which is more males than expected from studies of other harbour seal populations, where e.g. 47 %, 35 %, and 9 % were found among seals older than five years (Pitcher and Calkins 1979; Boulva and McLaren 1979; Bigg 1979). In addition, more mature (61 %, n = 433) than immature died than predicted from a platycurtic age structure in an increasing population.

This selective mortality has altered the age structure of the population. Different segments of the population have different affinities for haul-out and therefore surveys of seals on land may not be directly comparable before and after the epizootic. During past surveys low numbers of pups have been present on land in August (Heide-Jørgensen in litt.), and the absence of pups in 1988, will affect results from that year in an upward trend. This may, however, be counterbalanced by the reductions in males that, in other populations, are known to moult later than females (Thompson and Rothery 1987). The aerial surveys are conducted late in the moulting season and a smaller fraction of the males may be present in 1988 compared to previous years. The total effect of the assumed change in haul-out tenacity has not been evaluated in this study.

Although subject to various errors this study provides a crude estimate of the fraction of the entire population that is hauled-out during the surveys in 1988, and the estimate is of similar magnitude as those reported from radio-tagged individuals in other areas. Thompson (1987) monitored instrumented seals in Orkney, Scotland, and found that the seals were present on the haul-out site during 80 % of the days of the moulting season. In Alaska Pitcher and Calkins (1981) found that seals were hauled-out in approximately 50 % (n = 20) and 41 % (n = 13) of the days just prior to and after the moulting season.

The long-term effects of the seal plague have not been addressed in this study and the chances for recovery of the seal stocks can not be evaluated until the long-term effects have been quantified.

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Zusammenfassung

Die kurzfristigen Auswirkungen der Seehundpest in der Kattegat-Skagerrak-Region 1988

Zählungen der Seehund-Population im Kattegat und Skagerrak wurden durchgeführt, um die Auswirkungen des kürzlichen Massensterbens einzuschätzen. Sechs Luftphotozählungen sind im Jahre 1988 durchgeführt worden. Die Ergebnisse wurden mit dem Entwicklungsverlauf der Populationsgröße während der Jahre 1978–1986 verglichen. Die Anzahl der Seehunde zeigte sich um 60 % reduziert verglichen mit erwarteten Werten für das Jahr 1988. 47 % ist die entsprechende Zahl für das Jahr 1987. Die Reduktion war in drei verschiedenen Teilgebieten deutlich erkennbar, was zu dem Ergebnis führte, daß die Krankheit die gleichen Auswirkungen in allen Teilpopulationen hatte.

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Cold-adaptive modifications and torpor in the Cretan Spiny mouse (*Acomys minous* Bate, 1905)

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Abstract

Studied the effects of cold exposure, photoperiod, and food availability on metabolic rate and body temperature in the Cretan spiny mouse *(Acomys minous)*. In animals with food ad lib. exposure to ambient temperatures (Ta) auf 10 °C led to a gradual increase of the nychthemeral fluctuations of metabolic rate and body temperature. Within 3 days metabolic rates and body temperatures measured during the activity phase (night) were shifted to higher values while the corresponding values measured during the day remained unchanged. These effects which are regarded as cold adaptive modifications do not depend on the photoperiod. Food restriction (at Ta = 20 °C) induced torpor with a decline of the colon temperatures to 25.9 ± 1.6 °C (mean ± SD) and a decrease of the metabolic rates to 50 % of the initial values.

Experiments suggest that *Acomys minous* can cope with unfavourable low Ta by an increase of metabolism during the activity phase or by entry into torpor depending on food availability.

Introduction

In endothermic animals prolonged or repeated exposure to cold may cause adaptive modifications which reduce the physiological strain produced by the stressful environmental component (cf. Simon 1987; Brück 1986). These modifications may consist of an enhancement of the thermal insulation, e.g. growth of fur, or of various alterations in the thermoregulatory system. Latter effects of chronic could exposure, generally denoted as functional modifications, may be traced back to mainly two basic mechanisms: 1. changes in the capacity of the thermogenetic effector systems by development or enhancement of non-shivering thermogenesis (NST), and 2. changes in the regulatory characteristics, e.g. deviations of the threshold temperatures for the elicition of regulatory heat production (cf. Brück 1986).

Beside the development of specific adaptive modifications further strategies are known which enable some animals to cope with unfavourable environmental conditions. In many small mammalian species with body weights less than 100 g exposure to low ambient temperatures (Ta) is accompanied with the occurrence of shallow torpor which is characterized by a controlled lowering of the set point for body temperature regulation with a corresponding reduction in metabolic rate. In most species, however, induction of torpor is not directly caused by the low Ta. In the Djungarian hamster *(Phodopus sungorus)* daily torpor is a seasonal phenomenon, i.e. changes of the photoperiod is the most important factor in the control of torpor (Heldmaier and Steinlechner 1981). In pocket mice *(Perognathus californicus, P. longimembris, P. hispidus)* and in the kangaroo mouse *(Microdipodops pallidus)* there is a clear correlation between the incidence of torpidity and the availability of food (Tucker 1962; Bartholomew and Cade 1957; Wang and Hudson 1970; Bartholomew and Mac Millen 1961). In bats, on the other hand, torpor seems to be caused by the nychthemeral fluctuations of Ta (Kulzer 1965).

Under chronic cold exposure occurrence of daily torpor which usually lasts 8–12 h does

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not exclude the possibility to develop cold adaptive modifications. It was the aim of the present experiments to study the environmental factors that cause cold adaptation and torpor in the Cretan spiny mouse.

Materials and methods

Experiments were carried out in adult male and female Cretan spiny mice (*Acomys minous* Bate, 1905) wheighing 25–39 g. They were bred and raised in our laboratory. Animals were fed sunflower seeds, peanuts, oats, corn, Purina rat chow, and water ad libitum.

Animals were randomly divided into three groups which were kept under different environmental conditions for at least 8 weeks. One group was kept at Ta = 20 ± 1 °C and a 16 : 8 light-dark cycle. The other groups were exposed to 10 ± 1 °C and to either a long (LD 16 : 8) or a short (LD 8 : 16) photoperiod. Cold exposed animals were housed in individual cages.

As a measure of metabolic rate CO_2-production was determined by the open system method by means of a climatized metabolic chamber as described previously (Brück and Wünnenberg 1965). Within this metabolic chamber the unrestrained animal was supplied with food, water, and some nesting material with the exception of the tests in which the effects of starvation were studied.

Deep colon temperature (Tcol) was measured with fine thermocouples.

The U-test of Wilcoxon, Mann, and Whitney was used for statistical analysis.

Results

In all groups of Cretan spiny mice minimum observed metabolic rates (MOMR) and body temperatures showed a nychthemeral rhythm with maximum values during the night. In animals kept at Ta = 20 °C average CO_2-production during the day was $32.7 \pm 7.0\,ml \cdot kg^{-1} \cdot min^{-1}$ and $43.1 \pm 8.2\,ml \cdot kg^{-1} \cdot min^{-1}$ during the night. As soon as animals of this group (N = 8) were exposed to Ta = 10 °C, CO_2-production increased to $53.4 \pm 5.4\,ml \cdot kg^{-1} \cdot min^{-1}$ and $70.6 \pm 6.0\,ml \cdot kg^{-1} \cdot min^{-1}$, respectively (Tab. 1). As

Table 1. **Effects of cold exposure and photoperiod on minimum observed metabolic rate in *Acomys minous***
(mean ± SD, n = number of animals)

Cold exposure (Ta = 10 °C)	Photoperiod	CO_2-production ($ml \cdot kg^{-1}\,min^{-1}$) day	night	n
1st day	LD 8 : 16	53,4 ± 5,4	70,6 ± 6,0	8
2nd day	LD 8 : 16	53,5 ± 7,2	75,8 ± 6,8	8
3rd day	LD 8 : 16	54,2 ± 6,9	77,2 ± 7,8	7
8 weeks	LD 8 : 16	54,0 ± 8,7	74,1 ± 7,5	8
8 weeks	LD 16 : 8	61,1 ± 10,7	85,3 ± 15,6	5

demonstrated in Fig. 1 a continuation of the cold exposure has a considerable effect on the nychthemeral fluctuations of MOMR. While at the 3rd day of cold exposure average CO_2-production during the day did not show a significant change in comparison to the 1st day, the corresponding value measured during the night increased to $77.2 \pm 7.8\,ml \cdot kg^{-1} \cdot min^{-1}$. Similar effects of chronic cold exposure were observed when Tcol was measured (Fig. 1, lower part). Colon temperatures determined during the night continuously increased from 35.4 ± 0.9 °C (2nd day of exposure) to 36.9 ± 0.3 °C (4th day of exposure). Temperature values measured during the day, however, did not change significantly in the course of chronic cold exposure.

These changes of metabolic rate which developed within three days of cold exposure were not enhanced when the animals were adapted to Ta = 10 °C for 8 weeks (Tab. 1).

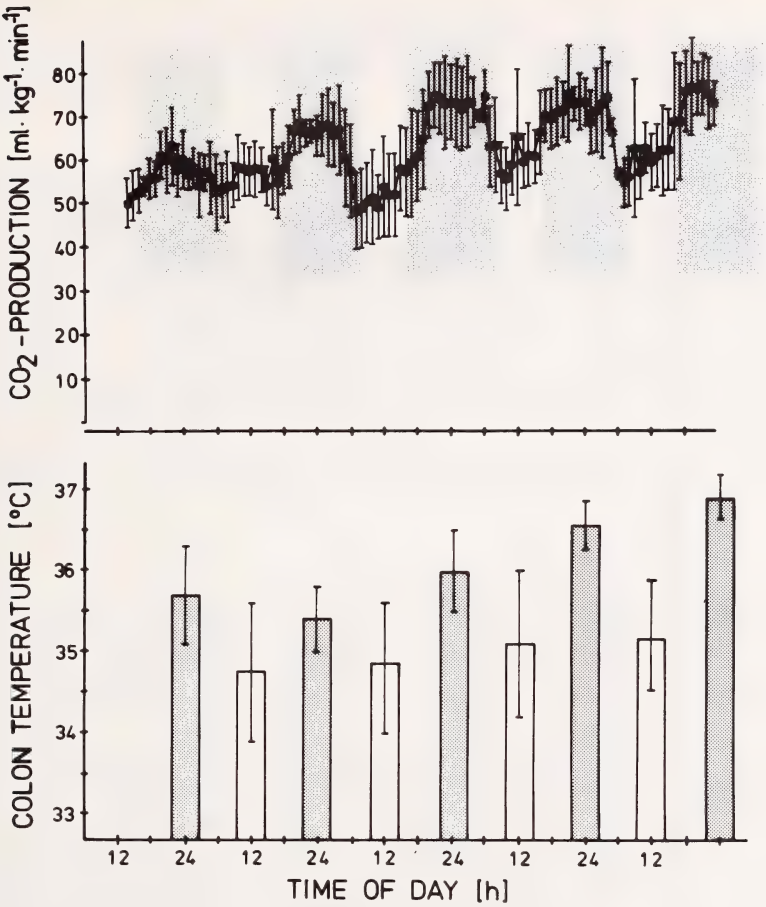

Fig. 1. Course of CO_2-production and colon temperature (mean ± SD) in *Acomys minous* exposed to Ta = 10 °C and a 8 : 16 light/dark cycle for several days. Shaded areas indicate scotophase

Furthermore, studies in 5 animals that were kept at Ta = 10 °C and a long photoperiod indicate that the increment of the nychthemeral metabolic fluctuations is mainly caused by the cold exposure (Tab. 1).

The effects of chronic cold exposure on MOMR and Tcol described above were all determined in animals that had free access to food and water. Food restriction (40 h) led to quite different results. Under this condition all animals (N = 23) entered into torpor during the day-time. Though cold stress was moderate (Ta = 20 °C) Tcol declined to 25.9 ± 1.6 °C and MOMR decreased but about 50 % of the initial value (Fig. 2). All animals quickly recovered after termination of the starvation experiments.

Discussion

It is well known that cold adaptation leads to an increase of the metabolic rate. At thermoneutral Ta as well as under cold stress cold-adapted dogs, rabbits, and rats, e.g., had considerable higher metabolic rates than the corresponding control animals (cf.

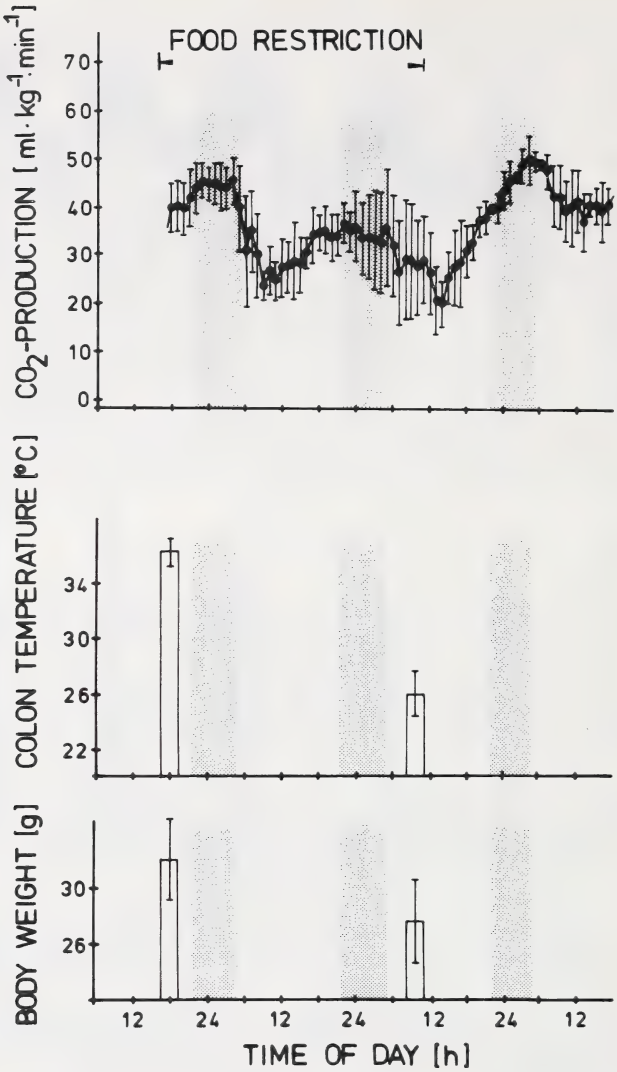

Fig. 2. Starvation induced torpor in *Acomys minous* at TA = 20 °C. Shaded areas indicate scotophase. (mean ± SD)

Precht et al. 1973). Our studies indicate that in *Acomys minous* total energy metabolism, related to 24 hours, only slightly increases during cold adaptation as a significant increase of the CO_2-production only occurs during the night hours. This cold-adaptive modification of the metabolic rate which seems to be independent of the photoperiod favours the adjustment of high body temperatures during the night when the Cretan spiny mice are active.

Development of adaptation, however, is not the only mode of coping with unfavourable environmental conditions. Our studies further show that *Acomys minous* exposed to a moderate cold stress enter into torpidity when food availability is restricted. Comparable results were obtained by studies in *Acomys cahirinus* (Müller et al. 1987) as well as by

numerous investigations in other species of rodents (cf. LYMAN et al. 1982; HUDSON 1978). Thus, our studies also support the hypothesis that torpor is used in "energy emergency" situations when energy availability is restricted relative to expenditures (HAINSWORTH and WOLF 1978; TUCKER 1966),

Zusammenfassung

Kälteadaptative Modifikationen und Torpor bei der Kreta-Stachelmaus (Acomys minous Bate)

Es wurden die Effekte niedriger Umgebungstemperaturen (Ta), der Photoperiode und des Nahrungsangebotes auf den Stoffwechsel und die Körperkerntemperaturen der Stachelmaus *(Acomys minous)* untersucht. Bei Tieren, denen Futter ad lib. zur Verfügung stand, führte Kälteexposition (Ta = 10 °C) bereits nach drei Tagen zu einer Zunahme der diurnalen Fluktuationen des Stoffwechsels und der Körpertemperaturen. Dabei stiegen die während der Aktivitätsphasen (Nacht) gemessenen Stoffwechsel- und Temperaturwerte an, während sich die entsprechenden Werte der Ruhephasen (Tag) nicht signifikant änderten. Diese Effekte, die als kälteadaptative Modifikationen angesehen werden, traten sowohl unter Kurztag- als auch unter Langtagbedingungen auf. Durch Nahrungsmangel (bei TA = 20 °C) wurde dagegen Torpor induziert. Die Körperkerntemperaturen der Tiere sanken auf 25.9 ± 1.6 °C (Mittelwert ± SD) ab, die Stoffwechselraten erreichten nur noch 50 % der Ausgangswerte.

Die vorliegenden Untersuchungen zeigen, daß bei *Acomys minous* eine mehrtägige Kältebelastung – in Abhängigkeit vom Nahrungsangebot – entweder zu einer Steigerung des Stoffwechsels (Kälteadaptation) oder zu einer deutlichen Stoffwechselreduktion (Torpor) führt.

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Thermoregulation and evaporative water loss in Spiny mice (*Acomys cahirinus* Desmarest, 1819)

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Abstract

Studied basal metabolism, thermoregulatory responses and evaporative water loss in spiny mice *(Acomys cahirinus)*. Oxygen consumption was lowest at $T_a = 32.5\,°C$ with a mean value of 1.0 ± 0.12 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, which is 24 % below the expected mass-specific level. At ambient temperatures below this narrow thermoneutral zone O_2-uptake did not increase linearly, but showed two clearely distinct segments with different slopes. The dry thermal conductance was found to be not a constant value, but decreased from 0.202 to 0.134 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$ with falling T_a; only at $T_a = 15\,°C$ it was in accordance with the mass-specific theoretical value. At $T_a = 32.5\,°C$ mean T_{re} was $36.4 \pm 0.4\,°C$. In the females T_{re} usually was about 0.5 °C higher than in the males. At $T_a = 20\,°C$ T_{re} decreased to $35.2 \pm 0.2\,°C$. In the heat T_{re} rose to $39.2 \pm 0.3\,°C$ ($T_a = 37.5\,°C$). Total evaporative water loss (TEWL) was rather low with 0.98 ± 0.3 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ (0.96 mg $H_2O \cdot$ml O_2^{-1}) at thermoneutral conditions. At $T_a = 35\,°C$ only 14.5 % of the metabolic heat production was dissipated through evaporative pathways. When exposed to dry air (r.h. = 15 %) TEWL increased to 1.53 ± 0.2 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ ($T_a = 33\,°C$). Respiration frequency showed no relation to humidity conditions, but was clearly correlated to ambient temperature.

Introduction

Among murid rodents (Family Muridae) spiny mice (genus *Acomys*) are probably the only truely desert adapted forms. They occur from the Indian peninsula westwards through the Middle East and from there southwards through North and East Africa down to the Cape Province. There also exist a few isolated populations in mountainous regions of the western Sahara and on islands in the eastern Mediterranean Sea. The common spiny mouse *(Acomys cahirinus)* is widespread in the Middle East and Northeast Africa, where it preferably inhabits crevices of rock outcrops in dry deserts and savannas, but in some places also lives in human dwellings (Delany and Happold 1979; Osborne and Helmy 1980).

Unlike most other desert adapted small mammals spiny mice do not dig burrows and are such more exposed to the often high air temperatures in their habitat. However, they not only live in dry hot areas with a mean annual rainfall less than 100 mm (Shkolnik 1966), but also occur at altitudes 2000 m above sea level, where temperatures at night can fall below zero (Shkolnik and Borut 1969). Though the microclimatic conditions in the rock crevices are more constant and less severe than in the open desert (Shkolnik 1966), spiny mice certainly suffer more from the stressful desert climate than burrowing species.

Apart from heat water shortage is the greatest threat to desert dwelling mammals. Water is especially needed for thermoregulatory purposes when ambient temperature exceeds body temperature. Under such conditions body heat can only be dissipated through evaporative pathways. The question, therefore, arises, whether spiny mice have developed special adaptations to economize water use for thermoregulatory purposes.

Information about this is contradictory. Shkolnik and Borut (1969) reported an extraordinary high value for total evaporative water loss (TEWL) of spiny mice at

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thermoneutrality: 1.96 mg $H_2O \cdot ml\ O_2^{-1}$ at T_a = 30 °C, which is the highest value ever reported for a desert adapted rodent of this size. In a more recent study Daily and Haines (1981) found that TEWL and water turnover rates in hydrated spiny mice fall in the midrange of values for small desert mammals; in water restricted individuals TEWL and water turnover could be reduced significantly. *Acomys* also has been found to possess an excellent capacity to maintain plasma volume during dehydration (Horowitz and Borut 1970). The concentrating ability of the kidney of spiny mice is comparable to that of other desert adapted small rodents (Shkolnik and Borut 1969; Buffenstein et al. 1985), a finding which is corroborated by the production of large quantities of antidiuretic hormone (Castel and Hochman 1976). In spite of these water-saving adaptations, *Acomys* obviously has a limited ability to acclimate to water shortage, as few animals were found to be able to tolerate chronic restriction of water uptake to 1/8 of the voluntary level (Daily and Haines 1981).

In view of the contradictory reports on total evaporative water loss in spiny mice we reinvestigated this point under controlled conditions of various humidities. Additionally, we looked at basal energetics and thermoregulatory capacities.

Material and methods

16 spiny mice (8 females, 8 males) were used for this study. They were taken from a breeding colony at our institute. The animals were 4–12 months old and their mean body mass was 48.5 g. They were kept in a climatic chamber, where ambient temperature and relative humidity were regulated to 25 ± 1 °C and 50 ± 10 % r.h. Lights in the chamber were on for 12 hours; a weak lamp served as illumination during the D-phase.

The spiny mice were housed singly or as unisexual pairs in plastic containers (41 × 26 × 15 cm). Food consisted of a mixture of wheat grains, sun flower seeds, rolled oats and pellets and was supplemented with apples, carrots and lettuce. Drinking water was not offered.

Energetics and thermoregulatory responses were measured in 8 spiny mice (4 females, 4 males) using an experimental set up similar to that described by Müller and Rost (1983) with the following alterations: No telemetric registrations of rectal temperature and heart rate were made in the present study. In addition CO_2-production was measured with an URAS MT (Hartmann and Braun). O_2-uptake was monitored with an Oxytest S (Hartmann and Braun). During the experiments the spiny mice were in a perspex box (volume 980 ml). Air flow was 18.7 l/h at T_a = 15–35 °C and 22.7 l/h at T_a = 37.5 °C. Relative humidity of the air entering the box was regulated to 40 %, only at T_a = 37.5 °C it was set to 20 %, humidity inside the box thus never exceeding 60 %. For measuring respiration frequencies a pressure transducer (Bell & Howell 4104, 0–35 mm Hg) was used. Rectal temperatures were determined by use of a thermistor (Ultrakust; accuracy ± 0.1 °C), which was inserted to a depth of 20 mm.

An experimental run lasted 2–4 hours and included an equilibration period of 1 hr. The measurements were always conducted during the L-phase. Each animal was tested twice at the various ambient temperatures. The mean from the two runs was used for further calculations. All gas volumes have been corrected to STPD-conditions.

In a second set of experiments total evaporative water loss and respiration frequency were measured in 8 other spiny mice (4 females, 4 males) at different relative humidities (6, 20 and 40 % r.h.) of the air entering the box. These experiments were done only at T_a = 25, 30 and 33 °C. Again each animal was tested twice at any given temperature/humidity combination.

Before testing mean values for the significance of differences (Student t-test or Welch-test) they were checked for homogeneity of variance (F-test). Regression lines were calculated using the method of least squares (Lorenz 1984). Values are given as mean ± S.D.

Results

Rectal temperature (T_{re})

At ambient temperatures from 25–32.5 °C mean T_{re} was 36.0 ± 0.5 °C (Fig. 1). When T_a dropped to 15–20 °C, T_{re} decreased to a mean of 35.2 ± 0.3 °C. At ambient temperatures above 32.5 °C T_{re} rose markedly (to 39.2 ± 0.3 °C at T_a = 37.5 °C).

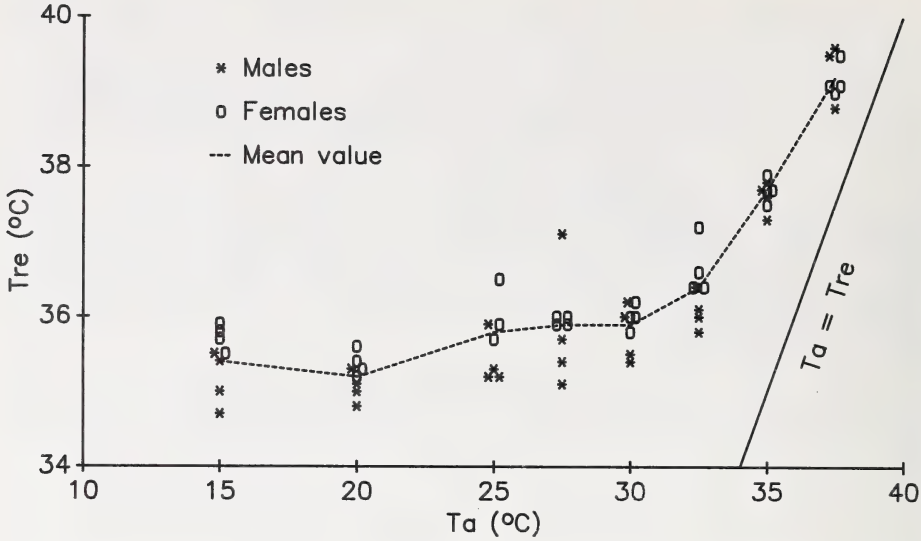

Fig. 1. Rectal temperatures after 2–4 hours exposure to ambient temperatures between 15–37.5 °C

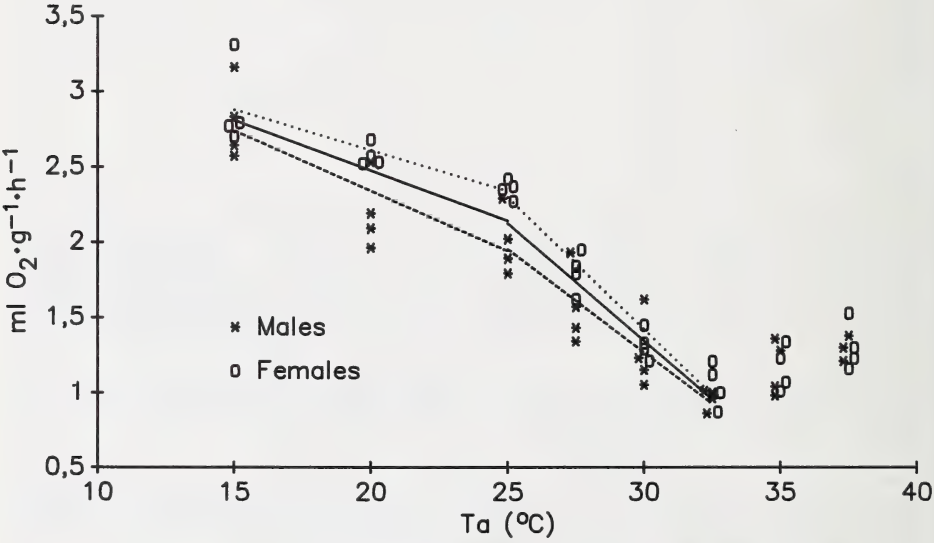

Fig. 2. O_2-consumption at ambient temperatures between 15–37.5 °C. Also given are the regression lines for males (----), females (····) and both sexes taken together (——); see also Table 1

The maximal T_{re} found was 41.4 °C, which was measured after 60 min exposure to T_a = 37.5 °C. In this case the experiment was disrupted because the animal exhibited signs of severe heat stress (restlessness, urination, defecation, uncoordinated movements). Brought back to the animal room (T_a = 25 °C) T_{re} of this spiny mouse decreased to 31.4 °C within three hours. However, the animal fully recovered and T_{re} rose to 35.2 °C without supplying external heat.

Oxygen consumption (VO_2) and basal metabolic rate (BMR)

Oxygen consumption was lowest at $T_a = 32.5\,°C$ (Fig. 2), the values at $T_a = 30\,°C$ ($\alpha = 0.005$) and $T_a = 35\,°C$ ($\alpha = 0.025$) being significantly higher. Within this narrow thermoneutral zone (TNZ) VO_2 was 1.0 ± 0.12 ml $O_2 \cdot g^{-1} \cdot h^{-1}$.

At ambient temperatures below the TNZ the increase of heat production as measured by VO_2 showed two segments with different slopes. Between $T_a = 25–32.5\,°C$ VO_2 increased much steeper than between $T_a = 15–25\,°C$. There was also a clear difference in the reaction of males and females: Except at $T_a = 15\,°C$ O_2-uptake was always considerably higher in the latter. The data are best described by different regression lines for each sex and temperature segment (Table 1).

At high ambient temperatures VO_2 increased less steep and was 30 % higher at $T_a = 37.5\,°C$ than at thermoneutral conditions.

Table 1. **Regression lines and regression coefficients for O_2-uptake at ambient temperatures below 32,5 °C**

	Ta = 15–25 °C
Males	$Y\ (ml\ O_2 \cdot g^{-1} \cdot h^{-1}) = 3.937 - 0.080 \cdot Ta\ (°C);\ r = -0.82$
Females	$Y\ (ml\ O_2 \cdot g^{-1} \cdot h^{-1}) = 3.688 - 0.054 \cdot Ta\ (°C);\ r = -0.83$
Both sexes	$Y\ (ml\ O_2 \cdot g^{-1} \cdot h^{-1}) = 3.813 - 0.067 \cdot Ta\ (°C);\ r = -0.75$
	Ta = 25–32,5 °C
Males	$Y\ (ml\ O_2 \cdot g^{-1} \cdot h^{-1}) = 5.375 - 0.137 \cdot Ta\ (°C);\ r = -0.90$
Females	$Y\ (ml\ O_2 \cdot g^{-1} \cdot h^{-1}) = 6.670 - 0.175 \cdot Ta\ (°C);\ r = -0.97$
Both sexes	$Y\ (ml\ O_2 \cdot g^{-1} \cdot h^{-1}) = 6.022 - 0.156 \cdot Ta\ (°C);\ r = -0.92$

Total evaporative water loss (TEWL)

With the air entering the respiration box having a relative humidity (r.h.) of 40 %, r.h. inside the box varied between 45–60 %. TEWL was lowest at $T_a = 27.5\,°C$ with 0.82 ± 0.13 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ (Fig. 3). It almost doubled when T_a rose to 35 °C. At $T_a = 37.5\,°C$ the spiny mice salivated profusely and spread saliva over the body surface, thereby increasing TEWL drastically to 4.8 ± 1.11 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$. However, it can not be excluded that saliva adhering to the walls of the box and to the wire mesh contributed to elevate the values.

If related to VO_2 TEWL showed a steady increase with increasing ambient temperatures (Table 2). Above the TNZ TEWL rose only slightly at $T_a = 35\,°C$, with 14.5 % of the

Table 2. **Respiratory quotient (RQ), total evaporative water loss (TEWL) and ratio evaporative heat loss vs. metabolic heat production (E/M) at various ambient temperatures**
(mean values ± S.D.)

Ta (°C)	RQ	TEWL ($ml\ H_2O \cdot kg^{-1} \cdot h^{-1}$)	TEWL ($mg\ H_2O \cdot ml\ O_2^{-1}$)	E/M (%)
15	0.82 ± 0.02	0.98 ± 0.12	0.35 ± 0.05	4.1
20	0.83 ± 0.02	0.91 ± 0.15	0.38 ± 0.06	4.5
25	0.84 ± 0.03	0.92 ± 0.20	0.42 ± 0.09	4.9
27.5	0.82 ± 0.02	0.82 ± 0.13	0.49 ± 0.05	5.8
30	0.89 ± 0.05	0.86 ± 0.15	0.67 ± 0.11	7.8
32.5	0.91 ± 0.02	0.98 ± 0.30	0.96 ± 0.23	11.4
35	0.86 ± 0.02	1.45 ± 0.32	1.25 ± 0.23	14.5
37.5	0.85 ± 0.02	4.80 ± 1.11	3.69 ± 0.81	43.7

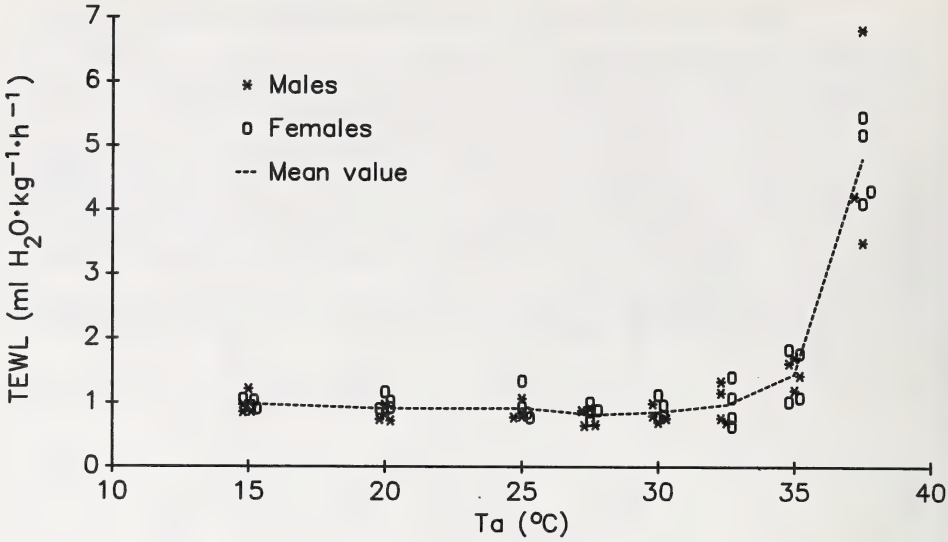

Fig. 3. Total evaporative water loss at ambient temperatures between 15–37.5 °C. During this type of experiments relative humidity inside the respiration box was 45–60 %

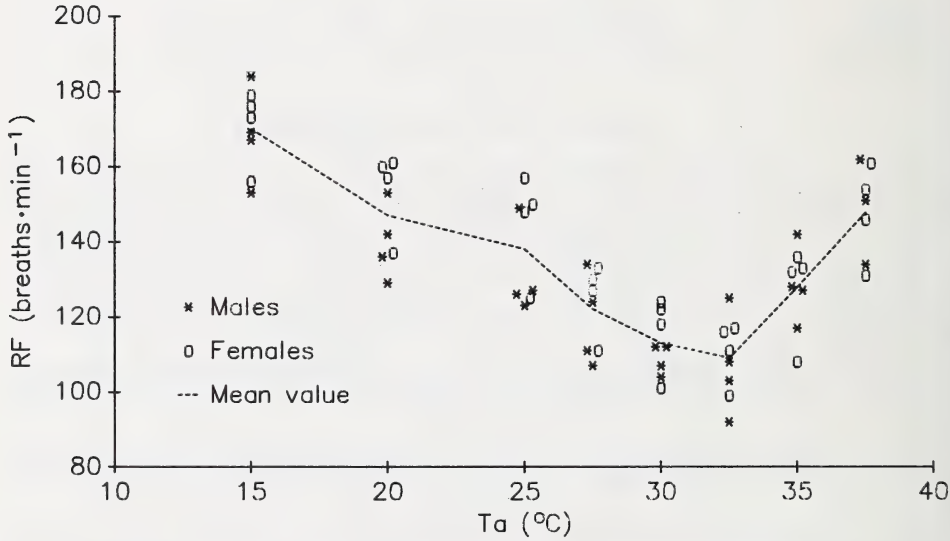

Fig. 4. Respiration frequency at ambient temperatures between 15–37.5 °C

metabolic heat production being dissipated through evaporative pathways, whereas at T_a = 37.5 °C more than 40 % of the endogenous heat was lost by evaporation.

Respiration frequency (RF)

Lowest RF was measured at T_a = 32.5 °C with a mean value of 109 ± 10.7 breaths·min^{-1} (Fig. 4). Like in VO_2 the increase between T_a = 25–32.5 °C was steeper than between 15–25 °C. At ambient temperatures above the TNZ RF increased almost linearly to 148 ±

12.2 breaths·min^{-1} at T_a = 37.5 °C. No panting-like acceleration of breathing could be noticed.

TEWL and RF at different relative humidities (r.h.)

When the air entering the box was regulated to 6, 20 and 40 % r.h., humidity inside the box averaged 15, 27 and 45 % r.h., respectively, the actual value depending on the water added by the evaporation of the tested individuals. TEWL did not differ at T_a = 25 °C and T_a = 30 °C (Fig. 5). At these ambient temperatures it rose from 0.742 at 45 % r.h. to 1.1 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ at 15 % r.h. At T_a = 33 °C TEWL was considerably higher, increasing from 0.927 (45 % r.h.) to 1.534 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ (15 % r.h.).

RF did not show a correlation to the moisture content of the air, being almost identical at all tested humidities (Fig. 6). Like during the measurements of thermoregulatory responses it exhibited a much closer relation to ambient temperature.

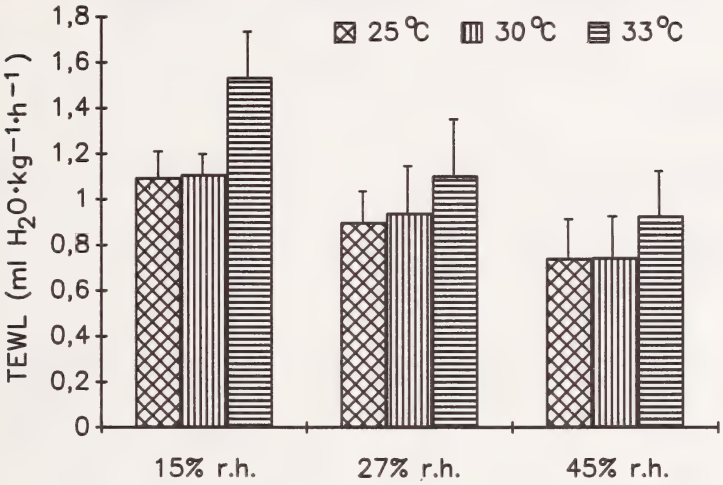

Fig. 5. Total evaporative water loss at various temperature/humidity combinations. Humidity is specified as it appeared inside the respiration box with an animal present. Ingoing air was regulated to 6, 20 and 40 % r.h., respectively

Discussion

If compared to data obtained in previous studies on TEWL in spiny mice, our results closely agree with those of Daily and Haines (1981) (Table 3), whereas they do not confirm the findings of Shkolnik and Borut (1969), who reported values, which were almost double as high. As Daily and Haines (1981) used the same technique for measuring TEWL as we did, it can be supposed that the discrepancies between the results for TEWL must be attributed to technical differences, the reason for the unusual high values in Shkolnik's and Borut's study remaining unclear. From the data now available it must be concluded that part of the adaptive strategies of spiny mice to desert conditions – like in other small desert rodents – mainly rests on an economical use of water for thermoregulatory purposes. This is in contrast to Shkolnik's and Borut's (1969) view, who – on the basis of their results – emphasized the ability of spiny mice to dissipate larger amounts of body heat through evaporative avenues.

The evaporative water loss which we measured at T_a = 30 °C falls in the midrange of

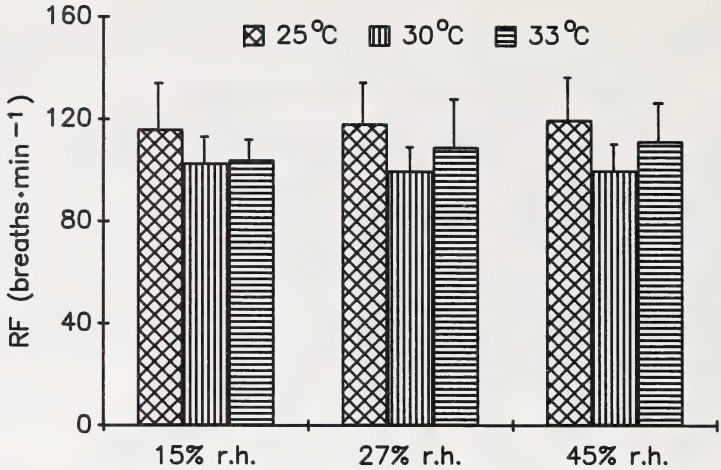

Fig. 6. Respiration frequency at various temperature/humidity combinations. Same experimental conditions as in Fig. 5

Table 3. **Total evaporative water loss (TEWL) in Spiny mice as measured by various authors**

Species	TEWL		VO_2	Ta	r.h.[a]	Source
	ml $H_2O \cdot kg^{-1} \cdot h^{-1}$	mg $H_2O \cdot ml\ O_2^{-1}$	ml $O_2 \cdot g^{-1} \cdot h^{-1}$	(°C)	(%)	
A. c.	2.09	1.9	1.1	30	15–30	Shkolnik and Borut (1969)
A. r.	1.84	2.3	0.8	30	15–30	Shkolnik and Borut (1969)
A. sp.	1.3	0.8	(1.63)[b]	?	ca. 50	Fertig and Edmonds (1969)
A. c.	0.86	0.84	1.02	30	ca. 50	Daily and Haines (1981)
A. c.	0.86	0.67	1.29	30	45–60	this study
A. c.	0.75	–	–	30	45	this study
A. c.	0.94	–	–	30	27	this study
A. c.	1.11	–	–	30	15	this study

A. c. = *A. cahirinus; A. r.* = *A. russatus*; [a]inside the respiration box; [b]estimated value

desert adapted small rodents (data summarized in Daily and Haines 1981; Müller 1985). The economic use of water for thermoregulatory purposes is corroborated by the finding that at an ambient temperature of 35 °C the spiny mice dissipated only 14.5 % of their metabolic heat through evaporative pathways. Instead of keeping T_{re} on the normal resting level, they rather relied on a water saving storage of heat as indicated by the elevation of the rectal temperature by about two degrees. The ability for the temporary storage of excess heat is favoured by the rather low level of T_{re} (< 36 °C) at ambient temperatures ≤ 30 °C.

Only at T_a = 37.5 °C the spiny mice increased TEWL drastically to over 5-times the value at T_a = 30 °C. About 40 % of the endogenous heat load was then evaporated. This rapid increase of TEWL was only possible because the animals salivated profusely. Salivation, however, is regarded as an uneconomic emergency measure. Additionally, at this high ambient temperature the spiny mice frequently changed their position in the respiration box, thus bringing their ventral surface into contact with cooler parts of the wire mesh material. This behaviour has already been noted by Shkolnik and Borut (1969) and certainly serves to increase conductive heat loss.

As long as ambient temperature did not exceed 30 °C, TEWL of the spiny mice remained fairly low. When exposed to the same relative humidity of the air, 15–28 % less water was evaporated at T_a = 30 °C than at T_a = 33 °C. The effect of different humidities on TEWL was more pronounced: At ambient temperatures from 25–33 °C TEWL decreased by 48–65 % when the relative humidity of the air increased from 15 to 45 %. This clearly demonstrates that searching for more favourable microclimatic conditions during the hottest parts of the day pays for the spiny mice with regard to their water budget.

As in most other rodents a panting-like acceleration of the breathing rate did not occur in the spiny mice. Respiration frequency seemed to be correlated to oxygen consumption rather than to the moisture content of the air. With falling ambient temperatures the increase of RF almost paralleled that of VO_2.

The low basal metabolic rate of spiny mice, which has also been found by other investigators (Shkolnik and Borut 1969; Wise 1977; Daily and Haines 1981; Haim and Borut 1981), is certainly advantageous in a habitat with regular periods of food and water shortage. A reduced basal heat production is common among small desert dwelling rodents (Müller 1985), as it contributes to minimize food and water requirements.

Thermoregulatory responses at temperatures below the TNZ differed from the usual picture in that VO_2 did not increase linearly, but showed two segments with different slopes. The flattening of the heat production curve below T_a = 25 °C was accompanied by a drop of T_{re} from 36.0 ± 0.5 °C at T_a = 25–32.5 °C to 35.2 ± 0.3 °C at lower ambient temperatures. Also dry thermal conductance proved to be not a constant value, but decreased from 0.191 at T_a = 25 °C to 0.134 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$ at T_a = 15 °C (Fig. 7). A similar reduction of C_{dry} in the cold has been reported for *Gerbillus perpallidus* (Müller 1985). Between T_a = 32.5 °C and T_a = 35 °C C_{dry} rose rapidly, indicating a marked increase of the heat loss by conduction and/or radiation, i.e. through water-saving avenues.

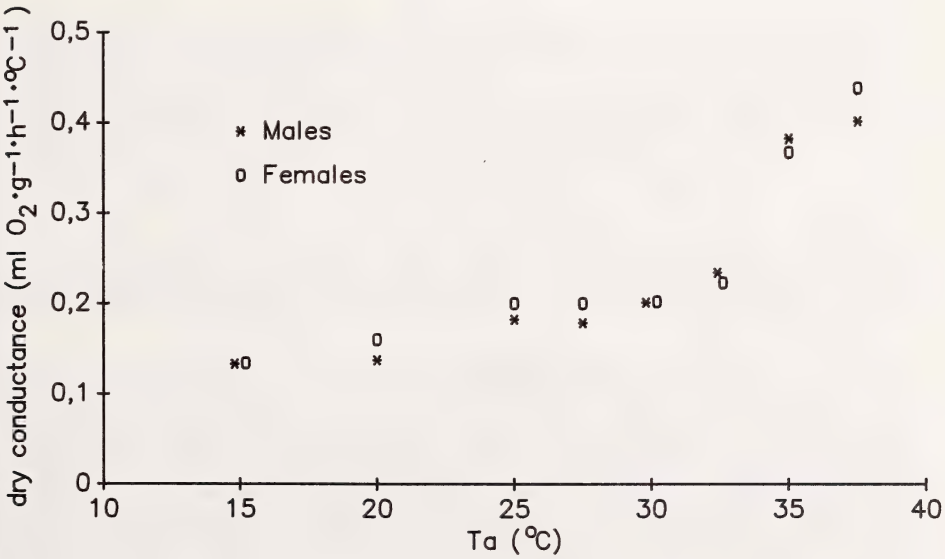

Fig. 7. Dry thermal conductance (C_{dry}) at ambient temperatures between 15–37.5 °C. Calculated after the formula:

$$C_{dry} = \frac{M - E}{T_{re} - T_a}$$

(M = metabolic heat production, E = evaporative heat loss, T_{re} = rectal temperature, T_a = ambient temperature)

These findings, however, do not indicate inappropriate thermoregulatory capacities of the common spiny mice in the cold, but rather represent a well controlled saving of energy by allowing a moderate decrease of the body temperature in a cold environment. Evidence for this comes from the fact that the flattening of the heat production was most pronounced when T_a fell from 25 to 20 °C. To a further drop of T_{re} the spiny mice reacted with an intensified heat production. Their recently found ability to enter torpor during prolonged periods of food reduction (Müller et al. 1988) also supports this view.

Zusammenfassung

Temperaturregulation und evaporative Wasserabgabe bei Stachelmäusen (Acomys cahirinus Desmarest, 1819)

An Stachelmäusen *(Acomys cahirinus)* wurden Basalstoffwechsel, Temperaturregulation und evaporative Wasserabgabe untersucht. Der O_2-Verbrauch war bei einer Umgebungstemperatur von 32.5 °C am niedrigsten und lag mit 1.0 ± 0.12 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ um 24 % unter dem gewichtsspezifischen Erwartungswert. Bei Umgebungstemperaturen unterhalb dieser engen thermischen Neutralzone stieg der O_2-Verbrauch nicht linear an, sondern zeigte zwei deutlich verschiedene Bereiche mit unterschiedlichen Steigungen. Die „trockene" Wärmedurchgangszahl war keine konstante Größe, sondern nahm mit sinkender Umgebungstemperatur von 0.202 auf 0.134 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$ ab; nur bei T_a = 15 °C stimmte sie mit dem gewichtsspezifischen Erwartungswert überein. Bei T_a = 32.5 °C lag die mittlere Rektaltemperatur bei 36.4 ± 0.4 °C. Bei den Weibchen war T_{re} im allgemeinen um 0.5 °C höher als bei den Männchen. Bei T_a = 20 °C sank T_{re} auf 35.2 ± 0.2 °C. Unter Hitzebedingungen (T_a = 37.5 °C) stieg T_{re} auf 39.2 ± 0.3 °C. Die evaporative Wasserabgabe war unter thermisch neutralen Bedingungen mit 0.98 ± 0.3 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$ relativ niedrig. Bei T_a = 35 °C wurden nur 14.5 % der im Stoffwechsel gebildeten Wärme durch Verdunstungskühlung abgegeben. In trockener Luft (r.h. = 15 %) stieg die evaporative Wasserabgabe bei T_a = 33 °C auf 1.53 ± 0.2 ml $H_2O \cdot kg^{-1} \cdot h^{-1}$. Die Atemfrequenz zeigte keine Beziehung zu den Feuchtebedingungen, war aber deutlich korreliert mit der Umgebungstemperatur.

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Was ist *Erythronesokia* Khajuria, 1981 (Mammalia : Rodentia : Muridae)?

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Eingang des Ms. 13. 4. 1989
Annahme des Ms. 25. 9. 1989

Abstract

What is Erythronesokia Khajuria, 1981 (Mammalia : Rodentia : Muridae)?

The main differences between the two rodent genera *Nesokia* and *Bandicota* consist in the greater relative rostrum length, and, especially, in the shorter absolute and relative length of the incisive foramina in *Nesokia*. Here, *Erythronesokia* with the only species *bunii* Khajuria, 1981 trends clearly to *Nesokia*. *Erythronesokia* is very similar to *Nesokia*, with greater size and the main differences in coloration and the relatively smaller mastoid and zygomatic widths. *Erythronesokia* is regarded by us to be not more than – if at all – a subgenus of *Nesokia*, but not a separate genus. The name of the species, therefore, is *Nesokia bunnii* (Khajuria, 1981). In addition, details on occurrence, ecology and behaviour of *N. bunnii* are given.

Einleitung

Die Gattung *Erythronesokia* mit der einzigen Art *E. bunnii* (Abb. 1) wurde von Khajuria (1981) anhand eines adulten Männchens mit defektem Schädel und eines Jungtieres beschrieben, das nur mit Vorbehalt identitfiziert werden konnte. Zusammen mit den uns vorliegenden 3 adulten Exemplaren, alles Männchen mit Schädeln und Bälgen, können wir nun eine bessere Beschreibung dieser Tiere geben.

Material und Methode

Die 3 genannten Exemplare gehören dem Basrah Natural History Museum (Nr. 164/177 und 188/1974) und dem Forschungsinstitut Senckenberg, Frankfurt (SMF 62925). Sie stammen von der Terra typica.

Ergebnisse und Diskussion

Erythronesokia ähnelt *Nesokia* Gray, 1842 und *Bandicota* Gray, 1873. Die Tiere sind groß: Die Kopf+Rumpf-Länge von 4 Exemplaren beträgt 230–260 mm. Der Schwanz ist lang, etwa ebenso lang wie Kopf + Rumpf und damit länger als bei *Nesokia* und *Bandicota*. Die Hinterfüße tragen schmale Hautsäume an den Zehenwurzeln zwischen 2., 3. und 4. Zehe, die beim Schwimmen helfen.

Die Rückenfärbung schwankt individuell zwischen dunklerem und hellerem Rostrot und wird an den Seiten heller. Beim einzelnen Rückenhaar ist die terminale Hälfte rostrot, die basale Hälfte dunkelgrau. Das Fell auf der Unterseite, an den Kopfseiten und den Extremitäten ist weißlich oder schmutzig grauweiß; hier ist das einzelne Haar einfarbig. Der Schwanz ist schwarzbraun mit nur wenigen Haaren, die nur auf der Schwanzunterseite dichter stehen.

Die Condylobasal-Länge ist größer als die Occipitonasal-Länge. Die Frontoparietal-

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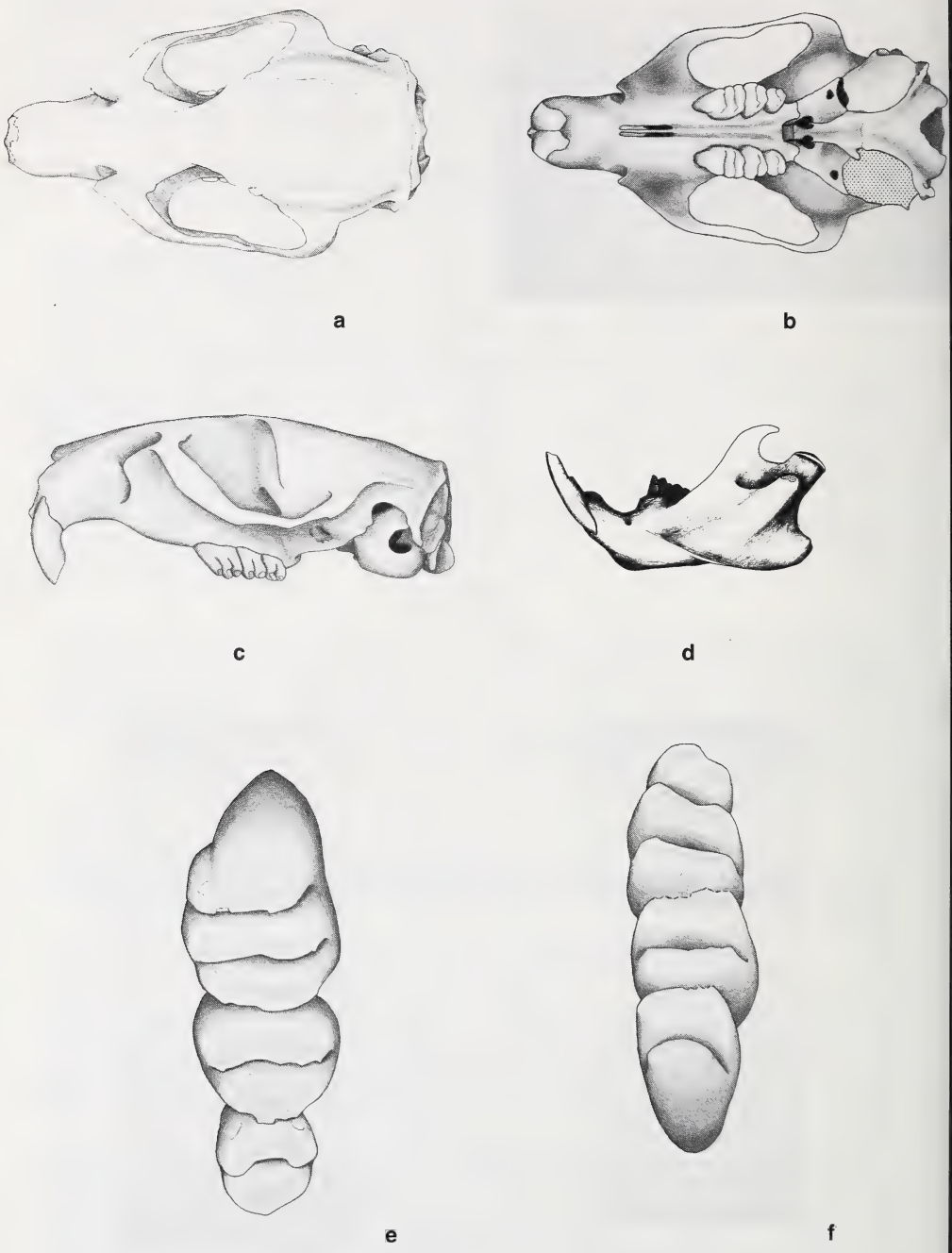

Abb. 1. Nesokia bunnii (Khajuria, 1981), Schädel SMF 62925. a–d = Schädel, e = linke obere Molaren, f = rechte untere Molaren. Zeichnung: Petra Friesleber, Senckenberg-Museum, Frankfurt

Leisten (Abb. 1a) reichen bis zum Hinterhaupt. Andeutungen von Postorbital-Fortsätzen sind vorhanden. Die Incisivi sind gelb, die Molaren hypsodont. Obere Molaren (Abb. 1e): einfach, wenn abgekaut mit ± geraden Querplatten; 3 Platten auf M^1, je 2 auf M^2 und M^3. M^3 kleiner als M^2. Bei einem unserer Exemplare (SMF 62925, Abb. 1e) hat der M^3 je einen kleinen anterointernen und anteroexternen Höcker (wohl t1 und t3); auf M^1 und M^2 keine Spuren solcher Höcker. Untere Molaren (Abb. 1f) mit transversalen Platten: M_2 mit 3, die anderen Molaren mit je 2 solcher Platten. An der Mandibel (Abb. 1d) sind Coronoid-Fortsatz und Condylus ähnlich wie bei *Nesokia* und *Bandicota*. Das seitlich am Gelenkfortsatz der Mandibel als Höcker hervorstehende Ende des Processus alveolaris steht in dessen Ausbildung und Lage zwischen den Situationen bei *Nesolia* und *Bandicota*.

Die Maße unserer 3 Exemplare zusammen mit denen des Typus (nach Khajuria 1981) finden sich zusammen mit *Nesokia*-Maßen in der Tabelle.

Maße von 4 Exemplaren von *Nesokia bunnii* (einschl. Typus-Exemplar nach Khajuria, 1981) und *Nesokia indica*

	Nesokia bunnii			*Nesokia indica*		
	n	min–max	M	n	min–max	M
Körper	3	230–260	247			
Kopf + Rumpf	3	250–271	257			
Schwanz	4	49–58	54			
Hinterfuß	3	62–64	63			
Vorderfuß	4	18–21	19			
Ohr	1		519 g			
Gewicht						
Schädel-Längen						
Occipitonasal-Lge	1		50,3	21	36,1–46,0	38,9
Condylobasal-Lge	3	52,1–56,6	53,6	25	38,7–50,2	42,5
Rostrum: M^3-Gnathion	3	32,0–34,7	33,2	31	22,8–30,4	25,8
Postmolare Lge	3	19,8–23,0	21,2	26	14,9–25,6	17,7
Diastema	4	16,3–18,2	17,3	31	12,2–17,0	13,95
Nasale	2	15,6–19,0	–	30	11,3–17,2	13,0
Nasale + Frontale	1		36,5	22	24,8–31,7	27,3
Parietale-Occiput	3	14,5–15,8	15,2	22	11,0–15,0	13,1
Foramen incisivum	4	6,7– 8,2	7,4	31	4,1– 6,8	5,0
Bulla	3	8,9–10,0	9,4	27	6,6– 9,1	8,1
Ob. Molaren (Kronen)	3	8,3– 9,8	8,9	32	6,2– 9,1	7,3
Ob. Molaren (Alveolen)	3	10,3–12,2	11,2	32	8,1–10,3	8,8
Schädel-Breiten						
Mastoid-Br.	3	18,9–21,0	19,9	23	15,7–19,5	17,0
Jochbogen-Br.	2	28,0–29,9	–	19	24,3–29,1	26,2
Ob. Molaren (Alveolen)	3	10,0–10,5	10,3	32	7,1– 9,5	8,15
Interorbital-Br.	4	7,4– 9,05	8,0	28	5,8– 7,35	6,45

Erythronesokia bunnii und *Nesokia indica* unterscheiden sich von *Bandicota* hauptsächlich durch einige unterschiedliche Schädel-Proportionen und, im Falle von *Erythronesokia*, durch die rötliche Rückenfärbung. Zum Vergleich unserer *bunnii*-Schädel mit *Nesokia indica* und *Bandicota* wurde folgendes Material herangezogen (alle Exemplare adult):

Nesokia indica (Gray und Hardwicke, 1831): Beluchistan: Panjgur, 10 Schädel (Zool. Staatssammlung München 547-551/1911, 557-559/1911, 565/1911, 583/1911). Afghanistan: Kabul, 13 Schädel (Sammlung Niethammer A. 86-87, A. 137, A. 539, A. 548, A. 1221, A. 1288, A. 1253, A. 1313, A. 1315, A. 1322, A. 1337; SMF 49455). Iran: Khusistan, 2 Schädel (Zool. Staatssammlung München 1957/287; SMF 48940); Fathabad, 1 Schädel

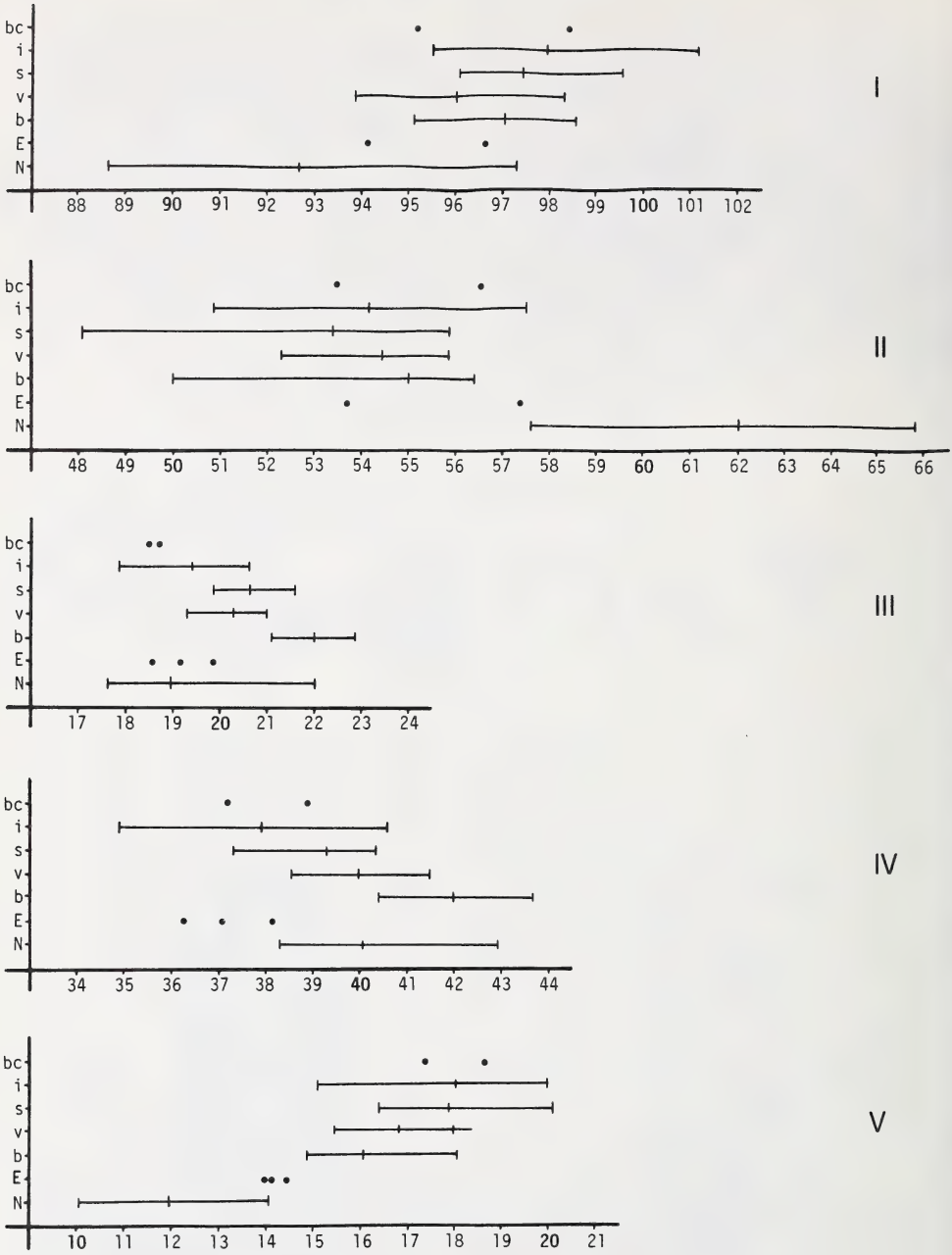
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Abb. 2

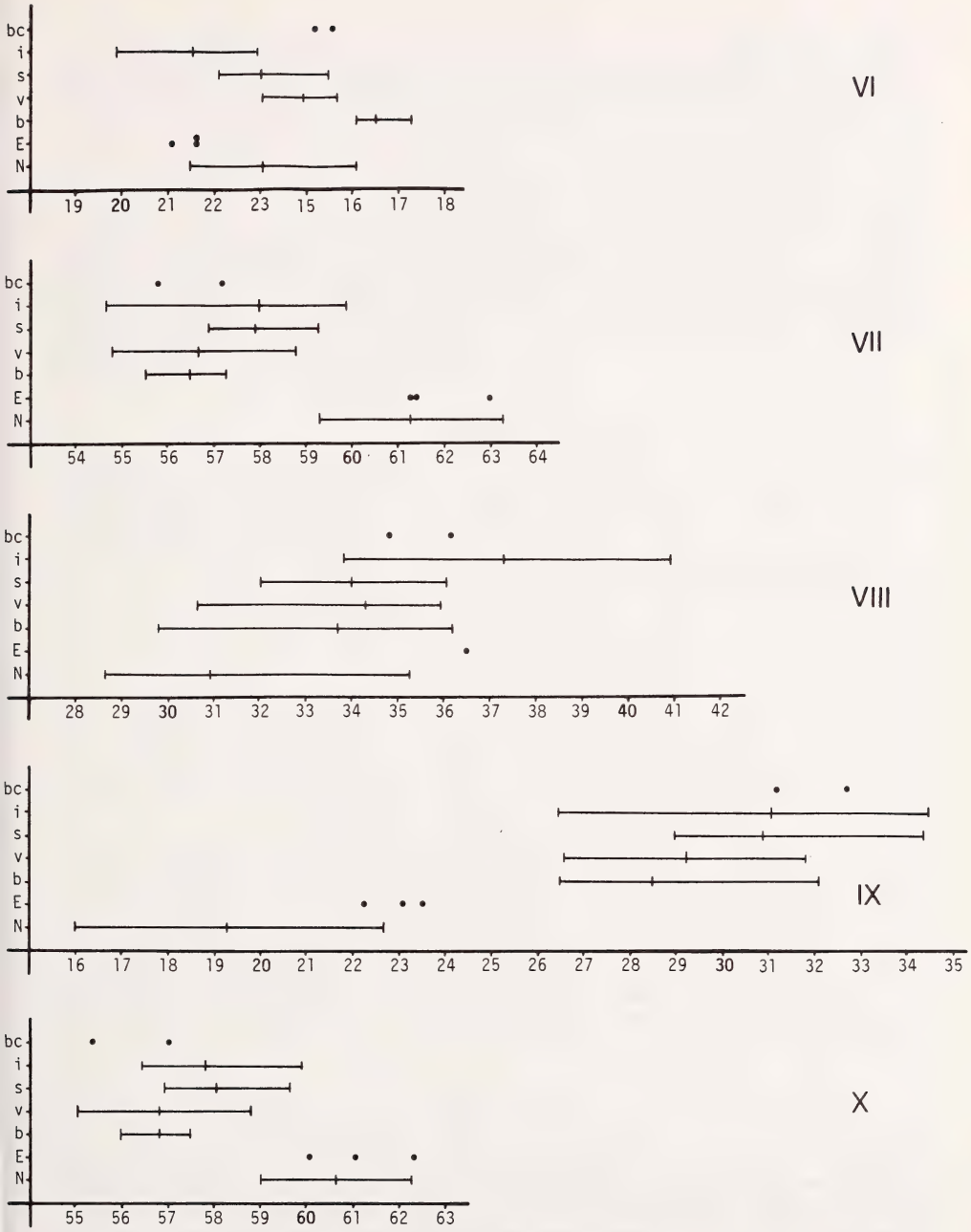

Abb. 2. Relative Schädelmaße von *Nesokia indica* (N), *N. bunnii* (E), *Bandicota bengalensis* (b), *B. varius* (v), *B. savilei* (s), *B. indica* (i) und *B. bangchakensis* (bc). I = Occipitonasale Länge in % der Condylobasal-Länge (Cbl). II = Jochbogen-Breite in % der Cbl. III = Breite über die oberen Molaren (alv.) in % der Cbl. IV = Mastoid-Breite in % der Cbl. V = Foramen incisivum-Länge in % der Cbl. VI = Länge der Bullae in % der Cbl. VII = Rostrum-Länge in % der Cbl. VIII = Nasal-Länge in % der Cbl. IX = Foramen incisivum-Länge in % der Rostrum-Länge. X = Rostrum-Länge (a) in Relation zur Postmolar-Länge (b) = a + b = 100

(SMF 46625). Syrien: Assad Lake, 1 Schädel (Sammlung Boessneck). Ägypten: Fayum, 1 Schädel (ZFMK Feld-Nr. 2). Iraq: Raum Qurna, 3 Schädel (Nat. Hist. Mus. Basrah 1–3).

Bandicota: Alle Exemplare aus Thailand (siehe Boonsong und Felten 1989): *Bandicota bengalensis* (Gray und Hardwicke, 1833): 8 Schädel (SMF 67741-8). *Bandicota varius* (Thomas, 1907): 11 Schädel (SMF 60165, 67749-58). *Bandicota savilei* Thomas, 1916: 14 Schädel (SMF 67759-72). *Bandicota indica* (Bechstein, 1800): 92 Schädel (SMF 60164, 60168-70, 60172-8, 60180, 60185-6, 67773-83, 67789-807, 67809-51). *Bandicota bangchakensis* Boonsong und Felten, 1989): 2 Schädel (SMF 67852-3).

Abb. 2 bringt verschiedene relative Schädel-Maße von *Erythronesokia, Nesokia* und *Bandicota*, um die verschiedenen Schädel-Proportionen gegenüberzustellen. In 2 Proportionen können *Erythronesokia* und *Nesokia* deutlich von *Bandicota* unterschieden werden:

1. Länge des Foramen incisivum: Es ist im Verhältnis zur Condylobasal-Länge mit 10,1–14,5 % deutlich kürzer als bei *Bandicota* (14,9 % und mehr). Im Verhältnis zur Rostrum-Länge ist es bei *Erythronesokia* und *Nesokia* mit 16,0–23,6 % deutlich kürzer als bei *Bandicota* (26,5 % und mehr). In beiden Fällen liegen die relativen Längen von *Erythronesokia* im oberen Bereich von *Nesokia*.
2. Rostrum-Länge: Im Verhältnis zur Condylobasal-Länge ist sie bei *Erythronesokia* mit 61,3–63 % innerhalb der entsprechenden Werte von *Nesokia* (59,3–63,3 %), aber länger als bei *Bandicota* (unter 59,9 %). Im Verhältnis Rostrum-Länge (a): Postmolar-Länge (b), (a + b = 100), finden wir eine ähnliche Situation: bei *Erythronesokia* und *Nesokia* ist die Rostrum-Länge größer als bei *Bandicota*.

Wir haben gesehen, daß *Erythronesokia* und *Nesokia* anhand von Schädel-Proportionen von *Bandicota* unterschieden werden können. Ist aber *Erythronesokia* in ähnlicher Weise von *Nesokia* zu trennen? Die relativen Schädelmaße in Abb. 2 zeigen, daß die Werte von *Erythronesokia* meist innerhalb der Variationsbreite der Werte von *Nesokia* liegen mit folgenden Ausnahmen: Die Mastoid-Breite ist bei *Erythronesokia* relativ geringer als bei *Nesokia*, aber ähnlich wie bei *Bandicota indica*; die relative Jochbogen-Breite ist bei *Erythronesokia* geringer als bei *Nesokia*, aber ähnlich wie bei *Bandicota*. Die Hauptunterschiede zwischen *Nesokia* und *Bandicota* liegen in der relativen Rostrum-Länge und, vor allem, in den absoluten und relativen Längen der Incisiv-Foramina; in diesen Fällen sind die Verhältnisse bei *Erythronesokia* ähnlich denen bei *Nesokia*.

Erysthronesokia steht unseres Erachtens *Nesokia* sehr nahe, wobei die Hauptunterschiede in der Färbung sowie den relativ geringen Mastoid- und Jochbogen-Breiten bei *Erythronesokia* liegen, was mit der nicht-grabenden Lebensweise in Verbindung stehen mag. Es fragt sich, ob diese Unterschiede gewichtig genug sind, um deswegen eine eigene Gattung aufzustellen. Wir halten *Erythronesokia* für nicht mehr als – wenn überhaupt – eine Untergattung von *Nesokia*. *Bunnii* ist eine gute Art, die neben *Nesokia (Nesokia) indica* die zweite Art der Gattung *Nesokia* bildet. Ihr Name ist dann *Nesokia (Erythronesokia) bunnii* (Khajuria, 1981).

Lebensweise

Nesokia bunnii lebt im Iran in den Sümpfen von El-Hamar in großen Schilfgebieten, die saisonal von den Flüssen Euphrat und Tigris überflutet werden. Diese Sümpfe sind gleichzeitig bedeutende Lebensräume für viele Wasser- und Watvögel. Im Sommer lebt *bunnii* in den Sümpfen, im Winter kommen die Tiere näher zu den Ufergebieten, wo junges Schilf verfügbar ist. Die Nester liegen etwa 0,5 m über der Wasseroberfläche und sind aus 2 Lagen Schilf geflochten. Die Öffnung liegt in mittlerer Höhe. Diese Ratten sind gute Schwimmer, wobei die Hautsäume an den Zehenbasen eine Hilfe sind. Sie können bis zu 5 Minuten unter Wasser bleiben. Die Nahrung besteht aus pflanzlicher und offensichtlich auch tierischer Kost. Sie wird aufrecht auf den Hinterextremitäten und dem Schwanz sitzend quer mit den Vorderpfoten gehalten. Es sind Würfe von 2 Jungen beobachtet worden.

Danksagung

Für das Ausleihen von *Nesokia*-Exemplaren haben wir den Herren Dr. Kraft und Prof. Dr. Boessneck, beide München, zu danken wie auch Prof. Dr. Niethammer, Bonn. Frau Petra Friesleber, Senckenberg-Museum Frankfurt, danken wir für die Anfertigung der Zeichnungen.

Zusammenfassung

Die Hauptunterschiede zwischen den Gattungen *Nesokia* und *Bandicota* bestehen in der größeren relativen Rostrum-Länge und vor allem in den kleineren absoluten und relativen Längen der Incisiv-Foramina bei *Nesokia*. Hier geht die Tendenz von *Erythronesokia* mit der Art *bunnii* eindeutig zu *Nesokia*. *E. bunnii* ist *Nesokia* sehr ähnlich bei überlegener Größe, unterschiedlicher Färbung und relativ geringen Mastoid- und Jochbogen-Breiten. Wir halten *Erythronesokia* höchstens für eine Untergattung von *Nesokia*, nicht jedoch für eine eigene Gattung. Der Artname von *bunnii* ist demnach *Nesokia (Erythronesokia) bunnii* (Khajuria, 1981). Zusätzlich werden Angaben über Vorkommen, Lebensweise und Fortpflanzung gemacht.

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Geographic variation in skulls of the nearly extinct Small Black rhinoceros *Diceros bicornis michaeli* in northern Tanzania

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Abstract

Skull parameters of Black rhinoceros *Diceros bicornis* (L., 1758) collected in Lake Manyara National Park and in the Ngorongoro Crater, both in northern Tanzania were measured. Statistical analysis showed that they belonged to two morphologically distinct sub-populations with only small overlap. The rhinoceroses from the two areas fall into the subspecies *D. b. michaeli* Zukowsky, 1964. The Ngorongoro area does not form an intergrade zone between the subspecies *michaeli* and *D. b. minor* Drummond, 1876. An analysis of the data published by Groves (1967) and those collected in the present study, shows that the group of skulls delimited as subspecies *minor* appear to be situated within a cline between subspecies *michaeli* and subspecies *D. b. ladoensis* Zukowsky, 1964. Even if the subspecies concept has no strict biological meaning, it has importance for nature conservation, and much effort should be concentrated on saving the Small East African black rhinoceros *D. b. michaeli,* as its numbers in the wild appear to be as low as fifty to one hundred.

Introduction

Until recently, the Black rhinoceros *Diceros bicornis* (L., 1758) was widely distributed in eastern and southern Africa and in the Sahel. At present, its range has been fragmented into small to very small areas (Haltenorth and Diller 1979), and total numbers have declined. For example, in Tsavo National Park, southern Kenya (Fig. 1), the population was estimated at approximately 8000 at the end of the 1960s (Goddard 1969), at 5600 in the mid-70s (Cobb 1976), but at present it has been reduced to a few dozen at most (W. van Wijngaarden pers. comm.). A likewise dramatic abatement took place in the Selous Game Reserve, southern Tanzania, where the population in the mid-70s was estimated to be at least 2500 (Douglas-Hamilton 1976), while in 1988 "a few" were left (M. Borner pers. comm.). These extreme declines are due to excessive poaching, just as elsewhere in most parts of Africa, and it is doubtful whether the species will survive in the wild for very long.

The Black rhinoceros as a morphological distinguishable taxon has a long history. It has been recorded in Africa from the Late Pliocene and Early Pleistocene (Guerin 1976; Hooijer 1969, 1976; Leakey et al. 1976; Harris 1983), and only minor evolutionary changes are observable in the fossil material (Harris 1983).

Seven subspecies have been distinguished and described by Groves (1967) on basis of skulls in museums. Because of the small number of skulls available, the discrimination between the subspecies is on statistical grounds not always very satisfactory. Corbet (1970) stated that "the chief obstacle to determining the pattern of variation in a species is the availability of samples that are sufficiently large and sufficiently random with respect to locality..., to allow the true pattern of variation in nature to be accurately inferred from the pattern of variation seen in the collected sample". As the number of living individuals is dwindling so fast, it is important for the systematics of the Black rhinoceros that as many individual skulls as possible are described before none are available anymore.

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The Small East African black rhinoceros *D. b. michaeli* Zukowsky, 1964, was described by Groves (1967) on basis of twenty-two adults (M_3 in wear), two subadults (M_3 just erupted) and two late juveniles (M_3 unerupted). The type specimen came from "the area between Engaruka and Serengeti" (Fig. 1). The village of Engaruka lies at present in the Tanzania's Eastern Rift Valley (longitude 3°19′ S, latitude 35°58′ E, 800 m above sea level).

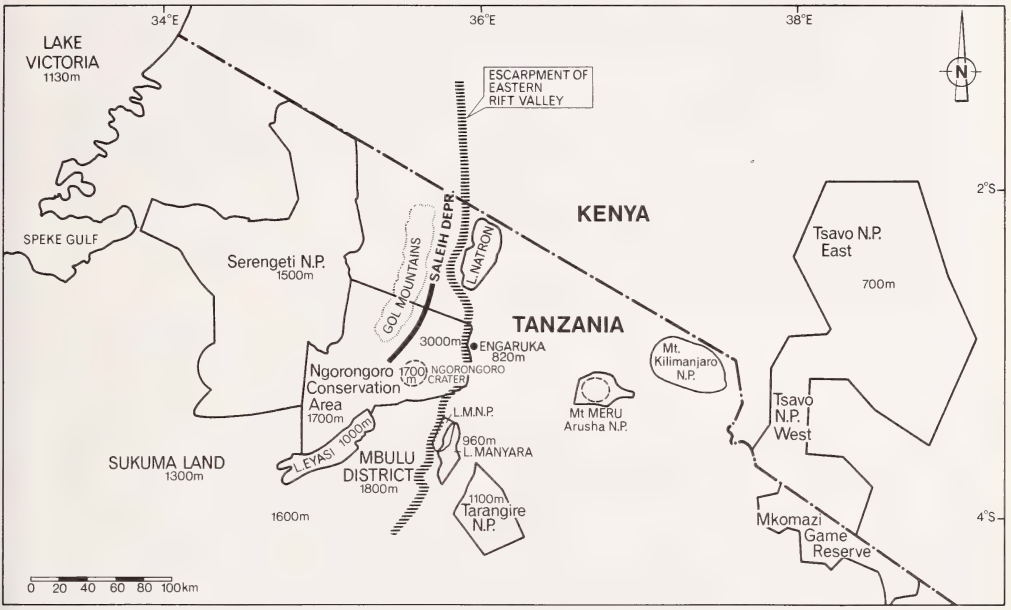

Fig. 1. Location of the study areas and of the geographical names mentioned in the text

The Serengeti short grass plain unfolds approximately 40 km due west, at the western side of the Ngorongoro Highlands, but good rhino habitat is not encountered again before the tall grass zone and woodlands some 40 km even further west (pers. obs.). There the Large East and South-East African black rhinoceros *D. b. minor* (Drummond, 1876) occurs (Groves 1967), although in very reduced numbers (less than 10, T. Caro pers. comm.). Groves (1967) considered the area between Engaruka and Serengeti, thus the Crater Highlands, and the area between Lakes Manyara and Eyasi, immediately south of the Ngorongoro Crater (Fig. 1), as an intergrade zone between the subspecies *michaeli* and *minor*.

Black rhinoceros skulls in the Ngorongoro Crater and in Lake Manyara National Park, both in Tanzania, were studied. Nearly all skulls derived from individuals killed by poachers. The objective of the paper is to describe these skulls, and to answer the question whether the rhinoceroses in Manyara and Ngorongoro belong to the same subspecies, and to what subspecies these individuals belong.

Material and methods

Twenty-two rhinoceros skulls were collected in Lake Manyara National Park (long. 3°42′ S., lat. 35°50′ E.), which is situated in the Rift Valley at approximately 1000 m a. s. l. and some 40 km South of Engaruka, and nineteen were collected in the Ngorongoro Crater (long. 3°7′ S., lat. 35°32′ E.), from which the floor is at about 1750 m a. s. l. The linear distance between Manyara and the Crater is

approximately 35 km (Fig. 1). Skulls were collected between 1979 and 1984. Discrimination of the sexes was not possible.

As during the field work we were not acquainted with rhinoceros craniology, we devised our own series of measurements (Fig. 2A and 2B):

A. Basal length, from the maxillary notch to the foramen magnum ridge between the occipital condyles. This parameter is (nearly) identical to Groves' (1967) "basal length".
B. Snout length, from the maxillary notch to the end of the palate. Basal length minus snout length is identical to "length palatonarial border to occipital condyles" (Harris 1983).
C. Width between the postglenoidal processes. Although this parameter is not equivalent to Harris' (1983) "width between occipital condyles", it appears to be roughly the same (Fig. 2B; compare Plate 4.6 in Harris 1983).
D. Squamosal width, measured at the lateral points of the fossae articularis, is apparently equivalent to Groves' (1967) "zygomatic breadth".
E. Snout width, measured at the most lateral points of the first molar and includes the maxillary bones.
F. Width foramen magnum, measured at the small caudal ridges of the foramen, is apparently equivalent to Harris' (1983) "width foramen magnum".
G. Height foramen magnum, measured in the medio-sagittal plane, and perhaps equivalent to Harris' (1983) "depth foramen magnum"?
H. Crown height of M_1, at the buccal side of the left and right first molar.
I. Horn boss diameter, as measured in the transversal plane.

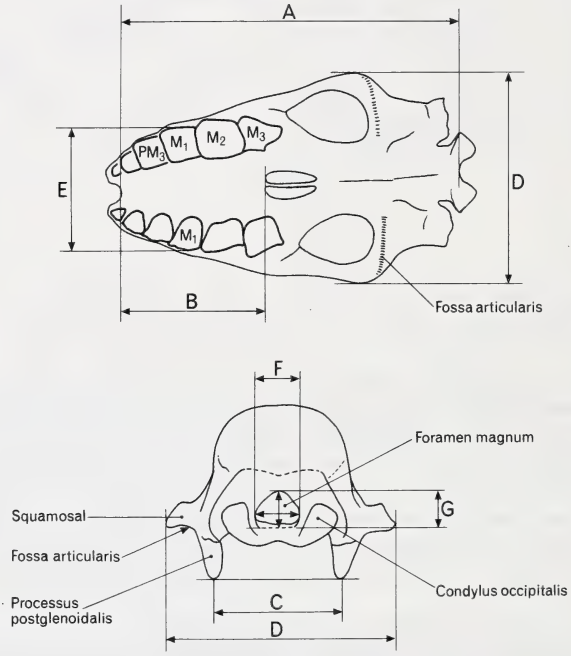

Fig. 2. The skull of a Black rhinoceros viewed from below (A) and from behind (B) to show skull parameters measured (see Methods)

All lengths were measured in mm, and analysed with Statistix soft-ware package. Two-tailed probability tests are quoted throughout the paper, and all parameters were tested for normality before choosing the appropriate test.

Coefficients of difference (CD) were calculated following Mayr (1969) as:

$$\frac{\text{mean length}_b - \text{mean length}_a}{SD_a + SD_b},$$

in which SD stands for the standard deviation of the sample, and sub-population are denoted with a and b.

Pearson's coefficient of racial likeness (CRL) was calculated as given by Sokal and Sneath (1963).

Three dimensional figures were prepared to show differences between the two subpopulations. In these figures, the axes stand for one skull parameter, and the sum of the three axes equal 100 % because each parameter is expressed as a percentage of the sum of the three linear values.

Differences between ratio's were t-tested after arcsine transformations. Not all measurements could be taken from each specimen for many were damaged, hence there is variation in sample size.

Results

For the Ngorongoro and Manyara material a distinction was made between adults (M_3 in wear), intermediates between adult and sub-adult stages (M_3 not fully in wear) and sub-adults (M_3 erupted). Only one skull of a juvenile rhino was found, which clearly confirms the notion that most of the skulls came from individuals killed for their horns. Many skulls had bullet holes, or showed traces of horn removal. Differences between the three age categories, or between adults and the combined other two categories, were not significant for the craniological parameters. Hence, in the analyses no further distinction was made between adult or sub-adult. As an additional measure of age, M_1 crown height was taken. Because of tooth wear, it is likely that older animals have shorter cheek teeth than younger ones. Table 1 shows that the skull parameters were not dependent on crown height within the data set of sub-adult and adult individuals. Although there are some exceptions (squamosal width for the Ngorongoro skulls and horn boss diameter for the Manyara skulls), the finding that the relations for the two localities were not both significant makes it safer not to reject the hypothesis that there is no effect of crown height, thus age, on the skull parameters.

The variation of the different characters is virtually independent of one

Table 1. **Linear correlations between Black rhinoceros skull parameters for two areas in northern Tanzania and the negative value of M_1 crown height**
Because of tooth abrasion, individual rhino with the lowest crowns are thought to be oldest. By using the negative values of crown heights, an indirect effect of inferred age on the skull parameters can be investigated. No consistent significant effect of age could be demonstrated within the data sets that comprised adult and sub-adult individuals

Skull parameters	Linear correlations with "age"	
	Manyara	Ngorongoro
Basal length	$r = 0.407$, $R^2 = 16.6$ %, n = 17; N.S.	$r = 0.040$, $R^2 = 1.6$ %, n = 16; N.S.
Snout length	$r = 0.232$, $R^2 = 5.4$ %, n = 17; N.S.	$r = 0.139$, $R^2 = 1.9$ %, n = 18; N.S.
Postglenoid width	$r = 0.256$, $R^2 = 6.6$ %, n = 17; N.S.	$r = 0.297$, $R^2 = 8.8$ %, n = 20; N.S.
Squamosal width	$r = -0.403$, $R^2 = 16.2$ %, n = 17; N.S.	$r = 0.580$, $R^2 = 33.6$ %, n = 19; $P < 0.02$
Snout width	$r = -0.322$, $R^2 = 10.3$ %, n = 15; N.S.	$r = 0.216$, $R^2 = 4.6$ %, n = 15; N.S.
Foramen magnum width	$r = 0.067$, $R^2 = 0.4$ %, n = 17; N.S.	$r = 0.464$, $R^2 = 21.5$ %, n = 17; N.S.
Foramen magnum height	$r = 0.402$, $R^2 = 16.2$ %, n = 17; N.S.	$r = 0.220$, $R^2 = 4.8$ %, n = 17; N.S.
Horn boss diameter	$r = 0.648$, $R^2 = 42.0$ %, n = 14; $P < 0.02$	$r = 0.243$, $R^2 = 5.9$ %, n = 6; N.S.
Snout length as % of basal length	$r = -0.205$, $R^2 = 4.2$ %, n = 17; N.S.	$r = -0.179$, $R^2 = 3.2$ %, n = 16; N.S.
Postglenoid width as % of squamosal width	$r = -0.014$, $R^2 = 0.0$ %, n = 17; N.S.	$r = -0.252$, $R^2 = 6.4$ %, n = 19; N.S.
Horn diameter as % of snout width	$r = 0.699$, $R^2 = 48.8$ %, n = 12; $P < 0.02$	$r = -0.635$, $R^2 = 40.3$ %, n = 4; N.S.

another. For example, basal length is not related to squamosal width (Manyara: $R^2 = 0.32$, n = 15, N. S.; Ngorongoro: $R^2 = 0.34$, n = 19, N. S.), neither is postglenoid width related to basal length (Manyara: $R^2 = 0.14$, n = 19, N. S.; Ngorongoro: $R^2 = 0.13$, n = 17, N. S.), nor is snout width significantly correlated with snout length (Manyara: $R^2 = 0.32$, n = 16, N. S.; Ngorongoro: $R^2 = 0.07$, n = 19, N. S.). However, for Manyara rhino postglenoid width is 0.286 * squamosal width + 16 mm ($R^2 = 0.29$, n = 18, $P < 0.05$) and for Ngorongoro rhino postglenoid width is 0.323 * squamosal width + 13 mm ($R^2 = 0.43$, n = 20, $P < 0.01$). It appears that, even if the correlations are significantly deviating from zero, the correlations are weak because the explained variance (R^2) is low.

The average values for the craniological parameters for the two sub-populations of Manyara and Ngorongoro are very similar but for a number of parameters (Table 2). Basal

Table 2. **Mean value and SD (in mm) for skull parameters for Manyara and Ngorongoro rhino**
Differences between the two sub-populations are tested with t-test for equal variance or unequal variance where relevant

Skull parameters	Manyara	Ngorongoro	Equal variance?	Difference
Basal length	503 ± 20 (N = 19)	500 ± 22 (N = 17)	yes	N.S.
Snout length	211 ± 10 (N = 19)	201 ± 10 (N = 19)	yes	P<0.01
Postglenoidal width	107 ± 7 (N = 19)	115 ± 9 (N = 21)	yes	P<0.005
Squamosal width	319 ± 14 (N = 19)	317 ± 17 (N = 20)	yes	N.S.
Snout width	165 ± 6 (N = 15)	160 ± 9 (N = 15)	P<0.1	P = 0.1
Foramen magnum width	55 ± 4 (N = 19)	55 ± 5 (N = 18)	yes	N.S.
Foramen magnum height	48 ± 4 (N = 19)	53 ± 4 (N = 18)	yes	P<0.001
Crown height	34 ± 10 (N = 17)	48 ± 7 (N = 21)	P<0.05	P<0.0001
Horn boss diameter	129 ± 13 (N = 16)	140 ± 4 (N = 7)	P<0.01	P<0.01

length, squamosal width, and foramen magnum width do not differ significantly. The Manyara rhinoceroses have a significantly longer snout length (10 mm), perhaps a wider snout width (5 mm; this is only significant at P = 0.1), a narrower postglenoid width (6 mm), a substantially smaller height of the foramen magnum (7 mm), and a smaller horn boss diameter (11 mm) than the Ngorongoro rhinoceroses. Moreover, the crown height of the first molar of the Manyara rhino is substantially lower than that of the Ngorongoro individuals (14 mm). Snout length as percentage of basal length is not related to presumed age, nor is postglenoid width as percentage of squamosal width, or horn boss diameter as percentage of snout width (Table 1).

Coefficients of variation are small, except for crown height (Table 3). Excluding this last

Table 3. **Coefficients of variation (%) for skull parameters for the two sub-populations of Black rhinoceros, and MAYR's coefficient of difference (see Methods)**

Skull parameters	Coefficient of variation (%)		Coefficient of difference for Manyara and Ngorongoro
	Manyara	Ngorongoro	
Basal length	4.0	4.4	0.071
Snout length	4.7	5.0	0.500
Posglenoidal width	6.5	7.8	0.500
Squamosal width	4.4	5.4	0.065
Snout width	3.6	5.6	0.333
Foramen magnum width	7.3	9.1	0.000
Foramen magnum height	8.3	7.5	0.625
Crown height	29.4	14.6	0.824
Horn boss diameter	10.1	2.9	0.647

parameter, the average coefficient of variation for the Manyara sub-population is 6.1 %, and for the Ngorongoro sub-population 6.0 %. Mayr's (1969) coefficient of difference is low for all parameters (ranging between 0 and 0.824) (Table 3).

The two populations can be fairly well separated by using three significantly differing parameters, for example, snout length, postglenoid width and crown height (Fig. 3 a), or snout length, postglenoid width, and foramen magnum height (Fig. 3 b). Because molars are subjective to wear from abrasive food, crown height is a less attractive parameter to include in the distinction of the two sub-populations. The Manyara rhinoceroses have a longer snout in relation to basal length than those of the Ngorongoro Crater (t-test after arcsine transformation: $t_{34} = 4.866$, $P < 0.005$), they also have a narrower postglenoid width in relation to the squamosal width ($t_{37} = 4.581$, $P < 0.005$), and their horn boss diameter may be narrower ($t_{14} = 1.843$, $P < 0.1$).

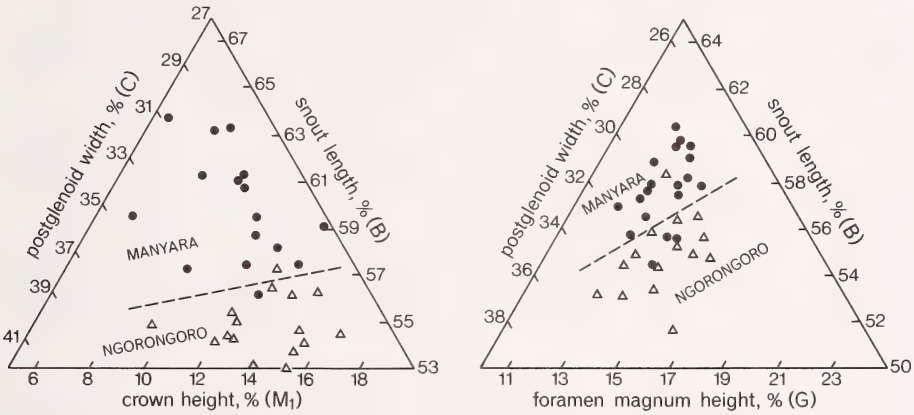

Fig. 3. The Black rhinoceros skulls from Lake Manyara National Park and from the Ngorongoro Crater fall into two distinct groups, although there is some small overlap. This indicates that the rhino from Manyara and those from the Ngorongoro Crater constitute two distinct sub-populations, and only rarely individuals move from one area into the other (see Discussion)

Discussion

As shown in Table 3, the coefficient of difference for all skull parameters is low and on average as small as 0.396. This value is much lower than the critical value of 1.28 needed if one is to speak of two different subspecies (Mayr 1969): the Black rhinoceroses of Manyara and Ngorongoro therefore clearly belong to the same subspecies. By the same token, the coefficient of racial likeness is only 0.313 (excluding crown height; if this parameter is included the CRL is 0.428). In terms of Pearson (1928), these two groups are "very intimate associated". It is likely that the number of characters studied is small in view of the genetic information contained in the genome and also that inclusion of more characters might change the similarity coefficient (Sokal and Sneath 1963, p. 110 et seq.). Nevertheless, the differences between the skull characteristics are large enough to make it likely that the rhinoceroses from Manyara and those from the Ngorongoro do represent two different sub-populations (Fig. 3 a and b). Manyara rhino have a relative longer snout and more space between the postglenoid and the outside of the squamosal, hence more space for jaw muscles. At present, rhino from the Ngorongoro Crater select herbs from between grasses, while those from Manyara typically browse from shrubs. It is possible that these different feeding habits have been selected for, together with small changes in

skull morphology. Because herbs are softer than twigs, this difference in diet could also explain the significant difference in tooth wear between Manyara and Ngorongoro rhino (Table 2).

However, the sub-populations are not totally isolated. Figures 3a and b show that some of the skulls from Manyara fall into the Ngorongoro group, and vice versa. The absence of a strict separation is confirmed by observations of rhino moving from the Ngorongoro into Manyara in 1968 (Wardens Reports 1968) and in 1983 (a female with her calf: pers. obs.). The Mbulu District, between the Ngorongoro Crater and Lake Manyara, although at present densely settled by humans, used to provide excellent rhino habitat (Baumann 1894), and even in the 1960s hundreds of rhino were killed in this area (Wardens Reports 1959–1973).

A comparison with the data provided by Groves (1967) (Tables 4 and 5), clearly shows that both the Manyara and the Ngorongoro rhino fall in the subspecies *michaeli,* as described by him. As cited above, the type specimen of this subspecies came from the area between Engaruka and Serengeti. By my reckoning it is highly likely that this statement refers to the Ngorongoro area, as it lies between Engaruka and the Serengeti. The conclusion that the skulls of Ngorongoro Crater rhino clearly fall into those of the *michaeli* subspecies group, confirms this notion. Hence, Groves' (1967) remark that the area between Engaruka and Serengeti falls into the intergrade zone between subspecies *michaeli* and subspecies *minor* ist not born out by the data. Apparently, the very dry Salei Depression, bordering the Ngorongoro Highlands to the northwest (Fig. 1), acted as an ecological barrier for rhino between the moist Ngorongoro area and the Serengeti woodlands. However, the Mbulu District in the direction of Lake Eyasi may have been an intergrade zone between the two named subspecies (Table 4). If this is true, rhino from the

Table 4. **Skull characteristics of three subspecies of Black rhinoceros and of two sub-populations from northern Tanzania**

All data, except from Manyara and Ngorongoro, from Groves (1967). Rhino from Lake Manyara National Park and from the Ngorongoro Crater are considered to belong to the *michaelis* group, but those from the Mbulu District and the vicinity of Lake Eyasi are intergrades between *michaelis* and *minor* (see Discussion)

	Basal length	Zygomatic breadth	Occipital breadth	Sample size
Lake Manyara and Ngorongoro Crater	501.4 ± 20.8	317.7 ± 15.8	–	38
subspec. *michaeli*	514.2 ± 14.2	326.8 ± 9.8	186.2 ± 10.1	22
Lake Eyasi and Mbulu District	525.8 ± 14.8	327.0 ± 12.8	187.7 ± 12.6	12
subspec. *minor*	545.5 ± 16.9	330.4 ± 10.5	188.2 ± 12.1	23
subspec. *ladoensis*	557.5 ± 14.2	347.7 ± 11.2	210.2 ± 6.3	6

subspecies *minor* must once have been living in Sukumaland (on the west side of Lake Eyasi) as they still do in the western Serengeti. The chance to confirm this hypothesis is remote, as it is extremely unlikely that rhino still live in Sukumaland.

North of the Serengeti (Fig. 1), between the White Nile and Lake Naivasha, Kenya, another subspecies of the Black rhinoceros occurs, *D. b. ladoensis* Zukowsky, 1964. This subspecies is even larger than *minor* (Groves 1964; Table 4). The rhino from Ngorongoro and Manyara, and the *michaeli* group are clearly distinct from *ladoensis,* and the coefficient of difference is (nearly) as high as advocated by Mayr (1969) to distinguish subspecies (Table 5). However, the value of this coefficient is not high enough to distinguish between *minor* and *ladoensis* (*pace* Groves 1967).

Based on data from Groves (1967), i. e. greatest skull length, basal length, zygomatic

breadth, and occipital breadth, but excluding teeth row length (as this parameter is subjective to shortening in older age because of teeth wear), coefficients of racial likeness (CRL) values have been calculated for *michaeli, minor,* and *ladoensis.* This value is highest for *michaeli* and *ladoensis* (CRL = 5.789), so these two subspecies are least alike. It is lowest for *ladoensis* and *minor* (CRL = 3.296), and intermediate for *minor* and *michaeli* (CRL = 4.630; all values with standard error of 0.477 and in the class "moderate" association' of PEARSON 1928). Together with the data presented in Table 5, the conclusion is that the subspecies *minor* ist not clearly distinct from either *michaeli* or *ladoensis.*

Table 5. **Coefficients for basal length (B) and zygomatic breadth (Z) for different pairs of groups of Black rhinoceros (upper right values), and average coefficients of difference for the same pairs (lower left values)**

Only the rhinoceroses from Manyara and Ngorongoro, and perhaps those from the *michaelis* group, differ enough from the *ladoensis* group to warrant subspecific distinction

	Manyara and Ngorongoro	Subspec. *michaeli*	Lake Eyasi and Mbulu District	Subspec. *minor*	Subspec. *ladoensis*
Manyara and Ngorongoro	–	B=0.366 Z=0.355	B=0.685 Z=0.325	B=1.170 Z=0.483	B=1.603 Z=1.111
Subspec. *michaeli*	0.361	–	B=0.400 Z=0.009	B=1.106 Z=0.177	B=1.525 Z=0.995
Lake Eyasi and Mbulu District	0.505	0.205	–	B=0.621 Z=0.146	B=1.093 Z=0.863
Subspec. *minor*	0.827	0.642	0.384	–	B=0.386 Z=0.797
Subspec. *ladoensis*	1.357	1.260	0.978	0.592	–

According CORBET (1970), "the concept of subspecies is meaningless unless it is restricted to discrete segments of a species. A distinction should be drawn between 'definite subspecies' that have been convincingly shown to be discrete entities in nature and 'provisional subspecies' that are based on discretely definable samples that are too small or non-random to indicate with a high degree of probability whether the populations from which they were drawn are or are not discrete entities". It appears that the forms described as *michaeli, minor,* and *ladoensis* may well represent clinal variation, with *minor* being the intermediate. If this is true, then *minor* should not be considered a "definite subspecies" (sensu CORBET 1970).

Although the difference between *ladoensis* and *michaeli* is not very large either, the fact that the fossil material from the Lake Turkana area, northern Kenya, from the Early Pleistocene yielded a rhino skull that would fall into the present-day small subspecies group (HARRIS 1983) increases the likelihood of a real distinction between a small and a large Black rhinoceros in East Africa. Added to this is that, as least in the border area between Tanzania and Kenya, there appears to be an ecological barrier between the two forms *ladoensis* and *michaeli* in the arid Salei Depression. This would counter the critique of *Corbet* (1970) that many subspecies have been described and subspecific boundaries drawn with little regard to the probability of either the range or the variation being continuous or discontinuous.

Several authors have suggested that the designation of subspecies would be helpful for the study of geographic variation but for the lack of a good biological definition of the subspecies (JOHNSON 1982; STORER 1982; ZUSI 1982). ELDREDGE and CRACRAFT (1980) do not even mention the subspecies, the species being considered the "minimal phylogenetic group" or the "taxon of the lowest categorical rank within the Linnaean hierarchy".

However, if by multi-variate statistical procedures groups of individuals can be distinguished, it could be possible that there are barriers in the gene flow between these groups or populations. "A name for such a population may be defensible on the grounds that it signals phenotypic divergence and a reduction of gene flow; in other words, the populations might be incipient phylogenetic species" (McKitrick and Zink 1988).

Whether or not the subspecies is a valid category in systematics, it is of value in nature conservation. Perhaps the observed degree of non-homogeneity within a species, such as in the Black rhinoceros, could result in new species in the future. Nature conservation is not only about maintaining what exists and has evolved, but should also concentrate on keeping open avenues for future evolution.

The situation for the Small black East African rhinoceros is very grim at present, and without very firm conservation measures it is doubtful whether the subspecies will survive another five or ten years. The range has been extremely fragmented, with perhaps a dozen or so still alive in Tsavo N. P., less than ten on Mts Kilimanjaro and Meru, thirty at the most in Tarangire N. P., perhaps ten or twenty in Manyara, and twenty in the Ngorongoro. The total population is therefore between 50 and 100, with the largest populations in the Tarangire-Manyara – Ngorongoro area. If subspecies *michaeli* is to be saved it should be by concentrating much of the conservation measures on this area, for example through extending Lake Manyara National Park (Prins 1987), by international financing of salaries of park rangers, and by education of the people living around the protected areas.

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Zusammenfassung

Geographische Variation der Schädel beim bedrohten Spitzmaulnashorn Diceros bicornis michaeli in Nordtansania

Schädelparameter des Spitzmaulnashorns *Diceros bicornis* (L., 1758), aus dem Lake Manyara Nationalpark und dem Ngorongoro-Krater – beide Lokalitäten liegen in Nordtansania – wurden vermessen. Die statistische Analyse zeigte, daß die Schädel zu zwei morphologisch unterscheidbaren Subpopulationen mit nur schmaler Überlappungszone gehören. Die Nashörner beider Gebiete werden der Unterart *D. b. michaeli* Zukowsky, 1964, zugeordnet. Das Ngorongoro-Gebiet stellt keine Übergangszone zwischen den Unterarten *michaeli* und *D. b. minor* Drummond, 1876, dar. Eine Analyse der Daten von Groves (1967) und jener, die für diese Studie gesammelt wurden, zeigt, daß Schädel, die zur Unterart *minor* gehören, zwischen den Unterarten *michaeli* und *D. b. ladoensis* Zukowsky, 1964, eingeordnet werden müssen. Selbst wenn man dem Konzept der Unterarten keine entscheidende biologische Bedeutung beimißt, ist es im Zusammenhang mit dem Naturschutz wichtig. Große Anstrengungen sollten zur Rettung des Spitzmaulnashorns *D. b. michaeli* gemacht werden, da in der freien Natur nur noch zwischen 50 und 100 Tiere leben.

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Naturally occurring suid hybrid in Java

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Abstract

A free-living hybrid between the Javan warty pig *(Sus v. verrucosus)* and the common wild boar *(S. scrofa vittatus)* was identified by physical characteristics including skull measurements. These species are sympatric on Java, and it is speculated that habitat reduction and the rarity of one parental species are environmental factors which result in localized hybridization.

Introduction

Twenty-five years ago very few genuine cases of hybridization between closely related sympatric species of mammals in the wild had ever been reported (Mayr 1963, p. 115), and at present such reports for species of larger mammals are still rare. Those encountered involve primates most frequently (Bernstein 1966; Aldrich-Blake 1968; Struhsaker 1970), but also include a well documented occurrence with canids (Nowak 1979). Among the ungulates, Bartos et al. (1981) mention that there is currently hybridization between sika deer *(Cervus nippon)* and red deer *(C. elaphus xanthopygus)* in natural contact in northwestern China. Roberts (1977) suggests that there may be natural hybridization between the straight horned markhor *(Capra falconeri jerdoni)* and the Persian pasang *(C. aegagrus)* in Pakistan, and an examination of specimens by one of us (CPG) leads him to concur with this assessment.

This paper describes the first recorded instance of natural hybridization between wild pig species, in this case the Javan warty pig (*Sus v. verrucosus* Müller, 1840) and the common wild boar (*S. scrofa vittatus* Boie, 1828). These species are naturally sympatric in java, *verrucosus* being endemic at subspecific level to the island and *scrofa* reaching the southern limit of its range there. Possible environmental factors which could cause a breakdown of the isolating mechanisms separating these species are examined, and the effects which hybridization could have on the gene pool of the Javan warty pig are discussed.

Material and methods

During a 1982 survey of the remaining *S. verrucosus* populations in Java (Blouch 1988), all recently killed adult wild pigs encountered were examined for indications of hybridization. An animal was classified as a possible hybrid if it showed a mixture of *verrucosus* and *scrofa* characteristics for such parameters as presence or absence of warts in the male, pelage colouration, and shape of the male's lower canine as described by Groves (1981). Among 31 recently killed specimens examined, one skull was provisionally identified as a hybrid. Its measurements were then compared with those of 19 adult male *S. s. vittatus* from Java and 27 adult male *S. v. verrucosus*. All material, including skulls collected during the survey, is housed in the collection of the Museum Zoologici Bogoriense, Bogor, Indonesia.

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Results

The evidence for the hybrid was the head of an adult male killed by a hunter in November 1982 in East Java near the village of Sumber Jambe about 150 km southeast of Surabaya. The common wild boar does not have warts, but in the putative hybrid a full complement of three pairs was present. These were smaller than normal for *verrucosus*, the infraocular being barely distinguishable and the mandibular extending less than 3 cm above the skin.

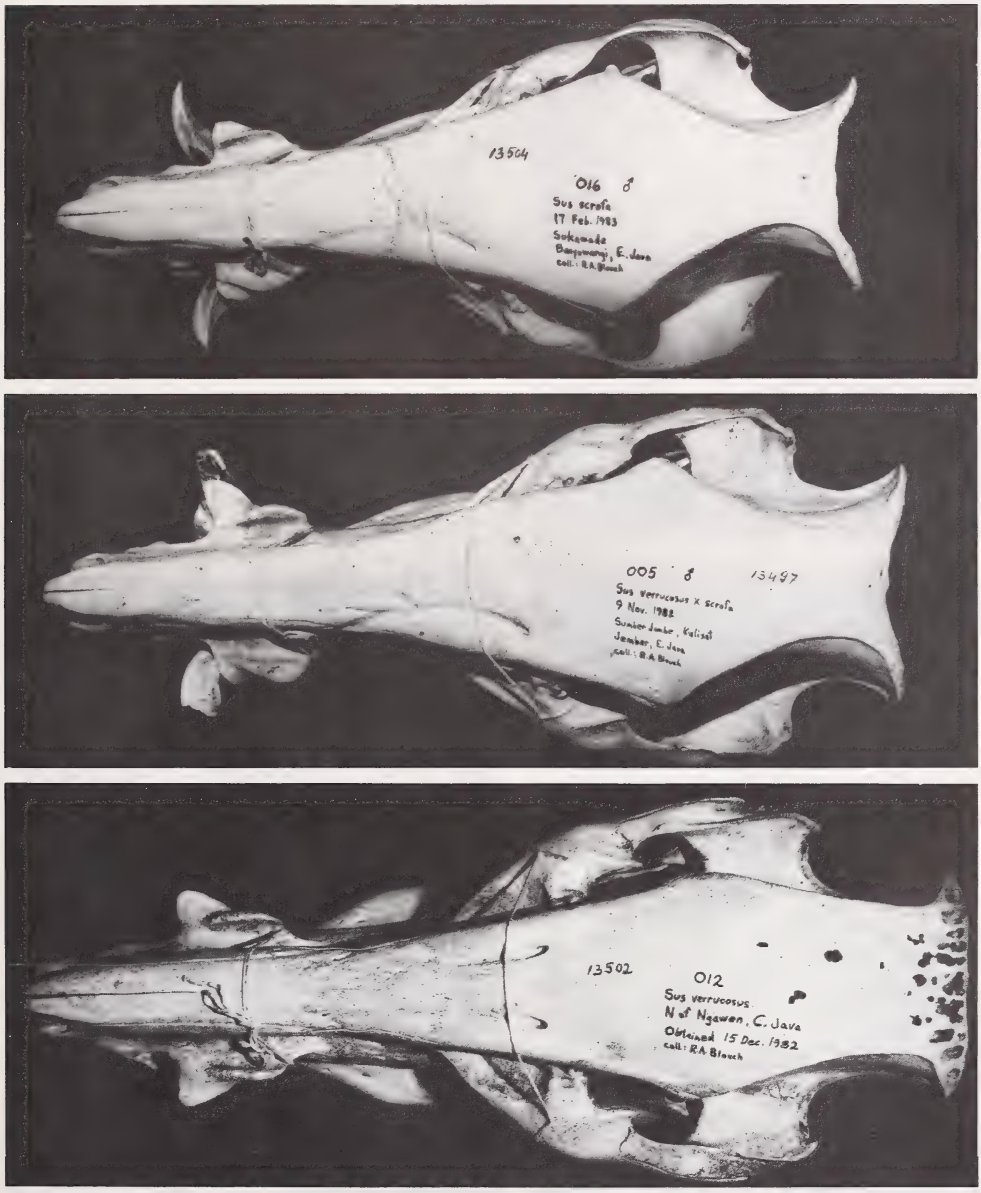
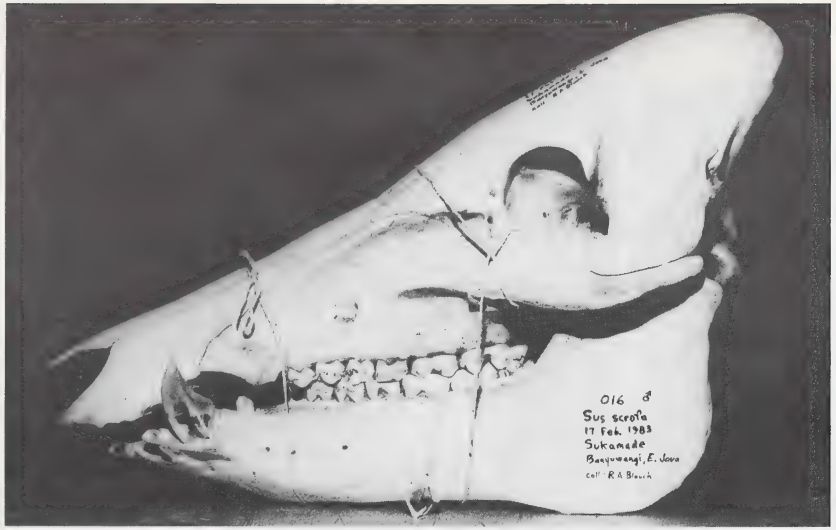
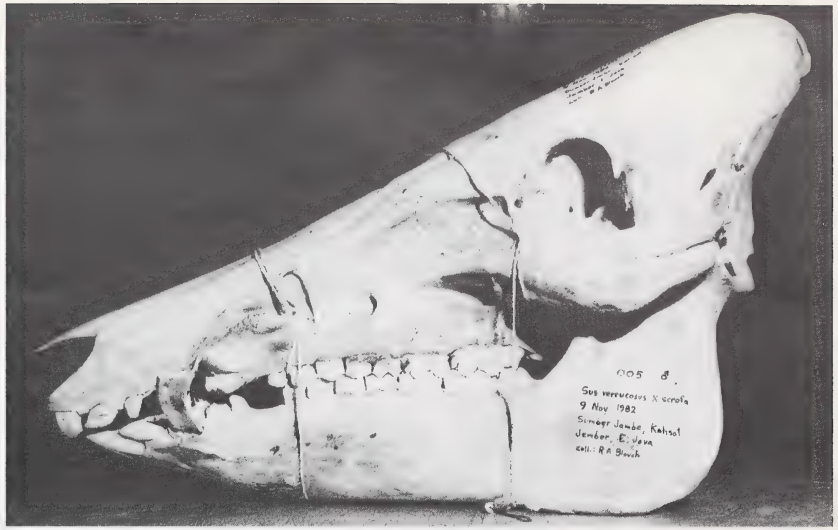


Fig. 1. Skulls of adult male pigs from Java, in lateral view. Above: *Sus scrofa vittatus,* MZB 016; centre: The putative hybrid, MZB 005; below: *Sus verrucosus verrucosus,* MZB 012





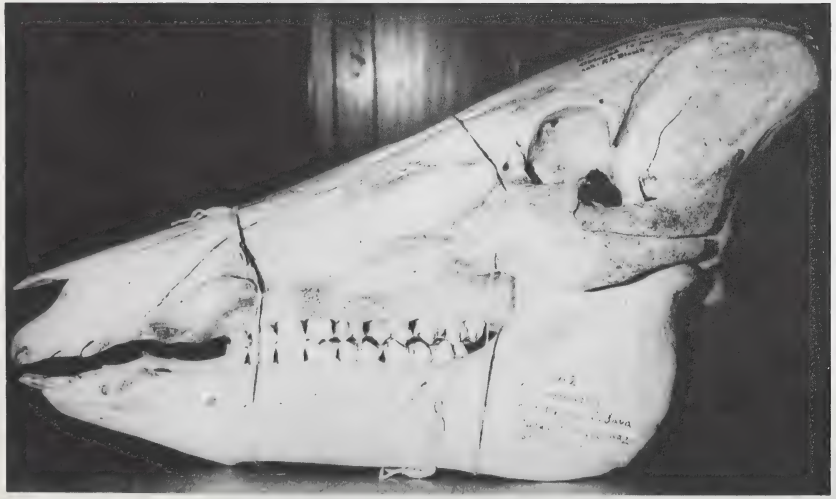


Fig. 2. Skulls of adult male pigs from Java, in dorsal view. *Above left: Sus scrofa vittatus,* MZB 016; *right:* The putative hybrid, MZB 005; *below: Sus verrucosus verrucosus,* MZB 012

The lower canines were typical of *scrofa*, having the posterior surfaces broader than the inferior surfaces. (Figs. 1, 2).

To test the skull's putative hybrid status further, a Discriminant Analysis was performed using seven measurements which were found by Groves (1981) to descriminate well between the two pigs sympatric on Java (Table 1). The Direct method (SPSS-X,

Table 1. **Skull measurements of *Sus scrofa vittatus, Sus verrucosus verrucosus* and the putative hybrid skull (in mm)**
Ranges are for fully adult males only

	Hybrid	*S. s. vittatus*	*S. v. verrucosus*
1 Greatest Skull Length	380	290–380 (21)	363–445 (27)
2 Condylobasal Length	328	267–335 (21)	321–369 (24)
3 Bizygomatic Width	150	121–155 (22)	154–189 (27)
4 Occipital Breadth	92	55–80 (22)	80–100 (27)
5 Nasal Length	188	134–187 (22)	185–222 (24)
6 Palate Length	230	170–231 (21)	229–270 (27)
7 Diastema Length	8	0–6 (15)	5–12 (14)

Measurement technique:
1 Tip of premaxillae to tips of occipital crest
2 Tip of premaxillae to posterior border of occipital condyles
3 Greatest span across zygomatic arches
5 Free ends of nasals to most posterior point on naso-frontal suture
4 Greatest width across occipital crest
6 Tip of premaxillae to most posterior point on margin of hard palate (lateral to choanal opening)
7 Length from posterior point on maxillary canine alveolus to most anterior point on anterior premolar alveolus

Discrimant program) was used, rather than Mahalanobis or Rao, as in this method the variables are not selected by rank according to their discriminating power, which tends, in a case such as this, to result in absolute size being the main discriminating factor. To reduce still further the chance of size being the main discriminant, two immature skulls of the larger-sized species, *Sus verrucosus*, were included in the sample for that species; and a few skulls of *Sus scrofa* from Sumatra, including unusually large specimens, were added to the *scrofa* sample which was otherwise composed of Java skulls. In the end, the following sample sizes were used: *Sus scorfa vittatus,* 14; *Sus verrucosus verrucosus*, 16.

The standardized Canonical Discriminant Function Coefficients were strongly positive for Palate Length, Bizygomatic Width, Diastema Length, and Nasal Length (in descending order), strongly negative for Condylobasal Length and fairly strongly negative for Occipital Breadth, and almost zero for Greatest Length. Thus, skulls scoring positively on the Discriminant Function would be those with long palate, diastema and nasals, and broad zygomata, compared to their size and occipital widths; those scoring negatively, the opposite. In the event (Fig. 3) all the *verrucosus* skulls except one scored positively; all the *scrofa* skulls, negatively. The single *verrucosus* skull scoring (just) on the negative side was not an unusually small sized one; a single *scrofa* skull, again not unusual as far as size was concerned, fell almost at zero. The putative hybrid fell exactly on the section point between the two species, with the same score as these two extreme individuals. We consider that this result strongly supports the hybrid status we have proposed for it.

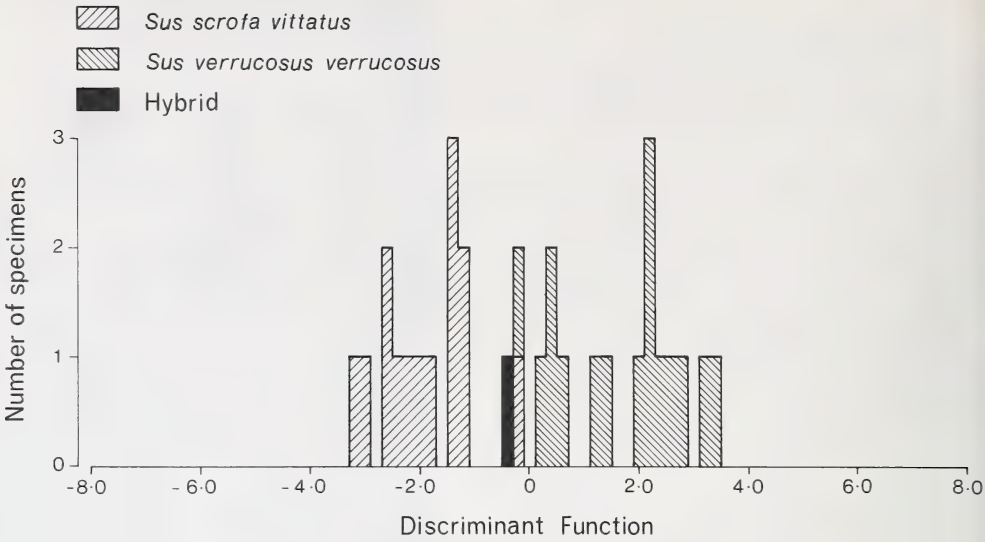


Fig. 3. Plot of Discriminant Function scores, showing intermediate status of the putative hybrid

Discussion

These results indicate that currently in East Java there is evidence of hybridization between free-living individuals of *scrofa* and *verrucosus*. Its frequency cannot be estimated from the single putative hybrid collected, but unconfirmed reports of hybrid wild pigs from two other locations in the province suggest this is more than an isolated instance. In the provinces of Central Java and West Java no evidence of hybridization has yet been found. This situation resembles "localized sympatric hybridization" as defined by Woodruff (1973), wherein highly localized hybridization occurs between two widely sympatric populations, often in association with habitat alteration and the breakdown of premating isolating mechanisms.

The habitat preferences of the two species differ, although they are by no means completely segregated in the wild (Blouch 1988). The Javan warty pig is found below about 800 m altitude and prefers extensive areas of secondary vegetation and grassland interspersed with clumps of forest; the common wild boar occurs at all altitudes in Java and inhabits dense forests as well as secondary vegetation. It seems that *scrofa* has a wider ecological amplitude than *verrucosus* and is generally better able to coexist with humans.

The putative hybrid from Sumber Jambe originated from about 650 m altitude on the western flank of Mt. Raung (3322 m). Here the distribution of the local *verrucosus* population is confined to a relatively narrow band around the sides of the volcano complex, delineated above by the altitudinal limit of the species and below by agricultural land with a moderate human population. In addition to occurring both above and below the elevations occupied by the Mt. Raung *verrucosus* population, *scrofa* also outnumbers the Javan warties even within their limited range (Blouch 1988).

Mayr (1963) mentioned the rarity of one parental species as an important factor contributing to the breakdown of isolating mechanisms. Individuals that occur beyond the solid range of their species often have difficulty in finding a conspecific mate and are apt to respond to individuals belonging to a different species. Such a situation appears to exist on Mt. Raung. Here, as natural vegetation was converted to agriculture on the lower slopes,

the *verrucosus* population was reduced and confined to a shrinking area at the upper edge of its altitudinal range. Under these conditions individual Javan warty pigs, particularly dispersing males, could easily become isolated from their conspecifics and, in the absence of their preferred mates, could breed with the available *scrofa*. Since *verrucosus* is the larger species, *scrofa* males would be unlikely to be able to prevent it.

In captivity, production of fertile offspring has been reported from interbreeding between *S. scrofa* and *S. barbatus*, a species closely related to *verrucosus* (Mohr 1960). Thus there is the possibility that introgressive hybridization between the two Javan wild pigs could occur, resulting in creation of a hybrid swarm. The extreme example of this is seen with the red wolf *(Canis rufus)* and the coyote *(C. latrans)* in North America where interbreeding was an important factor in the eventual disappearance from the wild of the red wolf (Nowak 1979). Although there is currently no evidence that hybridization is approaching levels which would threaten the *verrucosus* gene complex, a species having such a restricted range is especially vulnerable, and future monitoring of the situation is advisable.

Zusammenfassung

Natürliches Vorkommen von Suiden-Hybriden auf Java

Eine Hybride zwischen *Sus v. verrucosus* und *Sus scrofa vittatus* aus freier Wildbahn auf Java wurde über körperliche Merkmale und Schädelmaße identifiziert. Beide Arten kommen dort sympatrisch vor. Es wird angenommen, daß Habitatverminderung und die Seltenheit einer der Elternarten Umweltfaktoren darstellen, die zu Artbastardierungen führen könnten.

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The haemoglobins of wild cattle (Bovini Simpson, 1945)

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Abstract

The haemoglobins of nine bovines (anoa, Cape buffalo, European and American bisons, banteng, gaur, domestic yak, dwarf zebu, and taurine domestic cattle) were investigated by isoelectric focusing (and starch gel electrophoresis). The focusing patterns obtained were characteristic for each wild cattle species, with the exception of the two forms of the genus *Bison,* the haemoglobin of which could not be differentiated. Despite very small sample sizes, intraspecific variation of the red cell pigments were found in gaur, anoa and dwarf zebu. The genetic nature of this variability could be rendered likely by finding heterozygous individuals, and by densitometry which suggested dosage effects of genetic expression.

Introduction

In his description of a new haemoglobin polymorphism in Norwegian red cattle, Braend (1988) provided a short review of recent work about the population genetics of the bovine red cell pigment. So far, thirteen alleles of this protein have been detected in domestic taurine and zebu cattle. Haemoglobin alleles as genetic markers have served to reconstruct the phylogenetic descendance and breeding history of cattle races and population lines (Baker and Manwell 1980; Graml et al. 1986), as well as to analyse unknown pedigrees (e.g. Buschmann and Schmid 1968; Schleger and Soos 1967; Braend 1972). The haemoglobins of domesticated non-taurine bovines, such as the domestic water buffalo (Vella 1958), Bali cattle (Vella 1958; Namikawa and Widodo 1978), and the gayal or mithun (Winter et al. 1984) received less attention, with the exception of the Indian zebu (e.g. Naik et al. 1969; Manwell and Baker 1980). The study of wild bovine species has been largely neglected due to the difficulties implied in blood sampling, and only few studies are available on the haemoglobins of selected wild Bovinae, usually applying starch gel electrophoretic methods (Braend and Stormont 1963; Braend and Gasparski 1967; Davis and Read 1985; Davis et al. 1988; Hartl et al. 1988; Read et al. 1987). At the same time, the decrease in population numbers of several bovines in the wild and stricter laws concerning the trade in endangered wildlife imply that new blood is increasingly difficult to obtain for zoological gardens, and a better organization of the breeding management of the frequently very small captive populations is required for their long-term conservation. Stud-books and species management plans kept by zoos include those for the gaur *(Bos gaurus)*, the European bison *(Bison bonasus)*, and the wood bison *(B. bison athabascae)*. A stud-book for the anoa (*Bubalus depressicornis* ssp.) is being compiled (Seifert and Nötzold 1989). Major tasks for genetic research to support the captive breeding of wild cattle species include the necessity of finding genetic markers for the differentiation of the various described (or suggested) forms of anoa (which cannot be unambiguously determined by means of their phenotype), and an investigation of the alleged hybridization of captive bantends with either Bali or taurine cattle (Davis et al. 1988). Current efforts to bring founder animals of two critically endangered wild bovines into captivity, the

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kouprey *(Bos sauveli)* and the tamaraw *(Bubalus mindorensis)*, as a safeguard against extinction, increase the necessity of knowing genetic markers, in order to optimize breeding plans for the small initial populations.

For these purposes, blood samples were collected (and screened for their haemoglobins) from the wild cattle stock of the Berlin Zoological Gardens, when a transfer to new enclosures required the tranquilization of the whole population. Moreover, the fairly complete bovine collection of the Berlin Zoological Gardens permitted a comparison of electrophoretic patterns of bovine haemoglobins across the species boundaries.

Material and methods

Stabilized whole blood (EDTA) was mailed from Berlin Zoo to Heidelberg immediately after sample collection had been completed, and erythrocyte lysates could be frozen in liquid nitrogen within two days (and stored at −70 °C until analysis). The methods of preparation and purification of the haemolysates, and the details of isoelectric focusing and starch gel electrophoresis were essentially as described by Schreiber and Matern (1989). Prior to the runs, the haemoglobin concentrations of different haemolysates were brought to identical molarity by comparing their photometric extinctions at 410 nm, which corresponds to the maximum range of absorbance of taurine haemoglobin A. Isoelectric focusing was performed in thin (0.3 mm) polyacrylamide slab gels (4 % acrylamide, 0.16 % bis-acylamide, 5 % ampholines) polymerized on film foils (LKB). A LKB 2117 Multiphor II electrophoresis chamber, connected to a constant power supply (ECPS 3000/15, LKB), was used for electrophoretic separation. Approximately 5 µl of haemolysate (diluted 1:20) were applied to the gel, using a perforated rubber band as sample applicator. After a prerun of 10 minutes of 15 W (at maximal voltage and limiting current of 15 mA), focusing was performed at 20 W, 50 mA, and free voltage. When coloured isoelectric point markers (purchased from Promochem, Wesel) had reached their final position, the power was increased by 50 % to sharpen the bands. The ampholine gadients were tested after the runs by measuring the pH values of eluates from small successive gel portions cut from along the gradient. Stable and even ph-gradients in the banding region of haemoglobin were obtained by blending ampholines of different pH-ranges. The gels were photographed immediately after electrophoresis without artificial staining. For densitometric quantitation, a Chromoscan 3 (Joyce Loebl) was used. The scanning profiles are reproduced without any background correction.

The study of plasma proteins shortly mentioned was performed in an alkaline polyacrylamide gel as detailed by Schreiber and Matern (1989).

Results

Intraspecific variation

Individuals from nine bovines were included in the present investigation (see Table for their scientific names and specimen numbers). Three species exhibited more than one haemoglobin phenotype: three band patterns were descernible in the four gaurs (Fig. 1), and two in the three anoas (Fig. 2) and the two dwarf zebus.

Overview of the wild cattle species and specimen numbers sampled, and the number of haemoglobin phenotypes encountered

Species	Individuals sampled	Haemoglobin phenotypes
Lowland (?) anoa (*Bubalus depressicornis* ssp.)	3	2
Cape buffalo *(Synceros caffer)*	4	1
American bison *(Bison bison)*	3	1
European bison *(Bison bonasus)*	4	1
Banteng *(Bon javanicus)*	3	1
Gaurs *(Bos gaurus)*	4	3
Domestic yak (*Bos mutus* f. grunniens)	1	1
Dwarf zebu	2	2
Domestic taurine cattle (Buntvieh)	10	1

In the gaurs (Fig. 1a), the two less complex phenotypes are simultaneously present in two of the four individuals, suggesting a heterozygous condition. The densitometric analysis of the focusing patterns revealed that the bands of the presumably homozygous individuals contained approximately twice as much pigment (and hence proteid) each than the corresponding fractions of the heterozygous pattern (Fig. 1b). This suggests a simple gene dosage effect due to the expression of two codominant alleles. WINTER et al. (1984) suggested a haemoglobin polymorphism consisting of two alleles in the mithun, which is the domesticated form of the gaur. These authors included samples from three gaurs from Schönbrunn Zoo, Vienna, in their study, which lacked individual variation.

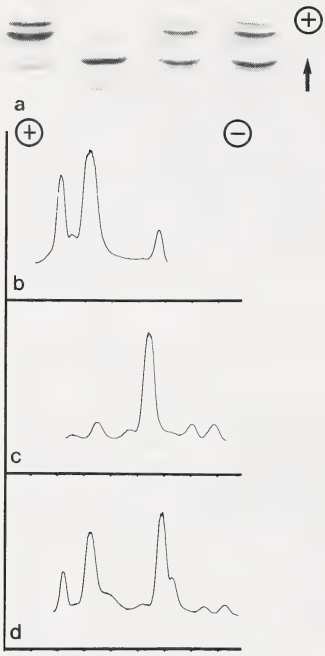

Fig. 1. Variability of gaur haemoglobin. a: Three phenotypes are evident after isoelectric focusing (pH 6–8, 4 % polyacrylamide). The first and second lanes depict the two alleles in homozygous patterns, while the remaining two patterns are interpreted as heterozygous. b–d: Densitograms of the gaur haemoglobins; b: Anodic allele (first lane in Fig. 1a), c: Cathodic allele (second lane in Fig. 1a), d: Suggested heterozygous pattern

In the three anoas, two animals showed a composed pattern which is interpreted as a heterozygous phenotype of two alleles (Fig. 2a). The anoa haemoglobin with faster mobility in starch gel, and the fraction with an isoelectric point shifted towards the acidic, is the only one found in the third specimen. An individual which is homozygous for the putative cathodal allele is lacking. The integrals of the densitometic peaks of the anoas again suggest a model of two codominant alleles with similar rates of genetic expression (Fig. 2b). The present study also suggested a postalbumin polymorphism in the Berlin anoas (which is not illustrated), but their transferrins are monomorphic.

One of the two dwarf zebus possessed a second haemoglobin (in addition to Hb A), which, on account of its close vicinity to Hb A, could have been Hb C (or the Hb X described by NAIK et al. 1969; review: SCHWELLNUS and GUÉRIN 1977). However, since the search in a small series of domestic cattle (Buntvieh) failed to discover Hb B which could have served as a reference marker, we cannot be certain as to the identity of the second, anodal dwarf zebu haemoglobin.

Neither the four Cape buffaloes, nor the three American and four European bisons, nor the three bantengs exhibited individual variation in the banding patterns of their haemoglobins; only one yak could be sampled.

The results concerning intraspecific variation must be interpreted against the back-

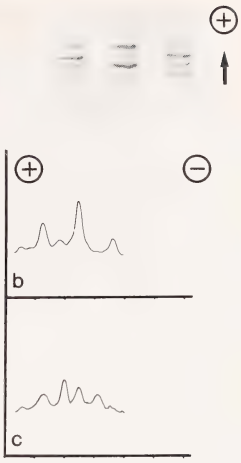

Fig. 2. Haemoglobin variation in the anoa. a: Both variants after focusing at pH 5–8 (4 % acrylamide). The first and third lanes are thought to show heterozygous haemoglobin patterns, and the central lane the anodic allele. b and c: Densitograms of these banding patterns; b: Anodic allele, c: Suggested heterozygous combination

ground of the small specimen numbers available. Furthermore, the lack of detailed data about the origin, and past breeding history of most individuals, renders certain conclusions difficult. Additional work about the bovine populations of other collections should follow soon, so that a more comprehensive understanding of the haemoglobin polymorphisms in wild cattle will emerge before the variation is lost in the tiny populations. Isoelectric focusing is suggested as the method of diagnosis, since it facilitates comparisons between the various, and unavoidably small, population samples available for study.

Comparative aspects

Most of the investigated cattle species (see Table) exhibited a distinctive haemoglobin band pattern both after isoelectric focusing (Fig. 3) and, albeit less conspicuously, starch gel electrophoresis (Fig. 4). The only exceptions were the American and European bisons, the

Fig. 3. Bovine haemoglobins after electrofocusing at pH 6–8 in a polyacrylamide gel (4 % acrylamide, 0.16 % bis). a: Domestic yak. b: European bison. c: American bison. d: Dwarf zebu. e: Banteng. f: Gaur (anodic allele, see Fig. 1). g: Cape buffalo. h: Anoa. (anodic allele, see Fig. 2). For explanation, see text

haemoglobins of which displayed identical electrophoretic mobilities and patterns (small differences in the focusing pattern of the minor haemoglobins seem possible, but this assumption requires confirmation in more specimens). Moreover, the cathodic allele in the

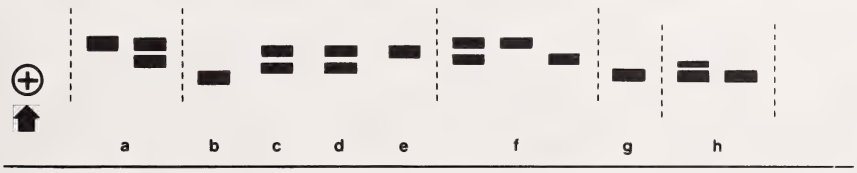

Fig. 4. Diagrammatic comparison of haemoglobin patterns from wild cattle after alkaline starch gel electrophoresis. a: Anoa. b: Cape buffalo. c: European bison. d: American bison. e: Banteng. f: Gaur. g: Taurine domestic cattle (haemoglobin A). h: Dwarf zebu

dwarf zebus (in starch gel) was indistinguishable from taurine Hb A. The high resolution properties of isoelectric focusing in thin-layer slab gels with species-specific patterns is noteworthy in view of the need to recognize the introgression of feral domestic cattle into some wild species. The resolution of the focused protein tetrameres into several bands indicates multiple haemoglobins, as in frequent in Artiodactyla (Butcher and Hawkey 1977). Figure 5 presents densitograms to facilitate interspecific comparisons of the protein fractions. The redundant peaks in the scanning profiles of the bisons and the yak might be

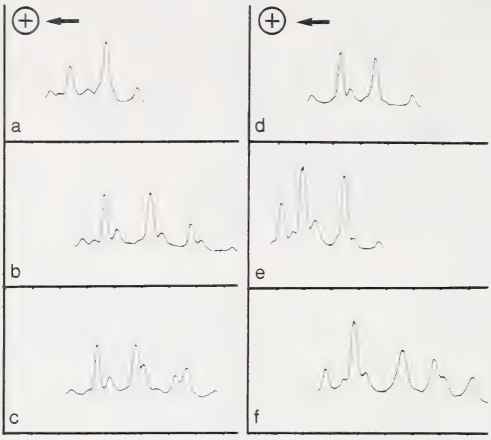

Fig. 5. Densitograms of focusing patterns of bovine haemoglobins (pH 6–8, 4% polyacrylamide). The anodic front is always oriented to the left. a: Anoa (anodic allele, see Fig. 2). b: Cape buffalo. c: European and American bisons. d: Banteng. e: Gaur (anodic allele, see Fig. 1). f: Domestic yak. Note: the bison and yak samples contained traces of methaemoglobin

due to the presence of partially oxidized haemoglobin: in these species, haemolytic plasma had to be used for electrophoresis instead of haemolysate, since the samples had been frozen prior to mailing (charged compounds of low-molecular masses, and salt present in blood plasma were removed by gel filtration in Sephadex columns, to prevent possible distortions of the electrophoretic results). Some of these minor bison haemoglobins grew weaker (or disappeared completely) after incubation of the proteins with 5 mM potassium cyanide for a few minutes (compare Bunn and Drysdale 1971). In starch gel, the bison haemoglobin was resolved into two bands. This must be due to gene duplication within the genome of each individual (and not to heterozygosity), because each specimen displayed the same pattern, and segregation was not observed. In ruminants, such multiple haemoglobins are frequently the result of a duplication of the alpha-globin chains. Like in the present study, no haemoglobin polymorphism could be detected in the 113 wild-living American bisons investigated by Braend and Stormont (1963), the largest population of any wild bovine species studied so far. The banding patterns obtained in that study (by starch gel electrophoresis) resembled those that were found in the Berlin bisons. Mazur et al. (1986) investigated one European bison from Munich Zoo which separated into two bands in a polyacrylamide gel. An identical pattern was observed with the Berlin samples when haemolytic plasma was separated in an alkaline polyacrylamide gel. Braend and Gasparski (1967) also resolved the haemoglobin of four European bisons into two bands (in starch gel). Butcher and Hawkey (1977) electrofocused the haemoglobins of one American and 6 European bisons; their micrograph does not show these details, but they listed two major bands (identical in both species), and 5 *(B. bison)* or 4–6 *(B. bonasus)* minor haemoglobins. The pattern of the single yak was complex. Lalthantluanga et al. (1985) described two variants in a sample of three (adult) yaks with the suggested heterozygous haemoglobin resolving into three, and the homozygous tetramere into two bands (in alkaline polyacrylamide gel electrophoresis). Yak occurs at elevated altitudes in the Central Asian mountain ranges, and it is capable of heavy work in an atmosphere of

very low oxygen pressure. Physiological adaptations can be expected to facilitate oxygen transport, and its supply to the tissues.

Discussion

Since the current efforts to compile a stud-book for the anoa, in order to improve the coordination of its conservation in captivity, is hampered by taxonomic uncertainties, the search for informative genetic markers is a priority in this small and phylogenetically interesting bovine (Seifert and Nötzold 1989): the breeding lines of its two morphologically distinctive subspecies, which are generally recognized, the lowland *(Bubalus d. depressicornis)* and the mountain anoa *(B. depressicornis quarlesi)*, cannot be separated merely on the basis of phenotypical evidence, such as body size, horn form, coat colour, and the texture of their fur. Indeed, the validity of (a) further subspecies has been suggested. The Berlin animals were at times thought to be mountain anoas, but this is now doubted. We preliminarily list them here as lowland anoas, according to recent karyotypic findings (Schreiber and Held, unpubl.). The occurrence of intermediate morphological types between both forms requires a comprehensive molecular investigation to improve the taxonomic basis for a sound conservation strategy. It remains unknown whether the existence of intermediate types is the result of a natural cline between two gradually differentiated subspecies, or is due to hybridization. Hardly anything has been published about the natural history of anoas in Sulawesi, and recent references treat the anoa forms as either ecologically separated subspecies, or, alternatively, suggest their true specific separation on account of a reported regional sympatric occurrence of both forms (e.g. Groves 1969; Honacki et al. 1982; review: Frädrich 1973; Seifert and Nötzold 1989).

Davis and Read (1985) screened the haemoglobins of 14 bantengs living in North American zoos. Other than in the present study, they found two haemoglobin variants (which they called B and C). Namikawa and Widodo (cited by Davis and Read 1985) found only one haemoglobin allele in bantengs sampled in Indonesia (the number of specimens is not cited). Davis and Read (1985) conclude from their finding that Hb A of domestic cattle was not present in American zoo bantengs, and that there were mutually exclusive alleles of acid phosphatase, that there is no reason to doubt the genetic purity of the American zoo population of *Bos javanicus* (against the view that it could contain cattle blood). Moreover, Davis et al. (1988) published a statistical model (on the basis of four blood proteins) suggesting a high probability that no significant introgression of taurine cattle have affected the North American zoo bantengs. The monomorphism of the Berlin bantengs coincides with the results by Namikawa and Widodo (although it appears from other publications that these authors do not always clearly differentiate between wild bantengs and Bali cattle). The bantengs in Berlin Zoo belong to the nominate subspecies *(Bos j. javanicus)*, and descend from founder specimens caught in Ujung Kulon National Park, Java. Ujung Kulon is one of the remote reserves in Java, and, lying in the moist western half of this island, mainly water buffaloes, and few Bali cattle are kept in the surroundings, thus minimizing the possibilities of hybridization. Unfortunately, the degree of inbreeding of the Berlin animals since their import in 1956 is unknown, and not all specimens could be included in the investigation. Follow-up studies in additional European zoo populations are desirable to determine if banteng haemoglobins are polymorphic. Given the insufficient knowledge of allele frequencies in Bali cattle, hybridization of zoo bantengs with their domestic conspecific will be very difficult to exclude. The Berlin bantengs display a strong sexual dimorphism in colour, and are therefore thought to be pure bred (Frädrich, pers. comm. 1989).

By now, the bisons are the best studied wild bovines in terms of protein elec-

trophoresis, and the results emerging are consistently showing very similar (or identical), multiple but monomorphic haemoglobins in both taxa. Both bisons experienced bottlenecks in their recent history, particularly the European form, which is reported to descend from 13 individuals (Slatis 1960; Pucek 1986). The investigation of one (or a few) loci prohibits taxonomic interpretations, and the small individual numbers investigated pose additional incertainties as to the homology of proteins (due to the possibility of the fixation of different alleles by founder effect). Still, the identity of the haemoglobin of both *Bison* forms is both remarkable and plausible, since they are closely related to each other and became separated only comparatively recently by the flooding of the Bering Strait. Indeed, there have been discussions by taxonomists as to their proper classification as distinct valid species (Bohlken 1967; review: Pucek 1986).

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Zusammenfassung

Isoelektrische Fokussierung von Rinderhämoglobinen

Die Hämoglobine von sechs Wildrindarten (Anoa, Kaffernbüffel, Wisent, Bison, Banteng, und Gaur) und drei domestizierten Rinderformen (Hausyak, Zwergzebu, und Bunvieh) wurden in Polyacrylamid-Dünnschichtgelen elektrofokussiert (sowie stärkegelelektrophoretisch aufgetrennt). Mit Ausnahme von identischen Proteinbanden bei Wisent und Bison und dem Übereinstimmen der kathodischen Hämoglobinallele von Zwergzebu und taurinem Hausrind konnten die Fokussierungsmuster aller Arten eindeutig differenziert werden. Bei Anoa, Gaur und Zwergzebu wurden Hämoglobinvarianten nachgewiesen. Das Auftreten (heterozygoter) Kombinationsmuster dieser Varianten legt ebenso die Annahme eines genetischen Polymorphismus mit zwei Allelen nahe wie eine quantitative densitometrische Auswertung der Proteinbanden. Die Möglichkeit der Anwendung dieser Befunde für die Erhaltungszucht der Arten wird angesprochen.

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WISSENSCHAFTLICHE KURZMITTEILUNG

Ein Nachweis der Zwergspitzmaus (*Sorex minutus* L., 1766) von der Insel Helgoland

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Eingang des Ms. 15. 1. 1990

Am 21. 10. 1987 erhielt ich (G. V.) von einem Kind (Marcia Gansekow) eine bereits verwesende Spitzmaus, die in einem Gebäude auf der Helgoländer Düne gefunden wurde. Die Bestimmung ergab (H. R.), daß es sich um die Zwergspitzmaus handelte. Körpermaße: KR-Länge 48 mm, Schw.-Länge 30 mm, HF-Länge 9 mm. Der Schädel war zerbrochen; am Unterkiefer wurden folgende Maße abgenommen (Meßstrecken nach Kahmann und Vesmanis 1974): Condylar-Länge 6,8 mm, untere Zahnreihen-Länge 6,0 mm, Coronar-Höhe 3,2 mm. Der Fund könnte ein weiterer Beleg dafür sein, daß – wenn auch sehr gelegentlich – Kleinsäuger, selbst Spitzmäuse, mit Faschinen oder anderen pflanzlichen Baumaterialien auf dem Wasserwege auf Inseln gelangen (s. dazu auch Ursin 1950; Goethe 1952; Krumbiegel 1955; v. Wijngaarden 1964; Schopf 1979; Hutterer 1981; v. Laar 1981).

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BUCHBESPRECHUNGEN

MUIZON, CH. DE.: **Les vertébrés fossiles de la formation Pisco (Pérou) III.** Les odontocètes (Cetacea, Mammalia) du Miocène. Trav. Inst. Franç. d'Etud. Andines 42 Paris: Éditions Recherche sur les Civilisations 1988. 244 S. FF 289,–. ISBN 2-86538-187-0

Im dritten Teil der Monographie über die fossilen Wirbeltiere der mio-pliozänen Pisco-Formation von Peru werden die Odontoceti des Miozäns beschrieben (vgl. Ref. über die Phociden [Teil 1] und die Zahnwale des Pliozäns [Teil 2] in Z. Säugetierkunde **47**, 1982, S. 124 und **51**, 1986, S. 326). Die Zahnwalreste (Zähne, Schädel, Periotica und auch postcraniale Elemente) stammen von mehreren Fundorten aus insgesamt fünf Horizonten des jüngeren Mittel-Miozäns bis zum jüngsten Miozän, welche einer Zeitspanne von etwa 10 Millionen Jahren entsprechen.

Die ersten Zahnwalreste hat bereits E. H. COLBERT 1944 als *Incacetus broggii* (ein Kentriodontide) beschrieben. Von den insgesamt 17 Taxa des Miozäns sind 7 spezifisch bestimmbar. Fünf davon sind neue Gattungen und Arten. *Lomacetus ginsburgi,* ein langschnauziger Phocoenide, wurde bereits 1986 vom Verf. bekannt gemacht. Demnach sind aus der miozänen Pisco-Formation folgende Zahnwalarten nachgewiesen:

Fam. Pontoporiidae: *Brachydelphis mazeasi* n.g.n.sp.; Fam. Phocoenidae: *Lomacetus ginsburgi* und *Australithax intermedia* n.g.n.sp.; Fam. Kentriodontidae: *Incacetus broggii, Atocetus iquensis* n.g.n.sp. und *Belonodelphis peruanus* n.g.n.sp.; Fam. Kogiidae: *Scaphokogia cochlearis* n.g.n.sp.

Scaphokogia ist als spezialisierte Form ein Vertreter einer eigenen Unterfamilie, *Brachydelphis* wird als kurzschnauziger Angehöriger der Pontoporiidae (U-Fam. Brachydelphininae) angesehen. Die Delphinoidea sind mit Kentriodontidae und Phocoenidae häufig nachgewiesen. Die ausführliche Beschreibung und Dokumentation (Fotos und Zeichnungen samt Rekonstruktionen von Schädeln) wird durch phylogenetische Schlußfolgerungen ergänzt: Die Platanistoidea (i. S. v. SIMPSON 1945) sind polyphyletisch, die Inoidea (i. S. v. MUIZON 1984) paraphyletisch. Auch die Monophylie der Kentriodontidae wird in Zweifel gezogen. Insgesamt ein wichtiger Baustein zur Cetaceenfauna des südamerikanischen Miozän.

E. THENIUS, Wien

REMANE, A., STORCH, V., WELCH, U.: **Kurzes Lehrbuch der Zoologie.** 6. neubearb. Aufl. Stuttgart, New York: Gustav Fischer Verlag 1989. 572 S., 283 Abb. DM 52,–. ISBN 3-437-20436-X

Das „Kurze Lehrbuch" liegt in seiner sechsten, von VOLKER STORCH und ULRICH WELSCH neu bearbeiteten Auflage vor und ist ein bemerkenswert inhaltsreiches Werk. Es ist auf völlig reflexfreiem Papier gedruckt und daher auch bei sehr intensiver Beleuchtung blendfrei zu lesen.

Mit einem klar formulierten historischen Abriß beginnt das Buch. Dieser Abschnitt schildert die Entwicklung der Zoologie von ARISTOTELES im vierten vorchristlichen Jahrhundert bis zur Aufsplitterung des Faches in viele Teildisziplinen in unserer Zeit. Im Haupttext wird dieser Zersplitterung erfreulicherweise entgegengewirkt. Den Autoren gelingt es trotz Schilderung vieler Einzelheiten, in diesen nicht zu „ertrinken", sondern das zoologische Grundwissen klar herauszuarbeiten.

Der erste Abschnitt behandelt die Allgemeine Zoologie und bietet zunächst eine Übersicht über die Zytologie (1. Kapitel), es folgt ein neu geschriebenes Kapitel über Gewebe und Gewebeflüssigkeiten. Die Kapitel 3 bis 11 beschäftigen sich mit Organsystemen und ihren Funktionen. Es folgt eine Darstellung der Individualentwicklung (Ontogenese) der Tiere, das anschließende 13. Kapitel behandelt die Vererbungslehre. Dann besprechen die Autoren die Evolution unter Berücksichtigung der Entstehung des Lebens auf der Erde, der Differenzierung echter Zellen (Eucyten) und der Evolution der Tiere. Je ein Kapitel über ökologische Probleme und die Verbreitung der Tiere auf der Erde schließen den allgemeinen Abschnitt des Lehrbuchs ab. Ungefähr das letzte Drittel des Buches beschäftigt sich mit der Systematischen Zoologie.

Der Inhalt des Textes ist außerordentlich befriedigend, doch hat der Rezensent einige Bemerkungen zum typographischen Erscheinungsbild zu machen: Stärkere Textgliederung durch Zwischenüberschriften und Einsatz von Kapitälchen oder Sperrung, sowie Hervorhebung von Kernbegriffen durch Fettdruck könnten die Lesbarkeit dieses gelungenen Lehrbuchs noch weiter steigern. Vor allem müßte aber ein Teil der Bilder überarbeitet werden. Es ist sehr schön, alte und bewährte Abbildungen in diesem modernen Lehrbuch wiederzufinden – dies sollte auch in den kommenden Auflagen der Fall sein. Durch „Zwischenüberschriften" in den aus Teilbildern zusammengestellten Abbildungen, d. h. beispielsweise durch Nennung der Taxa und ihre repräsentative Darstellung mit Tier-Umrissen, könnten viele Abbildungen übersichtlicher gestaltet werden. Einige *willkürlich* herausgegriffene Abbildungen, in denen derartige Verbesserungen vorgenommen werden könnten, sind die Nummern 70, 89, 91 oder 128. Durch „Zwischenüberschriften" in den Bildern könnte auch ein optisches „Ineinanderfließen" der Teilbilder (Abb. 141 h und i) vermieden werden.

Es fällt angenehm auf, daß die Autoren die Nutzung ihres Lehrbuchs durch Studenten im Auge

behielten. So werden im Literaturverzeichnis nicht nur gebundene Werke, sondern auch gute und preiswerte Taschenbücher genannt.

Es ist sicher, daß die sechste Auflage des Lehrbuchs von STORCH und WELSCH unter Studenten und Lehrenden wegen des klar formulierten Textes und der überlegten Stoffdarbietung viele zufriedene Leser gewinnen wird.

P. LANGER, Gießen

KINGDON, J.: **East African Mammals.** An Atlas of Evolution in Africa. Chicago: The University of Chicago Press. Vol. I: Introduction and Primates, 1971, US $ 40,25, ISBN 0-226-43718-3; Vol. IIA: Insectivores and Bats, 1974, US $ 37,00, ISBN 01-226-43719-1; Vol. IIB: Hares and Rodents, 1974, US $ 37,00, ISBN 0-226-43720-5; Vol. IIIA: Carnivores, 1977, US $ 43,25, ISBN 0-226-43721-3; Vol. IIIB: Large Mammals, 1979, US $ 43,25, ISBN 0-226-43722-1; Vol. IIIC: Bovids, 1982, US $ 37,00, ISBN 0-226-43724-8; Vol. IIID: Bovids, 1982, US $ 37,00, ISBN 0-226-43725-6

Diese dreibändige, aus 7 Lieferungen bestehende Darstellung über die Säugetiere Ostafrikas, die zwischen 1971 und 1982 publiziert worden ist, liegt jetzt vollständig als Paperback-Reprint zu einem verhältnismäßig erschwinglichen Preis vor: alle Bände zusammen kosten etwa US $ 270,00 gegenüber ungefähr US $ 650,00 für die Originalausgabe. Man kann daher hoffen, daß dieses Werk eine erheblich weitere Verbreitung als bisher finden wird.

Nach formalen Gesichtspunkten ist es hervorragend gegliedert mit diversen Hinweisen zur Stammesgeschichte, Verbreitung, Anatomie, Physiologie und Biologie für die einzelnen systematischen Einheiten. Jede Art wird ausführlich besprochen: dabei sind Volksnamen, Maße und Gewichte vorangestellt; die Darstellung ihrer Biologie nimmt breiten Raum ein unter Berücksichtigung vergleichender, ökologischer und evolutionärer Zusammenhänge. Hervorzuheben sind die textbegleitenden kunstvollen Zeichnungen, die über Verhaltenseigenarten – Körperhaltung, Bewegungsabläufe – Auskunft geben oder anatomische Sachverhalte wiedergeben, z. B. durch Darstellung von Skelett und Bezahnung sowie Muskel- und Organstudien. Verbreitungskarten sowie gelegentlich Graphiken und Tabellen runden die Einzelbeschreibungen ab.

Auf weitere Einzelheiten soll hier nicht eingegangen werden. Es sei auf die ausführliche Besprechung nach Erscheinen der Originalausgabe in dieser Zeitschrift (Bd. 48, S. 64, 1983) verwiesen.

D. HEINRICH, Kiel

GROTE, J. (Hrsg.): **Aktuelle Probleme der Atmungsphysiologie.** Funktionsanalyse biologischer Systeme Bd. 18. Stuttgart-New York: G. Fischer Verlag 1988. 283 S. DM 98,–. ISBN 3-437-30583-2

Der vorliegende Band faßt die Ergebnisse eines Symposiums zusammen, das aus Anlaß des 60. Geburtstages von Herrn Prof. Dr. Dr. THEWS im September 1986 in Mainz stattfand. Die Themenschwerpunkte entsprechen den Arbeitsgebieten der zahlreichen Schüler, Freunde und Kollegen des Jubilars. So werden neue Forschungsergebnisse zum Atemgastransport in der Lunge und im Gewebe vorgestellt und die zentralen und peripheren Regelungsmechanismen der Atmung diskutiert. In weiteren Beiträgen stehen pathophysiologische und sportphysiologische Aspekte im Vordergrund. Die Gesamtheit der einzelnen Arbeiten ergibt damit eine gute Übersicht über den gegenwärtigen Stand der Forschung auf dem vielseitigen Gebiet der Physiologie und Pathophysiologie der Atmung.

Es ist dem Herausgeber gelungen, die verschiedenen Berichte inhaltlich gut aufeinander abzustimmen. Kritisiert werden könnte lediglich, daß der Band nicht durchgehend in einer Sprache geschrieben wurde. Daß ein Buch mit einem deutschen Titel 14 deutschsprachige und 18 englischsprachige Beiträge enthält, wird sicher von den meisten Lesern aus dem deutschen Sprachraum akzeptiert werden – es stört jedoch, wenn in einem englischen Text Abbildungen mit deutscher und in einem deutschen Beitrag Abbildungen mit englischer Beschriftung erscheinen.

Das vorliegende Buch ist jedem zu empfehlen, der sich einen guten Überblick über den neuesten Wissenstand auf dem Gebiet der Physiologie des Gaswechsels verschaffen will. Es wird allerdings vorausgesetzt, daß der Leser mit den Grundproblemen der Atmungsphysiologie bereits vertraut ist.

W. WÜNNENBERG, Kiel

BENINDE, J.: **Zur Naturgeschichte des Rothirsches.** Reprint der Originalausgabe von 1937, mit einer Einführung von G. VOLQUARTS. Hamburg, Berlin: Verlag Paul Parey 1988. XI + 223 S., 29 Abb., 4 Karten, 1 Diagramm. Kart. DM 48,–. ISBN 3-490-22912-6

Obwohl es neuere Monographien über den Rothirsch gibt, wird im säugetierkundlichen und wildbiologischen Schrifttum immer wieder auf BENINDE's Studie zurückgegriffen, der sich nicht nur

theoretisches Wissen über den Rothirsch angeeignet hatte, sondern als Forstmann auch über reiche praktische Erfahrung mit diesem Wild verfügte.

Zweifellos kommt dem der Ökologie des Rothirsches gewidmeten Teil der Arbeit nach wie vor besondere Bedeutung zu. In diesem Kapitel wird, nach allgemeinen Erläuterungen zur Verbreitung, der Lebensraum des Rothirsches dargestellt unter Berücksichtigung von Klima, Vegetation und Landschaft. Beninde erkannte, daß diese genannten Faktoren, ferner die Größe des Lebensraumes und die Bestandsdichte in starkem Maße den Organismus, insbesondere die Körpergröße beeinflussen, und konnte das eindrucksvoll darlegen. Die übrigen Kapitel betreffen Paläontologie und Paläobiologie, Morphologie und Physiologie sowie Psychologie.

Es ist zu begrüßen, daß der Verlag Paul Parey dieses Werk nachgedruckt hat, das – schon längst vergriffen und schwer zugänglich – nun wieder einem breiten Leserkreis zur Verfügung steht. Abschließend sei G. Volquarts zitiert, der in seiner Einführung zu diesem Buch schreibt: „Es ist nicht veraltet, sondern auch heute beachtens- und lesenswert, gerade weil über das Rotwild, seine Ansprüche und seinen Lebensraum so lebhaft diskutiert wird." D. Heinrich, Kiel

Groves, C. P.: **A Theory of Human and Primate Evolution.** Oxford: Clarendon Press 1989. 375 pp. ISBN 0-19-857629-3

Der Verfasser – ein international bekannter Mammaloge – betrachtet die Evolution des Menschen nicht als Ergebnis von Mutationen und Selektion bzw. als Anagenese, sondern als gesetzmäßig gerichtete autonome Entwicklung, die unabhängig von der Umwelt verlaufen ist. Diese „neue" Evolutionstheorie entspricht der Nomogenese von Berg (1926) in etwas modifizierter und ausgearbeiteter Form.

Die Grundlage für die taxonomische Gliederung der Primaten bildet eine (mit etwas Vorsicht gebrauchte) kladistische Analyse.

Das Buch, das weder eine Einführung noch ein Lehrbuch („text-book") ist, gliedert sich in 8 Kapitel, von denen 3 allgemeinen Fragen der Taxonomie und Evolution gewidmet sind. Den Hauptteil bilden die Kapitel 4–7 (S. 64–297) mit einer ausführlichen taxonomischen Übersicht der Primaten, einschließlich des Menschen und seiner fossilen Vorkommen. Die Großgliederung erfolgt in Paromomyiformes (=Plesiadapiformes), Strepsirhini und Haplorhini; das madagassische Fingertier wird als eigene Infra-Ordnung (Chiromyiformes) klassifiziert. Als eigene Familien werden die Megaladapidae, Homunculidae, Aotidae, Callicebidae, Pitheciidae und Atelidae, Colobidae, Propliopithecidae, Proconsulidae und Dryopithecidae bewertet. Menschenaffen und Menschen sind als Hominidae mit zwei Unter-Familien (Ponginae und Homininae) klassifiziert.

Das Buch enthält eine Fülle von Daten und zahlreichen Abbildungen sowie Diskussionen über die Bewertung fossiler Hominiden, die für den speziell interessierten Leser sehr wertvoll sind. Nur einige taxonomische Bewertungen: *Paranthropus* = eigene Gattung; *Australopithecus afarensis* = paraphyletisch; *Afropithecus* und *Turkanapithecus* = keine Proconsulidae, sondern Hominidae; *Hemanthropus peii* = *Pongo*; der Ngandong-Mensch = *Homo erectus erectus*; Petralona- und Mauer-Mensch = *Homo sapiens heidelbergensis*; Steinheim-Mensch = *H. sapiens neanderthalensis* („early Neandertal-group").

Das abschließende Kapitel (Nr. 8) behandelt die morphologischen und ökologischen Aspekte der Menschwerdung. Dabei wird den gängigen Vorstellungen über die Bedeutung der Umwelt (Wald–Savanne; aufrechter Gang sowie Gehirnentwicklung und Werkzeugherstellung) die bereits genannte Nomogenese-Hypothese gegenübergestellt: „Endogenous genetic factors must play an enormous . . . role in human evolution; natural selection has an obvious role to play, but I believe more and more that the evidence allows it mainly a ‚fine-tuning' role, and that the course of evolution is determined for more by nomogenesis than by traditional adaptive mechanisms" (S. 321).

Ein ausführliches Literaturverzeichnis (S. 322–360) und ein Index (Autoren- und Sachverzeichnis) ergänzen das Buch. Auch wenn im Literaturverzeichnis sogar nicht-englische Zitate enthalten sind, so vermißt man u. a. Literatur über Prädisposition (= „exaptation"), Neotenie und Fetalisation. Ein Buch, das sicher seine Leser finden wird. E. Thenius, Wien

Boessneck, J.: **Die Tierwelt des Alten Ägypten, untersucht anhand kulturgeschichtlicher und zoologischer Quellen.** München: C. H. Beck Verlag 1988. 197 S., 275 Abb., DM 88,–. ISBN 3 406 33365 6

Auf der Grundlage kulturhistorischer (bildlicher) Zeugnisse und naturgeschichtlicher Quellen (Knochenfunde) entwirft der Verfasser ein Bild von der Tierwelt des Alten Ägypten, das sich vielfältiger und schillernder kaum denken läßt. Die Zahl der auf den Abbildungen (allerdings nicht immer eindeutig) erkennbaren und anhand von Knochenfunden und Mumien bestimmbarer Tierarten ist groß. Neben weit über hundert vorwiegend summarisch erwähnten Wirbellosen, etwa 40 Fisch-, drei Amphibien-, 15 Reptilien- und rund 155 Vogelarten werden auch rund 70 Säugetierspezies namentlich genannt, die das Land am Nil jahrtausendelang besiedelten und in vielfältiger Beziehung zum

Menschen standen (als Fleischlieferant, Rohstoffquelle, Speiseopfer, Last- und Zugtier, Jagdobjekt, Heim- und Spieltier, Machtsymbol). Es war nicht das Ziel des Verfassers (und es konnte es auch nicht sein), die Tierarten in zoologisch-systematischer Reihenfolge zu behandeln. Die Darstellung orientiert sich vielmehr an historischen und kulturgeschichtlichen Kategorien. Einem der Geographie und Topographie Ägyptens gewidmeten Kapitel schließen sich folgende Abschnitte an: Die vorgeschichtliche Zeit vom Neolithikum bis zum Beginn der dynastischen Zeit, Frühdynastisches, Wild und Wüste, im Papyrusdickicht, Einfuhren aus Süd und Ost, Palast- und Lieblingstiere, Kleinsäuger und die echten Haustiere in der dynastischen Zeit. Danach folgen Abschnitte, die sich mit Tiergruppen befassen: Die Vogelwelt, Reptilien und Amphibien, Fische, Schnecken, Muscheln und Tintenfische, Gliederfüßer. Zwischengeschaltet ist ein Abschnitt über die Tiermumien. Ein Schlußwort, zahlreiche Anmerkungen und ein umfangreiches Literaturverzeichnis beschließen den etwa zwei Drittel des Buchumfanges ausmachenden Textteil, der eine unverzichtbare Ergänzung durch zahlreiche altägyptische bildliche und figürliche Darstellungen erfährt. Die Bildquellen unterstreichen, daß die Haustiere mit Rind, Schaf, Ziege, Schwein, Esel, Pferd, Maultier, Maulesel, Hund, Katze und Gans wie auch die sogenannten halbdomestizierten Arten (manche Gazellen und Antilopen, die Streifenhyäne [?]) im Alten Ägypten wichtige Wirtschafts- und Kultobjekte waren. Auch viele wildlebende Arten spielten eine große Rolle, wie den Jagdszenen auf Säugetiere und Vögel und den Fischfang darstellende Bilder entnommen werden kann. Eine besonders ergiebige Quelle zur Erforschung der altägyptischen Tierwelt stellen die mumifizierten und die in Gräbern mit beigesetzten Tiere dar. Das vorliegende Buch wendet sich mit Sicherheit nicht nur an die Ägyptologen, die die Erforschung der Tier- und Pflanzenwelt des Alten Ägypten bislang nur wohlwollend unterstützt haben. Es wurde auch für jene geschrieben, die sich mit vor- und frühgeschichtlichen Haustieren befassen. Auch diejenigen werden es mit Gewinn zur Hand nehmen, deren Interesse auf zoogeographischem Gebiet angesiedelt sind. Es enthält eine Fülle oft sehr ins Detail gehender Informationen, die aus vielen Quellen gespeist werden, wie dem über 450 Titel umfassenden Literaturverzeichnis zu entnehmen ist. Zum Schluß zwei kritische Anmerkungen: Da in dem vorliegenden Buch sehr viele Tierarten erwähnt werden (auch wiederholt erwähnt werden), wäre ein Arten-Index dem leichteren Auffinden dienlich gewesen. Und: der mit der altägyptischen Geschichte nicht Vertraute vermißt eine Zeittafel, aus der ersichtlich ist, wann und wie lange eine kulturgeschichtliche Periode oder Dynastie bestanden hat. Diese Anmerkungen schmälern nicht die Leistungen des Autors, der nach kritischem Studium der zoologischen und kulturgeschichtlichen Quellen ein Buch vorgelegt hat, das unsere Kenntnisse über die vor- und frühgeschichtliche Tierwelt des östlichen Mittelmeergebietes erweitert und als beispielhafter Beitrag in das archäologische Schrifttum Eingang finden wird.

H. Reichstein, Kiel

NATUR + RECHT

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Z. Säugetierkunde 55 (1990) 4, 217–288

Hugo Stünzi / Eugen Weiss

Allgemeine Pathologie für Tierärzte und Studierende der Tiermedizin

8., neubearbeitete Auflage

Herausgegeben von Prof. Dr. Dr. h.c. Hugo Stünzi, ehem. Direktor des Instituts für Veterinärpathologie der Universität Zürich, Thalwil, Schweiz, und Prof. Dr. Eugen Weiss, Direktor des Instituts für Veterinär-Pathologie der Justus-Liebig-Universität Gießen. Mit Beiträgen von Prof. Dr. K. Dämmrich, Berlin, Dr. E. Karbe, Wuppertal, Prof. Dr. H. Loppnow, Berlin, Prof. Dr. DDr. h.c. A. Mayr, München, Prof. Dr. J. Pohlenz, Hannover, Prof. Dr. A. Pospischil, Zürich, Prof. Dr. J. von Sandersleben, München, Prof. Dr. Th. Schließer, Gießen, Prof. Dr. Dr. h.c. H. Stünzi, Thalwil, Prof. Dr. E. Weiss, Gießen.

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Die allgemeine Pathologie beschäftigt sich mit der Erforschung der Grundphänomene, dem Erkennen allgemeiner Gesetzmäßigkeiten bei den Krankheitserscheinungen und den sich daraus ergebenden Folgerungen, die artübergreifend auf alle Haustiere anwendbar sind. Sie ermöglicht eine Interpretation und Wertung der mit den einzelnen Krankheiten einhergehenden pathologischen Merkmale und damit die Diagnose und Therapie. Dieses vor fünfzig Jahren von Prof. Dr. Dr. h.c. Walter Frei begründete Lehrbuch hat sich seitdem bereits in sieben Auflagen bewährt. Es wurde von Auflage zu Auflage den neuen Erkenntnissen und Fortschritten der Human- und Veterinärmedizin, insbesondere der Pathologie, angepaßt. Prädestiniert durch ihre Tätigkeit als Forscher und Lehrer in Pathologie und Mikrobiologie haben Herausgeber und Autoren der nun vorliegenden 8., neubearbeiteten Auflage wiederum ihre vielschichtigen Beobachtungen und Erfahrungen eingebracht und ein umfassendes und modernes Werk geschaffen, das sowohl den Anforderungen der Studierenden an ein didaktisch modernes Lehrbuch als auch den Bedürfnissen der bereits im Beruf stehenden Tierärzte nach einer Gesamtdarstellung der allgemeinen Pathologie in jeder Weise entspricht.

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Records of young hedgehogs (*Erinaceus europaeus* L.) in a private garden

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Institute of Zoology and Zoophysiology, University of Aarhus, Aarhus, Denmark

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Abstract

Young hedgehogs attracted to a private, suburban garden by supplementary food were recorded over 6 successive autumns. Individual recognition at a distance was made possible using a code pelage marking system. Altogether 55 young were initially recorded in September (n = 6), October (n = 36) and November (n = 13), the earliest and latest occurrence being September 8 and December 6, respectively. Most hedgehogs paid frequent visits to the feeding area during some weeks, though 10 individuals only appeared once.

The initial body weight was mainly less than 500 g. Most young grew heavier during the recorded period. The growth rate averaged 7 g/day in 35 specimens initially captured during September–October, whereas 7 specimens marked during November 1–14 gained 2 g/day. The pre hibernation body weight was 400–800 g. 44 young individuals retired during November.

The spring recapture rate was 47–100 %, averaging 69 %. It is claimed that the food supplemented to the natural diet was not crucial for winter survival. Further, it is maintained that previous estimates of winter mortality in young hedgehogs has been overrated, and there is hardly any indication of low survival rate among young deriving from late born litters.

Introduction

For any hibernator, a critical minimum body weight preceding the cold season is necessary to make winter survival possible. Speculations on this matter may lead to the hypothesis that late born young frequently have particular problems in attaining a sufficient size to prevent winter starvation.

Regarding the hedgehog (*Erinaceus europaeus* L.), Morris (1984) maintains that young from late litters are unlikely to survive the winter. Mortality of young during the cold season has been estimated to be 70 % to 80 % (Hoeck 1987 citing Esser 1984; Obermaier 1985). According to published measurements, however, these winter losses are much less (Kristiansson 1984).

The minimum body weight required for hedgehogs when entering hibernation has been discussed in a public debate in Germany. It was maintained that small young should be actively searched for, rescued and housed from September–October onwards (Nowak 1977; Bestajovsky 1979). Optimal body weight prior to hibernation was claimed to be 700–900 g (Jungbluth 1978; Bestajovsky 1979). Recent scientific literature, however, concludes the German figures to be over-generous, referring to estimates of minimum body weight necessary for winter survival (Morris 1984).

The present capture-mark-recapture study is concerned with the measured body weight increase of young hedgehogs prior to hibernation and their fate during the winter.

Material and methods

Daily records of hedgehogs visiting a private garden (1300 m^2) were kept for 8 summers, i.e. from July 1977 to November 1984. The garden, established 70 years ago, is situated in the town of Ølstykke,

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located 30 km to the west of Copenhagen. The town (12 500 inhabitants), is mainly a residential area with some 3500 private houses surrounded by gardens.

Food which attracted the hedgehogs was regularly put out towards sunset every day. The standard diet offered mainly consisted of light bread (400 g) and boiled milk (1 l) with wheat flower to which margarine and sugar were added in minor quantities.

The hedgehogs were fed in a specially constructed food shelter (40 cm high) roofed with two window frames in oblique positions. The broad rectangular entrance (10 × 100 cm) to the shelter was provided with a lamp (12 V, 15 W) and a photo relay. When animals passed by, the broken light beam activated an alarm bell in the private residence. An electric lamp (40 W) illuminated the feeding area. The electric installations facilitated observation of the visiting hedgehogs when records were made i.e. usually between sunset and midnight.

Body weight was the sole criterion used to separate young from adults. During an individual's initial visit to the feeding area, it was permanently marked and sexed and body weight (± 5 g) was ascertained. Over the subsequent period weighing was repeated at irregular intervals, when possible. In order to secure observations of known individuals, a code pelage marking system was used (cf. Parkes 1975; Berthoud 1982). This marking involved clipping the spines from no more than two locations and subsequently painting these areas white or yellow. Thus the hedgehogs could be recognized at a distance without hampering their normal activities.

The observation period mainly comprised the seven months May to November, with occasional records made in April and December. This paper deals only with the young hedgehogs appearing during the six successive autumns 1977 to 1982. The remaining records are dealt with elsewhere.

Results

Altogether 55 young were recorded. The number occurring per year varied between 3 and 19, with highest numbers appearing during two successive autumns (Table 1). The male sex predominated.

The initial records of young were mainly made after the period when numerous adults came into the garden (Fig. 1). All young appeared within the period September 8 to November 29, viz. 6, 36, and 13 in the three months respectively. Ten specimens paid a sole visit to the feeding area, while the great majority appeared more or less regularly during some period of time, i.e. up to more than two months (Fig. 2). In all years there was a peak period for records from early October and the subsequent six weeks. In 1979 when the feeding season was extended, records of 4 young were made in early December. The majority of multiply recorded hedgehogs (n = 45) paid frequent visits to the feeding area, i.e. that they were seen in the garden on most days during their recorded period (Figs. 2 and 3).

Initial body weight tended to be below 500 g and was frequently less than 400 g (Fig. 4). Most young (37) grew heavier during the recorded period, while only 5 specimens were found to lose body weight. The available weight records show that 42 young were weighed twice or more (Table 2). During September and October all but one of the

Table 1. Sex and spring recapture rate of 55 young hedgehogs recorded during six successive autumns

Year	Records			Spring recapture rate	
	N	Sex		N	%
		♀♀	♂♂		
1977	7	2	5	7	100.0
1978	19	9	10	9	47.4
1979	16	6	10	12	75.0
1980	6	3	3	4	66.7
1981	4	1	3	4	100.0
1982	3	2	1	2	66.7
Sum	55	23	32	38	69.1

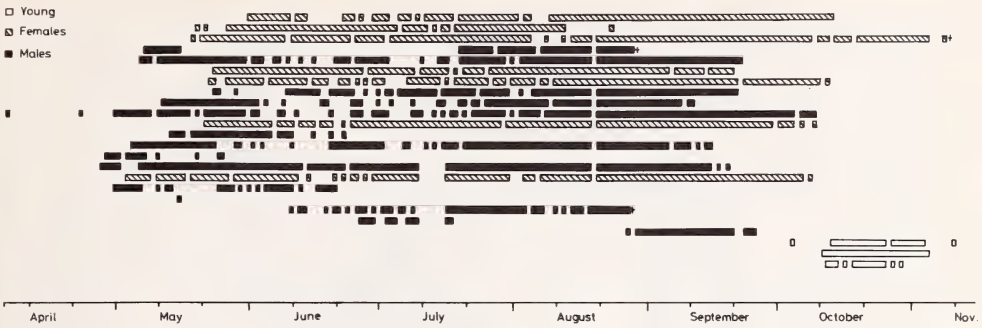

Fig. 1. Records of 21 adult (7 ♀♀, 14 ♂♂) and 3 young hedgehogs in the private garden during the summer of 1982

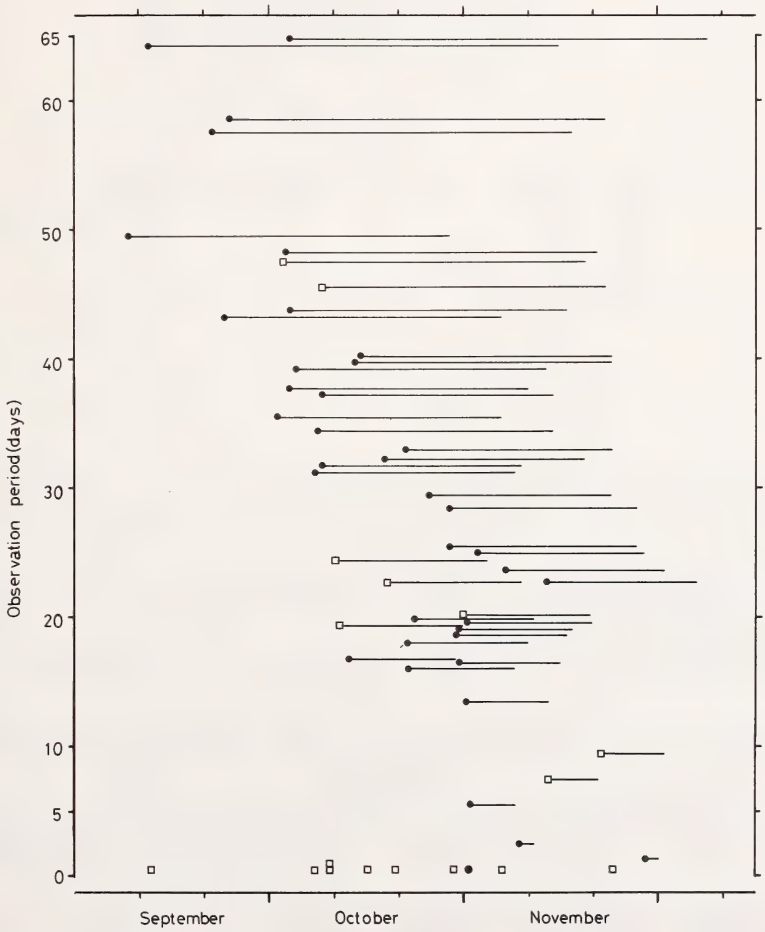

Fig. 2. The day of initial capture of 55 young hedgehogs is either marked with a black circle (specimens re-seen after the winter) or with an open square (non-recaptures in following years). Horizontal lines indicate periods during which 45 multiply recorded specimens were observed

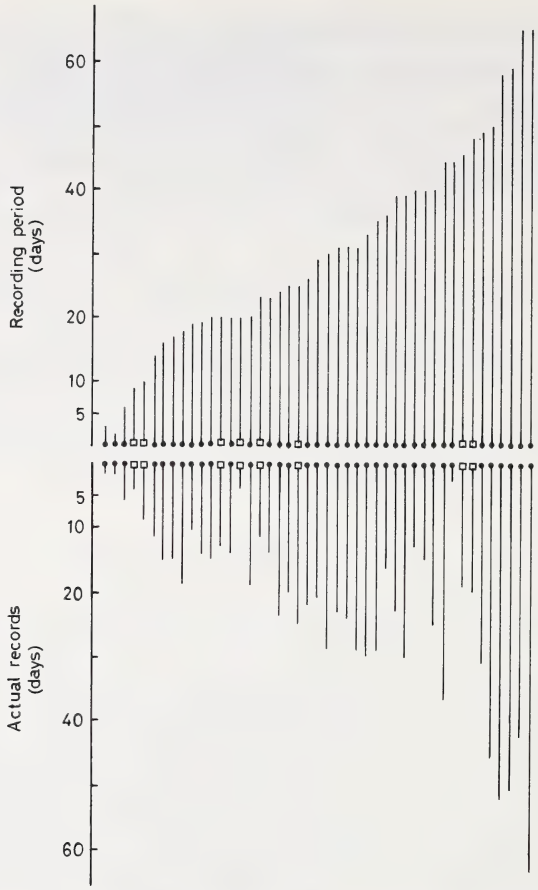

Fig. 3. Vertical lines depict periods through which 45 multiply recorded young were observed, and the number of days each individual was actually seen, respectively. Circles and squares: cf. Fig. 2

multiply weighed specimens increased their body weight. The growth rate of these young averaged 7 g per day. Among those being recorded for the first time in November, the majority hardly put on weight (Fig. 4).

The final body weight, mainly reached during November, amounted to 400–800 g in most young (Fig. 5, Tab. 2). Among 17 young with no further observations in subsequent

Table 2. **The overall increase in body weight of young hedgehogs during autumn, and their spring recapture rate**

N	Dates of weighings		Days of growth (in total)	Body weight increase (g)		Fate after winter	
	initial	final		In total	Individual (average/day)	Recaptured	Unknown
5	8–25 IX	21 X–18 XI	258	1850	7.0	5	0
30	2–30 X	23 X–1 XII	819	6075	7.4	25	5
7	1–14 XI	19 XI–3 XII	114	190	1.7	4	3
13	7 IX–29 XI	none				4	9

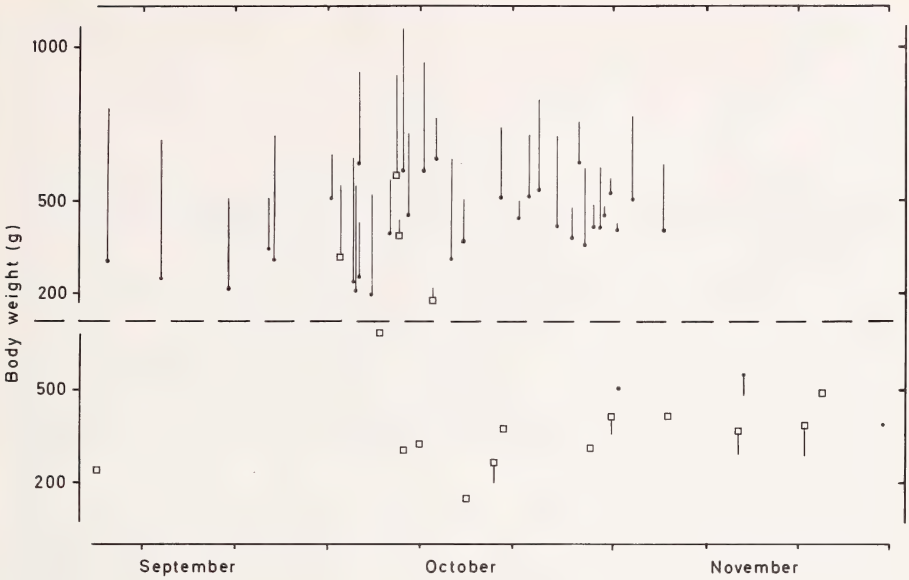

Fig. 4. Circles and squares (cf. Fig. 2) depict date of initial weighing and body weight for 55 young hedgehogs. Vertical lines indicate weight increase (upper) or weight loss (lower) for 42 multiply weighed specimens

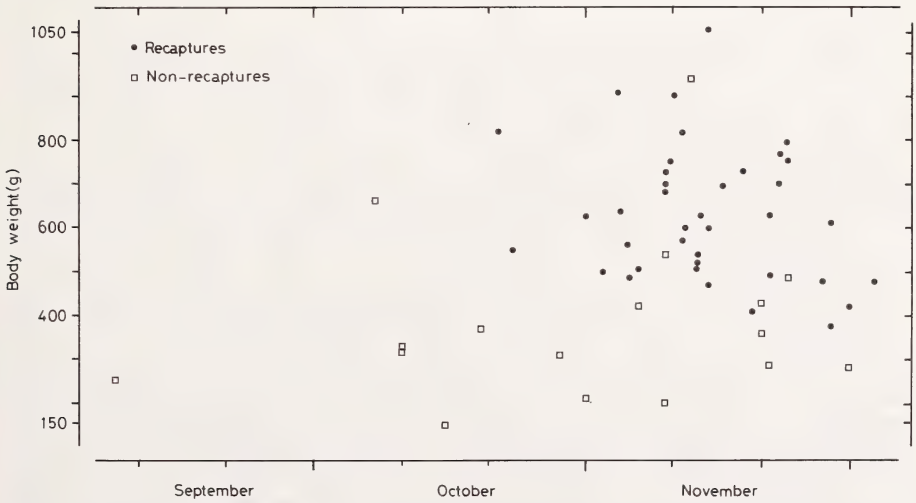

Fig. 5. Circles and squares (cf. Fig. 2) illustrate the latest recorded body weights, during autumn for 55 young hedgehogs (cf. Fig. 4 and Tab. 2)

years, 12 finally weighed between 150 and 380 g. The latest recorded body weights of the remainder were from 380 to 1050 g, their spring recapture rate was 90 %.

On average, 69 % of the young marked in the autumn were recaptured in the following spring. The recapture rate, however, varied greatly between years (Tab. 1). The majority of young (44) was found to enter hibernation during November (Fig. 2). The earliest and

latest final records of overwintering specimens were made on October 21 and December 3, respectively.

Discussion

None of the young recorded appeared with their mother and thus evidently were non-suckling. Furthermore, this indicates that females regularly visiting the garden (cf. Fig. 1) did not bring their offspring to the feeding area. There was no correlation between the number of regularly appearing adult females and the number of young visiting the garden in various years. Hence, it is believed that the number of young recorded (Tab. 1) was casual and did not reflect real fluctuations in juvenile production.

Most young appeared after the period when numerous adult hedgehogs had been recorded (Figs. 1 and 2). During the weeks (Sept. 7–Dec. 3) when the young visited the garden, very few initial records of adults were made, and the period when most young appeared was in succession with the records of adults. Furthermore the body weights alone clearly separated the two age categories.

The initial body weights of young varied from 150 to 700 g (Fig. 4). 29 individuals weighed 400 g or less, mainly below 345 g. This indicates that most initial captures represented recently weaned litters (Morris 1966). As the young remain with their mother for at least 40 days, the 21 earliest captures (Sept. 7–Oct. 10) are most probably from litters born before September 1., i.e. the period when most Danish hedgehogs breed (Walhovd 1984). Another 12 young, initially captured after October 10 with weights of 500–700 g, most likely also derive from the peak breeding season. The remaining 22 young, appearing October 11–November 29, were most probably from late born litters as their initial body weight was only 150–490 g.

Among the 45 young appearing over 2–11 weeks (Fig. 2), 38 were actually seen in the garden on most days, i.e. a frequency of occurrence of more than 50 %. Among these, 11 in particular were feeding often. They had been recorded as non-visiting for 0–5 days only. Obviously, gardens where supplementary food is regularly available attract some hedgehogs more strongly than others (cf. Fig. 1).

On the other hand 12 young were seen at the feeding bowls only once or twice. Furthermore, a few visited the garden on occasional evenings over several weeks (Fig. 3). For instance, no. 19 appeared only on 3 nights during September 24–November 6. These infrequently appearing hedgehogs apparently were not addicted to supplementary food and probably relied mainly on natural food items.

The measured postweaning development varied widely (Fig. 4). Among those young increasing their body weight, 13 put on 290–520 g. The recorded frequency of occurrence at the feeding site for these hedgehogs averaged 80 % and the food supply may have contributed to the enhanced condition of some young (Morris 1985). The natural diet is probably more crucial for winter survival than is supplementary food which alone proved to be an unsuccessful pre hibernation forage among confined young leading to high winter losses (Walhovd 1978). It is most likely, therefore, that the offered food supplemented the natural diet and did not replace it. However, during November when most young retired for the winter (Fig. 2), frequent cool and occasional frosty nights probably reduced the activity of invertebrate life and hedgehogs may have depended more heavily on other sources of food.

Those young losing or hardly gaining weight mainly appeared from mid-October onwards. Their initial size was mostly below 400 g and thus they are likely to have derived from the latest born litters (Walhovd 1984). Cold nights probably affected the foraging activity of these small young more severely than larger individuals (Walhovd 1975).

Postnatal growth of hedgehogs has been studied in a limited number of young raised in

captivity (Herter 1938; Morris 1967; Król 1985). The data available are mainly from the suckling period.

In 10 cases investigated, however, the rapid growth initiated during the lactation period proved to continue after weaning when the young attained body weights of 700–1200 g within 100 days (Herter 1938; Król 1985). Thus, all the young recorded in the garden were probably in the fast-growing phase of their development (Fig. 4). The initial growth of 6 monitored specimens (Król 1985) was 6–8 g/day, which is in accordance with the average daily increase in body weight during September–October of 35 young in the present study (Tab. 2). It should be noted, however, that the growth rate among those putting on weight, varied widely. For example, no. 101 increased by 350 g during October 11–November 2, while no. 66 gained only 230 g during October 4–December 1 despite having visited the feeding bowls on at least 40 nights. The much reduced growth or weight loss of 7 young recorded during November (Fig. 4) may partly be due to frequent near-zero temperatures causing moderate or no surface activity of earthworms (Edwards and Lofty 1976), the most strongly selected prey item of hedgehogs (Wroot 1985).

Measurements of adult and sub-adult home range sizes are plentiful (Parkes 1975; Berthoud 1982; Reeves 1982; Kristiansson 1984; Boitani and Reggiani 1984; Morris 1988) while, to the author's knowledge, movements of recently weaned young hedgehogs never have been monitored. In the present study, captures of numerous young specimens in some years (Tab. 1) makes it likely that they derived from various litters born in different gardens of the town. Frequent occurrence of great variation in body size among initially captured young on successive days suggests that the feeding bowls were discovered fortuitously by solitary living young that may have travelled considerable distances (Morris 1988).

Final records of multiply captured young were made mainly during November, with a few even during December, which is in accordance with other experimental work (Walhovd 1978). However, the previous inclusion of November in the "hedgehog winter" (Walhovd 1975) should be modified. Rather, this month is a period when some young continue natural foraging and gain weight.

After a period of mainly rapid growth, the final body weight of multiple captured animals was roughly 400–800 g (Fig. 4). Thus in Denmark, most young hedgehogs are probably not fully grown before hibernation which seems to contrast with the conditions in England (Morris 1977). The moderate growth or even loss in weight of some young was partly due to their initial late appearance and small size.

The final body weight in autumn of the young recorded to hibernate successfully mainly exceeded 400 g which is in accordance with previous estimates (Morris 1984). These young mostly retired during November after a period of rapid growth (Figs. 2 and 4).

Previous observations indicated a high winter mortality among small, juvenile hedgehogs (Walhovd 1975, 1978). This trend has not been confirmed in the present study, as 69 % were recaptured after their first hibernation season (Tab. 1). Additional young may have overwintered successfully since they were not of particularly small size as compared to others (Fig. 4). These probably derived from distantly born litters which apparently foraged elsewhere, like some recaptured specimens (Fig. 3). The young either losing weight or growing very slowly, however, are likely to have succumbed early in the winter (Fig. 4). A few others from the young missed in spring may have been lost by road accidents since a high road mortality rate was ascertained among the adults recorded in the same garden.

The present study illustrates that trends found during previous experimental work (Walhovd 1978) do not fully reflect the natural hibernation success of young hedgehogs in Denmark. Among the 22 recorded young estimated to have been derived from late born litters, 13 (60 %) were recaptured in spring, and even some more may have hibernated

successfully as already justified. Also, it is possible that previous estimates of winter mortality in young hedgehogs from other sources (e.g. Morris 1984; Hoeck 1987) may have been overrated. In conclusion, the present study supports the view that the hedgehog is extremely well adapted to winter life.

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Zusammenfassung

Untersuchungen über junge Igel (Erinaceus europaeus L.) in einem privaten Garten

Durch Futter in einem Villengarten angelockte junge Igel wurden jeweils im Herbst in 6 aufeinanderfolgenden Jahren untersucht. Die individuelle Beobachtung aus der Ferne war durch Markierung der Stachelkleider möglich. Insgesamt wurden 55 Junge gezählt, 6 im September, 36 im Oktober und 13 im November; die ersten Jungen wurden am 8. September, und die letzten am 6. Dezember gesichtet. Die meisten Igel suchten die Futterstelle mehrmals während einiger Wochen auf, 10 wurden nur einmal beobachtet.

Das Anfangsgewicht betrug meistens weniger als 500 g. Die meisten Jungen wurden während der Untersuchungsperiode schwerer. Die Wachstumsrate wurde an 35 Igeln, die in den Monaten September und Oktober gefangen wurden, mit 7 g pro Tag ermittelt. Sieben zwischen dem 1. und 14. November markierte Tiere nahmen nur 2 g pro Tag zu. Das Gewicht vor dem Winterschlaf lag meist zwischen 400 und 800 g. 44 Junge zogen sich im Laufe des Novembers zurück.

Die Rate der im Frühjahr wiedergefangenen Jungigel lag zwischen 47 und 100 %, im Durchschnitt aller Jahre bei 69 %. Die Befunde sprechen dafür, daß die Zufütterung nicht ausschlaggebend für das Überleben im Winter war. Frühere Schätzungen der Wintersterblichkeit junger Igel scheinen zu hoch zu sein. Es gibt kaum Anzeichen für eine niedrige Überlebensrate junger Igel der letztgeborenen Würfe.

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Spermatogenesis in Schlieffen's bat, *Nycticeius schlieffenii* (Chiroptera: Vespertilionidae)

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Abstract

Investigated spermatogenesis in Schlieffen's bat, *Nycticeius schlieffenii*. Schlieffen's bat exhibits an extended spermatogenesis with the various cell stages easily identifiable in the sequence of events. From late September to October there is only a slow increase in type A spermatogonia while proliferating type B5 spermatogonia predominate in the seminiferous tubules during the period November–February. December–February can be regarded as the time when change over to primary spermatocytes occurs, although at a very slow rate. March is an active month when all spermatogenic cells can be found. Spermatozoa only start to accumulate in the epididymes in April (mid-autumn), i.e. about three months before the first copulations.

Introduction

Schlieffen's bat is one of the smaller South African bat species, with males averaging 4.7 g and females 5.1 g (Rautenbach 1982). It has a distinct easterly distribution within South Africa, but is one of the more common species of bat within its range. *N. schlieffenii* does not migrate seasonally, as they were collected from the same area throughout the year. During the day this species roosts at sites such as hollows in trees (Verschuren 1957) or rock crevices (Pienaar et al. 1987).

Copulation commences during June and the females have spermatozoa in the uterine horns from then until the end of August when ovulation occurs. These bats are seasonally monoestrous with births occurring during November (van der Merwe and Rautenbach 1987).

The purpose of this study is to describe the male reproductive cycle.

Material and methods

Specimens of Schlieffen's bat were collected at monthly intervals with macro-mistnets (Rautenbach 1985) at several localities at Pafuri (22° 25′ S; 31° 12′ E) in the northern region of the Kruger National Park, Eastern Transvaal lowveld. At least five male specimens were collected for each calender month. At the field laboratory the bats were sacrificed with technical ether. The testes were dissected out and preserved in Bouin's fixative for histological examination. Following routine paraffin wax embedding, all testes and epididymes were sectioned at 5 μm, mounted and stained with Ehrlich's haematoxylin and eosin.

Results

During August (end of winter) the testes were inactive with no sign of spermatogenic activity in the seminiferous tubules although some spermatozoa from the previous cycle could still be found in the caudae epididymides. The relatively large lumina of the

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seminiferous tubules were lined with a compact layer of Sertoli cells and only occasional stem spermatogonia could be found against the basal lamina (fig. 1). At this stage the Leydig cells were small and compact.

The first signs of spermatogenic activity were towards the end of September when a few spermatogonia undergoing mitosis were found. Within the epididymes only cell debris could be found with no sign of spermatozoa. Leydig cells were similar in appearance to the previous month.

Towards the end of October (mid-spring) the number of type A spermatogonia had increased considerably resulting in the formation of a near complete layer of cells on the inside of the basal lamina (fig. 2). A few type B spermatogonia were also present. The Leydig cells were still compact.

By the end of November a marked increase in type B spermatogonia was found (fig. 3) while the Leydig cells were still compact.

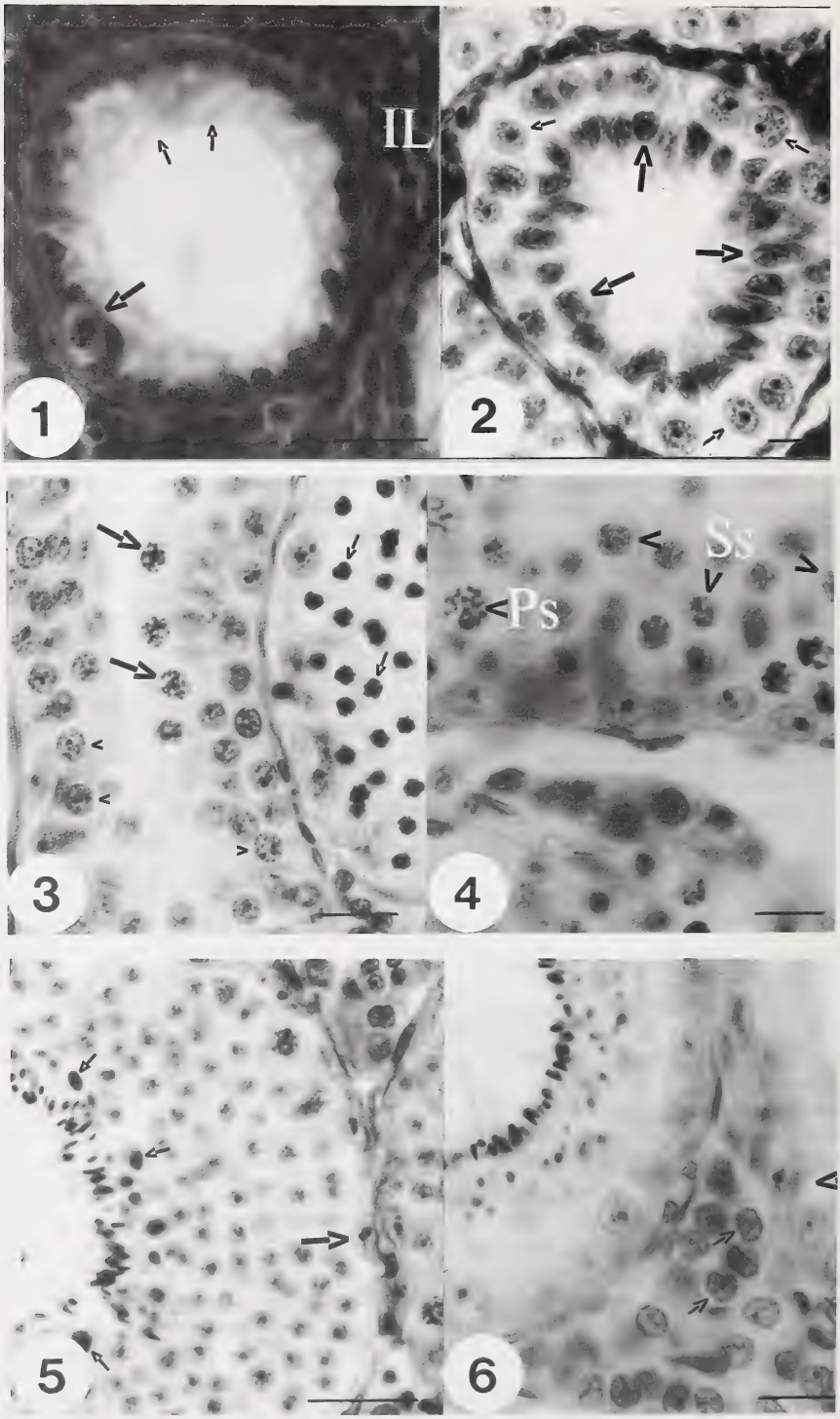
Towards the end of December resting type A spermatogonia, many type B spermatogonia (both undergoing mitosis) and a few primary spermatocytes could be found (fig. 3). The Leydig cells were still compact although some showed vacuoles.

From January towards the end of February the Leydig cells were swollen with vacuoles. During both months many type B spermatogonia were present, the majority had completed the mitotic divisions, and were in the growth phase. Primary spermatocytes were still scarce at the end of January, but they were more numerous towards the end of February.

From the end of February to the end of March nearly all stages in germ cell development could be found including the short lived secondary spermatocytes (fig. 4). During this period spermatozoa were still absent from the epididymes. Primary spermatocytes and spermatids were abundant with large numbers of type B spermatogonia in the growth phase. The first time that spermatids with condensed nuclei (undergoing spermiogenesis) and a few spermatozoa were found, was at the end of March and beginning of April. At this stage, however, they were still very scarce.

Towards the end of April primary spermatocytes and spermatids with condensed nuclei were abundant. Numerous spermatozoa were attached to Sertoli cells or accumulated in the lumina of the seminiferous tubules while large numbers were also present in the epididymes. There was a drastic decrease in the number of type B spermatogonia while against the basal lamina only a few resting type A spermatogonia could be found (fig. 5). At this stage spermiogenesis was actively taking place with cytoplasmic residual bodies very conspicuous (fig. 5). The caudae epididymides were crowded with spermatozoa while the Leydig cells were swollen.

Between May and June (beginning of winter) the situation changed with a decrease in the number of primary spermatocytes. Spermatids and spermatozoa were abundant and the caudae epididymides crowded with spermatozoa. A few individual type B spermatogonia were still present. Spermiogenesis was continuing with an abundance of cytoplasmic residual bodies. Although the majority of Leydig cells were still swollen, some of them were becoming compact with darker, more unevenly shaped nuclei. At the end of July the seminiferous tubules were exhausted. With the exception of some spermatozoa, and a few resting (stem) type A spermatogonia, no spermatogenic cells could be found (fig. 6). In the majority of seminiferous tubules the nuclei of the Sertoli cells were lying against the basal lamina with no spermatogenic cells present except individual stem type A spermatogonia. The caudae epididymides were still crowded with spermatozoa. Most of the Leydig cells were compact with shrunken nuclei of uneven dimensions.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Discussion

Vespertilionid bats in the temperate zones generally copulate during autumn with the spermatozoa being stored in the female uterus until the following spring when ovulation and fertilization occur (Racey and Potts 1970). In the subtropical climate of Pafuri, copulation in Schlieffen's bat is initiated towards the end of June (early winter) with the first ovulations towards the end of winter (Van der Merwe and Rautenbach 1987). Spermatozoa were found in the uterus of females collected at the end of June and end of July while four out of five females collected at the end of August were pregnant (Van der Merwe and Rautenbach 1987). At present it is not certain whether the females store spermatozoa during June till August, as males have epididymes crowded with spermatozoa during the same period. At present it appears likely that frequent copulations occur during this period.

From the same study area van der Merwe and Rautenbach (1989) have also found prolonged spermatogenesis in the lesser yellow house bat *Scotophilus borbonicus*. The present study agrees with their findings that spermatocytogenesis is extended but not spermiogenesis.

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Zusammenfassung

Spermatogenese bei Schlieffens Fledermaus, Nycticeius schlieffenii (Chiroptera: Vespertilionidae)

Untersucht wurde die Spermatogenese bei Schlieffens Fledermaus *Nycticeius schlieffenii*. Vom späten September bis Oktober vermehren sich Typ-A-Spermatogenien nur langsam, während von November bis Februar Typ-B-Spermatogenien, die sich rasch vermehren, in den Hodentubuli vorherrschen. Von Dezember bis Februar beginnt – allerdings in geringem Umfang – die Bildung primärer Spermatozyten. Im Monat März sind alle spermatogenen Zellen vorhanden, und im April (in der Mitte des Südherbstes), d. h. etwa drei Monate vor den ersten Paarungen, beginnen sich Spermatozoen im Nebenhoden anzuhäufen.

Fig. 1–6. Sections through parts of testes collected during different months. *Fig. 1.* At the end of August showing a seminiferous tubule lined with Sertoli cells (small arrows) and one stem spermatogonium (large arrow). The interstitial cells of Leydig (IL) can be seen between the tubules. Bar = 25 µm. – *Fig. 2.* At the end of October showing a seminiferous tubule with type A spermatogonia (small arrows) against the basal lamina and the nuclei of the Sertoli cells (large arrows) on their inside. Bar = 25 µm. – *Fig. 3.* At the end of December showing numerous type B spermatogonia undergoing mitosis (small arrows), with mature type B spermatogonia (arrow heads) and a few primary spermatocytes (large arrows). Bar = 25 µm. – *Fig. 4.* At the end of March showing primary spermatocytes (Ps) and secondary spermatocytes (Ss). Bar = 10 µm. – *Fig. 5.* At the end of April showing a seminiferous tubule with masses of spermatozoa and of cytoplasmic residual bodies (small arrows). Against the basal lamina a few resting type A spermatogonia can be seen (large arrow). Bar = 25 µm. – *Fig. 6.* At the end of July showing one seminiferous tubule with numerous spermatozoa and cytoplasmic residual bodies while the adjacent one is empty with only Sertoli cells (large arrow) lining the basement lamina. The uneven shape of the nuclei of the interstitial cells of Leydig is indicated with small arrows. Bar = 15 µm

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Notes on the breeding biology, gular gland and roost habits of *Molossus sinaloae* (Chiroptera, Molossidae)

By P. D. Heideman, K. R. Erickson and J. B. Bowles

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Abstract

Greasy, odoriferous marks on the dorsum of female *Molossus sinaloae* are apparently produced through contact with the male gular gland. Male gular glands were largest and produced the most secretory material around the time of parturition, when most marks were observed and when lacerations on males were also most frequently observed. The ecological and evolutionary significance of marking is not yet clear.

Introduction

A distinctive morphological feature of many species of molossid bats is the gular gland, a conspicuous structure on the throat (Werner and Lay 1963; Horst 1966; Quay 1970) that produces an oily, musky-smelling exudate. Although the gland is usually apparent only in males, it has been reported to be equally well developed in males and females of a few molossid species (Quay 1970). Horst (1966), observed seasonal fluctuations in male gland size corresponding to breeding cycles in *Molossus rufus* (= *M. ater*), and observed involution of the gland following castration; on the basis of these observations he speculated that the gland's secretions had some role in reproduction. Rasweiler (1987) noted that female *Molossus ater* often nuzzled the gland of a male prior to mating, and (1988) that males sometimes rubbed their gland against females.

In this paper we present observations on the gular gland of male *Molossus sinaloae,* presented in the context of the breeding biology and roosting habits of this species.

Materials and methods

Data were collected in or near Merida, Yucatan, Mexico during ten field seasons (March–May 1971, 1973, 1975; June 1978, May–August 1979; September–November 1976, 1977, 1979, 1983; December–January 1979–1980). The two principal study sites after 1976 were a large, clay-tiled, suburban dwelling (La Casa, in the north-central part of the city) and a man-made pond at a country club on the northern edge of the city, approximately three km NNW of La Casa (Campestre-see Birney et al. 1974, for a detailed description). *Molossus sinaloae* and two other molossids (*M. ater* and *Eumops bonariensis*) roosted in roof crevices at La Casa; Campestre was a *M. sinaloae* drinking site.

Bats were captured in mist nets; bats were either tattooed (Bonaccorso and Smythe 1972) or tagged with numbered, color-coded plastic wing bands (males banded on the left forearm, females on the right forearm). For each capture we recorded: capture time, band or tatoo number (if present), sex, age (neonate, juvenile, subadult, and adult; based upon weight and epiphyseal fusion), forearm length (recorded only once/year/individual), weight, gular gland size (small, medium, or large) and gular gland condition in males (no secretions present, low level of secretion, copious secretions), teat size and lactational status, and presence/absence of embryos by palpation (detectable only during late gestation). Beginning in 1979, we recorded the presence/absence and position of wounds and distinct areas of fur that appeared moistened with light oil (see below). For La Casa captures, precise capture location was also recorded.

Activity within roosts was observed using headlamps and binoculars and, from December 1979 to January 1980, a nightviewing scope. Observations were limited to events at the front of the openings created by the overlapping (pantiled) roof tiles.

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Voucher specimens of *M. sinaloae* were deposited at the Biology Department, Central College, Pella, Iowa; The Museum, Texas Tech University, Lubbock, Texas; and Departamento de Conservación, Mexico D. F., Mexico.

Rainfall and other climatic data were recorded daily at the study site during our field seasons. Annual rainfall data for Merida were taken from the world-wide Airfield Summary, National Climate Data Center, Ashville, NC, USA.

Statistical analyses were carried out using the MIDAS computer program of the University of Michigan Terminal System (Fox and Guire 1976), using the SPSS statistical package on a PDP-11 computer at Central College, or on a hand calculator following Sokal and Rohlf (1981).

Results

Only one *Molossus sinaloae* roost area was found in the Merida area, at which bats roosted in gaps beneath ornamental roof tiles on a house (La Casa) (Bowles et al. in press). The roosts were 2.5 to 15 m high and ranged from fairly shallow (< 0.15 m) to moderately deep (0.5–1.0 m).

There was a daytime mean of 20 adult bats present at La Casa during 1979–1980, the year for which our data are most complete. However, typically at least twice that many individuals were captured at La Casa during any given field season, and in one year, 1977, 106 individuals were captured there (vegetation blocked access to some roosts in later years, causing a decline in the number of bats present). There was substantial variation in population size both within and between years. One of the 106 bats banded at La Casa in 1977 was recaptured there six years later, and 15 recaptures (approximately 8 % of the total marked with bands) were made two or more years after marking. However, many bats left La Casa roosts for periods ranging from a single night to many nights, indicating that fidelity to this single roost site was rather low.

Females in this population gave birth to single young synchronously in June in 1978 and again in 1979 (Bowles et al. in press). Macroscopically visible embryos (conceptus size of 2–3 mm) first appeared in March or April (Fig. 1). The very small number of reproductively inactive females (10 of 358) captured either at La Casa or at Campestre during this period suggests that female *M. sinaloae* are reproductively active during their first year. The duration of lactation is approximately 6–8 weeks (Bowles et al. in press). None of 40 adult females captured from September 1979 through January 1980 had embryos detectable by palpation, nor were any lactating. Thus, *M. sinaloae* in the Merida area apparently have a single annual birth period (Bowles et al. in press).

The size and secretory activity of the gular gland in *M. sinaloae* varied through the year, with a high proportion of males with large, copiously secreting glands in May–August (193 of 207 secreting), and a lower proportion in September–January (12 of 25 secreting) (G-test for independence, $G = 29.81$, $df = 1$, $P < 0.0001$; Sokal and Rohlf 1981).

The secretions from the gular gland were highly distinctive: greasy or oily in appearance, viscous, and with a very characteristic and pungent odor. The skin and hair around a copiously secreting gland became matted and greasily moist or wet in appearance. A slight pressure on the edges of the gland often produced a drop of the gland's contents.

In June of 1979 we noted that many captured bats had patches of dorsal fur that appeared matted and wet or greasy. These patches smelled very strongly of the distinctive odor of male gular glands, suggesting that bats might somehow be smeared with the glands during incidental or intentional contact with secreting males. On 23 July 1979, a male within a roost was observed apparently sniffing or searching the dorsum of a female, after which he climbed atop her dorsum and pressed closely against her in a manner which must have forced the gular gland into contact with the inter-scapular region of the female. During this time, the female's 4 week-old pup was roosting within a few cm of the pair. It was not possible to determine if the adult pair was mating, but if the male's gular gland was secreting copiously (as was true of over 90 % of all males at that time) his actions would

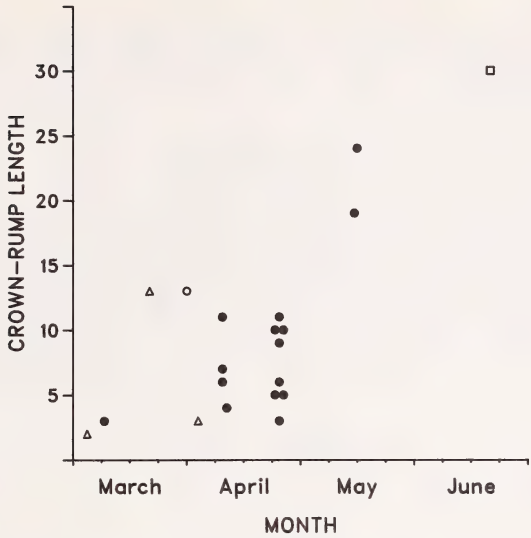

Fig. 1. Crown-rump length of embryos of autopsied female *Molossus sinaloae* from May through June (1971–1978). (Open circle = 1971 [from Bowles 1973]; open square = 1973 [from Birney et al. 1974]; solid circles = 1975; open triangles = 1978.)

have resulted in the smearing of fluid from the gland onto the female. Also in July 1979, an unmarked female was observed to enter a roost containing a secreting male and leave with a dorsal mark. On six subsequent occasions, freshly marked females were captured exiting a roost within 20 minutes of the departure of a secreting male. These observations suggest that the viscous, pungent exudate from the gular gland of adult male *M. sinaloae* is used to mark other individuals.

The marks were oily, strong-smelling spot(s) covering up to four cm^2 of the fur of the marked bat, usually on the dorsum. Marked females that were released immediately after capture and then recaptured within 30 minutes always retained a mark (although it was often less extensive in area, suggesting that marks may have dried or been incompletely groomed away), but on those recaptured after longer intervals marks were often dried, with the fur matted, or were no longer apparent. All but two of the 134 marked animals we captured were females ($P < 0.01$; binomial test, Sokal and Rohlf 1981), and none were neonates or juveniles. Marked females were more common from June to August (132 marked of 236 adult females examined) than from September to January (2 of 29 females) (G-test for independence, $G = 28.94$, $df = 1$, $P < 0.0001$). It is possible that the gland may also be used to mark other substrates (e.g. roosts), but we never found marks near or within roosts at La Casa.

Injuries were uncommon on *M. sinaloae* at most times. Most types of injuries (e.g. broken phalanges and torn wing membranes) were rare, and equal in frequency on both sexes. One category of injury, deep lacerations (typically 2–5 mm in length), were most commonly observed on males, and were a common occurrence for only a small part of the year. Fewer than 1 % of all captured animals had lacerations, but almost all the lacerations observed occurred in June and July. There were significantly more wounded males (11 of 155) than females (4 of 280) at Campestre during this period in 1979 (G-test for independence with Williams correction for small cell sizes [Sokal and Rohlf 1981]; $G = 8.89$, $df = 1$, $P < 0.01$). In nine of the males the lacerations were on the head (v.s. only one female). The proportion of males with lacerations was less than 2 % (2 of 85) from 6–22 June, was 18 % (7 of 39) from 28 June–8 July, and 6 % (2 of 31) from 25–31 July. The

variation among periods was significant (G-test for independence with William's correction, G = 8.28, df = 2, P < 0.05; Sokal and Rohlf 1981). Males with lacerations were very uncommon during other months in which data were collected (January, May and August through December).

There were three classes of roost associations at La Casa: (1) resident males that were always solitary (N = 5), (2) multiple male groups (mean = 2.5 males, range = 2–3, N = 2 groups), and (3) female groups (rarely occupied by only one of the resident females) with occasional or frequent male visitors (mean = 3 females, range = 1–8, N = 4 groups). Three of the five resident solitary males and the members of the multiple male groups were never found visiting female groups. In contrast, the other two resident solitary males were frequent visitors to the four female groups, one male visiting at least three of the four female groups and the other visiting at least two. Relationships among the bats were complicated by occasional non-resident male visits to all of the female groups, frequent appearance at La Casa of non-resident solitary males, moves of individual resident females to different groups or away from La Casa for one or more nights, and occasional appearances of non-resident females, usually in one of the female groups, but occasionally in otherwise-unused roosts. Some members of the groups were not recorded at La Casa for periods of weeks or months.

Discussion

The gular glands of male *Molossus sinaloae* are apparently the source of the marks observed on females. It is not clear if the marks were an incidental effect of contact between males and females, or if the marks are deliberately placed by the males. It appeared that both males and females were interested in scents on the dorsum of other bats, as both sexes often sniffed or nuzzled the dorsum of bats newly arrived at the entrance to a roost. Other investigators have hypothesized that male molossids may use the gland to mark roosts (Horst 1966; Quay 1970); we have no evidence to support this hypothesis for *M. sinaloae,* but cannot reject it.

The greater frequency of lacerations in males than in females, particularly on the head, suggests that lacerations are incurred during some behavior that is more common in males. In *Molossus sinaloae,* males are 20 % heavier than females, an unusual degree of sexual dimorphism in a small insectivorous bat (Findley and Wilson 1982; Ralls 1976; Myers 1978). It is possible that lacerations are incurred in aggressive encounters with males. In a captive colony of a related species, *Molossus ater,* J. J. Rasweiler IV (pers. com.) observed that captive mature males can normally be held in groups, but when males that have recently mated are returned to cages holding other males, fights erupt rapidly. These generally include biting attacks at the face, and males often lock jaws, suggesting that facial wounds are a likely outcome. In *M. sinaloae,* the peak of observed lacerations on males fell within the period immediately following parturition and within the period when gular glands were most active and the proportion of marked females was highest.

The evolutionary and ecological significance of *M. sinaloae* marking is uncertain. The peaks in gular gland activity and of marks on females were in May/June through August, which include the second half of pregnancy and the first two months after parturition. It is possible that males attempt to sequester mates during this time of the year; but why this should occur months before the appearance of macroscopically visible embryos in March (Fig. 1) is problematical unless there is some form of post-copulatory delay mechanism such as sperm storage or other post-copulatory delay mechanism. Although Molossids have, heretofore, been thought to lack such delays, two recent studies have reported prolonged periods of mating and/or presence of spermatazoa in the female reproductive tract of two neotropical molossid species (*Molossus ater*, Rasweiler 1987; and *Molossus fortis,* Krutzsch and Crichton 1985) but this has not been reported in *M. sinaloae*. In

addition, if males do mark females in an attempt to sequester mates, it is not clear why the roost associations at La Casa did not reflect female defense by males (e.g. a male defending each female group) instead of the rather loosely structured female groups which were visited by more than one male.

Acknowledgements

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Zusammenfassung

Beitrag zur Reproduktionsbiologie, Gulardrüse und zum Sozialverhalten von Molossus sinaloae (Chiroptera, Molossidae)

Fetthaltige, stark duftende Marken auf dem Rücken von weiblichen *Molossus sinaloae* entstehen offenbar durch Kontakt mit der Gulardrüse männlicher Tiere. Während der Gebärphase weiblicher Individuen waren die Gulardrüsen der Männchen am größten und produzierten am meisten Sekret. In dieser Phase wurden bei den Weibchen die meisten Duftmarken und bei den Männchen die meisten Fleischwunden festgestellt. Die ökologische und evolutive Bedeutung dieser Duftmarkierung ist ungeklärt.

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Analysis of pairing-parturition- and interbirth-intervals in a colony of Common marmosets *(Callithrix jacchus)*

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Abstract

Investigated the pairing-parturition-intervals (PPIs) and interbirth-intervals (IBIs) of marmoset females *(Callithrix jacchus)* with particular emphasis on prolongations. 28 PPIs and 166 IBIs of 31 females were considered. Comparison with endocrinological data of marmosets shows that conception usually takes place during the first or second ovarian cycle after pair formation. Our data indicate a two-peak-distribution of IBIs, that is 17 % of IBIs refer to conceptions during second or subsequent post-partum ovulation. About 45 % of these prolonged IBIs occur between the first and second, 21 % between the second and third delivery of each female. A relation was found between survival of the infants of the first and/or second litter in their native family and prolongation of the following IBI. The results are discussed in comparison with data from other colonies and with respect to the social system of marmosets.

Introduction

Common marmosets have been kept and bred successfully under laboratory conditions for many years. Due to a mean gestation length of 144 days (Hearn 1983) and no delay in ovulation when lactating, conception usually occurs some days after birth (Lunn and McNeilly 1982). The interbirth-intervals are therefore usually 150 to 160 days (see e.g. Poole and Evans 1982; Box and Hubrecht 1987). However, a considerable fluctuation in the length of pairing-parturition-intervals and IBIs can also be observed (see e.g. Evans and Poole 1983; Phillips 1976). In *C. jacchus* prolongation of PPI has been reported to be due to the young age of females at pair formation (Evans and Poole 1983), but explanations for prolongations of IBIs are still lacking. In other Callitrichids it has been found that decreasing daylight and humidity might be involved in triggering the conception (Kirkwood et al. 1983; for *Saguinus oedipus*). Removal of the infants shortly after birth may cause a reduction of IBI (Wolfe et al. 1975; Kirkwood et al. 1983; for *Saguinus* sp.).

The present paper analyses a relatively large sample (n = 194) of PPIs/IBIs. The possible causes and consequences of prolongation are discussed.

Material and methods

The marmosets were housed in cages or rooms of 1.0 m × 2.0 m × 2.5 m up to 5.0 m × 7.0 m × 3.0 m. The groups usually could not see each other, however, auditory and olfactory communication was possible. Housing conditions were maintained at a temperature of around 25 °C and 65 % humidity. In addition to daylight, a 12 hour light cycle was maintained using artificial lightning. All animals were fed twice daily; in the morning with a rice and porridge mixture with additional vitamins, protein and minerals; in the afternoon with fresh fruit and vegetables. Additionally the animals received crickets, mealworms, live newborn mice, boiled chicken and boiled veal. Unsweeted black tea was always available.

The data refer to 31 breeding females including six wild caught females. In order to exclude some possible influences of different social conditions only those families were taken into account, which

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Table 1. **Estimation of PPI and IBI ranges**

	mean (days)	range (days)
gestation[1]	144.0 ± 2.0	141–146
post partum ovulation[1]	10.5 ± 0.7	5– 17
follicular phase[1]	8.3 ± 0.3	—
luteal phase[1]	19.2 ± 0.6	—
PPI – conception at:		
first ovulation a.p.	—	141–174
second ovulation a.p.	—	170–202
IBI – conception at:		
first ovulation p.p.	154.5 ± 4.5	146–163
second ovulation p.p.	182.0 ± 4.9	174–191

[1]data published by HEARN (1983).
a.p. – after pair formation; p.p. – post partum.

were set up as pairs (no trios, or multi-male/multi-female groups). All females apart from one, were at least 18 months old when paired; the one exception was 15 months old. With the exception of one laboratory born and the wild caught females with unknown parity, all the other females were nulliparous. Except for one unintended pair formation (the male was 9.5 months old) all the other laboratory born males were no younger than 17 months.

Based on the endocrinological data published by HEARN (1983) we calculated expected PPI and IBI ranges by summing up the interval ranges of ovarian cycle and gestation period. These interval ranges were estimated from the mean values by Gaussian distribution. Depending on the conception date a number of discrete intervals, in which the IBIs should occur, could be found (during the first, second, or even later post-partum ovulation; table 1 and fig. 2, marked intervals). In contrast to the calculated IBIs, the expected intervals for PPIs overlapped in such a manner, that only an approximate determination was possible (table 1 and fig. 1, marked intervals).

The observed IBIs of all 31 breeding females were numbered chronologically. The intervals preceding abortions and premature births were excluded, whereas the IBIs between these events and the following births were included in the analysis. Additional information on the physical condition and illnesses of the animals, abortions, premature births as well as all disturbances (e.g. rehousing) to which the breeding groups were exposed, were used for a more detailed interpretation of the PPI and IBI data.

In order to examine a possible relationship between prolongation and seasonality in births, we looked for a correlation not only between the time of pair formation and first delivery but also the second delivery as well as the associated IBI and PPIs. Our hypothesis is, if there is an effectual seasonality in parturition, depending on the time of pair formation, a perceptible prolongation in PPI and IBI would be expected in order for the births to occur at the correct time of year.

Possible relationships of IBI length to group size (i.e. number of helpers) were examined by comparison of IBIs of successive deliveries of viable offspring.

Results

Pairing-parturition-intervals (PPIs)

Since two of the 31 females aborted and one female was already pregnant when paired, the data refer only to 28 deliveries. The lengths of the PPIs show a large spread between 144 and 402 days, however, most of the deliveries occured between 144th and 185th day after pair formation (fig. 1). 23 (82 %) of the observed deliveries occured during that interval. The respective females are likely to have conceived during the first or second ovulation after pairing (compare marked interval fig. 1). The prolongation of at least three of the remaining five PPIs (18 %) could possibly be related to disturbances in daily routine (n = 2) and to an unintended pair formation (n = 1, see above). A relationship between prolongation and seasonality could not be detected, as prolonged PPIs occured the whole year round (see also prolongations of IBIs).

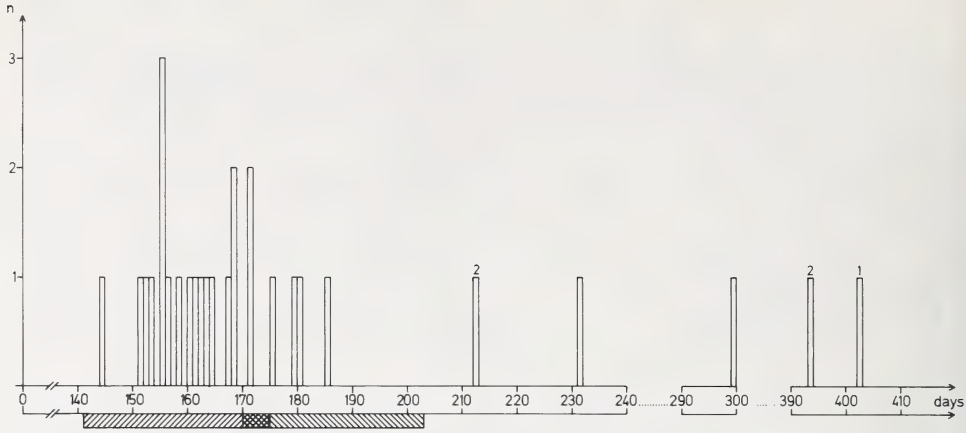

Fig. 1. Distribution of pairing-parturition-intervals

[1] – unintended pair formation (male 9.5 months old)
[2] – prolongation presumably caused by illness or disturbances
– conception at first ovulation after pair formation (estimated interval)
– conception at second ovulation after pair formation (estimated interval)

Interbirth-intervals (IBIs)

The data refer to 166 deliveries excluding two abortions and one premature birth. 137 (83 %) of the IBIs could be allocated to the interval between day 147 and 167; most of which can be found between day 150 and 157 with maxima on the 152th and 155th day (fig. 2). A second minor concentration of IBIs occurs between 173 to 192 days (n = 15, 9 %). 14 (8 %) of the IBIs were longer than 196 days. These IBIs nearly totally agree with the two expected ranges of IBIs for conception after 1. the first ovulation (146 to 163 days) and 2. the second ovulation post partum (174 to 191 days; compare marked intervals fig. 2). In conclusion this means that only 17 % of all conceptions occured during the second or subsequent ovulation post partum.

Prolongation of IBIs

One explanation for prolongation may be that regular breeding is interrupted or prevented by illnesses of the breeding pair or by external and/or social disturbances. The appendices in fig. 2 show that a considerable number of prolonged IBIs (n = 5, 17 %) may be influenced by such disturbances (n = 3) or occured after an abortion (n = 2). Nevertheless regular IBIs occured also after abortions (n = 3). Also no apparent relationship could be detected between prolongation and seasonality. Moreover, females which bred for several years in our facility gave birth the whole year round.

Apart from the possible influence of disturbances on IBI length, it is striking that 45 % (n = 13) of all prolonged IBIs (n = 29) were associated with the second delivery with a smaller peak in association with the third delivery (21 %, n = 6). This is also true for wild caught females, as two of the six females showed prolonged IBIs for their second delivery. This result was not caused by a possible bias due to different numbers of deliveries of different females. Table 2 shows the frequency of the IBI categories of 21 females which gave birth to at least five litters. The IBIs are listed according to the sequence of successive

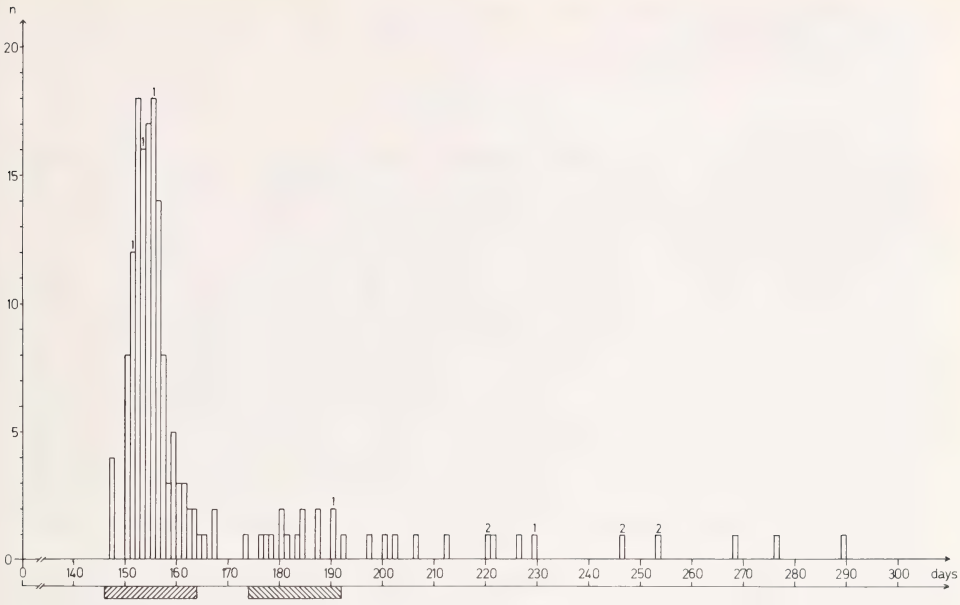

Fig. 2. Distribution of interbirth-intervals

[1] – one IBI after abortion
[2] – prolongation of one IBI presumably caused by illness or disturbances
– conception at first ovulation post partum (estimated interval)
– conception at second interval post partum (estimated interval)

deliveries of viable and reared offspring (litter 02 to litter 05) and are compared to those IBIs where all infants of a given litter died or were removed within 10 days (IBI^x). 41 % of IBIs of the second and 32 % of the third litter were prolonged. In comparison IBI^x shows a prolongation of the IBIs rather similar to that of the fourth and fifth deliveries (6 to 17 %).

Table 2. **Frequencies of IBI categories of 21 females from litter 02 to 05**

		Ranges for IBIs (in days) 147–167	173–192	>196	Σn
litter 02	n	10[1]	4	3[2]	17
	%	58.8	23.5	17.7	
litter 03	n	13	4	2	19
	%	68.4	21.1	10.5	
litter 04	n	18	0	2[22]	20
	%	90.0	0	10.0	
litter 05	n	15[1]	1	0	16
	%	93.7	6.3	0	
IBI^a	n	10	2	0	12
	%	83.3	16.7	0	

[1] One IBI after abortion. – [2] One IBI presumably caused by illness or disturbances. – IBI^a – all infants of a given litter died or were removed within 10 days after birth.

Overall this means that 72 % (n = 13) of prolonged IBIs of these 21 females occured in the second and third parturition.

Discussion

Our data indicate that in the common marmoset a rather large proportion of conceptions occur during the first or second ovarian cycle of newly paired females. Evans and Poole (1983) found 50 % of all deliveries in their *C. jacchus* colony to occur between day 140 and 200 after pair formation. These authors explain the strikingly increased PPIs of the remaining females to be due to the young age of those females (< 18 months) when paired for the first time. We cannot comment on this interpretation. Our data confirm another observation of Evans and Poole (1983) that there is no relationship between the females' age at pair formation and the lengths of PPIs, if the paired females were older than 18 months. With the exception of the three prolonged PPIs in our sample which were probably caused by external factors, our data allow one to speculate that under normal conditions nearly all females would have given birth about 185 days following pair formation. This could also be true for females which live in their native groups until shortly before pair formation, since ovulation occurs almost immediately following the females' removal from their native family (Abbott 1984; Epple and Katz 1984; Evans and Hodges 1984).

As a consequence of this result it is not necessary to investigate further a possible seasonal dependence of deliveries in captive *C. jacchus* females. Although two breeding peaks have been observed in wild marmoset groups (Hubrecht 1984; Rylands 1981), this may be altered by housing conditions in captivity. Nevertheless, if birth peaks are observed under laboratory conditions, one has also to examine other possible reasons apart from just seasonal dependence, i.e. more or less identical time of pair formation or synchronisation between breeding females as to ovulation cycles (see French and Stribley 1987 for *Leontopithecus rosalia*).

In our colony most IBIs had a length of 150 to 157 days. The mean and median values for IBIs found in the literature generally range from 154 to 205 days (Box and Hubrecht 1987; Hiddleston 1978; Lunn and Hearn 1978; McIntosh and Looker 1982; Phillips 1976; Poole and Evans 1982). However, as the observed IBIs of our *C. jacchus* colony and their expected intervals indicate a two (or more)-peak-distribution, the use of mean or median values are neither meaningful nor correct. Unfortunately we do not have enough data from our colony at present to undertake a more suitable statistical evaluation, which considers both the dependence and distribution (e.g. maximum likelihood). Apart from this, the rather regular IBIs and prolongation of IBIs seem comparable to other studies (e.g. Box and Hubrecht 1987). Our data show that the prolongations are regularly associated with the second and third deliveries of viable offspring. On the other hand, if infants are removed shortly after birth, the following IBI lengths are comparable to those of the fourth and fifth deliveries. This indicates a relationship between survival of the infants of the first two litters and prolongation of the following IBIs in wild caught as well as in laboratory born females (compare Wolfe et al. 1976 and Kirkwood et al. 1983 for *Saguinus* sp.). Newly paired marmosets are confronted with a strikingly new situation following parturition of their first young, as the parents will have to carry their infants during sexual and copulatory activities, whereas after the second delivery only unexperienced helpers are available. Both of these factors may possibly handicap the animals and prevent the female from conceiving during the first ovarian cycle post partum. Conception would be more probable during the second or later ovarian cycles, because at this time the infants are more independent and move around on their own. Therefore, the prolongation of the second and/or third IBI in the females' life may have a natural cause and should not be compensated by removal of the young.

On the other hand, if breeding pairs tolerate experienced related or unrelated conspecifics as helpers, they could possibly increase their potential time of reproduction by reducing the nonreproductive intervals. It has to be considered that this hypothesis cannot directly be extended to natural conditions.

Since wild marmosets have been observed to exhibit birth peaks (Hubrecht 1984; Rylands 1981), a reduction of the nonreproductive interval would not necessarily result directly in a higher reproduction rate with a greater number of offspring. It has to be ensured that the births do not occur in a period of limited food resources which would result in higher infant mortality; therefore any reduction or prolongation of the nonreproductive interval leading to such an unfavourable time of birth would have to be avoided. In order to analyse these contrasting models it would be necessary to know firstly how long marmosets maintain their reproductive privilege in wild groups (to decide whether the regulation of the time of birth is associated to one or more females within a group) and secondly what the prerequisites for tolerance against strange conspecifics of either sex are. Although high turnover rates in *C. jacchus* groups had been observed (Scanlon et al. 1988) and new groups may be formed by more than one male and one female (Ferrari, pers. comm. 1988; for *C. flaviceps*), we urgently need more data to clarify the possible coherence between the presence of additional helpers, the tolerance against them and the reproductive benefits for the breeding animals.

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Zusammenfassung

Analyse von Verpaarungs-Geburt- und Intergeburten-Intervallen in einer Kolonie von Weißbüschelaffen (Callithrix jacchus)

Untersucht wurden Verpaarungs-Geburten-Intervalle (PPIs) und Intergeburten-Intervalle (IBIs) von Weißbüschelaffen-Weibchen *(Callithrix jacchus)*. Für die Untersuchung standen 28 PPIs und 166 IBIs von 31 Weibchen zur Verfügung. Im Vergleich mit endokrinologischen Daten zeigt sich, daß die Weibchen normalerweise während des ersten oder zweiten ovarialen Zyklus' nach Verpaarung konzipierten. Die IBIs lassen eine zwei(oder mehr)-gipflige Verteilung vermuten, d. h. 17 % der IBIs lassen sich auf Konzeptionen bei der zweiten oder einer späteren Ovulation post partum zurückführen. Etwa 45 % dieser verlängerten IBIs folgen auf die erste Geburt, 21 % auf die zweite Geburt jedes Weibchens. Es kann eine Beziehung zwischen dem Überleben der Jungtiere des ersten und zweiten Wurfes und der Verlängerung der folgenden IBIs festgestellt werden. Die Ergebnisse werden im Vergleich mit anderen Untersuchungen und in Hinsicht auf das Sozialsystem der Marmosetten diskutiert.

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Ovulation rates in European lynx, *Lynx lynx* (L.), from Norway

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Abstract

Variation in ovulation rates in European Lynx, *Lynx lynx*, was studied with reference to condition and availability of prey species.

Over a period of 17 years, the mean ovulation rate of 83 females older than two years was 3.10 ± SD 1.87. No significant relationships were found between ovulation rate and important parameters like food availability, general condition of the female, age or year.

Introduction

Brand and Keith (1979) found significantly lower ovulation rates in Canadian lynx, *Lynx canadensis,* during a snowshoe hare *Lepus americanus* decline in Alberta, Canada, than during increases.

The snowshoe hare is the major food of the Canadian lynx, and lynx numbers fluctuating with hare abundance in approximately 10-year cycles (Keith 1963).

In Norway the European lynx, *Lynx lynx,* is not nearly as restricted to only one prey species as it's North American counterpart (Birkeland and Myrberget 1980), and fluctuations in abundance are small.

Materials and methods

From 1960 to 1981, the Norwegian state bounty on lynx required that the skinned carcasses were to be sent to the Directorate for Nature Management. The present study is based on samples accumulated from 1960 through 1976, and includes skulls and reproductive tracts with ovaries of 176 females.

Ovaries were macroscopically examined for form, colour, size and stage of development, sectioned by a freezing microtome and stained with Heidenhain's haematoxylin (Romeis 1948; Baker 1966). Sections were analysed with a microscope, and Graafian follicles and corpora lutea were counted.

Fresh luteal bodies can be found the year round. Normally they are easily distinguishable from luteal bodies of the previous cycle (Crowe 1975). There are differences in colour and consistency. Fresh luteal bodies are light yellow. One year later, when they turn into "lutein bodies of the previous cycle", they are red-brownish or gray with a significantly less grainy appearance. Luteal bodies from three cycles have been observed in eight cases.

Ovulation rates were calculated by counting the fresh luteal bodies and Graafian follicles in ovaries (Cheatum 1949; Duke 1949; Gashwiler et al. 1961). Age was determined by means of incremental lines in tooth cementum (Kvam 1984).

In order to avoid bias due to lower ovulation rates in young individuals, only females older than 2 years were used. A total of 83 females were investigated.

Since hunting of lynx is almost exclusively restricted to the period from January through April, the youngest individual investigated was almost 3 years old. Lynx kittens are born in May or early June, and the rutting season takes place from January through April.

According to Birkeland and Myrberget (1980) reindeer, *Rangifer tarandus*, roedeer, *Capreolus capreolus,* Mountain hare, *Lepus timidus* and small rodents Microtinae made up respectively 31 %, 17 %, 19 % and 8 % by number of the inspected stomach contents of 146 lynx from Norway.

Official hunting statistics for these major prey species except rodents were compared with annual

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records of the number of lynx killed, in order to study fluctuations in population size in relation to lynx condition and ovulation rates.

Small rodent abundance in Norway follows approximately a 4-year cycle. Peak years, based on data from Myrberget (1973) and Christiansen (1983) are plotted in Fig. 1.

Specimens were assigned an index value from 1 (low) to 5 (high) indicating general condition, based on results of initial laboratory examinations of intestine fat deposits, and kidney fat index (Langvatn 1977).

Results

The annual kill of lynxes in Norway around 1960 was relatively low. A positive trend which peaked in 1968 was followed by a decline in the 1970s, and numbers started increasing again in 1977 (Fig. 1).

There is no correlation between hunting statistics for European lynx and roedeer the same year in the period 1960–1981 (Fig. 1) ($r = -0.41$, $n = 22$, $P = 0.43$ Pearsons corr.).

There is no significant correlation between lynx ovulation rate and roedeer hunted the same year ($r = -0.04$, $n = 83$, $P = 0.35$ Pearsons corr.).

Individual lynx ovulation data were compared to roedeer hunted the year each animal was born, to see if the condition of the mother, which might be connected to roedeer availability, had influence on the reproductive performance of the young. The correlation was statistically significant, but not very high: $r = +0.31$, $n = 83$, $P = 0.002$ (Pearsons corr.).

Hunting statistics are available for mountain hare after 1971 (Fig. 1). Correlation with numbers of lynx killed is low and even negative: $r = -0.16$, $n = 11$, $P = 0.32$ (Pearsons corr.). Possible correlation between lynx ovulation rate and statistics on mountain hare hunting cannot be tested, since data on both parameters are available for only five common years. The lynx is most abundant in areas of Norway where reindeer husbandry is practised, and therefore comparisons with statistics on hunting of wild reindeer would be futile. No statistics on reindeer husbandry were available before 1980.

Fig. 1 shows that there is no obvious correlation between small rodent peak years and lynx population size as measured by annual numbers of lynx killed.

Correlations between mean numbers of corpora lutea and numbers of lynx killed annually are low and not significant ($r = 0.20$, $n = 17$, $P = 0.21$ Pearsons corr.).

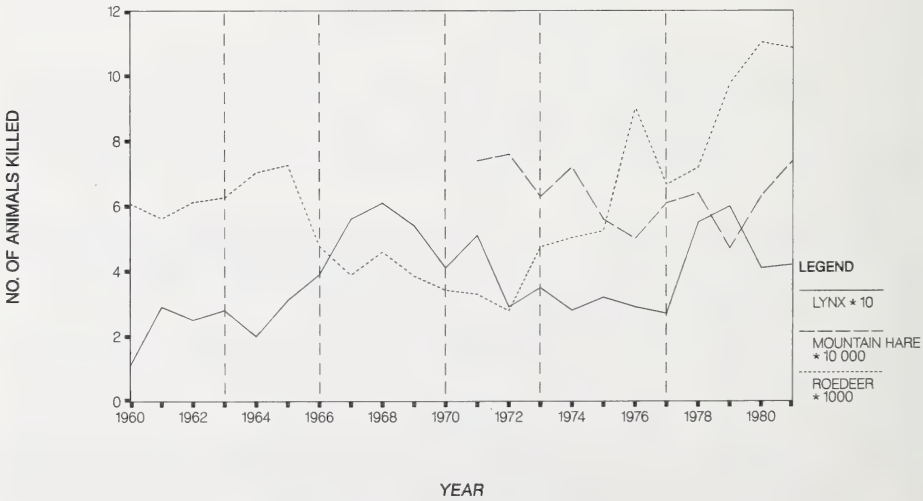
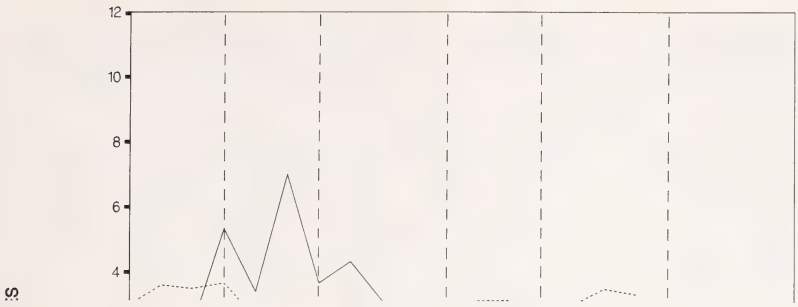


Fig. 1. Numbers of European lynx, *Lynx lynx* × 10, mountain hare *Lepus timidus* × 10 000 and roedeer *Capreolus capreolus* × 1000 killed per year in Norway since 1960 according to official hunting statistics. Small rodent peak years are indicated by vertical dotted lines



Erratum

Zeitschrift für Säugetierkunde, Band 55, Heft 4, S. 253–259 (1990)

VERLAG PAUL PAREY

Im Beitrag K. Al-Robaae und H. Felten, „Was ist *Erythronesokia* Khajuria, 1981 (Mammalia: Rodentia: Muridae)?" muß es im Kapitel „Lebensweise" (S. 258) in der ersten Zeile heißen:
Nesokia bunnii lebt im Irak . . .

4, 3 and 1 fresh corpora lutea. The resulting mean ovulation rate was 2.66, which was far below 3.10, the mean ovulation rate for the entire sample. Only one female was classified in the general condition index 1, indicating "lean". Although this female was 17 years old (No. 3/74), she carried 4 fresh corpora lutea and 1 luteal body of previous cycles. The result does not indicate the difference between ovulation rates in animals of extremely bad and extremely good condition to be significant when speaking in terms of population biology.

Discussion

The European lynx is a known predator on a variety of animals, from small rodents to ungulates (Birkeland and Myrberget 1980; Breitenmoser and Haller 1987; Dulkeit 1953; Haglund 1966; Hell 1973; Jonsson 1980; Pulliainen 1974, 1981; Pulliainen and Hyypia 1975; Suminski 1973). Prey preferences seem to differ between different parts

Table 1. **Ovulation rate expressed by number of fresh corpora lutea and Graafian follicles ranged according to age classes**

Age in years	x̄	SD	N	Range
2	3.09	1.57	22	0– 7
3	3.80	2.17	20	0– 8
4	2.91	2.62	11	1–10
5	2.40	1.65	10	1– 5
6	1.83	1.16	6	0– 3
7	3.20	1.10	5	2– 4
8—9	3.16	1.47	6	1– 5
10–17	3.67	1.53	3	2– 5
Total	3.10	1.87	83	0–10

Table 2. **Ovulation rate expressed by number of fresh corpora lutea and Graafian follicles ranged according to year of killing**

Year	x̄	SD	N
1960	1.00	0	1
1961	2.17	1.60	6
1962	2.33	2.08	3
1963	5.33	4.16	3
1964	3.40	2.70	5
1965	7.00	0	1
1966	3.67	2.07	6
1967	4.33	2.00	9
1968	3.13	0.64	8
1969	2.88	1.69	9
1970	2.00	0	1
1971	3.00	1.31	8
1972	3.00	1.70	8
1973	3.00	1.41	2
1974	2.00	0.82	4
1975	2.33	1.37	6
1976	2.00	1.73	3
Total	3.10	1.87	83

Table 3. **Ovulation rate expressed by number of fresh corpora lutea ranged according to a general condition index**

Gen. condition index	N	x̄	SD
1	1	4.00	0
2	8	2.63	2.45
3	54	3.06	1.71
4	13	3.62	2.36
5	3	3.00	1.73
(No index)	4	2.75	1.89
Total	83	3.10	1.87

Legend to general condition indexes: 1 = "lean"; 2 = not too good; 3 = normal; 4 = very good; 5 = fat

of the distribution area of the lynx, dependent on availability of relevant prey species (Breitenmoser and Haller 1987; Pulliainen et al. 1988).

It has previously been demonstrated that roedeer may represent a major part of the diet of the European lynx (Birkeland and Myrberget 1980; Egorov 1965; Johnson 1980). Roedeer were not originally members of the native Norwegian fauna before 1900, and regular hunting for roedeer was not registered before 1927 (Olstad 1944). The annual numbers of lynx killed before the turn of the century were much higher than in more recent years. Although the roedeer is an important food resource when available, it is consequently in no way a prerequisite to the survival of lynx in Norway.

Haglund (1966) and Birkeland and Myrberget (1980) report a shift in the diet of lynxes from predominantly small game during autumn, to cervids in winter. Small game and rodents are inaccessible under deep snow, and cervids experience difficulties moving in deep snow, while a lynx with its well adapted large paws travels with ease in snow covered terrain (Formozov 1946).

The European lynx is bigger than the other *Lynx* species (Kurten and Rausch 1959; Matjuschkin 1978; Werdelin 1981), and may therefore be more ready to accept larger prey species (Moors 1980; Stenseth et al. 1977; Werdelin 1981).

Small game in Northern Europe follow a 4-year-cycle similar to that of small rodents (Hagen 1953; Myrberget 1984; Østbye and Mysterud 1984). As the European lynx

readily accepts a variety of prey species, it is only slightly influenced by such cycles as long as alternative prey is available. PULLIAINEN et al. (1988) report a significant difference in available prey, stomach-contents and condition between lynxes in Tavastland and in South-Eastern Finland in the 1980s. The lynx in Tavastland had the opportunity of switching to white-tailed deer *Odocoileus virginianus* when hare populations were low, while the lynx in SE-Finland did not have this opportunity. Switching for prey (MURDOCH and OATEN 1975) in the European lynx is also indicated by BREITENMOSER and HALLER (1987), and in the Canada lynx by BERGERUD (1967, 1971, 1983).

The Norwegian lynxes show no fluctuations in number or ovulation rate comparable to variations in abundance of its most important prey species over a 17 year period. The most likely explanation seems to be prey switching, which imply dampened tendency for individuals to deviate too much from normal condition. The Norwegian lynx has a variety of prey species available, and thereby the necessary prerequisite for stable condition and stable ovulation rate.

Zusammenfassung

Ovulationsraten beim Europäischen Luchs, Lynx lynx (L.), aus Norwegen

Die Ovulationsrate norwegischer Luchse *(Lynx lynx)* wurde in Beziehung zur Häufigkeit ihrer Beutetiere und zu ihrer Kondition untersucht. Für 83 Weibchen betrug die mittlere Ovulationsrate in 17 Jahren 3,10 ± 1,87 (SD). Signifikante Beziehungen ergaben sich weder hier noch zwischen Ovulationsrate und Alter oder Ovulationsrate und Erlegungsjahr.

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Interspecific odour discrimination in four *Gerbillurus* species

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Abstract

Interspecific odour discrimination was investigated in an attempt to identify possible mechanisms of species recognition in four *Gerbillurus* species. Four-way choice-chamber tests of preference for odours of the opposite sex of *G. paeba, G. tytonis, G. setzeri,* and *G. vallinus* were conducted. When test animals were prevented from physically contacting the odour source (soiled sand), males showed more evidence of discrimination than females, but only male *G. tytonis* significantly preferred conspecific odours. Males showed less discrimination among odours of females which had been injected with hormones to induce oestrus.

When test animals were allowed to contact the odour source females showed more evidence of discrimination in two-way and four-way choices. Female *G. tytonis* and *G. vallinus* showed significant preference for conspecific odours in two-way tests.

It is suggested that males responded to a volatile chemosignal of females, but this response diminished if males were permitted to sniff the odour source. Females responded to non-volatile chemosignals deposited by males. However, little evidence for preference of conspecific odours is provided. Physical contact between animals may be necessary for precise species recognition.

Introduction

Olfactory communication is implicated in mate selection, reproduction, territoriality, and parent-offspring interactions in many rodent species (Brown 1985). The vomeronasal organ, which assists in odour detection, is well developed in rodents (Eisenberg and Kleiman 1972), and permits precise discrimination at the level of individuals in some species (Johnston 1982; Young 1988).

Pheromones may be present in urine, faeces and saliva, and also in secretions from glands around the eyes, mouth, genital organs, and skin (Brown 1985). Sandbathing, which is exhibited by many desert rodents, serves a marking as well as a pelage-dressing function (Eisenberg and Kleiman 1972; Brown 1985). Specific scent-marking behaviour includes perineal dragging and ventral-gland marking in *Meriones unguiculatus* (Thiessen and Harriman 1983). Harderian gland secretion mixed with saliva is spread over the face during grooming and serves a communication function in *M. unguiculatus* (Thiessen et al. 1976).

Volatile chemosignals may act as long-distance attractants or territorial indicators, while low-volatile and non-volatile substances may permit acute, short-range identifications which precede sexual and aggressive behaviour (Nyby 1982; Brown 1985). The odour of an oestrus female mammal has been identified as one of the prime stimuli indicating her condition to the male (Eisenberg and Kleiman 1972).

The use of odour differences among closely-related rodent taxa as a means of maintaining reproductive isolation has been investigated in speciating *Spalax ehrenbergi* (Nevo et al. 1976), *Clethrionomys glareolus* (Godfrey 1958), and *Peromyscus* spp. (Smith 1965; Moore 1965; Doty 1972). Preference for conspecific odours was not always exhibited (Moore 1965), and the oestrus condition of females was important for discrimination in some species (Doty 1972; Nevo et al. 1976).

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In this study, four species of the genus *Gerbillurus* were included in a comparative study of communication in the genus. Preferences for conspecific and heterospecific odours were investigated in a series of experiments based on a choice-chamber technique.

Study species were *G. paeba, G. tytonis, G. vallinus* and *G. setzeri.* Previous research has shown that *G. paeba* and *G. tytonis* (2n = 36) are closely related, while *G. vallinus* and *G. setzeri* (2n = 60) are a separate, closely-related species-group (Schlitter et al. 1984; Dempster and Perrin 1989a). Three species, *G. tytonis, G. vallinus* and *G. setzeri*, are allopatric, with evidence of occasional and localised overlap in distribution of *G. tytonis* and *G. setzeri* (De Graaff 1981). *G. paeba* occupies areas of allopatry, but also occurs sympatrically with *G. vallinus* and *G. setzeri,* and syntopically with *G. tytonis* locally and seasonally (Boyer 1987; Erasmus, in litt.; Dempster, Perrin and Downs pers. obs.).

Gerbillurus species lack a ventral gland, as occurs in *M. unguiculatus* and *M. hurrianae* (Brown 1985; Prakash et al. 1988). The only glands found in the skin of *G. paeba* were on the naked toe-pads of fore- and hindfeet (Green 1988). Scentmarking behaviour in the form of perineal dragging occurs rarely (Dempster pers. obs.). All *Gerbillurus* species sandbathe by rolling rapidly from the side to the dorsum (Dempster pers. obs.). *G. paeba* and *G. tytonis* selected fine dusty sand for sandbathing in preference to coarser grades of sand (Hamer 1985). *Gerbillurus* spp. maintained in laboratory cages are remarkably odourless to humans except for *G. tytonis* individuals, whose odour is distinctive (Dempster pers. obs.).

In the present study, olfactory preferences of males and females were tested using odours of the opposite sex in each test combination. Tests in which animals were prevented from contacting the odour source were compared with tests in which contact was permitted. In addition, male preferences for odours of females in artificially-induced oestrus were tested.

Materials and methods

Details of numbers of individuals, sexes, and trap localities are given in Table 1. Laboratory maintenance of animals is described elsewhere (Dempster and Perrin 1989b). The choice chamber used in tests of olfactory preference is illustrated in Figure 1.

All tests were of the heterosexual type, i.e. if males were the odour sources, females were test animals and vice versa. A test animal was placed in the central arena and permitted to investigate the apparatus for 5 min. In the following 15 min, the animal's visits to and time spent in each tunnel were recorded using a programmed microprocessor. After each observation, the whole apparatus was

Table 1. **Number of individuals, sexes and trap localities of gerbils used in olfactory preference experiments**

Species	Sex	N	Trap locality
G. paeba	Males	11	Swakopmund, Namibia
	Females	16	Swakopmund, Namibia
	Males	9	Kuiseb River, Namibia
	Females	7	Kuiseb River, Namibia
G. tytonis	Males	12	Namib dunefield
	Females	18	Namib dunefield
G. setzeri	Males	5	Arandis, Namibia
	Females	5	Arandis, Namibia
	Males	9	Gobabeb, Namibia
	Females	9	Gobabeb, Namibia
	Males	8	Donkerhoek, Namibia
	Females	1	Donkerhoek, Namibia
G. vallinus	Males	14	Kenhardt, N. Cape
	Females	11	Kenhardt, N. Cape

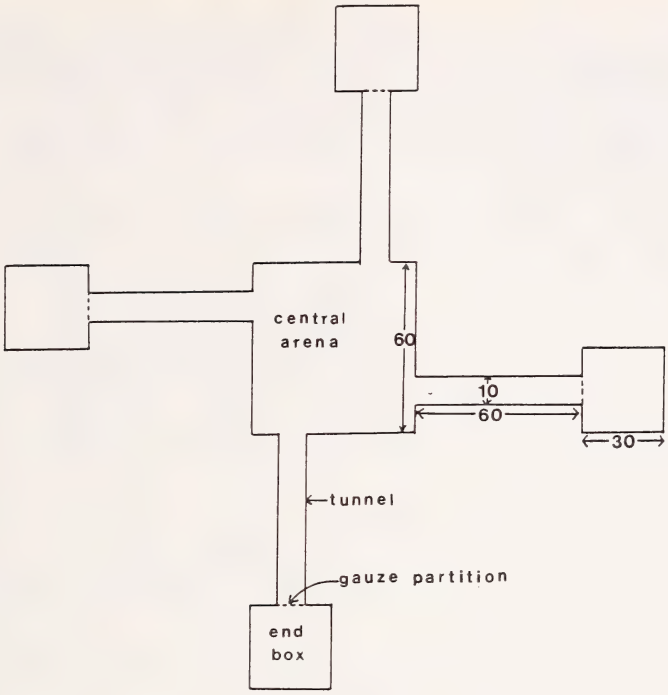


Fig. 1. Choice chamber used in olfactory preference tests. Measurements are given in cm

washed out with odourless soap and water. The allocation of odour source to tunnel was changed on each day of testing.

Observations were conducted in a quiet, window-less room, with lighting provided by a single red light positioned above the centre of the apparatus. Two animals of each species, i.e. eight individuals, were tested on each day of testing, and tests were conducted at weekly intervals.

Three experimental procedures were followed:

Experiment I: Clean sand was placed in each of the end boxes. Four animals of the same sex, but of different species, were placed singly in the end boxes for 18 h, after which they were removed and testing as described above commenced.

Experiment II: Sand from the cages of four individuals of the same sex, but of different species, was used as the odour source. Animals had been housed singly in cages for at least one week prior to testing. A glass petrie dish containing 20 ml of sand was placed approximately 5 cm inside the entrance to each tunnel. The sand was changed after each observation.

Experiment III: The choice chamber was divided in half by a metal partition. Four animals of the same sex and of different species were placed in containers which held 250 ml clean sand. After 1 h the animals were removed and the containers sealed. A glass petrie dish containing 20 ml of this sand was placed approximately 5 cm inside the entrance to each tunnel. The sand was changed after each observation. Two-way tests of *G. vallinus*-*G. setzeri* and *G. paeba*-*G. tytonis* combinations were conducted.

The oestrus condition of females was not considered in these experiments, since vaginal smears were not reliable indicators of the oestrus cycle in *Gerbillurus* species (Dempster and Perrin 1989b). One set of observations in Experiment I used as odour sources females of all species which had been injected with 0.006 mg oestradiol-17B and 0.4 mg progesterone to induce oestrus.

Results of four-way choice experiments were analysed using Friedman's 2-way analysis of variance with correction for tied ranks (ZAR 1974). Wilcoxon T-test (one-tailed) was used to test the hypthesis that each species preferred conspecific odours in Experiment III.

Results

Results for animals that visited less than two tunnels in the entire observation period were discarded. This accounted for 15 % of all observations. The number of visits made and the time spent in each tunnel varied considerably among individuals. Results for number of visits are presented in Tables 2 to 4, while results for duration of visits are presented as box-and-whisker plots (STATGRAPHICS) in Figs. 2–4.

Table 2. **Mean (± s.d.) number of visits to odours of different species in Experiment I**

Test Animal	n	Odour sources				Friedman's
		G. vallinus	*G. setzeri*	*G. paeba*	*G. tytonis*	X^2
Males			Females			
G. vallinus	18	13.4 ± 13.6	11.3 ± 8.6	15.4 ± 12.5	10.8 ± 9.1	6.7 n.s.
G. setzeri	17	8.8 ± 4.0	9.1 ± 3.8	8.5 ± 5.4	8.8 ± 4.7	1.8 n.s.
G. tytzonis	18	7.1 ± 4.4	9.2 ± 4.6	7.3 ± 3.6	8.9 ± 3.9	7.2 n.s.
G. paeba	18	12.9 ± 18.5	13.2 ± 15.8	13.3 ± 11.9	7.3 ± 7.1	3.6 n.s.
Females			Males			
G. vallinus	15	15.8 ± 23.3	13.1 ± 18.9	11.5 ± 16.4	10.9 ± 19.3	4.5 n.s.
G. setzeri	15	11.5 ± 5.4	11.6 ± 5.4	10.9 ± 3.9	10.2 ± 3.8	1.9 n.s.
G. tytonis	15	7.9 ± 3.9	9.6 ± 5.6	10.6 ± 6.3	8.3 ± 5.8	7.6 n.s.
G. paeba	13	11.1 ± 7.8	12.6 ± 9.7	13.1 ± 11.9	10.9 ± 10.7	2.3 n.s.

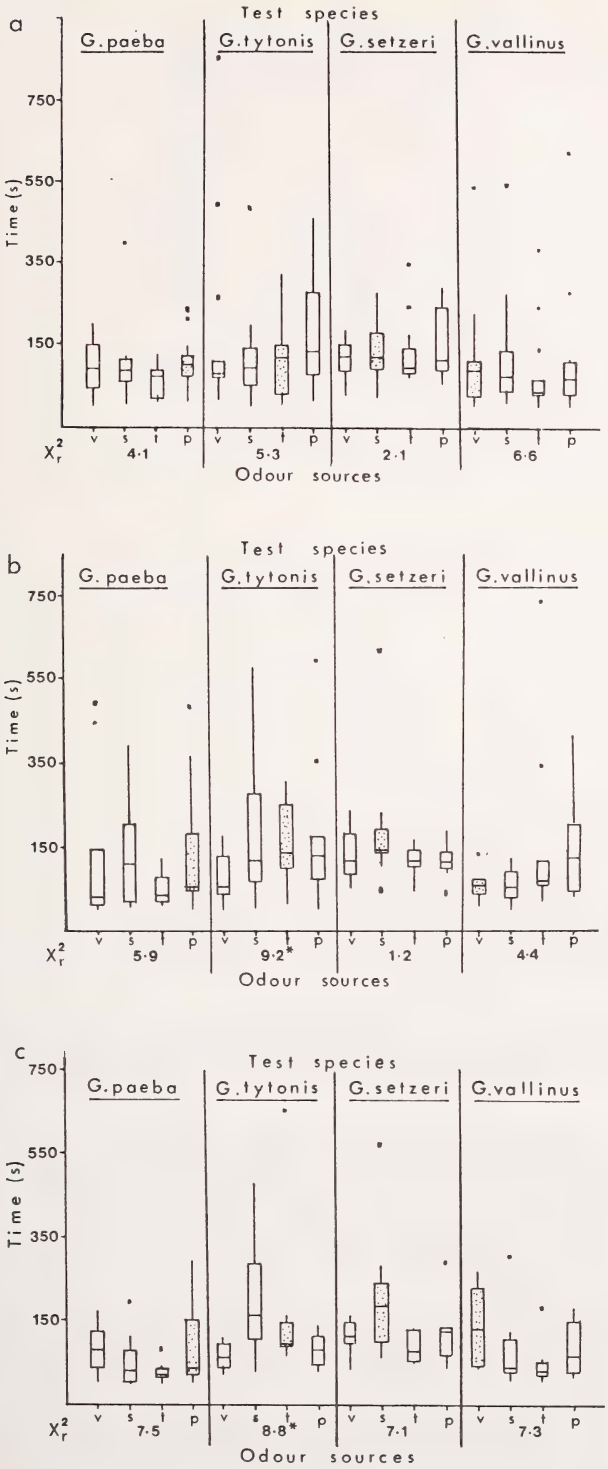
Table 3. **Mean (± s.d.) number of visits to odours of different species in Experiment II**

Test Animal	n	Odour sources				Friedman's
		G. vallinus	*G. setzeri*	*G. paeba*	*G. tytonis*	X^2
Males			Females			
G. tytonis	10	6.8 ± 4.1	8.2 ± 4.5	12.5 ± 12.6	11.6 ± 14.1	0.8 n.s.
G. paeba	10	21.4 ± 19.1	19.7 ± 26.6	22.7 ± 25.2	22.7 ± 26.7	0.4 n.s.
G. setzeri	10	10.2 ± 4.4	10.1 ± 8.1	11.1 ± 10.4	9.7 ± 11.7	0.8 n.s.
G. vallinus	10	7.7 ± 6.7	6.3 ± 4.7	5.1 ± 4.5	5.5 ± 3.5	0.7 n.s.
Females			Males			
G. tytonis	10	10.6 ± 7.0	9.8 ± 4.4	7.5 ± 3.3	9.5 ± 4.1	2.0 n.s.
G. paeba	10	15.9 ± 18.9	12.6 ± 11.9	14.8 ± 17.8	12.5 ± 17.8	0.2 n.s.
G. setzeri	10	11.5 ± 6.0	12.5 ± 6.7	10.5 ± 5.9	12.0 ± 10.7	3.6 n.s.
G. vallinus	10	4.8 ± 3.9	4.8 ± 3.4	6.0 ± 3.5	7.0 ± 6.0	2.8 n.s.

Table 4. **Mean (± s.d.) number of visits to odours of different species in Experiment III**

Test Animal	n	Odour sources				Wilcoxon
		G. tytonis	*G. paeba*	*G. vallinus*	*G. setzeri*	T
Males			Females			
G. tytonis	10	20.5 ± 15.0	18.2 ± 20.9			24.5 n.s.
G. paeba	10	24.9 ± 24.8	11.0 ± 10.8			19.0 n.s.
G. setzeri	10			29.7 ± 37.3	35.9 ± 42.2	21.0 n.s.
G. vallinus	10			11.5 ± 9.6	16.7 ± 18.7	10.0 n.s.
Females			Males			
G. tytonis	10	23.3 ± 9.7	19.3 ± 7.5			2.0*
G. paeba	10	14.2 ± 7.8	26.3 ± 27.3			24.5 n.s.
G. setzeri	9			14.9 ± 10.8	12.2 ± 5.6	5.0*
G. vallinus	9			25.2 ± 21.0	18.6 ± 11.6	8.0*

* = $p \leq 0.05$



Results of Experiment I are given in Table 2 and Figure 2. Number of visits to odours of different species did not differ significantly in any species or sex. *G. tytonis* males and females and *G. vallinus* males were nearest to significance at the 95 % probability level, but in no case did this indicate a greater number of visits to conspecific odours.

Durations of visits differed significantly in only two test situations. Male *G. tytonis* spent more time with conspecific odour of injected females and avoided *G. vallinus* odour. However, for untreated females, male *G. tytonis* preferred the odour of *G. setzeri* and, avoided *G. vallinus* and *G. paeba*. Males discriminated more among untreated females than among injected females, and two species, *G. vallinus* and *G. setzeri*, preferred conspecific to heterospecific odours. X_r^2 values for these tests approached significance at the 95 % probability level. *G. tytonis* odours were avoided by all species except *G. tytonis* males.

Female *G. vallinus* were the only species which showed a preference for male conspecific odours, but differences were not significant.

Fig. 2. Durations of visits made by a) females to odours of males (n = 13 for *G. paeba*, n = 15 for other species); b) males to odours of treated females (n = 10 for each species); c) males to odours of untreated females (n = 8 for each species). ✳ = $p < 0.05$; all other X_r^2 values not significant

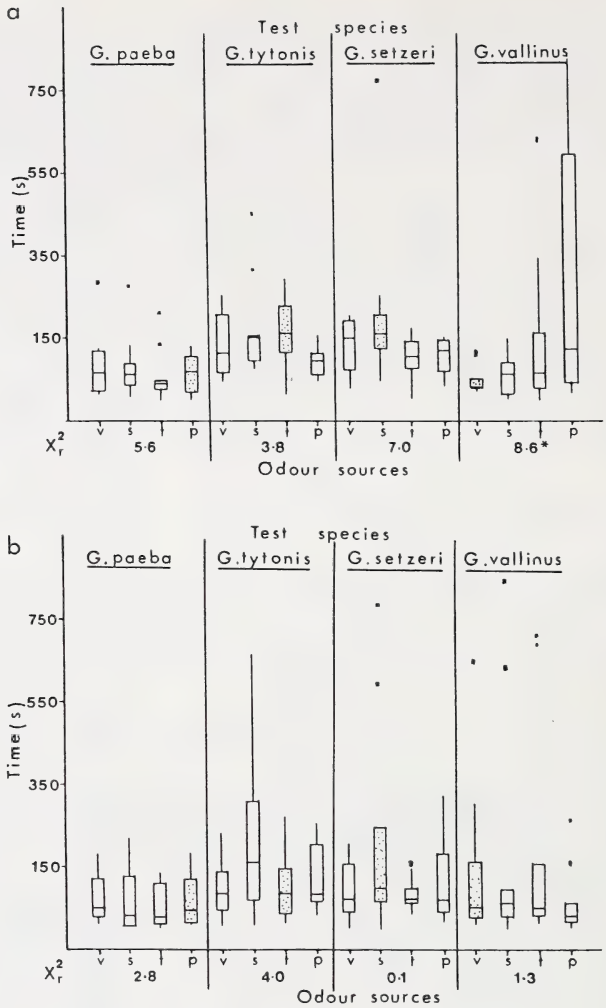


Fig. 3. Durations of visits made by a) females to odours of males (n = 10 for each species); b) males to odours of females (n = 10 for each species). ✳ = $p < 0.05$; all other X_r^2 values not significant

Results of Experiment II are shown in Fig. 3 a) and b) and Table 3. Numbers of visits to different odours did not differ significantly in any species or sex, and high probability values were calculated in all tests. Durations of visits varied significantly in only one species; *G. vallinus* females avoided conspecific odours and preferred male *G. paeba* odours. Female *G. setzeri* preferred conspecific odours, and this result approached significance at the 95 % probability level.

Results of Experiment III are shown in Fig. 4 a) and b) and Table 4. No significant differences were noted in the number of visits made to female odours by males. *G. setzeri* males spent more time near conspecific odours, but differences for this and other species were not significant.

Female *G. setzeri* visited male *G. vallinus* odours significantly more frequently than male *G. setzeri* odours, but durations of visits were not significantly different. *G. vallinus*

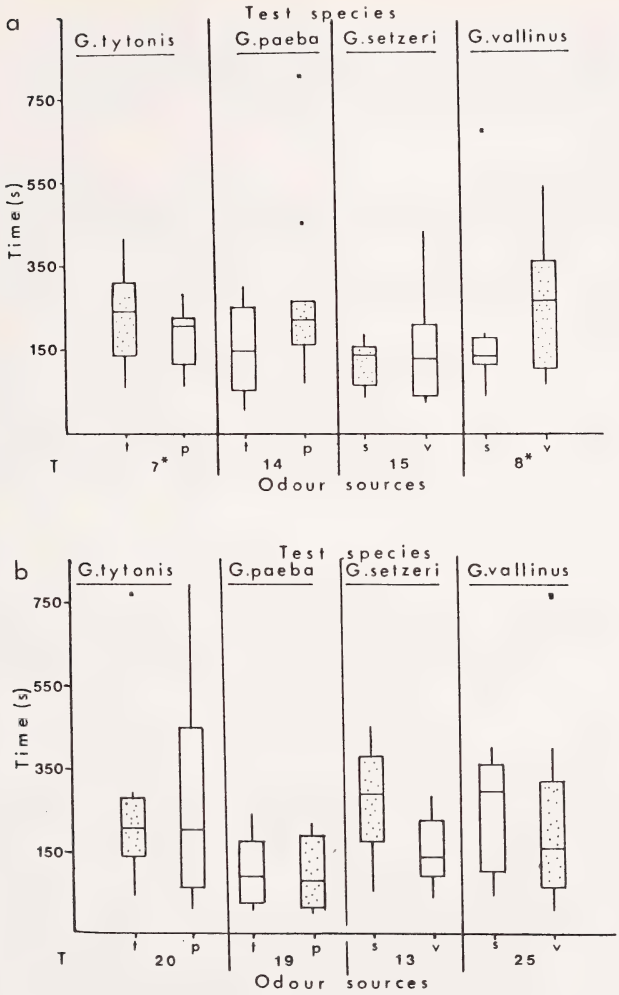


Fig. 4. Durations of visits made by a) females to odours of males (n = 9 for *G. vallinus* and *G. setzeri*, n = 10 for *G. paeba* and *G. tytonis*); b) males to odours of females (n = 10 for all species). ✳ = $p \leq 0.05$, all other T values not significant

and *G. tytonis* females visited conspecific odours significantly more frequently and for a longer time than heterospecific odours. Female *G. paeba* preferred conspecific odours, but this difference was not significant.

Discussion

Male *Gerbillurus* spp. showed more discrimination when they were prevented from making contact with the odour source, while females showed more discrimination when they were able to make contact with the odour source. Sexual dimorphism of odours is indicated by these results, as occurs in other rodent species (Nyby 1982). Male rats demonstrated a preference for odours of oestrus females over dioestrus females, but this preference disappeared when males were allowed physical contact with the odour source.

A similar effect occurred in mice and hamsters, and may partially account for differing results obtained by different researchers (Nyby 1982).

Nyby (1982) has suggested that a volatile chemosignal which serves as a long-range sex attractant is produced by several female rodent species; male response to this signal is dependent on previous sexual experience. For *Gerbillurus* species, a volatile chemosignal of females appears to exist.

Male *Gerbillurus* spp. discriminated less clearly among odours of oestrus-induced females than among untreated female odours. Artificial induction of oestrus in female *Gerbillurus* rarely resulted in copulatory behaviour, although 80 % of females had vaginal smears which were devoid of leucocytes after hormone treatment (Dempster and Perrin 1989b). The lack of response of male *Gerbillurus* may have been due to failure to induce oestrus effectively.

Response to the volatile chemosignal of oestrus female rats, mice, and hamsters appears to be dependent on prior sexual experience of males (Nyby 1982). Animals used in this study were wild-caught as adults and rarely bred in captivity (Dempster and Perrin 1989b). Thus, lack of sexual experience may have contributed to the present results. However, male *Dipodomys merriami* and *M. unguiculatus* did not prefer the odour of urine from oestrus or prooestrous females to that of non-oestrus females (Gregg and Thiessen 1981; Randall 1983).

Male odours accelerate puberty in juvenile female rodents of a number of species (Brown 1985). Oestrus female *D. merriami* (Randall 1983) and *M. unguiculatus* (Gregg and Thiessen 1981) preferred urine of intact males to that of castrated males, and oestrus female *Spalax ehrenbergi* preferred homochromosomal odours of cage litter or urine (Nevo et al. 1976). In *Gerbillurus* species, females were more discriminating if they were permitted to make contact with the odour source, indicating that they were responding to non-volatile chemosignals. However, few results were statistically significant. The oestrous condition of female *Gerbillurus* may have influenced the present results. Anoestrus female *S. ehrenbergi* did not discriminate among male odours (Nevo et al. 1976). Oestrus female *D. merriami* (Randall 1982) and *M. unguiculatus* (Gregg and Thiessen 1981) showed greater response to intact male urine than did anoestrus females.

Although discrimination as measured by time occurred in a few species, this did not always indicate a preference for the odour of conspecifics. Males preferred conspecific odours in 6/16 test situations, and females preferred conspecific odours in 6/12 test situations, but differences were significant in only 3/28 test situations. Male *G. tytonis* preferred injected conspecific odours in Experiment I; female *G. vallinus* and *G. tytonis* preferred conspecific odours in Experiment. III. Other significant results were ambiguous: female *G. vallinus* preferred male *G. paeba* and avoided conspecific odours, male *G. tytonis* preferred untreated female *G. setzeri* odours, and female *G. setzeri* preferred male *G. vallinus* odours in Experiment III.

Results of two-way choice tests were similar to those obtained in Experiment II. Thus lack of detection of olfactory preference was not due to confusion resulting from a testing procedure which was too complex. Using freshly-collected odours in Experiment III also had little effect on the results, indicating that lack of conspecific preference was not due to bacterial decay of chemosignals.

The results presented here negate the hypothesis that *Gerbillurus* species identify conspecifics by response to deposited chemosignals. *Gerbillurus* differed considerably from some other rodent species, which differentiated among odours of individuals (Johnston 1982; Young 1988). Male bank voles preferred the scent of their own race (Godfrey 1958) and mated preferentially with their own race. House mice, however, did not differentiate among individuals of other populations (Perrigo and Bronson 1983). Several studies have investigated olfactory discrimination as a sexual isolating mechanism in *Peromyscus* species and subspecies. Oestrus female *P. maniculatus bairdi* and *P. leucopus*

noveboracensis preferred conspecific male odours (Doty 1972). Moore (1965) has suggested that species discrimination of odours has evolved in *P. maniculatus* because of coexistence with other *Peromyscus* species, while no conspecific preference was exhibited by the geographically-isolated *P. polionotus.* Male *P. eremicus* and *P. californicus* from areas of sympatry showed stronger preference for conspecific odours than did allopatric animals (Smith 1965).

Gerbillurus individuals used in this study were from geographically separated populations. Detailed data on distribution of *Gerbillurus* species is lacking, but areas of sympatry and allopatry do exist (Boyer 1988; Erasmus in litt.; Griffin in litt.). Results presented here suggest that species discrimination of deposited chemosignals has not evolved in allopatric populations. *Gerbillurus* species produced small volumes of urine (Downs and Perrin pers. obs.) and few sudoriferous glands were found in the skin of *G. paeba* (Green 1988). Nasonasal sniffing was frequently observed in staged male-female encounters; anogenital sniffing occurred more rarely (Dempster 1986). Randall (1982) reported that male *D. merriami* were attracted to the vaginal odour of oestrus females, but needed to actually sniff the female's vaginal area before responding. The present results suggest that deposited chemosignals play a limited role in species discrimination in *Gerbillurus* species; physical contact with a potential mate may be necessary.

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Zusammenfassung

Zwischenartliche Geruchsunterscheidung bei vier Gerbillurus-Arten

Die geruchliche Unterscheidung zwischen Angehörigen der vier Arten der Gattung *Gerbillurus* wurde bei Männchen und Weibchen aller dieser Arten untersucht. In Vierfachwahlversuchen konnte sich jedes Versuchstier für den Geruch eines Tieres des entgegengesetzten Geschlechts von *G. paeba, G. tytonis, G. setzeri* oder *G. vallinus* entscheiden. Hatten die Versuchstiere keinen Zugang unmittelbar zur Geruchsquelle (imprägniertem Sand), unterschieden die Männchen deutlicher als die Weibchen. Aber nur männliche *G. tytonis* bevorzugten signifikant den Geruch konspezifischer Weibchen. Die Männchen unterschieden weniger deutlich zwischen Weibchen, die hormonell behandelt worden waren, um bei ihnen Oestrus zu induzieren.

Durften die Versuchstiere die Duftquelle berühren, unterschieden die Weibchen deutlicher in Zweifach- als in Vierfachwahlen. Im Zweifachwahlverfahren bevorzugten weibliche *G. tytonis* und *G. vallinus* signifikant arteigene Gerüche.

Vermutlich reagieren die Männchen auf flüchtige Duftstoffe der Weibchen, unterscheiden aber weniger deutlich, wenn sie die Duftquelle beriechen können. Die Weibchen reagierten auf nicht flüchtige, von den Männchen abgegebene chemische Signale, zeigten aber kaum eine Bevorzugung der Gerüche von Artgenossen. Der physische Kontakt zwischen den Tieren ist vermutlich zum sicheren Erkennen des Artgenossen notwendig.

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Sparring in White-tailed deer *(Odocoileus virginianus)*

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Abstract

The occurrences of sparring, aggressive, and sexual behavior in bucks of different antler classes were studied in a white-tailed deer *(Odocoileus virginianus)* population in Virginia from September 11 until December 31 1983. Sparring activity showed two distinct peaks. One preceded the rut, the other was observed at the height of the rut. At the first peak bucks of higher antler classes predominated whereas bucks of the lower antler classes were mainly involved at the second peak. Most aggressive behavior was recorded at the height of the rut. Bucks of higher antler classes showed significantly more aggressive behavior than bucks of lower antler classes. Sexual behaviour was predominantly shown by bucks of higher antler classes. Our findings confirm the assumption that sparring in older males serves to establish a social hierarchy before the actual breeding season starts. In young bucks sparring could serve as means to gain fighting and social experience. During the height of rut aggressive postures were employed by older males to confirm their rank and to achieve access to females in estrus.

Introduction

The shape and mass of antlers can play an important role in determining the social rank of cervids. While shape and mass of antlers in red deer *(Cervus elaphus)* are relearned every year by „Fighting Play" and „Shadow Fighting", recognition of the relative status value of the own and of other antlers has to be obtained by sparring (Bubenik 1968). Sparring behavior in connection with the rut has been observed and described in many cervids, including North American moose *(Alces alces)* (Geist 1963); Axis deer *(Axis axis)* (Schaller 1967); white-tailed deer *(Odocoileus virginianus)* (Brown 1971; Hirth 1977; Michael 1968), and mule deer *(Odocoileus hemionus)* (Kucera 1978; Wachtel et al. 1978) and many other cervids. In white-tailed deer, despite the extensive literature on behavioral aspects of this species, few detailed and quantitative data analyzing the role of sparring are available. Hirth (1977) concluded that sparring permits the establishment of a hierarchy before the actual breeding season starts and that older bucks participated more in sparring early in the breeding season than later on. The literature on sparring in mule deer is more extensive and detailed (Kucera 1978; Wachtel et al. 1978; Koutnik 1983). Koutnik (1983) suggested that dominant bucks initiate sparring to reinforce their social status prior to the breeding season, thus insuring access to females, and that sparring in young bucks primarily serves as a means to gain social experience by interacting with older bucks in a relatively low risk, ritualized agonistic encounter. Kucera (1978) and Wachtel et al. (1978) came to similar conclusions.

The purpose of this study was a.) to provide quantitative data on sparring in white-tailed deer b.) to correlate frequencies of sparring with frequencies of aggressive and sexual behavior and c.) to differentiate between bucks of different antler classes in these behavior categories.

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Study area and methods

The National Zoological Park's Conservation and Research Center is located south of Front Royal, Virginia. The study area encompasses 510 ha and was partially enclosed by a 1.8 to 2.5 m high chain-link fence. Since no hunting has been allowed since 1974, except a controlled hunt in 1981, and there was only little predation by domestic dogs, population density increased up to 0.44 deer per ha in 1983 (Stüwe 1986). In order to reduce the density, several 30 meter sections of the fence were removed in October 1983.

The topography with ridges, hollows and steep slopes varies in elevation from 250–650 m. Eighty percent of the area is convered by mixed hardwood forest, the rest by meadows. The vegetation was severely damaged by overbrowsing and bark stripping.

Field observations were conducted from 11 September until 31 December 1983 as part of a telemetry study on the breeding season of white-tailed deer (Fleischer and Schwede 1985; Hölzenbein and Schwede 1989), and resulted in 88 hours of direct behavioral observations. Additional behavioral observations were made during 1248 hours of radio-tracking.

The study began when the first buck was seen in hard rack and ended when the first buck dropped his antlers. Observations were made during the evening hours from treestands or vehicles using 8 × 56 binoculars and a 30 × 75 spotting scope.

The behavior patterns recorded (Tab. 1) were classified in three categories: 1. sparring, 2. aggressive behavior, and 3. sexual behavior. Detailed descriptions of all behavior patterns were given previously by Thomas et al. (1965), Michael (1968), and Hirth (1977). In order to detect changes in behavior frequencies over time, the study was divided into 14 eight-day periods. The division into eight-day periods was a result of a specific data collection schedule serving different objectives of the study. The rut was defined by the first (21 Oct. 83) and the last (7. Dec. 83) occurrence of courtship pursuit (Michael 1965). The time before the rut (11 Sep.–21 Oct.) is termed "PRE RUT", the time after (7–31 Dec.) as "POST RUT".

Table 1. **List of the observed behavior patterns**

1. Sparring	
2. Aggressive behavior	
a. Low aggressive behavior	– Hard look ear drop
	– Head low threat
	– Head high threat
b. High aggressive behavior	– Sidle
	– Rear
	– Strike
	– Chase
c. Specific rutting postures	– Present threat
	– Rush
3. Sexual behavior	– Courtship pursuit
	– Tending

Since the level of interaction and aggression may have influenced group composition, interaction rates were calculated for all groups consisting of at least one male and one female or two males. The method of calculation follows that of Struhsacker (1967b). These rates express interactions within a group on a pair-minute basis. Pair-minutes are the number of different pair combinations of animals within a group multiplied by the number of minutes the group was observed. The rate of interaction per pair-minute was corrected for groups of different size and observations of varying length.

The size of antlers and number of points proved to be a good indicator of relative size and condition of bucks. Usually 10-point bucks were larger than 8-point bucks, and 8-point bucks were larger than 6-point bucks, etc. Therefore, based on the total number of points, including brow tines, bucks were classified into seven different antler size classes (ASC) (Tab. 2). Because of considerable variation in body and antler size within the 8-point class, this group was split up into three subclasses,

Table 2. **Antler class categories**

Antler class	Number of points
1	2
2	4
3	6
4	8 (s)
5	8 (m)
6	8 (l)
7	>8

termed small (s), medium (m) and large (l) according to body size and antlerbeam length. By comparing the size and form of antlers, as well as body size of all bucks to 13 well known marked individuals, bucks of ASC 1–4 were classed as young (yearling to 3.5 year old) and ASC 5–7 as old bucks (3.5 and older). All possible pair combinations were analyzed among bucks of all antler classes and between does and members of the seven antler classes. Thus, we were able to partition the overall interaction rate of one observed group into rates for each of the possible antler class-sex pair combination.

Frequencies of sparring, aggressive, and sexual behavior were compared to a uniform distribution using the Kolmogorov-Smirnov test. Observed and expected participation of bucks of each antler class were compared using the Chi-square goodness-of-fit test. Results were considered significant at $P \leq 0.05$. Expected participation was calculated from the total time bucks of each antler class were observed in a group.

Results

Sparring

Sparring matches were initiated when one buck presented antlers to another, and the second buck responded similarly. Such an antler presentation never involved the "hard look ear drop" seen in aggressive encounters. After presenting their antlers both bucks moved forward and engaged their antlers. Then they twisted their heads from side to side while pushing against each other. Matches were terminated when one or both bucks simply disengaged their antlers or one was forced to jump away. Losers of such matches were never seen being pursued, as in aggressive encounters. While all observed sparring matches appeard playlike, the intensity of sparring matches varied: mild matches involved only

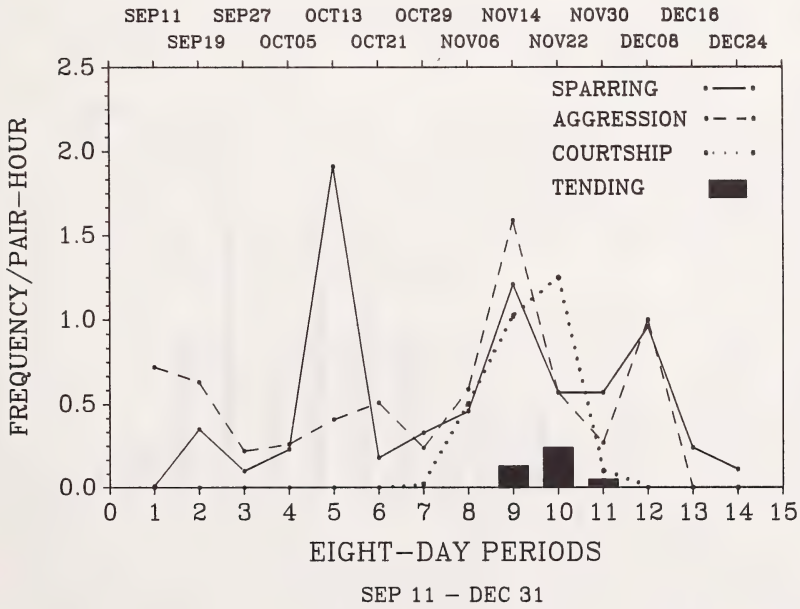

Fig. 1. Seasonal changes in the frequencies of sparring and aggression (buck/buck hours, n = 220.9 h), courtship pursuit and tending (buck/doe hours, n = 483.9 h) over eight-day periods

touching of antlers. Matches of moderate intensity involved head twisting and pushing back and forth. In violent matches the winner pushed the opponent several meters away or threw him off balance. In most mild and moderate matches no winner could be determined. Mild intensity matches usually occurred when opponents differed in ASC or when both sparring partners were of low ASC.

An unusually long encounter involving five sparring matches took place on 30 October between bucks of ASC 4 and 5. Both bucks sparred over a period of 70 minutes, and matches varied in length from 20 seconds to 4 minutes. The smaller buck initiated each time and displayed the submission posture after each match. As soon as a match ceased, both bucks resumed feeding, until the smaller one initiated the next match by licking the muzzle region of the larger buck.

A total of 94 sparring matches were observed from 24 September, (two weeks after the first buck was seen in hard rack) to 27 December (two weeks before the first buck dropped his antlers). Distribution of sparring matches over the 14 periods showed significant differences (DN = 0.615, $p < 0.05$) (Fig. 1). Two peaks of sparring activity were observed, one in period 5 preceding the breeding season and the other subsequent to it in period 9. Sparring activity was higher at the first peak than at the second peak. At the end of the rut in period 12 there was a third peak at a lower level. Sparring activity was low when the most sexual behavior was observed in period 10.

Until period 5 bucks of higher antler classes (ASC 5–7) participated in most (76 %) sparring matches (Fig. 2). After period 5 younger bucks of lower antler classes (ASC 1–4) became more prominent in sparring. They were engaged in 76 % of all observed matches during the actual rut. No sparring activity in older bucks was observed when most sexual behavior was recorded (period 10). All bucks did not participate equally in sparring matches. A Chi-square goodness-of-fit test indicated a significant difference ($\chi^2 = 19.03$, df = 6, $p < 0.01$) between the antler class frequency of bucks in sparring matches and the antler class frequency of all bucks (Fig. 3).

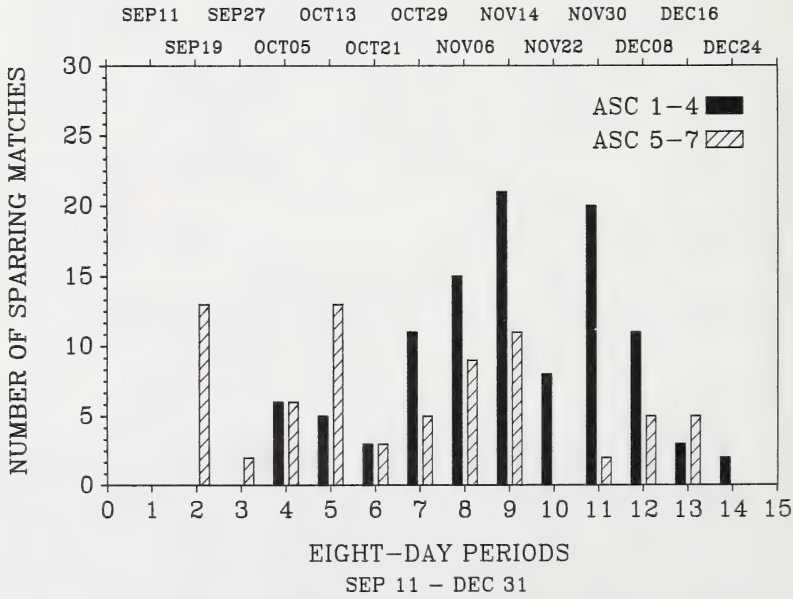

Fig. 2. Seasonal changes in the absolute number of sparring matches involving young (ASC 1–4) and old (ASC 5–7) bucks

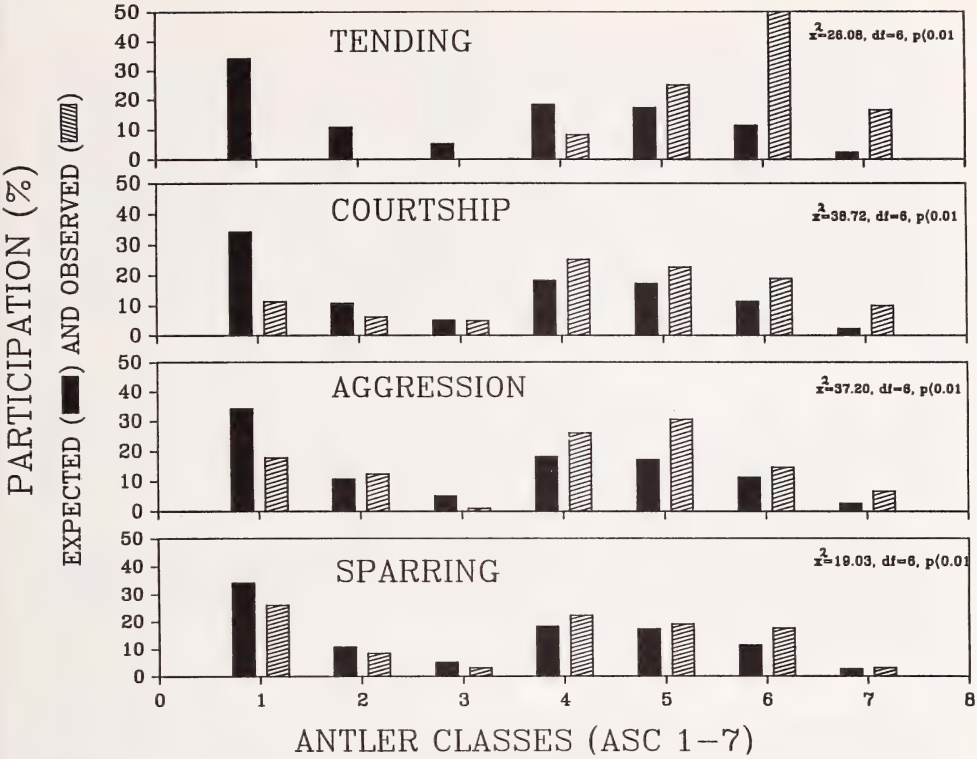

Fig. 3. Overall percentage of participation of each antler class in sparring behavior, aggressive behavior, courtship pursuit and tending. Expected frequencies are based on the total time each antler class was observed in a group

Sparring matches tended to occur between individuals of different antler size classes (Tab. 3). In 71 % of all matches partners of different antler size classes were involved. Smaller bucks challenged larger bucks to spar more often than vice versa. Before challenging a partner of a higher antler class, bucks, in particular contestants of ASC 1–4, licked the muzzle-forehead region, before presenting their antlers. Bucks sparring with opponents of smaller size seldom did more than rattle antlers with them rather than sparring more vigorously as they did with a partner of equal size.

Table 3. **Pair combinations of sparring matches**
Total number of matches is 94

	Antler classes						
	1	2	3	4	5	6	7
1	12	5	3	9	6	–	2
2		1	1	–	5	3	–
3			–	2	1	–	–
4				3	10	10	4
5					2	10	–
6						5	–
7							–

Aggressive behavior

A total of 88 aggressive interactions between bucks were recorded. In 72.2 % of these interactions low aggressive postures were observed. Only 21.6 % were classified as high aggressive and 5.7 % as specific rutting postures. The overall distribution of aggressive postures differed significantly (DN = 0.615, $p < 0.05$) (Fig. 1). After an initial decline towards period 4 the frequency increased slightly at the beginning of the rut in period 6, before dropping in period 7. Most aggressive behaviour was observed in period 9 just before the height of the rut. Participation in aggressive behavior was not equally distributed among all seven ASC (Fig. 3). Bucks of higher ASC showed aggressive behavior at a significantly higher rate than expected, whereas bucks of lower ASC showed less aggressive behavior than expected $\chi^2 = 37.20$, df = 6, $p < 0.01$).

Sexual behavior

Courtship pursuit was observed 79 times between period 6 and period 13. The frequency increased significantly (DN = 0.769, $p < 0.01$) in period 9 and reached its peak in period 10 (Fig. 1). A similar trend at a lower level was indicated by the distribution of 12 tending bonds witnessed between period 9 and period 11 (Fig. 1).

Bucks of all ASC participated in courtship, whereas, in tending, only bucks of ASC 4–7 were involved (Fig. 3). A significant difference in courtship ($\chi^2 = 38.72$, df = 6, $p < 0.01$) and tending ($\chi^2 = 26.08$, df = 6, $p < 0.01$) was found between expected and observed participation.

Discussion

Environmental factors including the photoperiod influence the timing of the breeding season (Goss 1969a, b). The period prior to the breeding season is characterized by rapidly increasing testosterone levels, correlated with the shedding of velvet and an increase in testicular volume (Lincoln et al. 1972; McMillin et al. 1974). The peak output of testosterone is reached by the middle of October, two months before the peak of the rut. At this time we observed an increase in sparring activity and a decrease in aggressive behavior. The coincidence of the reported peak of testosterone and the observed high frequency of sparring activity could imply that sparring is dependent on high levels of testosterone. By replacing aggressive behavior which increases until the shedding of velvet (Thomas et al. 1965), sparring could serve to establish a dominance hierarchy among bucks as soon as they can use their antlers. By participating in sparring matches as soon as the velvet is stripped, bucks can relearn the shape and recognize the status value of their own and other antlers (Bubenik 1968). During the first five periods until sparring activity reached its highest frequency, older males (ASC 5–7) predominated in sparring matches. This preponderance of older males in sparring at this time, supports the wide spread assumption that one function of sparring is the establishment and reinforcement of the social hierarchy before the actual breeding period starts (Hirth 1977; Townsend and Bailey 1981; Koutnik 1983). Expending energy in sparring at this time to establish a rank in the hierarchy instead of during the rut may be bioenergetical efficient (Koutnik 1983, for mule deer), since older males expend considerable energy during the rut by looking for does in estrus. The function of sparring to define positions in the hierarchy was also reflected in the intensity of sparring matches. Most of the matches at this time, involving contestants of higher and more evenly matched ASC, were of moderate to violent intensity with an obvious loser and winner. The lower participation (24 %) of older bucks at the second peak and after the rut coincides with findings by Koutnik (1983) on mule deer and is probably related to their predominant participation in aggressive behavior and almost exclusive participation in sexual behavior at this time. The increased aggression in older

bucks at the height of the rut is probably based on the access to and defense of females in estrus, as in the maintenance of the hierarchy assuring the strongest males the highest reproductive success. During this time, when bucks have only little excess energy and dominance relationships are well established, energy conservative, low intensity threat patterns are more efficient than energy and time consuming sparring matches to achieve those goals.

A frequent participation of young males in sparring matches is apparently common in Cervids *(Alces alces)* (Geist 1963), white-tailed deer *(O. virginianus)* (Brown 1971; Hirth 1977; Michael 1968; Ozoga and Verme 1985) and mule deer *(O. hemionus)* Kucera 1978; Wachtel et al. 1978; Koutnik 1983). The difference between observed and expected sparring in younger, lower ranking bucks in our study could be partly due to the history of the population. High population density as well as limited chance for emigration and immigration until October 1983 could have enhanced social stability (Bartos and Haynek 1982). Stüwe (1986) who studied the behavior and ecology of the resident population, hypothesized that the high density of dominant males caused young males (ASC 1–4), independently exploring the vicinity of their mothers, to retreat to familiar ranges. Home range data on 6 young males (ASC 1–4) showed that all stayed in their mother's home range (Fleischer and Schwede 1985) throughout the breeding season and even into the following year. Other studies have demonstrated that these age classes are most likely to disperse (Hawkins et al.; Nelson and Mech 1984). By staying close to their mothers and suppressing, to a certain extent, any rutting behavior, they may have provoked less pressure from older males. Ellenberg (1978) reported for roe deer, that young males that were not aggressive and behaved "female like" were chased and attacked less than more aggressive ones. We conclude that social pressure may have caused a reduction in sparring activity in younger bucks.

The observed predominance (76 %) in sparring of young males that displayed only little agonistic and sexual behavior, at the second peak and after the rut could be proximately related to a more gradual decline in their plasma testosterone levels. Leader-Williams (1979) found some evidence in reindeer that older males show a rapid decline in plasma testosterone levels immediately following the rut whereas younger males show a more gradual decline from peak values. Data by Stüwe (1986) showing that, in 1983, yearling bucks stripped their velvet three weeks later than adult bucks, support this. Ultimately sparring in young males probably serves as means to gain social experience by interacting with other males. By participating in sparring with partners of higher ASC, characterized by a great tolerance of the larger bucks and play like behavior, the young bucks can probably test their strength, establish their position in the hierarchy (Hirth 1977) and learn the use of antlers as visual status cues (Schaller 1967, Geist 1971) without taking the risk of injuries. In younger bucks the frequently observed licking of the muzzle-nose of the older bucks before sparring could have been a submissive signal from the subordinate to assure their tolerance and reduce possible aggressive responses following the presentation of antlers. Sparring between bucks of different antler classes accounted for 71 % of all encounters indicating that bucks tend to spar with closely matched, but not identical, partners. Similar results were reported by Michael (1968) and Brown (1974). Maynard Smith and Parker (1976) suggested that asymmetric conditions of opponents in a contest usually give some advanced information about the probable outcome of the encounter thereby avoiding an escalation. Escalation is predicted to occur only if opponents are closely matched or information about the asymmetry is imperfect (Maynard Smith and Parker 1976). Our data support their suggestion by showing the asymmetry of sparring partners and the characteristic of matches. As Koutnik (1983) reported for mule deer, the intensity of sparring matches seemed to be related to the antler class of the participants. The greater the difference in ASC, between opponents, the milder the intensity of the match. Violent matches were only observed between closely matched partners.

Acknowledgements

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Zusammenfassung

Kampfspiele beim Weißwedelhirsch (Odocoileus virginianus)

Vom 11. September bis 31. Dezember 1983 wurden an einer Weißwedelhirschpopulation in Virginia Daten zum Kampfspiel, zum aggressiven und zum sexuellen Verhalten erhoben. Anhand von 88 Beobachtungsstunden wurden die Verhaltenshäufigkeiten und die Beteiligung von Männchen verschiedener Geweihklassen verglichen. Die Häufigkeitsverteilung der Kampfspiele zeigte zwei deutliche Gipfel. Beim ersten Gipfel, der vor der Brunft lag, waren zu 76 % die Männchen höherer Geweihklassen beteiligt. Beim zweiten Gipfel, der während des Höhepunktes der Brunft auftrat, waren es hauptsächlich (76 %) die Männchen unterer Geweihklassen, die an den Kampfspielen teilnahmen. Aggressives Verhalten wurde am häufigsten zum Höhepunkt der Brunft beobachtet. Bei Männchen höherer Geweihklassen lag die Häufigkeit der aggressiven und sexuellen Verhaltensweisen signifikant höher als bei Männchen unterer Geweihklassen. Die Ergebnisse bestätigen die Annahme, daß bei älteren Männchen eine der Funktionen von Kampfspielen darin liegt, die Rangordnung festzulegen, bevor die eigentliche Brunft beginnt. Während der Hauptbrunftzeit, wenn die meisten Weibchen in den Östrus kommen und die Rangordnung relativ stabil war, zeigten die älteren Männchen vermehrt aggressives Drohverhalten, um ihren Rang zu behaupten und Zugang zu den Weibchen zu erhalten. Für die jüngeren Männchen, die nur wenig aggressives und sexuelles Verhalten während der Brunft zeigten, ist die Funktion von Kampfspielen mehr in dem Gewinn sozialer Erfahrungen sowie dem Erlernen der Bedeutung und der Benutzung des Geweihs zu sehen.

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Marking behaviour and dominance in Suni antelope *(Neotragus moschatus)*

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Abstract

Studied the antorbital gland, pedal gland and elimination product marking in 3 groups of captive suni *(Neotragus moschatus)*. Antorbital gland marking was performed almost exclusively by dominant (territorial) males and gas chromatograms of dominants marks differed from subordinates. Marking posts are short vertical twigs in open areas away from paths, with highly visible bulbs of deposit and arranged in concentric rings. Their unusual distribution may be associated with the suni's specialised forage. Based on site marking frequency, marks last 4 days. Strange secretions are recognised but not marked over. Pedal gland marking was assumed to be highest on paths, a characteristic feature of suni territories. Paths had a consistent density independent of enclosure size. Midden sites do not appear to serve a marking function. Strange elimination products are marked over by the dominant male. The findings are discussed in relation to the "scent matching" hypothesis.

Introduction

Suni *(Neotragus moschatus)* are one of the smallest of the antelopes with a mean shoulder height of 350 mm and a mean mass of 5 kg (Smithers 1983). The species has a patchy distribution throughout the eastern regions of Africa in areas where the preferred habitat – dense woody vegetation with a high stem density in the shrub layer and low ground cover – is present (Lawson 1986). Ansell (1971) recognises five subspecies. This study was conducted on the most southerly of the five, *N. m. zuluensis* (Thomas 1898) which is distributed along the coastal area of Natal northwards to southern Mozambique and Zimbabwe (Heinichen 1972).

Very little is known about the behaviour of the suni, which is listed in the South African Red Data Book as being an endangered species. Its ecology in Natal-KwaZulu has been studied in detail by Lawson (1986). However, owing to its small size and shy habits, detailed observations on various behaviour pattern complexes are either sparse or lacking, especially information on marking behaviour.

Suni possess at least three means of indicating their presence olfactorally. These are the secretions from the extremely large antorbital glands, secretions from the pedal glands and elimination products, which are usually deposited in middens. Antorbital glands differ widely in size, type and functional ability in Artiodactyls (see Gosling 1985 for a review) but are conspicuous in all Neotraginae. These, together with the duikers (Cephalophinae), are classified by Jarman (1974) as category A species and hold either individual or pair territories.

The use of olfactory cues to indicate spatial tenure is widespread amongst mammals (Müller-Schwarze 1971; Stoddart 1976; Leuthold 1977; Brown 1979; Brown and MacDonald 1985) and scent marking has been shown to be associated with dominance or intolerance of conspecifics in a number of species (see Ralls 1971 for a review). Suni are territorial with partial overlap between territories of male and female (Lawson 1986). This

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study investigates the olfactory means by which territory occupancy could be indicated. Heinichen (1972) was unable to observe marking behaviour in a free-living Kenyan suni population but hypothesised, on the basis of deposits found, that territorial males marked objects in their territories. Lawson (1986) reports that, in captive groups, scent marking comprises 0.3 % of the male total activity patterns and 0.1 % of those of females in winter (July) but marking is infrequent (absent?) in summer (Dec.–Jan.). No further reference to marking in this species exists.

Material and methods

The study was conducted on 4 captive groups of suni held at De Wildt Cheetah Research and Breeding Station near Brits, Transvaal. The group size and composition was as follows (M = male, F = female): Group A – 1M, 2F; Group B – 1M, 2F; Group C – 4M; Group D – 3M. Heterosexual groups were held in enclosures of 290 m^2 while male bachelor groups had enclosures of 80 m^2. A covered shelter, bushes and trees were present in each enclosure and enclosures were separated from one another by a 2 m high wooden fence. Observations were conducted from a hide at one end of the enclosure. Apart from the natural forage present, the animals' diet was supplemented with lucerne and antelope pellets and water was available ad libitum.

Observations were conducted on 3 different groups (A, B, C) from mid-February to mid-September for a total of 101 hours, with observation periods being arranged to cover the entire timespan from 0630 to 1800 h. All instances of marking with the antorbital glands were recorded together with the duration, location, sequence of behaviour patterns performed and the individual performing them. Since marking with the pedal glands is considered to occur passively when the animals walk (Gosling 1985), no quantitative data on marking frequency by this means could be obtained, although the paths used by the animals in the enclosure were mapped. Practically the entire enclosure was used, however, when the animals foraged.

To determine the responses of animals to foreign marks, two marking posts were moved from group C's enclosure to group A's on different occasions and the behaviour of the animals encountering the mark recorded for 1 h after introduction of the marking post.

A series of experiments were performed to ascertain the role of middens as olfactory territorial marking sites (Rasa 1973). To determine whether middens were site specific, the original midden site was thoroughly cleaned and covered with fresh sand in group A and group B's enclosures and the elimination products removed to a site 2 m away. To determine whether personal elimination products alone acted as attractive elements in the choice of elimination sites or whether faeces and urine of strange individuals were also attractive, the middens in the same 2 enclosures were thoroughly cleaned, as above, and the elimination products of another group placed at a different site, also 2 m away. In all cases, the behaviour of the animals was recorded for 1 h after manipulation. Each set of experiments was conducted once in each of the two enclosures to minimise disturbance effects. Faeces quantity at the sites was estimated visually at 24 h intervals for comparison of site usage. Since a large and variable number of small pellets are produced at each defaecation, the actual number of defaecations could not be measured.

Although suni are active throughout the 24 h period (Lawson 1986), observations could only be conducted between 0630 and 1800 h, the hours of winter daylight. Quantitative data on marking frequencies are therefore probably biased towards low values since only the diurnal part of the activity cycle could be monitored.

To ascertain whether differences were present in the marking substances from the antorbital glands of dominant and subordinate animals, marking posts were collected for analysis of volatiles by the dynamic solvent effect (see Apps et al. 1987 for the chromatographical sampling techniques used). Posts were removed shortly after they had been actively marked and placed in closed test-tubes on crushed ice until analysed. Two samples were taken from the dominant male in group C, one from the dominant male in group D and two from two subordinate males in group D.

Statistical tests used are mentioned at appropriate points in the text.

Results

Marking behaviour

Antorbital gland marking consisted of a sequence of behaviour patterns with a mean duration of 7.5 sec (range 1.5–24 sec, n = 111). The four behaviour patterns involved were 1. olfactory monitoring of the marking post (sniffing), 2. insertion of the tip of the marking

post into one of the everted antorbital gland pouches and moving the head vertically with a short jerky motion (mean = 1.09 strokes, range = 1–4 for a mean duration of 2.2 sec, range = 1.5–8.5 sec) termed marking, 3. licking the marking post and 4. insertion of the tip of the tongue into the antorbital gland (licking gland).

Of the 141 observed contacts with marking posts, 21 % consisted of olfactory monitoring only. For the 111 cases of antorbital gland marking recorded, olfactory monitoring of the marking post preceded marking on 104 (93.7 %) of the occasions. By far the majority of contacts with marking posts consisted of olfactory monitoring followed by marking only (58.6 %). All 20 cases where animals were observed to lick their antorbital glands followed marking of the post. For the 9 records of licking the marking post, 4 occurred after marking and 5 took place between olfactory monitoring of the post and marking. The sequence in which marking behaviour patterns occur in suni therefore appears to be highly stereotyped, only licking the marking post, a relatively uncommon behaviour, being variable in its sequential positioning. The basic sequence can, however, be repeated up to three times and fragmentation of the sequence can occur at any point during repetition.

During a single marking sequence, only one antorbital gland is used for marking. However, glands may be alternated in sequential marks. Of the 48 marks recorded for the territorial male in group A, 24 were performed with the left and 24 with the right gland. The male in group C, however, performed significantly more marks with the left gland than the right ($x_1 = 2$, $N = 14$, $p = 0.019$ Binomial Test). The frequency of left or right gland useage therefore appears to differ amongst individuals.

Self-anointing with the antorbital glands was not observed. Allomarking with these glands has been reported for several antelope species (Ralls 1974; Leuthold 1977). It did not occur in the suni groups studied, although licking of the partner's antorbital gland occasionally took place.

Marking posts

Antorbital gland marks are confined to definite marking posts. These were all firm, sharp objects such as twigs, sprouts of wild asparagus (*Protasparagus* spp.) and grass stalks, which appeared to have been bitten off close to the ground with a mean height of 75 mm (range 15 to 280 mm, n = 19). The secretion dried to a hard, greyish-black, crystalline substance that, due to accretion, formed highly visible bulbs of deposit.

Each enclosure contained numerous marking posts. The two 290 m^2 enclosures contained 41 and 65 posts each, the 80 m^2 enclosure contained 14. This gave a mean density of 0.184 ± 0.043 posts/m^2 i.e. approximately one post/5 m^2.

Posts were sited both singly and in groups. Of the 120 posts recorded for the three enclosures, 54 were within 1 m of each other with a distance greater than 2 m between them and their nearest neighbour. Groups had a mean size of 3.18 ± 1.33 posts (n = 17, range = 2–7).

There was significant tendency in the larger enclosures containing heterosexual groups for posts to be located more than 1 m away from regularly used paths. In enclosure A, only 10 of the 41 posts (24.9 %) were located near paths (Binomial Test, $x_1 = 10$, $N = 41$, $p = 0.001$), in enclosure B, 18 of the 65 posts (27.7 %) were near paths (Binomial Test, $x_1 = 18$, $N = 65$, $p = 0.0003$). In contrast, in the bachelor group in enclosure C, all 14 posts were sited within 1 m of paths. This finding could, however, be influenced by the small enclosure size (8 × 10 m). The vegetation also influenced marking post distribution. In enclosure A, none of the posts were in grass-covered areas and in enclosure B, only 2 were on the fringes of grassy patches (3.1 %). There was no grass in enclosure C. Posts therefore appear to be restricted almost entirely to areas of open ground and, at least in heterosexual groups, only a small proportion of posts are located near the network of regularly used pathways.

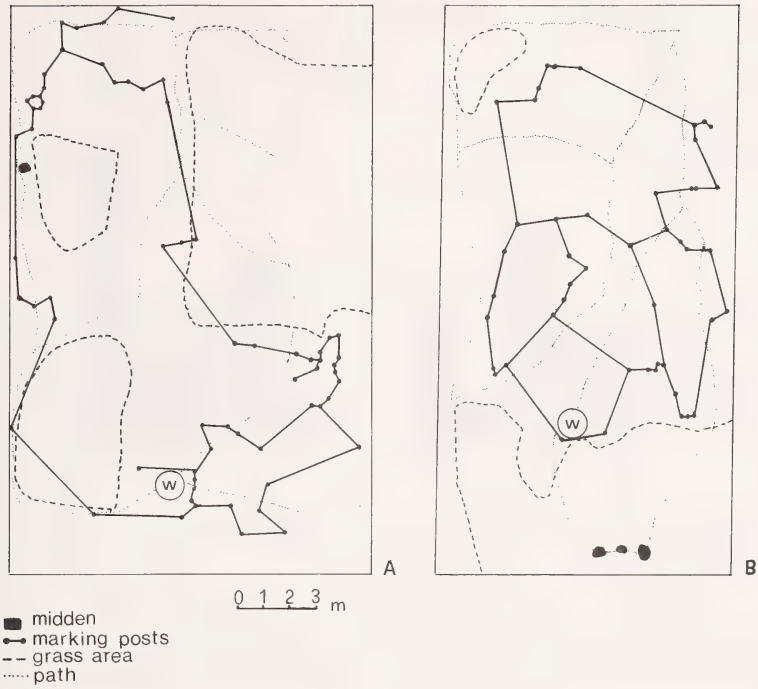

Fig. 1. Maps of enclosures A and B drawn to scale showing the pattern of marking posts, connected using the "nearest neighbour" method. These form concentric rings, especially obvious in enclosure B. No marking posts are present in grassy areas. The network of paths joining salient sites in the enclosures and the position of middens is illustrated. W = waterhole

Using the nearest neighbour method (Gośling 1981) to investigate the pattern of marking sites, a large ring of marking posts could be demonstrated in enclosures A and B (Fig. 1a and 1b). Since the animals were held in enclosures, the enclosure walls could be equated with the territory boundaries. The enclosure was, however, much smaller than the territory sizes mapped by Lawson (1986) for free-living suni. In the Tembe Elephant Reserve these varied from 0.49 to 3.61 ha. A second circle within the boundary circle, but containing fewer marking posts can also be constructed for both territories with connections between the two circles. In both enclosures, neighbouring groups, which were not visible but which could be detected by sound and odour, were present adjoining the whole length of the north and south walls of the enclosures. There appeared to be no tendency for a higher aggregation of marks to occur along these boundaries. In enclosure A, only 5 of the 41 posts were within 1 m of the N and S boundary fences with none located on the east and west sides. For enclosure B, 6 of the 65 posts were within 1 m of the N and S fences and 4 were adjacent to the E and W ones.

Frequency of marking

The frequency of marking by various individuals in the three groups A, B and C was recorded. The 9 individuals involved (5 M, 4 F) marked a total of 73 times in 67 observation hours. Of these, 67 (91.2 %) marks were made by the dominant males in each of the groups. The subordinate male which was second in rank in bachelor group C was observed to mark twice (2.7 %). The lowest-ranking male in this group was never

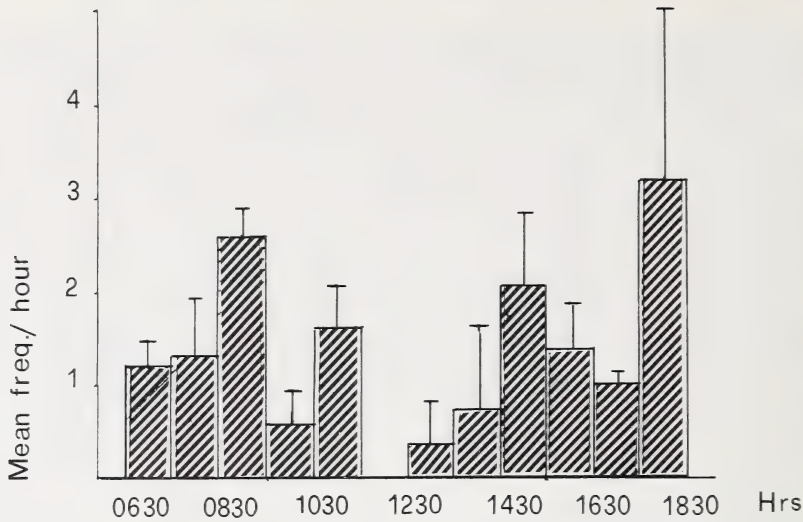

Fig. 2. Mean frequency of marking per hour, with standard deviations of the means, from sunrise to sunset during winter (February to September, 100 hours total)

observed marking. Only one of the 4 females, the dominant in group A, marked. This occurred 4 times (5.5 %) immediately after the original dominant male in the enclosure had been replaced by another adult male. (This exchange of breeding males is performed yearly to mitigate inbreeding effects.) These findings indicate that antorbital gland marking is performed almost exclusively by dominant males, although females do mark under exceptional circumstances.

An incidental observation which supports this is the change in marking frequency of the subordinate male in group C, mentioned above, after transfer to group D containing 3 young males. He assumed dominant status within 3 days and his marking frequency increased from 0.07 marks/h, observed in the original enclosure, to 8.57 marks/h in the new group.

To determine whether marking activity showed temporal patterning, data from all 4 groups were pooled and the mean frequency of marking/hour calculated for each hourly interval from 0630 to 1830 h. Marking showed two peaks of activity during the daylight hours (Fig. 2). The highest mean marking rate, however, occurred just prior to sunset and may indicate increased marking activity during the early evening. This section of the animals activity cycle could not, however, be monitored.

If, however, as Lawson (1986) has shown, suni activity continues throughout the night also in captive groups, and assuming that marking shows the same relatively even temporal pattern found during daylight for the entire 24 hour cycle, then the frequency of marking for the territorial male in group A could be estimated at a mean of 24.88 marks/day (1.12 marks/h × 24). Enclosure A contained 41 marking posts and enclosure B, 65 posts. Assuming that the males' marking was evenly distributed between posts, for which there is no contrary evidence from the daytime observations, then the male in group A could mark each site every 1.65 days and the group B male every 3.98 days.

Response to foreign marking posts

Two marking posts from enclosure C were introduced at different times into enclosure A and positioned in the same way as natural posts (i.e. vertical and approximately 8 cm above

ground level). On both occasions the dominant male in the group approached the strange post first and responded by sniffing and jerking its head back abruptly. This sequence was repeated 3 times, after which the post was ignored. The same behaviour patterns were recorded for the dominant female but here, the sniff/head-jerk was repeated only twice on both occasions. None of the animals marked over the marking post in the 1 hr observation period subsequent to its encounter. Similar behaviour was never observed in response to "own" marking posts. This behavioural difference suggests that the odour eminating from the introduced post was identified as being unfamiliar.

Antorbital gland activity

Dominant males appeared to have highly active antorbital glands, suggested by their "wet" appearance, with secretion extruding from the gland orifice. This was not the case for subordinate males, where the gland appeared "dry". The amount of secretion produced appears to correlate with gland useage. As previously stated, dominant males are responsible for 91.2 % of the total marking observed, subordinates for only 2.7 %. The earliest observed case of antorbital gland activity, inferred by active marking behaviour, was in an 11 month old male.

Pedal gland marking and pathways

Since pedal gland marking occurs passively while the animals walk, quantitative measures of marking intensity or frequency could not be conducted. However, particular routes within the enclosure were used with such regularity that obvious paths were formed. The assumption is that such paths, owing to disproportionately frequent useage in contrast to the rest of the enclosures, would have a greater concentration of pedal gland secretion present than areas which were infrequently traversed.

Paths were not distributed randomly throughout the enclosures but connected salient sites within it i.e. shelter, waterhole, artificial feeding site, midden and preferred resting sites. In enclosure A there were 83 m of paths, in enclosure B 93 m, and in the smaller enclosure C, 34 m. This gave a mean of 1 m of path/2.8 m^2 for enclosure A, 1 m/2.5 m^2 for enclosure B and 1 m/2.4 m^2 for enclosure C. The mean for all enclosures was 1 m of path/2.57 $\pm$ 0.21 m^2. The close agreement between the figures suggests that paths, at least in these captive groups, tend to show a rather typical density independent of enclosure size. This could not be attributed to the fact that the salient sites of enclosures A and B were similar and the animals had to adopt the same path patterns to reach them. As Figs. 1a and 1b show, the path networks in the two enclosures were very different. For enclosure C, the salient sites were arranged in a completely different pattern from those in the other two enclosures, yet the path length/m^2 was approximately the same.

Apart from pedal gland secretion, elimination products might also be used to passively mark paths, owing to the dominant male occasionally performing scraping motions with the forefeet in the contents of middens (see below).

The use of middens as marking sites

Suni urinate and defaecate almost exclusively at certain places in the enclosure, termed middens. These are used by all group members. Enclosure B contained only a single midden, enclosure A had 3 adjacent ones and enclosure C, 3 widely separated ones. All middens were sited at the periphery of enclosures. Animals urinated and then defaecated on the sites but did not scrape middens with their forefeet during normal elimination.

To determine whether middens were sited so as to function in olfactory demarcation of the territory, or whether the choice of elimination site was arbitrary and dependent on the presence of the elimination products themselves, the experiments described in the

Table 1. **Response of groups A and B to manipulation of the midden site in their enclosures**

	Group A		Group B	
	24 h	48 h	24 h	48 h
I. Own faeces				
Old site	0	0	75	0
New site	100	100	25	100
II. Strange faeces				
Old site	0	0	50	0
New site	100	100	50	100

In experiment I, own elimination products were placed approximately 2 m away from the old, cleaned site. This was termed the new site. The same procedure was followed in experiment II but using elimination products from a strange group of animals. Midden usage was estimated by the approximated percentage of faeces deposited at the two sites during the two subsequent 24 hour intervals

"Methods" section were conducted. The hypothesis tested was that if the site of the midden was important in territory boundary demarcation, animals would continue to defaecate on the original site rather than change to a new site. The results are shown in Table 1.

The findings indicate that elimination products, whether familiar or unfamiliar, act as attractants for subsequent urination and defaecation. In no case was fidelity to the previously used site observable after 24 hours. Group A changed midden sites immediately. In the case of group B, the original midden site was large and well established. The 24 h delay before the new site was used exclusively could have been dependent on elimination product odour (especially urine) remaining at the old site.

Animals in experiment I showed no behavioural change except transfer of their elimination behaviour to the new site. In experiment II, however, there was a marked behavioural response to the strange elimination products. In group A, only the dominant male approached the site within the first hour following introduction of the strange elimination products. His response was intense olfactory monitoring followed by urination and defaecation on the site. Subsequent to this, the site was scraped repeatedly with the forefeet with olfactory monitoring occurring between scraping bouts. The entire sequence was repeated twice within the first 20 min after which the male ignored the site. In group B the dominant male's response was more intense and the above behaviour patterns, especially scraping with the forefeet, were performed almost continuously for 18 min. During this period, the male urinated on the site 4 times. These observations indicate that strange elimination products are recognised as such but that the dominant male superimposes his own faeces and urine on them, the frequent scraping with the forefeet probably serving to mix his own and the strange elimination products as well as cover the latter. The midden is then adopted for future use rather than the site being avoided.

Chromatographic profiles of dominant and subordinate males' marks

The volatile components of antorbital gland secretion deposited on marking posts by dominant and subordinate males and analysed by the dynamic solvent effect, were qualitatively and quantitatively different. The gas chromatograms of the dominant males in groups A and D are shown in Fig. 3a and 3b and those of the two subordinate males in group D in Fig. 3c and 3d. The antorbital secretions of dominant males contained greater numbers and larger quantities of highly volatile substances than those of subordinate males. The components concerned, however, have not yet been chemically identified. Dominant and subordinate animals therefore differ in the chemical composition of their antorbital gland secretions.

Discussion

The study has shown that suni territories are liberally provided with olfactory cues indicating occupancy. Male suni mark posts in their territories with secretions from the

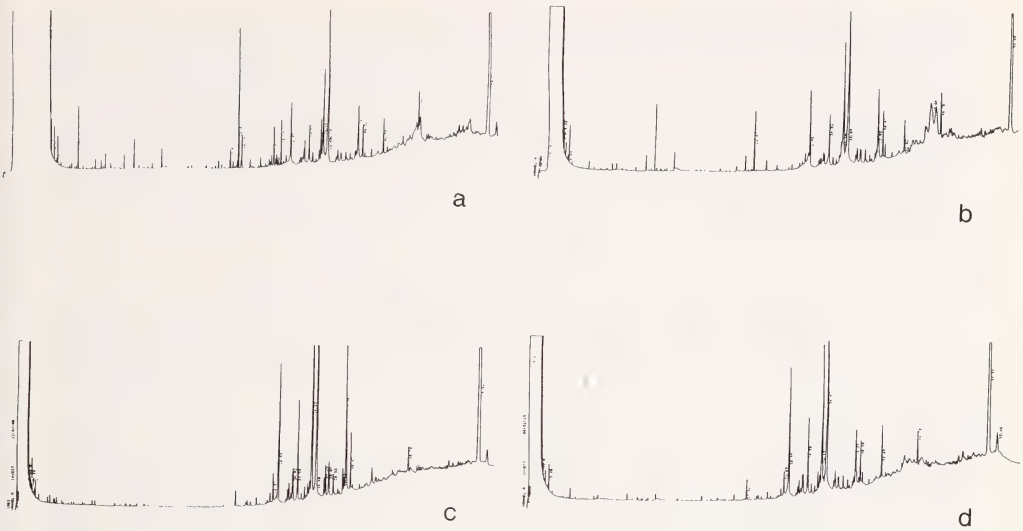

Fig. 3. Gas chromatograms of the antorbital secretions of 2 dominant (a, b) and two subordinate (c, d) suni males, obtained using the dynamic solvent method. Chromatograms of dominants show qualitative and quantitative differences from those of subordinates

antorbital glands while such marking in females is rare. This tendency for male Artiodactyls to be most active in territorial marking has been reported for oribi *Ourebia ourebia* (Gosling 1972), pronghorn antelope *Antilocapra americana* (Kitchen 1974), Coke's hartebeest *Alcelaphus buselaphus cokei* (Gosling 1974), impala *Aepyceros melampus* (Jarman 1979), blackbuck *Antilope cervicapra* (Hediger 1949), Grant's gazelle *Gazella granti* (Walther 1965) and Thompson's gazelle *Gazella thomsoni* (Gosling 1985), amongst others. Only dominant male suni show high rates of antorbital gland marking. As Ralls (1971) indicated, high marking frequency is associated with intolerance of conspecific rivals and Lawson (1986) has shown that the territories of male suni are almost mutually exclusive.

Although the majority of sightings of free-living suni indicate that the species is probably pair-living, male and female territories do not show the degree of coincidence found in the dik-dik *Madoqua kirki* (Hendrichs 1975) and a single male may show territorial overlap with two or more females. Even groups of a single male and up to 4 females have occasionally been sighted (Lawson 1986). Mutual exclusivity is thus not typical of female ranges and may be associated with low marking frequency in females.

Marking appears to be suppressed in subordinate animals of both sexes. No subordinate female was ever observed marking and the subordinate male in bachelor group C marked rarely until he became the dominant male in group D. Other subordinate males did not mark or only at very low frequencies. The gas chromatograms of antorbital gland secretions from dominant and subordinate males show clear differences in their volatile components. This suggests that status related physiological differences exist between territorial and non-territorial males and that these changes can occur rapidly, in the abovementioned case, within 3 days. Dominance is therefore not only reflected in the constituents of the antorbital marking secretion but also in marking frequency.

The sequence of behaviour patterns in suni antorbital gland marking was found to be highly stereotyped and marking was almost always preceded by olfactory monitoring of the marking site. Vertical up and down movements of the head during marking have been reported for most antelope species which mark with antorbital glands (Gosling 1985).

Compared with other Artiodactyls (Walther 1979), however, suni are unusual in that typically only one of the glands is used during any one mark and the majority of marks consist of a single stroke only, rather than a repeated nodding movement of the head. The actual performance of marking does not appear to have a signal value, as has been reported for hartebeest (Gosling 1984), impala (Jarman 1979) or chital *Axis axis* (Schaller 1967) probably owing to its brevity and relative inconspicuousness. Licking of the gland after marking has not been reported for other species to date.

Marking posts

Marking posts appear to be manufactured by biting off the plant just above ground level, although this was not actually observed. All the plants used as marking sites are normally at least 0.5 m high and *Protasparagus* and grasses are not forage plants. It is therefore unlikely that the short stumps used were the byproducts of normal feeding. Manufacture of marking sites has been recorded for oribi (Gosling 1972), pronghorn antelope (Kitchen 1974) and chevrotains (Dubost 1975). Only 2 marking sites were on twigs of overhanging branches and by far the majority of posts were 7 cm or lower. Gosling's (1981) maximum mark detection hypothesis states that marking posts should be sited so as to maximise the chances of encounter. Gerenuk and oribi place their antorbital gland marks at head-height for detection by a walking intruder (Gosling 1972, 1981). For suni, however, this would be approximately 30 cm, yet marking posts are practically at ground level. It is during foraging that the head would be carried low, suggesting that the posts are "aimed" at intruding foragers.

A further corollary of Gosling's "maximum detection" hypothesis is that marks should be located near routes regularly used by potential territorial invaders i.e. pathways and game trails. This has been demonstrated for pronghorn antelope (Gilbert 1973), gerenuk (Gosling 1981) and dik-dik (Gosling 1985). In suni there was a significant tendency for marks to be sited in open areas away from regularly used pathways. The differences between the findings for the bush-savannah/open grassland living species and suni may be associated with their differing food sources. Oribi, gerenuk and dik-dik are either browsers or grazers on short grass swards. Suni live in woodlands and are specialist feeders, foraging mainly on fallen leaves (especially *Ficus* spp.), flowers and fruit (Lawson 1986). As Gosling (1985) points out, territory owners would be expected to mark near objects that are likely to attract other animals. Since the suni's preferred food items are patchy resources, in contrast to bushes and grass, and tropical woodland trees are rarely synchronised in their flowering and fruiting cycles (Frankie et al. 1974), a tree which is either dropping its leaves, flowers or fruit would be a relatively isolated food patch. This would serve as a strong attractant for other animals. A territory owner should thus mark where encounter rate by an exploiting invader would be highest i.e. near ground level and in the open around or under such trees.

The high visibility of suni marking sites also suggests that their function is in forage resource demarcation. All marking sites except two were on open ground and away from grassy areas which would obscure the large blackish-grey bulb of secretion. A relationship between marking site and preferred food has been demonstrated for gerenuk (Gosling 1981) and the evidence presented for suni suggests strongly that a similar relationship is present in this species.

The spatial patterning of marking posts agrees well with Gosling's (1981) economic marking hypothesis. This states that, if the pattern of marks is adapted to intercept animals entering the territory, marks should be concentrated at the territory boundary and should it be to the owner's advantage that more than one mark be encountered, then concentric circles should be formed. The pattern of marking sites revealed by the mapping of "nearest neighbour" marks shows that suni mark predominantly along the territory boundary and

that smaller concentric circles may be present. Similar patterning of antorbital gland marking sites has been demonstrated for gerenuk (Gosling 1981) and Thompson's gazelle (Gosling 1985 redrawn from Walther 1978a).

Gosling (1985) hypothesises that territorial animals should concentrate their marking sites in areas where the likelihood of encounters with neighbouring males would be high. Enclosures containing territorial males adjoined the N and S sides of enclosures A and B. Although these adjacent groups were not visible, owing to the fence, their presence was known, as evidenced by the "butting" fights directed at the fence by neighbouring males. However, there was no tendency for marking sites to be concentrated at these boundaries.

In gerenuk, marking sites tended to occur close together more frequently than if they were randomly distributed (Gosling 1981). In this study, approximately half the total number of suni marking posts occurred in groups with a mean of 3 posts within 1 m of one another. The significance of this clumping of marking sites is unknown, but may aid in forage site defence.

From the frequency of marking per site calculated from the observed marking frequency/hr during daylight, the known activity cycle of suni and the number of marking posts present, the male in group A could mark each site every 1.65 days and the group B male every 3.98 days. These values compare well with those found for other Artiodactyls (4.5 days/site for gerenuk [Leuthold 1978], 2.8 days/site for Thompson's gazelle [Walther 1978a, b, in Gosling 1985]). The intervals between site marking given above suggest that there is an upper time limit beyond which a mark loses its effectiveness and that this is relatively short and consistent for the species studied to date, ranging between 1.6 and 4.5 days. Whether these are maximum or minimum times between mark deposition and loss of effectiveness is unknown.

Pedal gland marking

All enclosures had a network of paths connecting salient sites within them. These paths are a recognised feature of suni territories (Heinichen 1972). In the captive animals, paths showed a consistent density independent of enclosure size, path pattern and salient site distribution. If pedal gland secretion is present in higher concentrations on such paths than on the surrounding areas, then consistent path density may indicate that paths have a marking function. No quantitative data are available, however, for free-living suni.

On paths, marks from both males and females would be present, in contrast to the male antorbital gland marking sites. In addition, paths would also indicate the intensity of range useage (Gosling 1985). They are unlikely to reflect the presence of preferred forage, a function of pedal gland secretion suggested for grassland Artiodactyls such as Coke's hartebeest (Gosling 1974) and reindeer (Müller-Schwarze et al. 1978), since the majority of suni forage is sited away from paths. A combination of pedal gland secretion on paths and antorbital gland marks away from paths would thus almost completely olfactorally delineate the range occupied but by different means.

Middens

With one exception, enclosures contained more than one midden. Their positioning, however, appeared to bear no relationship to the presence of neighbouring groups. The natural siting of middens does not suggest their role as territory markers, as has been found for dik-dik (Hendrichs 1975). This is supported by the results of the experiments conducted. Where the midden is sited appears to be unimportant, since animals changed their elimination sites completely within 48 h of the site being artificially changed. The presence of elimination products themselves appeared to determine where further elimination occurred and there was no fidelity to the previous site even after long-term useage.

However, the response of the territorial males to elimination products from a strange suni group placed in the enclosure indicates that they do carry olfactory cues associated with identity. Strange elimination products evoked attempts, at least on the part of the male, to cover the odour with his own. After this, they were used as the focus of a new midden. Similar findings have been recorded for a carnivore, the dwarf mongoose *Helogale undulata rufula* (Rasa 1973). These experiments contrasted with those where strange antorbital gland secretions were introduced into the territory. Although these marks were identified by both male and female as being unfamiliar, no attempt was made to mark over them and they were avoided or ignored.

The functional significance of marking

Several hypotheses have been put forward as to the functional significance of territorial marking in Artiodactyls, ranging from threats (Ralls 1971) and deterrents (Hediger 1949) to "increased self confidence" (Richter 1972) and as an "aid in self orientation" (Walther 1978a). Gosling (1985) suggests that Artiodactyl territorial marking functions in "scent-matching", allowing a territory owner to be identified and "assessed" by an opponent, thus reducing the time and energy spent in territorial defence. According to this hypothesis, only intruders intending to compete for territory ownership would then engage in a possibly costly fight. The four predictions which arise from this hypothesis are a. the territory owner will mark the area in a way that maximises mark detection; b. will mark himself with the same marking substances; c. remove or replace marks that do not match his own; d. make himself available for scent-matching.

The first prediction holds true only when antorbital gland marking is taken in conjunction with pedal gland marking. Then, both paths and areas between paths are marked, the latter in concentric rings, suggesting boundary marking. However, suni do not actively anoint themselves with their antorbital glands which, however, are large and under muscular control. It is likely that the secretion exuding from the "wet" glands of territorial males is sufficient to provide the necessary odour cues. As far as prediction c. goes, suni show no tendency to remove or replace strange antorbital gland marks but rather to avoid or ignore them. This was not the case for elimination products, however. Whether territorial male suni make themselves available for scent-matching in agonistic encounters is speculative. Owing to the captive conditions under which the animals were held, open encounters were not possible, although fights between territorial males occurred through the fences. The observation that suni occasionally lick each others' antorbital glands and also lick marking posts may indicate that scent-matching behaviour may form part of an assessment process, although in the observed cases, this licking was probably affiliative rather than agonistic, occurring between pair partners. Similar behaviour, pressing of the antorbital glands of partners against one another, is recorded in Maxwell's duiker (Ralls 1974).

Fights only occurred between territorial males, even though the opponents were not clearly visible to each other, suggesting that there is some mechanism of olfactory recognition of dominant/territorial status. The gas chromatograms of antorbital gland secretions from dominant and subordinates differed qualitatively and quantitatively in volatile content. It is likely that these volatiles indicate status, identifying potential competitors. Further experiments are necessary to determine the existence of individual scent-matching. For a territorial male, there would be no advantage in attacking all intruders, since this strategy is energy consuming and would also exclude females. Competing males, however, should be rapidly identified as such and excluded. The volatile components of the antorbital gland secretions could serve as the means by which this rapid identification could be achieved.

In summary, marking behaviour in suni fulfills the predictions of Gosling's "scent-

matching and assessment" hypothesis only if all means of marking are taken into account. The hypothesis does not hold for antorbital gland marking alone since prediction c) is not fulfilled, but does if it is considered in conjunction with marking with elimination products at middens, where prediction a. does not hold. Prediction d. can, at present, only be related to status and not to individuals and prediction b. may not apply to this species, owing to the size of the antorbital glands in relation to body mass. The use of different modes of olfactory communication to construct a single "message" has been demonstrated for dwarf mongooses (Rasa 1973) and may be a more widespread phenomenon than hitherto recorded.

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Zusammenfassung

Markierungsverhalten und Dominanz bei der Suni-Antilope (Neotragus moschatus)

Untersucht wurde Markieren durch Voraugendrüsen, Interdigitaldrüsen und Ausscheidungsprodukte bei 3 gefangengehaltenen Suni-Gruppen *(Neotragus moschatus)*. Voraugendrüsenmarkierung findet fast ausschließlich bei dominanten (territorialen) Männchen statt, und Gaschromatogramme der Sekrete von dominanten und subdominanten Männchen zeigen Unterschiede. Markierungsstellen sind kurze, senkrecht stehende Zweige, in offenen Gebieten zu konzentrischen Kreisen angeordnet. Die außergewöhnliche Anordnung der Markierungsstellen könnte mit den spezialisierten Futterquellen der Suni zusammenhängen. Die Wirkung des Markierungssekretes hält ungefähr 4 Tage an. „Fremde" Sekrete werden identifiziert, aber nicht übermarkiert. Es wird angenommen, daß die höchste Konzentration des Sekrets der Interdigitaldrüsen auf Pfaden vorkommt, die typisch für Suni-Territorien sind. Pfade haben eine fast konstante Dichte, unabhängig von der Gehegegröße. Kotplazierung scheint keine Markierungsrolle zu spielen. Fremde Ausscheidungsprodukte werden von dominanten Männchen jedoch übermarkiert. Die Befunde werden in bezug auf die „Geruchsschätzungs"-Hypothese diskutiert.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Aspects of nasal gland function in the opossum (*Didelphis virginiana* Kerr, 1792) as indicated by carbohydrate histochemistry

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In the opossum (*Didelphis virginiana* Kerr), a rather basic species, the general pattern of mammalian nasal gland types in the regio respiratoria is already present. Relatively early in nasal cavity development of this animal, the glandulae nasales laterales and the glands of Jacobson's organ can be distinguished, whereas the glandulae nasales mediales (GNM) appear later (Tsuda 1924), probably latest in all mammals (Broman 1921). The overall organization and arrangement of these glands in the nasal septum mucosa of the opossum compares closely to that found in Rodentia (Fig. 1; see also Bojsen-Møller 1964). In this connection, using nasal septum samples from six adult animals of both sexes, the present study focusses on carbohydrate histochemical peculiarities of the GNM as, probably, related to specific glandular functions. The methods applied are described in detail by Meyer and Tsukise (1989), including the control of lectin residue demonstration by addition of inhibitory sugars to the respective lectin solution (see Table).

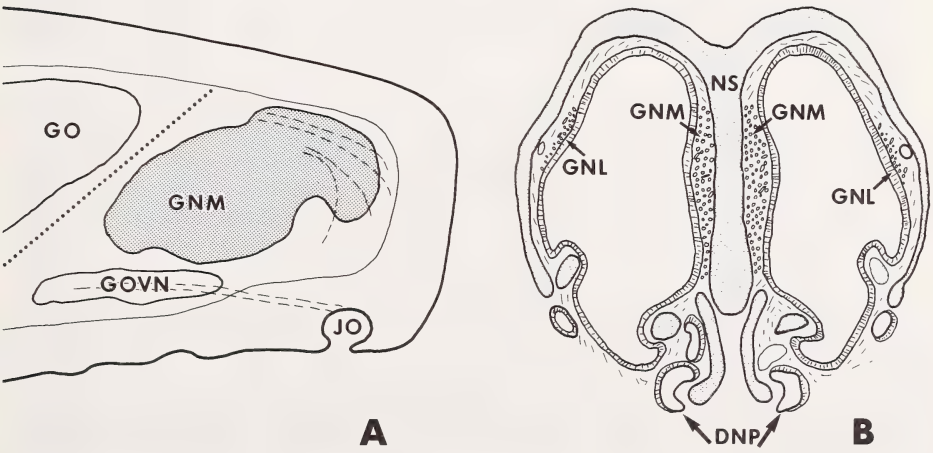

Fig. 1. Position of the GNM at the nasal septum. A: lateral view in regio respiratoria, B: frontal section through nasal cavity; schematically after Tsuda (1924) and original. DNP = ductus nasopalatinus, GNL = glandulae nasales laterales, GNM = gll. nasales mediales, GO = gll. olfactoriae (Bowman's glands), GOVN = gll. organi vomeronasalis, JO = Jacobson's organ, NS = nasal septum

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Carbohydrate histochemical reactions in the glandulae nasales mediales of the opossum

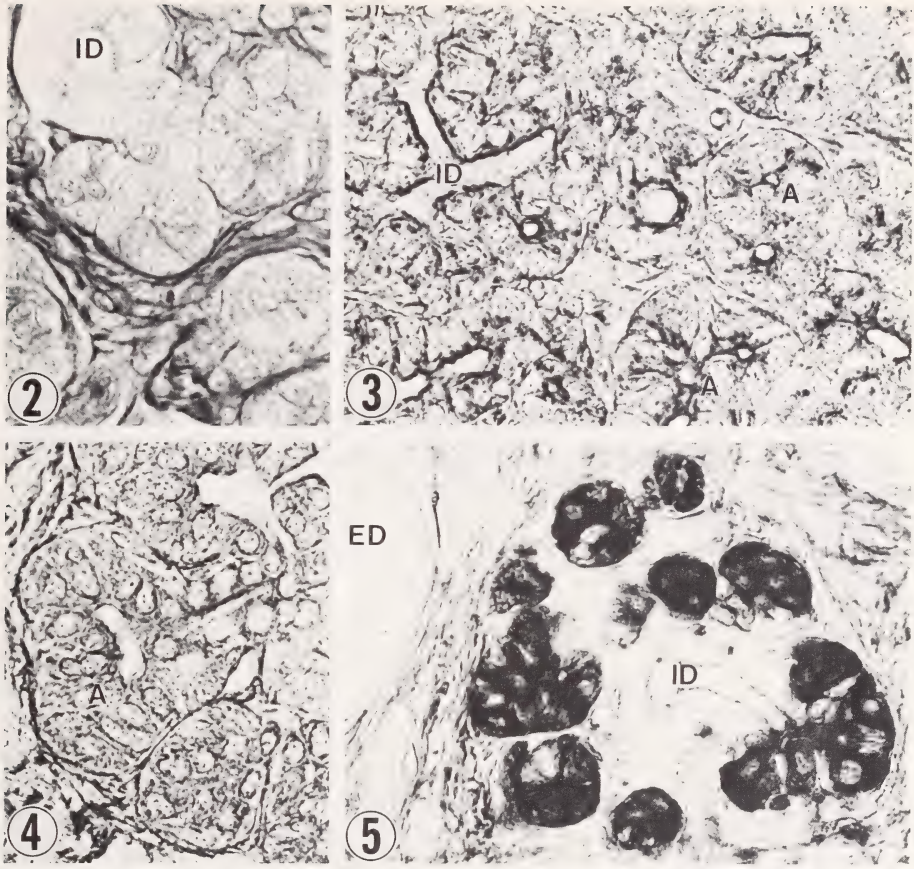
Reactions	Secretory cells	Luminal secretion	Excretory duct cells	Inhibitory sugars for lectins
PAS	2	0	0	
AB (pH 1.0)	0	0	0	
AB (pH 2.5)	0–1	1	0	
DI-FCY	1	1	1	
AB (pH 2.5)-PAS	2	0	0	
Sul-AB (pH 1.0)	2–3	0–1	0	
Amyl-PAS	2	0	0	
PO-Con A-DAB	2–3	2	3[a]	D-Man
PO-RCA-I-DAB	1–4	3–4	3–4[a]	D-Gal
PO-PNA-DAB	2–3	2–3	2–3[a]	D-Gal
PO-SBA-DAB	1–2	3–4	3–4[a]	D-GalNAc=D–Gal
PO-MPA-DAB	1–2	2–3	1–2[a]	D-Gal
PO-DBA-DAB	0	0	0	D-GalNAc
PO-UEA-I-DAB	4–5	1	0	L-Fuc
PO-WGA-DAB	1–2	1–2	1–2[a]	D-Glc
PO-LPA-DAB	2	2	1–3[a]	NeuNAc

Reaction intensities: 0 = no reaction, 1 = very weak, 2 = weak, 3 = moderate, 4 = strong, 5 = very strong. a: free surface only in collecting duct system.

The GNM of the opossum consist of cells which are located in acini and can be identified as serous type from their fine cytoplasmic granules and the central or slightly basal, roundish nucleus. The serous acini are connected by short intercalated ducts which penetrate partially into the acini, in this way producing centro-acinar cells (Figs. 2–5). The intercalated ducts drain into smaller and larger interlobular ducts with a single-layered epithelium. Typical striated ducts, as known, for example, of mammalian salivary glands, could not be detected. The glandular components are generally surrounded by many blood capillaries and numerous mast cells. The reactions for the different carbohydrate histochemical staining procedures, as summarized in the Table, demonstrated some neutral, but only very few acidic glycoproteins in the GNM (Fig. 2). This is in general accordance with observations from serous or seromucous glands of human nasal mucosa or nasolabial glands of different mammals (Thaete et al. 1981; Tsukise et al. 1988; Meyer and Tsukise 1989). However, in the opossum, the serous cells reacted negatively for glycogen.

The lectin reaction pattern in the GNM showed certain similarities to mammalian salivary and nasolabial glands (Laden et al. 1984; Tsukise et al. 1988; Meyer and Tsukise 1989), with the following spectrum of terminal saccharide residues: α-D-mannose, α-D-galactose, β-D-galactose, β-D-galactose-D-N-acetyl-galactosamine, α-L-fucose, sialic acid. This is especially true of the presence of α-L-fucosyl residues in the serous cells, a feature also observed in this cell type in other mammalian glands (Mazzuca et al. 1982; Laden et al. 1984; Tsukise et al. 1988). In the opossum, the respective UEA-I reaction is very strong, particularly in the cell wall or, possibly, in intercellular material (Fig. 5). The significance of such an abundance of fucose in serous cells or their cell walls, respectively, is unknown but the relative hydrophobicity of this sugar may, to some extent, be correlated with specific cellular or membrane transport functions (Schulte et al. 1985). Thus, the reaction for UEA-I may be typical for serous cells during active secretion production, and generally affirm the basic role of serous gland cells in water and ion transport (Thaete et al. 1981).

These observations could be related to general functions of the secretion type produced by such glands, as to dilute mucus in ciliated areas of the nasal cavity or to humidify the air stream and the snout surface. Considering, however, the specific structure of the opossum



Figs. 2–5. 2: Alcianblue (pH 2.5) – PAS; *3:* PO-RCA-I-DAB; *4:* PO-PNA-DAB; *5:* PO-UEA-I-DAB. A = acini, ED = excretory duct, ID = intercalated ducts; (all 340×)

snout with a deep medial cleft leading into Jacobson's organ (Meyer and Tsukise 1990), the nonviscous serous fluid of the GNM flowing down could also carry smelling substances which would be sucked into the organ for an additional olfactory evaluation. This may be particularly important for nocturnal animals such as the opossum, a species that needs excellent olfactory properties in discriminating many possible food sources.

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The shrew (*Crocidura* sp.) of Gozo, a probable survivor of the Pleistocene fauna of Mediterranean Islands

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The Pleistocene fauna of Mediterranean islands comprises several endemic mammals all of which are now extinct. The only known exception is *Crocidura zimmermanni,* the endemic shrew of Crete (Reumer 1986). Many of the species became extinct only after the arrival of man during the Neolithic period. Man, either accidentally or consciously, introduced most of the presently occurring mammals, such as hedgehogs, mice, rats, ungulates, and so forth (summarized by Vigne and Alcover 1985). According to these authors, *Suncus etruscus* and two species of the genus *Crocidura, C. suaveolens* and *C. russula,* which presently occur on several of the Mediterranean Islands, have also been introduced by man. This interpretation was confirmed for some islands by Poitevin et al. (1986) and Vogel et al. (1986).

The shrews of Sicily, however, could not be confidently referred to one or the other species and, until recently, have been variously assigned to *C. caudata, C. sicula, C. suaveolens, C. leucodon,* or *C. russula* by various authors (Miller 1901; Vesmanis 1976, among others). The recent discovery of a particular karyotype with 2n = 36 chromosomes has now demonstrated that the Sicilian shrew is a separate species (Vogel 1988), related to *C. canariensis* (Maddalena 1990), a species endemic to the Canary Islands and which has a similar karyotype (Hutterer et al. 1987).

Once the species was recognized, the question arose as to its origin. Was it introduced by man as many other mammals, or was it a relic of the local Pleistocene fauna? Kotsakis (1986) has described a Pleistocene species of *Crocidura* from Spinagallo cave in Sicily, together with remains of the dwarf elephant *Palaeoloxodon* and the giant dormouse *Leithia.*

Kotsakis (1986) has also referred material from the Pleistocene of Malta (reported by Malec and Storch 1970) to his new species from Sicily, which he named *Crocidura esui.* Both islands share a more or less common Pleistocene vertebrate fauna. If the extant shrew was a descendant of the Pleistocene species, then one would expect the same species to occur also in the Maltese archipelago. Shrews from the Upper Pleistocene and Holocene of the Ghar Dalam cave, Malta, were reported as *C. cf. russula* by Malec and Storch (1970). The species is now extinct on Malta, but on the Island of Gozo, 5 km northwest of Malta, specimens were recently found and referred either to *C. russula* or to *C. suaveolens* (Sultana 1971; Schembri and Schembri 1979; Schembri and Cachia Zammit 1979; Vesmanis and Vesmanis 1982). These identifications would imply that the Pleistocene species became extinct and has now been replaced by a continental species, as proposed by Kotsakis (1986) for Sicily. To solve the problem, we obtained alive shrews from Gozo and studied their karyotype.

We collected three specimens of *Crocidura* sp. on Gozo in March 1989. The colour of these animals, especially in the juvenile pelage, is characterised by a dark back and a bright belly which are separated by a clear line of demarcation. However, in older animals this

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Fig. 1. Adult male *Crocidura sicula* from Gozo

line is not as sharp (Fig. 1). The chromosomal analysis revealed a karyotype of 2n = 36 (Fig. 2), which agrees with the one previously reported from Sicily (Vogel 1988), and which differs from both *C. russula* and *C. suaveolens.*

These results confirm our assumption that the extant shrews of Sicily and Gozo occurred there before the arrival of man and therefore provide strong evidence that they have survived since the Pleistocene. As a consequence, it was possible to restudy the morphology of the Sicilian and Maltese populations (Vogel et al. 1989) and to conclude that *C. caudata* is a synonym of *C. sicula*, and that the shrews of the Egadi Island also belong to this species which we call *C. sicula.*

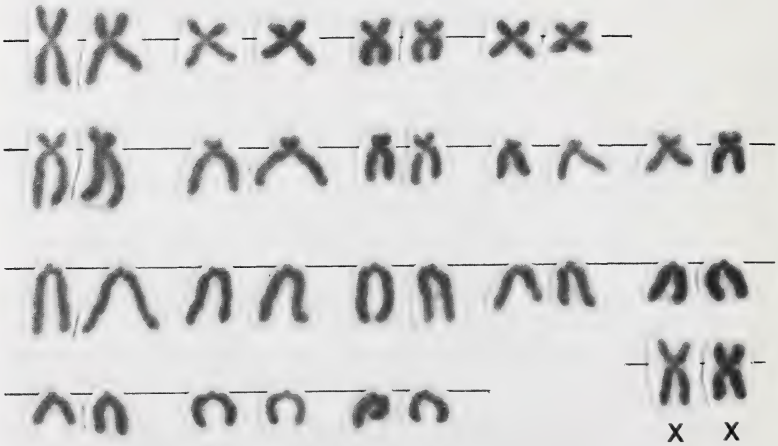

Fig. 2. Karyotype of *Crocidura sicula* from Gozo (female IZEA 3525)

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BUCHBESPRECHUNGEN

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Das Buch enthält Manuskripte und Kurzfassungen von 38 Autoren zu Vorträgen, die im November 1987 anläßlich eines Symposiums der British Mammal Society zum Thema „Mammals as Pests" gehalten wurden. Bei dieser aus dem Blickwinkel des Naturschutzes sehr aktuellen Tagung wurden grundsätzliche Fragen gestellt wie zum Beispiel: „Was ist ein Schädling?" Von der Beantwortung dieser Frage hängt es ab, ob eine Tierart geschützt, geduldet oder verfolgt wird. Der Herausgeber diskutiert denn auch in seinem Vorwort zunächst die verschiedenen in der Vergangenheit gegebenen Definitionen, einige der Autoren kommen in ihren Beiträgen später darauf zurück. Das Spektrum der behandelten Säugetiere reicht von den Insectivora (Maulwurf) über die Rodentia (Mäuse, Wühlmäuse, Grauhörnchen, Nutria), Lagomorpha (Kaninchen) und Carnivora (Dachs, Fuchs, Mink, Seehund, Hauskatze) bis zu den Artiodactyla (Reh, Sika-, Rothirsch). Behandelt werden direkte und indirekte Schäden durch Fraß, Schälen von Baumrinde, Verwühlen etc., die Rolle von Säugetieren als Vektoren (Tollwut: Fuchs; Rindertuberkulose: Dachs; Weilsche Krankheit: Nager), und es wird berichtet über Erfahrungen bei der Entwicklung neuer Abwehrsubstanzen und beim Einsatz von Tötungsmitteln. Die meisten Betrachtungen sind sehr differenziert, und zuweilen kommen die Autoren zu überraschenden Schlußfolgerungen. So waren Seehunde und der Mink in Großbritannien wohl nicht die Schädlinge, für die sie lange gehalten wurden, und die Mittel, die für ihre Bekämpfung ausgegeben wurden, waren nicht gerechtfertigt. Von Dachs und Maulwurf verursachte Schäden werden nicht generell, sondern bestenfalls als lokales Ärgernis ohne nationale ökonomische Bedeutung angesehen. Auf der anderen Seite werden kommensale Nager und Wühlmäuse als potentiell schwere Schädlinge von nationalökonomischer Bedeutung eingestuft. Auch Kaninchen und Hirsche können bedeutende Schäden in der Land- und Gartenbauwirtschaft verursachen. Bei anderen Arten muß im Einzelfall geprüft werden, welche objektiven Schäden sie anrichten und welche Abwehrmaßnahmen angemessen sind. Insgesamt betonen die Autoren und der Herausgeber die Bedeutung von exakten und objektiven Daten zur Beurteilung jedes Schadenfalles und der eventuell daraus resultierenden Maßnahmen. Das Buch ist ein wichtiger Schritt zur differenzierten Betrachtungsweise von „Schädlingen" und kann deshalb allen Lesern empfohlen werden. Vor allem aber gehört es in die Hände der Behördenvertreter, die über Schadensfälle urteilen oder neue Gesetze und Vorschriften entwerfen. R. HUTTERER, Bonn

PFLUMM, W.: **Biologie der Säugetiere.** Pareys Studientexte Nr. 66. Berlin, Hamburg: Verlag Paul Parey 1989. 565 S., 413 Abb., 4 Tab. DM 58,–. ISBN 3-489-63534-5

Im vorliegenden „Studientext" werden nach Behandlung der Frage, was ein Säugetier sei (Kapitel I), und der Schilderung der Charakteristika des Körperbaus der Säugetiere (II) Probleme besprochen, die mit dem Energiewechsel und dem Wärmehaushalt in engerem oder weiterem Zusammenhang stehen (III bis V). Fortpflanzung und Jungenaufzucht (VI, VII), Anpassungen an die Lebensräume (VIII), Gehirn, Sinne und Verhalten (IX), Nahrungs-Erwerb und -Verdauung (X) sowie die Evolution der Säugetiere (XI) werden behandelt. Ein abschließendes Kapitel bringt eine Übersicht über das System der Mammalia (XII). Mehrere Register erschließen den Inhalt des Werkes.

In weiten Abschnitten werden die Fakten in anekdotischer Form dargeboten, was zwar die Lesbarkeit steigert, doch die Dichte der Information nicht fördert. Das Buch, welches auf insgesamt 565 Seiten ein so weites und differenziertes Feld wie die Säugetierkunde behandelt, kommt mit nur vier Tabellen aus!

Das Werk hinterläßt einen widersprüchlichen Eindruck. Einerseits stellt es eine Zusammenstellung großer Informationsmengen dar und betont physikalische, biochemische, anatomische und physiologische Gesichtspunkte, doch seine Gliederung und Darbietung der Fakten sind in einigen Fällen höchst eigenwillig und schwer nachvollziehbar. Es fragt sich, ob beispielsweise „Carnivora" mit dem deutschen Begriff „Reißtiere" allgemeinverständlich benannt sind (fünf ausführliche Wörterbücher der deutschen Sprache erwähnen diese Bezeichnung nicht), oder die verbreiteten Begriffe „Eutheria" und „Placentalia" durch „Choriata" ersetzt werden sollten. – Zusammenfassend muß festgestellt werden, daß der „Studientext" als Lehr- und Arbeitsbuch den Studierenden der Biologie und Schülern der Sekundarstufe II nicht uneingeschränkt empfohlen werden kann. P. LANGER, Gießen

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Z. Säugetierkunde 55 (1990) 5, 289–360

Andrej P. Dyban / Wladislaw S. Baranow

Die Zytogenetik der Säuger-Embryogenese

Experimentelle Studien zu den Irrwegen und zur Auslese während der Verteilung des Genoms

Pareys Studientexte Nr. 64

Von Prof. Dr. Andrej P. Dyban und Prof. Dr. Wladislaw S. Baranow, beide Akademie der Medizinischen Wissenschaften, Leningrad. Aus dem Russischen übersetzt von Petra Pawel. Deutsche Bearbeitung von Prof. Dr. Walter Sachsse, Institut für Genetik der Johannes-Gutenberg-Universität, Mainz.

1990. 276 Seiten mit 8 Abbildungen, 28 Tafeln und 36 Tabellen. 23,5 × 15.5 cm. Kartoniert DM 38,– ISBN 3-489-51016-X

Zytogenetische Untersuchungen während der Embryogenese sind heute unabdingbar als medizinisch-biologische Grundlagenforschung. Es gibt sogar noch Lücken in unserem Wissen über die normalen Vorgänge, obwohl diese Wissenschaftssparte Pate stehen sollte für die Analyse von Spontanaborten und diese dann wiederum für die pränatale Diagnostik. Zytogenetik, alias Chromosomenkunde, umfaßt das, was vom Vererbungsvorgang und -material sichtbar zu machen ist und richtet sich im hier vorliegenden Werk besonders auf die Vereinigung der Keimzellen, natürlich mit Berücksichtigung der vorausgehenden Prozesse sowie der nachfolgenden, eigentlichen Embryogenese. Heute ist dieses Fach über eine humangenetische Grundlage hinaus Basis und Angelpunkt für die Biotechnologie.

Aufbauend auf den Erfahrungen langjährigen Experimentierens gibt dieser Studientext die gesamte Palette dessen wieder, was sich sichtbar darstellen läßt, also Haploidie und Polyploidie, numerische sowie strukturelle Chromosomenaberrationen, Mosaiken und Chimären, genetische Aktivität von Chromosomen bis zu Verhaltensstörungen bei balancierten und unbalancierten Translokationen; dabei werden jeweils die Entstehungsweisen und die Konsequenzen unter die Lupe genommen und das spontan Auftretende dem experimentell Induzierbaren gegenübergestellt. Dyban und Baranow haben von Anfang an in der Mitte des noch jungen Faches, der zytogenetischen Teratologie, gestanden, vom Experimentellen an bis zu den Auseinandersetzungen um die theoretische Anwendbarkeit in der Humangenetik.

Daraus ergibt sich die Bedeutung dieses erfolgreichen, zuerst in der UdSSR erschienenen Buches auch für den deutschsprachigen Raum, denn es gilt, eine Generation von Medizinern und Biologen detailliert in die Grundlagen einzuführen, bevor sie in die Diskussion hineingezogen oder gar vor Probleme, Entscheidungen oder Aufgaben gestellt werden.

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Cytogenetics and karyosystematics of South American oryzomyine rodents (Cricetidae: Sigmodontinae)

II. High numbered karyotypes and chromosomal heterogeneity in Venezuelan *Zygodontomys*

By O. A. Reig, M. Aguilera, and A. Perez-Zapata

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Receipt of Ms. 11. 12. 1989
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Abstract

Studied karyotypes in savanna mice of *Zygodontomys microtinus thomasi* and *Z. m. stellae* from sixteen localities in Venezuela. Fifteen males and thirteen females from ten populations of the former, and three males and two females from one population of the latter showed a 2n = 84, FN = 116–118 karyotype comprising mostly small bi-armed autosomes and an XY-XX sexual pair. C-banding showed that a great deal of the genome was heterochromatic, including pericentromeric, whole arm, and whole chromosome heterochromatin types. Three males and six females from one population of Monagas State (Isla Guara), which did not differ in morphology from *Z. m. thomasi*, showed a different karyotype of 2n = 88, FN = 116–118 which can be derived from the former by two Robertsonian fissions. The taxonomy of *Zygodontomys* is briefly discussed.

Introduction

The chromosomes of the cricetid savanna mouse *Zygodontomys microtinus* were briefly described twenty years ago on the basis of specimens from several localities in Venezuela (Kiblisky et al. 1970). The karyotype comprised 2n = 84 chromosomes, at that time the highest chromosome number for a mammal, only matched by a similar diploid number previously communicated for the black rhinoceros (Hungerford et al. 1967). Later on, two papers reported chromosome numbers or briefly described the karyotypes in samples of *Zygodontomys* from other localities (Gardner and Patton 1976; Tranier 1976). However, neither an accurate description, nor an illustration of the chromosomes of a species of this genus has been published so far.

During the last 15 years we have obtained new information on chromosomes of Venezuelan *Zygodontomys*. The recent discovery of polytypic variation in the karyotypes of *Zygodontomys* (Perez-Zapata et al. 1984) added to our increasing interest in the biology (Aguilera 1985), and systematics (Reig 1987) of species of this genus and induced us to present our results.

Material and methods

Forty-two specimens of *Zygodontomys* (twenty-one of each sex) are included in the present study (see specimens examined). Animals were captured by live trapping at sixteen localities covering a large portion of Venezuela (Fig. 1).

All animals processed were deposited in the collection of mammals of the Museum of Biology, Central University of Venezuela, Caracas, Venezuela (MBUCV), and the Museum of Natural Sciences of the Simón Bolivar University in Caracas (USB).

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Fig. 1. Map of Venezuela showing localities of the studied specimens of *Zygodontomys*. Numbers at each marked point correspond to localities as defined in the text under "Specimens examined"

All specimens were brought alive to the laboratory for standard bone-marrow chromosome preparations (Reig et al. 1971). A few animals were also processed following Fredga's (1964) cornea technique. C-banding was obtained in a few of them following Sumner (1972). A few males were also processed for meiotic chromosomal preparations after Pathak and Hsu (1979). For nomenclature of chromosomes we followed Levan et al. (1964). For the assortment of chromosomes into size classes, we called medium-sized those between 5.5 and 9.0 % of the length of the female haploid set (LHS); small those between 2 and 5.5 %, and minute those <2 % of the LHS. Fundamental number (FN) is the number of autosomal arms.

Specimens examined

Localities and collection numbers are as follows: 1. Barinitas, Barinas State: one male (USB K-097). 2. Tierra Buena, Portuguesa State: one male (USB K-416). 3. Turén, Portuguesa State: one female (USB K-059). 4. La Batea-Morón, Carabobo State: one female (USB K-803). 5. Manuare, Carabobo State: one male (USB K-081). 6. Calabozo, Guarico State: four males (MBUCV 1-1838; USB K-197, K-237, K-242) and six females (MBUCV 1-1839, 1-1840, 1-1841; USB K-238, K-241, K-310). 7. Hato "El Frío", Apure State: two males (USB K-441, K-480) and one female (USB K-474). 8. San José de Guanipa, Anzoátegui State: one female (USB K-796). 9. Río Pao-Hato San Antonio, Anzoátegui State: two males (USB K-654, K-657). 10. Paso Bajito-El Tigrito, Anzoátegui State: one female (USB K-645). 11. San Vicente, Sucre State: two males (USB K-691, K-693) and one female (USB K-692). 12. San Juan de las Galdonas, Sucre State: one female (USB K-670). 13. Isla Guara,

Monagas State: three males (USB K-621, K-624, K-627) and six females (USB K-617, K-620, K-622, K-636, K-637, K-638). 14. Ciudad Bolivar, Bolivar State: one male (MBUCV A-365). 15. El Guri, Bolivar State: one male (MBUCV 1-1657). 16. La Esmeralda, Amazonas Federal Territory: three males (MBUCV 1-1763, 1-1931, 1-1953) and two females (MBUCV 1-1932, 1-1954).

Fig. 2. Representative 2n = 84 bone-marrow karyotype of *Zygodontomys microtinus thomasi* and *Z. m. stellae*, as shown in a female individual from Paso Bajito-El Tigrito, Anzoátegui State, Venezuela. Illustrated are also the sex chromosomes of one male from Rio Pao-Hato San Antonio in the same State. Bar represents 5 μm

Results

A karyotype of 2n = 84 was found in all individuals examined, except those from Isla Guara (Fig. 2). This number was confirmed by 42 bivalents counted in several diakineses, and by the same number counted in meiotic II metaphases. This karyotype is composed of 41 pairs of gradually decreasing autosomes and an XY/XX gonosomal set (Fig. 2). Of the autosomes, chromosomes of pair 1 are middle-sized submetacentrics amounting to 5.8 %

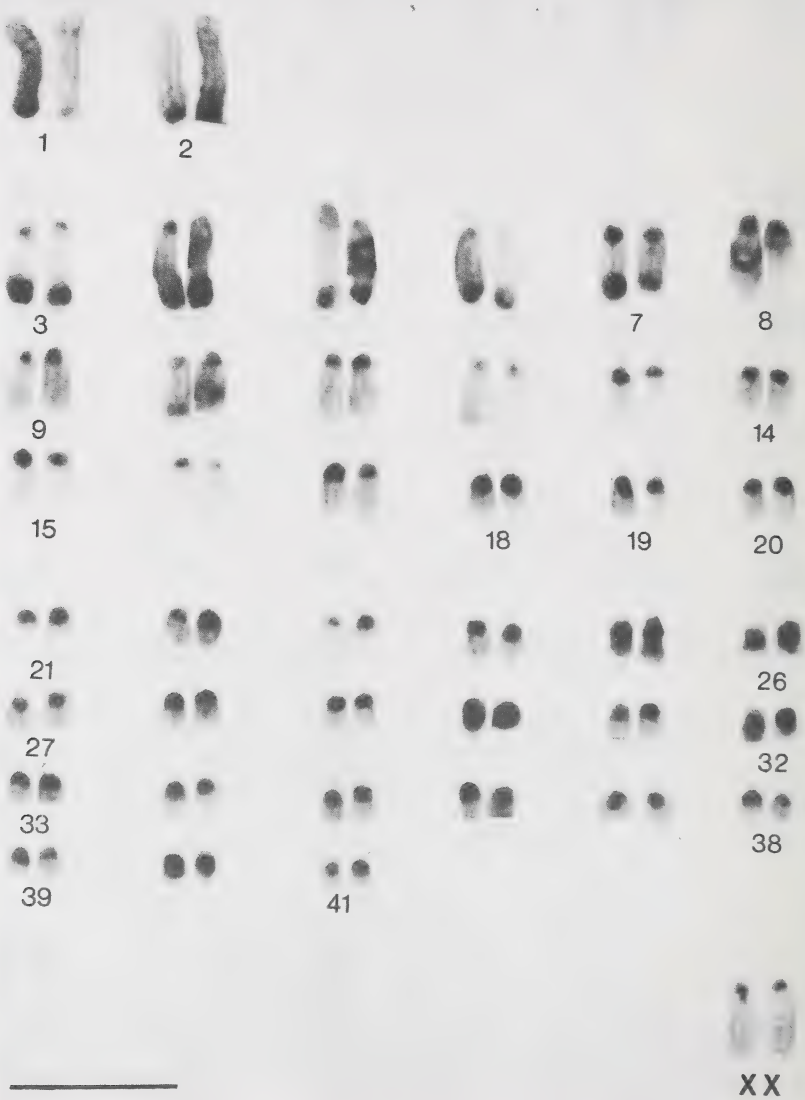

Fig. 3. Representative C-banded bone-marrow karyotype of *Zygodontomys microtinus thomasi* of a female individual from Paso Bajito-El Tigrito, Anzoátegui State, Venezuela. Bar represents 5 μm

LHS, and an average of 3.8 (3.0–4.8) μm of absolute size. Those of pair 2 are subtelocentric a little smaller than the former (5.5 %). Pairs 3 to 20 are small sized autosomes gradually decreasing in size from 4.6 % to 2.0 % LHS, and pairs 21 to 41 are minute chromosomes very similar in size, which also gradually decrease from 2.0 to 1.0 % LHS. Due to the small size of most autosomes, it was hard to recognize the morphology of many of the chromosomal pairs in all individuals examined. Moreover, the heterochromatic nature of some of the short arms (see below), may be responsible for polymorphic variants in the morphology of several autosomes among different individuals. The following description is based on the best-defined karyotypes from Anzoátegui (Fig. 2). Of the small sized series made of chromosome pairs 3 to 20, pairs 3, 7 and 18 are subtelocentric and pairs 15 and 19 are submetacentric and metacentric, respectively. The remaining pairs are either telocentric or show an indication of a very small short arm. Of the 21 pairs of minute autosomes, four

Fig. 4. 2n = 88 bone-marrow karyotype of *Zygodontomys microtinus thomasi* of a male individual from Isla Guara, Monagas State, Venezuela. Illustrated are also the sex chromosomes of one female from the same locality. Bar represents 5 μm

pairs are likely to be metacentric, and further six or seven are also clearly biarmed, whereas in the remaining pairs the presence or absence of short arms cannot be decided. Therefore, of the 41 autosomal pairs, 17 or 18 are biarmed, and 24 or 23 are likely to be telocentric chromosomes, allowing us to tentatively estimate the autosomal FN as made of 116 or 118 arms. Autosomes of pair 36 are telocentric showing a secondary constriction. The X-chromosome is a small-sized subtelocentric (r = 3.39) amounting 4.1 % LHS, and the Y-chromosome is a subtelocentric of minute size.

Although C-banding was not very clear in overall resolution in all treated cells and specimens, it allows us to conclude that a great deal of the genome is C-positive (Fig. 3). However, the small size of most chromosomes makes it difficult to ascertain the C-pattern of each chromosomal pair. The following description is based on a few good C-band resolutions we obtained in specimens from Anzoátegui. Chromosomes of pairs 1 and 2 lack a striking C-staining region, whereas those of pairs 3 to 7 exhibit both pericentromeric heterochromatin and a clear-cut terminal heterochromatic block. All the remaining autosome pairs show different degrees of C-staining. Those of the small-sized series exhibit in all cases a neat centromeric banding, and in addition three of them, corresponding to pairs 15, 18 and 19, have a full small arm heterochromatic block in all examined cells. Five of the minute autosomes are entirely C-positive, and the remaining sixteen pairs are C-positive in one third or more of their lengths, suggesting either large pericentromeric or full-arm blocks. The X-chromosome is C-positive only at the centromeric region, and the banding pattern of the Y-chromosome was not clearly defined.

Another slightly different karyotype was found in the nine analyzed specimens from Isle Guara. Here we have a karyotype of 2n = 88, FN = 116–118 (Fig. 4). The difference in diploid numbers affects the set of autosomes of the minute-sized class, where the addition of two pairs of autosomes is observed. Therefore, the autosomal set of the minute-sized series of the 2n = 88 is made of 23 pairs, instead of the 21 pairs found in the 2n = 84 complement. Besides, the small-sized series maintains the same number of 18 pairs, but the metacentric and the submetacentric pairs found in the 2n = 84 karyotype are lacking here. These differences can be easily explained by two Robertsonian fissions affecting pairs 15 and 19 of the 2n = 84 karyotype. However, because of the lack of good G-band resolution confirming the arm homologies, this interpretation is merely tentative. One specimen from Isla Guara produced successful C-banding. Here again a great deal of the genome was C-positive, although the small size and high number of chromosomes hampered efforts to obtain a clear-cut banding pattern in each of the pairs. It is evident, however, that eleven pairs of minute autosomes are fully C-positive, and five pairs of the small-sized series also appear to be fully heterochromatic.

Discussion

Zygodontomys has been difficult to classify among the groups of South American cricetids, which are currently divided into seven tribes (Reig 1980). Of these, it has been more frequently grouped with the Akodontini (Thomas 1916; Ellerman 1941; Vorontzov 1959; Cabrera 1961; Gardner and Patton 1976), but Tate (1932) considered it to belong to the Oryzomyini, and Hershkovitz (1962) argued that it must be grouped with the Phyllotini. On the grounds of its chromosomal characteristics, one of the present authors concluded that *Zygodontomys* should be removed from the Akodontini, and may represent a direct oryzomyine derivative, which because of its dubious relationships would better be placed as a Sigmodontinae *incertae sedis* (Reig 1980, 1987). We now believe that the high-numbered chromosomal complement of *Zygodontomys* is more likely to represent a primitive oryzomyine condition, as very high chromosomal numbers are more common in members of the tribe Oryzomyini than in members of the remaining tribes of the Sigmodontinae. Of the 18 species of mammals showing diploid numbers of 80 or

Mammalian species with diploid numbers equal or higher than 2 N = 80

Taxon	2n	FN	Source
RODENTIA, MYOMORPHA			
CRICETIDAE, SIGMODONTINAE			
Ichthyomyini			
Chibchanomys trichotis	92	102	GARDNER 1971; VOSS 1988
Ichthyomys pittieri	92	98	SCHMID et al. 1988
Sigmodontini			
Sigmodon alstoni	80–82	—	REIG 1987
Oryzomyini			
Oecomys "bicolor"	80	134–136	GARDNER and PATTON 1976
Oecomys "concolor"	80	112	GARDNER and PATTON 1976
Oryzomys "albigularis"	80	92	GARDNER and PATTON 1976
Oryzomys nitidus	80	86	GARDNER and PATTON 1976
Oryzomys macconelli	80	—	LEITAO and BARROS 1977
Delomys dorsalis collinus	82	—	YONENAGA 1975
Zygodontomys brevicauda	84	—	GARDNER and PATTON 1976
Zygodontomys microtinus	84–88	—	GARDNER and PATTON 1976
Zygodontomys microtinus	84	—	KIBLISKY et al. 1970
Zygodontomys microtinus	88	—	PEREZ-ZAPATA et al. 1984
Zygodontomys microtinus	84–88	116–118	This report
RODENTIA, CAVIOMORPHA			
CAPROMYIDAE			
Geocapromys browni	88	136	GEORGE and WEIR 1972
PERISSODACTYLA			
RHINOCEROTIDAE			
Ceratotherium simum	82	—	HEINICHEN 1969
Diceros bicornis	84	172	HUNGERFORD et al. 1967
Rhinoceros unicornis	82	—	WURSTER and BENIRSCHKE 1968
TAPIRIDAE			
Tapirus terrestris	80	—	MATTHEY 1973
PRIMATES			
TARSIIDAE			
Tarsius bancanus	80	94	CHIARELLI et al. 1979
Tarsius syrichta	80	94	CHIARELLI et al. 1979

FN = Number of autosomal arms. See under "References" for source of information.

more chromosomes, 6 species other than the sigmodontines *Chibchanomys trichotis* (= *Anotomys leander,* see VOSS 1988), *Ichthyomys pittieri, Sigmodon alstoni* and those of *Zygodontomys*, are members of the tribe Oryzomyini, whereas the remaining 7 species are assorted among the Perissodactyla, Caviomorpha and Primates (Table). These data certainly support GARDNER and PATTON's (1976) conclusion that the structurally primitive group of the oryzomyines is characterized by high chromosome numbers, and that a diploid number near 70 or 80 most likely is the progenitor state for oryzomyines and South American cricetids in general (but see BAKER et al. 1983). Thus, karyological data strongly support the hypothesis that *Zygodontomys* is closely linked to the early radiation of the Oryzomyini, and is better classified within that tribe, as originally held by TATE (1932).

It is now generally agreed that the name *Zygodontomys* should be limited to the "northern group" of HERSHKOVITZ (1962) (see REIG 1987; MACEDO and MARES 1987). But there is extensive disagreement about the number of species to be recognized within that assemblage. Opinions vary from recognizing ten (TATE 1932) or four species (CABRERA 1961), to the extreme position held by HERSHKOVITZ (1962), who only recognizes one species: *Z. brevicauda*, a view that has been accepted uncritically by most later authors (see, for instance, HONACKI et al. 1982).

After a regrettably brief examination of the types and other original materials in the British Museum, one of us (OAR) concluded that the taxonomy of *Zygodontomys* is much more complex than what Hershkovitz supposed. Morphological and geographical discontinuities in the material examined allowed for provisional recognition of four species and 13 subspecies: *Z. brevicauda* (including *brevicauda, cherriei, tobagi, soldadoensis, seorsus*); *Z. microtinus* (including *microtinus, thomasi, stellae*); *Z. punctulatus* (including *punctulatus, griseus, fraterculus*), and *Z. bruneus* (including *bruneus*, and *sactaemartae*). An additional probable member of *Zygodontomys* is *Oryzomys borreroi* Hernandez (1957) (see Gardner and Patton 1976). As regards *Z. reigi* from the French Guiana (Tranier 1976), the senior author, after the study of the type and original series, did not find reasons to separate those specimens from *Z. m. microtinus*, as reported by Husson (1978) for specimens of Surinam.

Specimens from the Venezuelan states of Guárico, Barinas, Sucre, Carabobo, Apure, Portuguesa, Bolivar, and Anzoátegui, are similar in size, fur color and morphology, and they agree with the type of *Zygodontomys microtinus thomasi* Thomas, being thereby identified as belonging to that taxon. The specimens from Isla Guara, though they differ in chromosome number, were indistinguishable from the former in overall morphology, and are thus identified as a chromosomal variant of the same taxon. The single sample from La Esmeralda clearly belongs to *Z. microtinus stellae* Thomas. Specimens of this sample differ from the former in being darker in fur color and larger in size. The fact that they belong to the same species was supported by obtaining viable laboratory hybrids from one male of the later and a female of the former (Garcia 1970).

Tranier (1976) based *Z. reigi*, among other characters, in the possession of 2n = 78 instead of 2n = 84 chromosomes. This was probably a miscount easy to occur when dealing with high chromosomal numbers, as other slides from the same locality observed by one of us (OAR) gave a normal 2n = 84 count.

Gardner and Patton (1976) reported a karyotype of 2n = 84 for *Z. brevicauda* from Costa Rica. At the same time, these authors found a karyotype of 2n = 88 in a *Z. microtinus* from Villavicencio, Colombia. The first report can be interpreted as an indication of karyotypic stability among different species of *Zygodontomys*. The second is congruent with our discovery of karyotypic poltypy in *Z. microtinus*. However, we need better knowledge of the chromosomes of additional samples of *Zygodontomys* to further settle the question of the interspecific and intraspecific variability of karyotypic constitution in this genus. In view of the extensive occurrence in the studied karyotypes of great amounts of heterochromatin both of the pericentromeric and of the whole-arm and even whole-chromosome type, it is expected that a great amount of polymorphism and polytypism will be demonstrated when more evidence becomes available.

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Zusammenfassung

Zytogenetik und Karyosystematik bei südamerikanischen Rodentia der Gruppe Oryzomyini (Cricetidae: Sigmodontinae). II. Hohe Chromosomenzahl und Karyotyp-Heterogenität bei Zygodontomys microtinus in Venezuela

Die Chromosomen von 42 Mäusen der Art *Zygodontomys microtinus* von 16 Herkünften aus Venezuela wurden untersucht. 33 dieser Tiere aus den beiden Unterarten *O. m. thomasi* und *O. m. stellae* hatten 2n = 84 Chromosomen und FN = 116–118. Die C-Banden zeigten, daß Heterochromatin, das perizentromer über ganze Chromosomen und Chromosomenarme verteilt ist, einen großen Teil des Genoms darstellt. 9 Exemplare der Herkunft Isla Guara (Monagas), die sich morphologisch nicht von *Z. m. thomasi* unterschieden, hatten 2n = 88 Chromosomen. Ihr Karyotyp ist von dem sonst gefundenen durch zwei Robertsonsche Fissionen ableitbar. Nach Ansicht der Autoren umfaßt die Gattung *Zygodontomys* 4 Arten und gehört wahrscheinlich zu den Oryzomyini.

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Evolution morphologique de la première molaire inférieure des campagnols souterrains d'Europe (Arvicolidae, Rodentia)

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Abstract

Morphological evolution of the first lower molar in the European ground-voles (Arvicolidae, Rodentia)

The morphology of the first lower molar (M1) of the European ground-voles, subgenus *(Microtus) Terricola*, was studied in different present and fossil species. Three dental characters summarize the morphological evolution of the M1: the development of the anterior part, the *Pitymys* rhombus and the anterior loop. Each character was compared between the species by the one-way analysis of variance (ANOVA). The *Pitgymys* rhombus is the best character for discrimining the present species, identified by an inclined *Pitymys* rhombus, from the fossil species, identified by a poorly inclined pitymys rhombus.

The anterior loop enables to classify the *Terricola* into two geographical groups: the Middle-European and Atlantic group with the fossil species *M. (T.) gregaloides* and *M. (T.) vergrannensis* and the present species *M. (T.) subterraneus, M. (T.) multiplex* and *M. (T.) pyrenaicus*, characterized by a closed anterior loop; the Mediterranean group with the species *M. (T.) tarentina* and *M. (T.) duodecimcostatus*, characterized by an open anterior loop.

The development of the anterior part is often more reduced in the Mediterranean species than in the Middle-European species.

The paleontological data show that the separation between the two groups is prior to 700 000 BP.

Introduction

L'application des techniques de la génétique des populations (électrophorèse des protéines) à l'étude des mammifères a beaucoup fait progresser leur systématique depuis une vingtaine d'années. En particulier l'étude de différentes espèces européennes et américaines de campagnols du genre *Microtus* (Graf 1980) a montré que les campagnols souterrains d'Europe ne sont pas génétiquement plus proches des campagnols souterrains d'Amérique que des autres espèces européennes de *Microtus* (sensu stricto). Aussi les espèces de campagnols souterrains d'Europe ne peuvent plus être rangées dans le sous-genre américain *Pitymys* McMurtie, 1831, dont l'espèce type est *M. (P.) pinetorum* d'Amérique du nord, mais doivent être attribuées au sous-genre européen *Terricola* Fatio, 1867 (Chaline et al. 1988). Les campagnols souterrains d'Europe se caractérisent par un polymorphisme chromosomique important (Matthey 1957, 1964; Meylan 1970, 1972; Winking et Niethammer 1970; Winking 1974, 1976; Graf et Meylan 1980) et une répartition géographique des espèces souvent restreinte et/ou discontinue (Niethammer et Krapp 1982; Fayard 1984) qui font de ce groupe un matériel particulièrement intéressant pour l'étude de l'évolution, de la spéciation en particulier.

L'étude des populations fossiles du Pléistocène moyen et supérieur est restée très fragmentaire jusqu'à récemment (Brunet-Lecomte 1988a) en raison du fait que seule la première molaire inférieure (M1) permet de distinguer les espèces de *Terricola* des autres espèces européennes de *Microtus*. La mise au point d'une morphométrie précise de la M1 (Brunet-Lecomte et al. 1987) suivie de l'utilisation des analyses statistiques multivariées

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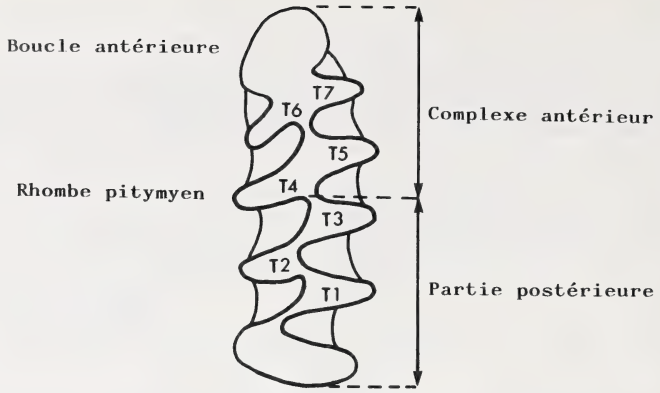

Fig. 1. Morphologie de la première molaire inférieure des campagnols souterrains d'Europe, sous-genre *Terricola*. Les triangles 1 à 7 sont nommés T1 à T7. Remarquer la confluence des triangles T4 et T5 formant le rhombe pitymyen

faites sur un nombre important de populations actuelles et fossiles a permis d'affiner la systématique des espèces fossiles (Brunet-Lecomte 1988b), de présenter la répartition géographique des espèces au Pléistocène moyen et supérieur (Brunet-Lecomte 1989) et de préciser l'évolution morphologique du groupe en Europe occidentale depuis le Pléistocène moyen.

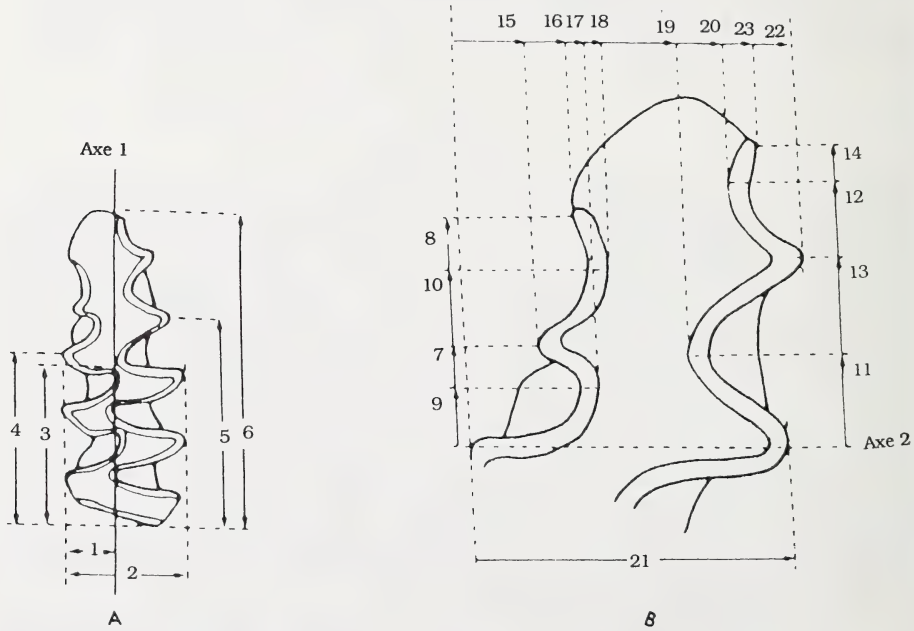

Fig. 2. Morphométrie de la première molaire inférieure des campagnols souterrains d'Europe, sous-genre *Terricola*. A = vue d'ensemble de la dent, B = partie antérieure de la dent. Les mesures 1 et 2 sont perpendiculaires à l'axe 1, les mesures 3 à 6 sont parallèles à l'axe 1; les mesurs 7 à 14 sont perpendiculaires à l'axe 2, les mesures 15 à 23 sont parallèles à l'axe 2

L'objet de cet article est de présenter les résultats obtenus par la comparaison entre les différentes espèces actuelles et fossiles des campagnols souterrains d'Europe des trois caractères dentaires qui résument le mieux l'évolution de la M1 dans le groupe depuis le Pléistocène moyen par la méthode de l'analyse de variance à 1 facteur. La synthèse de ces résultats permet d'affiner les relations de parenté entre les espèces fossiles et actuelles.

Matériel et méthode

La M1 inférieure des campagnols souterrains est une molaire à croissance continue dont la surface occlusale est composée de triangles rentrants. Si les trois premiers triangles sont clos chez toutes les espèces de *Microtus* d'Europe les quatrième et cinquième triangles sont opposés et confluent chez les *Terricola* en un rhombe caractéristique, le rhombe pitymyen (fig. 1), et clos chez les autres espèces européennes de *Microtus*.

En tout 23 mesures sont prises sur la partie occlusale de la M1 inférieure (fig. 2). Chacune de ces mesures correspond à une variable, nommée respectivement var 1 à var 23. Toutefois l'analyse des dents fossiles ayant montré que la mesure des variables var 14 et var 23 n'était pas fiable, celles-ci n'ont pas été retenues pour les analyses statistiques.

Les mesures 1 à 6 sont prises par référence à un premier axe passant par les bords externes de l'émail des premier et quatrième angles rentrants. Les mesures 7 à 23 sont prises par référence à un second axe joignant les deux points limités extérieurement par les mesures 4 et 5. Les mesures 7 à 14 sont perpendiculaires à cet axe et les mesures 15 à 23 parallèles. Les mesures sont prises avec une précision de 1/1000 de millimètre, mais toutefois les variables var 1 à var 23 sont exprimées en 1/100 de millimètre.

La description des variables est la suivante:

Variables mesurant la longueur de la dent: longueur totale: var 6; longueur de la partie postérieure de la dent: var 3 (rhombe pitymyen non compris), var 4 (partie postérieure jusqu'au bord intérieur de l'émail de la base du triangle T4 et var 5 (rhombe pitymyen compris).

Variables mesurant la largeur de la dent: largeur du bord du triangle 4 à l'axe: var 1, largeur totale entre les triangles T4 et T3: var 2.

Variables du complexe antérieur: longueur et largeur de la dent comprises entre les bords extérieurs des triangles T4 et T6: var 7 et var 15; longueur et largeur de la dent comprises entre les bords extérieurs du triangle T4 et de la boucle antérieure: var 8 et var 16; longueur et largeur de la dent comprises entre de bord extérieur du triangle T4 et le bord intérieur de l'angle rentrant situé entre les triangles T4 et T6: var 9 et var 17.

Longueur et largeur de la dent comprises entre le bord extérieur du triangle T4 et le bord intérieur de l'angle rentrant situé entre le triangle T6 et la boucle antérieure: var 10 et var 18; longueur et largeur de la dent comprises entre le bord extérieur du triangle T4 et le bord intérieur de l'angle rentrant situé entre les triangles T5 et T7: var 11 et var 19; longueur et largeur de la dent comprises entre le bord extérieur du triangle T4 et le bord intérieur de l'angle rentrant situé entre le triangle T7 et la boucle antérieure: var 12 et var 20; largeur et la dent comprise entre les bords extérieurs des triangles T4 et T5 (largeur du rhombe pitymyen): var 21; longueur de la dent et largeur de la dent comprise entre les bords extérieurs des triangles T4 et T7: var 13 et var 22.

Matériel

Le matériel analysé dans cette étude provient de différents échantillons obtenus à partir des populations suivantes.

Populations appartenant aux six espèces actuelles d'Europe occidentale: *M. (T.) subterraneus* (223 dents de France, Suisse et Pologne), *M. (T.) multiplex* (222 dents de France, Italie et Suisse), *M. (T.) savii* (130 dents d'Italie et Suisse), *M. (T.) pyrenaicus* (69 dents de France), *M. (T.) lusitanicus* (439 dents d'Espagne) et *M. (T.) doudecimcostatus* (257 dents de France et Espagne).

Populations fossiles des gisements suivants: Bourgade (Hérault, 69 dents classées en deux populations C1 et C2 de 27 et 42 dents), Orgnac 3 (Ardèche, population H de 10 dents), l'abri Vaufrey (Dordogne, population J2 de 103 dents) et Vergranne (Doubs, population O1 de 105 dents) pour la France; Villa Castelli (Taranto, population P de 40 dents) pour l'Italie; Atapuerca (Burgos, 35 dents classées en deux populations S1 et S2 de 17 et 18 dents) pour l'Espagne; West Runton (Norfolk, 18 dents classées en deux populations U1 et U2 de 5 et 13 dents) pour la Grande Bretagne; Villany 6 et 8 pour la Hongrie (34 dents classées en deux populations V1 et V2 de 17 et 17 dents).

La description et la chronologie des gisements fossiles ont été présentées par ailleurs (Brunet-Lecomte 1988a, 1989).

Analyse statistique

L'étude de la morphologie comparée des populations actuelles et fossiles a porté sur les trois caractères qui synthétisent le mieux l'évolution morphologique de 1a M1 depuis le Pléistocène moyen: le développement de la partie antérieure de la dent, noté vart 1 (var 1 = [var 6–var 3]/var 6); l'inclinaison du rhombe pitymyen, notée vart 2 (vart 2 = var 4–var 3)); la fermeture de la boucle antérieure, notée vart 3 (vart 3 = var 20-var 18).

La variable vart 1 est sans dimension, les variables vart 2 et vart 3 sont exprimées en 1/100 de millimètre.

La méthode choisie pour comparer l'évolution de chacun des caractères entre les espèces et/ou les populations est l'analyse de variance à un facteur (ANOVA).

Pour préciser l'évolution respective de chacun de ces caractères au cours du temps, trois groupes d'analyses de variance à un facteur (classe) ont été faites pour chacun des trois caractères. Le facteur classe comporte, toutes ou partie, des 18 espèces, ou populations suivantes.

Classe 1: *M. (T.) subterraneus*, notée 1; Classe 2: *M. (T.) multiplex*, notée 2; Classe 3: *M. (T) savii*, notée 3; Classe 4: *M. (T.) pyrenaicus*, notée 4; Classe 5: *M. (T.) lusitanicus*, notée 5; Classe 6: *M. (T.) duodecimcostatus*, notée 6; Classe 7: Population West Runton = *M. (T.) arvalidens*, notée U1; Classe 8: Population West Runton = *M. (T.) gregaloides*, notée U2; Classe 9: Population Villany, population attribuée à *M. (T.) gregaloides*, notée V1; Classe 10: Population Villany = *M. (T.) hintoni*, notée V2; Classe 11: Population Bourgade = *Microtus (Allophaiomys) pitymyoides*, notée C1; Classe 12: Population Bourgade = *M. (A.) nutiensis*, notée C2; Classe 13: Population Atapuerca = *M. (A.) chalinei*, notée S1; Classe 14: Population Atapuerca = *M. (A.) species*, notée S2; Classe 15: *M. (T.) mariaclaudiae*, notée H; Classe 16: *M. (T.) vaufreyi*, notée J2; Classe 17: *M. (T.) vergrannensis*, notée O1; Classe 18: *M. (T.) tarentina*, notée P;

Les classes 1 à 6 correspondent aux six espèces actuelles d'Europe occidentale, les classes 15 à 18 aux espèces du Pléistocène moyen d'Europe occidentale (âge compris entre 500 000 et 80 000 BP), et les classes 7 à 14 (toutes d'âge antérieur à 600 000 BP) soit à des espèces anciennes (U1, U2, V2, C1, C2 et S1) soit à des populations de statut spécifique incertain (V1, et S2).

Pour le premier groupe d'analyses de variance (ANOVA 1), les analyses ont été faites entre toutes les classes (variation maximale du facteur temps).

Tableau 1. **Moyenne ± écart-type des variables vart 1, vart 2 et vart 3 chez les classes de campagnol souterrain d'Europe**

La variable vart 1 est sans dimension, les variables vart 2 et vart 3 sont exprimées en 1/100 de millimètre

Variable Classe	Vart 1	Vart 2	Vart 3
1	0,528 ± 0,013	0,3 ± 4,4	14,7 ± 4,9
2	0,514 ± 0,019	1,4 ± 2,4	22,1 ± 8,7
3	0,508 ± 0,017	0,2 ± 4,0	27,9 ± 5,7
4	0,510 ± 0,012	−1,5 ± 3,7	24,5 ± 6,1
5	0,507 ± 0,013	−4,8 ± 5,1	21,4 ± 7,2
6	0,494 ± 0,015	−4,0 ± 4,5	34,8 ± 8,1
U1	0,512 ± 0,027	5,6 ± 4,0	24,4 ± 7,6
U2	0,532 ± 0,024	14,8 ± 3,2	25,3 ± 5,5
V1	0,515 ± 0,017	10,5 ± 6,5	30,1 ± 7,5
V2	0,510 ± 0,014	20,3 ± 3,8	39,1 ± 5,5
C1	0,514 ± 0,021	15,3 ± 3,9	38,8 ± 9,1
C2	0,516 ± 0,012	16,6 ± 3,8	36,5 ± 5,9
S1	0,498 ± 0,016	14,6 ± 2,8	36,2 ± 4,9
S2	0,496 ± 0,019	15,3 ± 3,7	37,2 ± 4,8
H	0,516 ± 0,011	2,1 ± 2,9	24,8 ± 3,6
J2	0,527 ± 0,022	7,5 ± 9,0	28,3 ± 5,1
O2	0,522 ± 0,009	0,5 ± 3,0	27.1 ± 4,6
P	0,484 ± 0,021	−1,6 ± 5,1	48,3 ± 7,9

Légende des classes: 1 = *Microtus (Terricola) subterraneus*, 2 = *M. (T.) multiplex*, 3 = *M. (T) savii*, 4 = *M. (T.) pyrenaicus*, 5 = *M. (T.) lusitanicus*, 6 = *M. (T.) duodecimcostatus*, U1 = *M. (T.) arvalidens*, U2 = *M. (T.) gregaloides*, V1 = Population de Villany attribuée à *M. (T.) gregaloides*,, V2 = *M. (T.) hintoni*, C1 = *Microtus (Allophaiomys) pitymyoides*, C2 = *M. (A.) nutiensis*, S1 = *M. (A.) chalinei*, S2 = *M. (A.)* species d'Atapuerca, H = *M. (T.) mariaclaudiae*, J2 = *M. (T.) vaufreyi*, O1 = *M. (T.) vergrannensis* et P = *M. (T.) tarentina*.

Pour le deuxième groupe d'analyses de variance (ANOVA 2), les analyses ont été réalisées entre les classes définies par les espèces actuelles (classes 1 à 6) et les espèces fossiles d'âge moyen, classes 15 à 18 (variation moyenne du facteur temps).

Pour le troisième groupe d'analyse de variance (ANOVA 3), les analyses ont été faites entre les seules espèces actuelles, classes 1 à 6 (facteur temps constant).

Afin de réduire le biais qu'aurait pu introduire une trop grande variation dans les effectifs entre les classes, il a été choisi de limiter à 20 individus au plus les effectifs de chaque classe. Pour cela un tirage aléatoire a été fait parmi les classes ayant un effectif supérieur à 20 individus (classes 1, 2, 3, 4, 5, 6, C1, C2, J2, O1 et P). Pour les autres classes les effectifs correspondent au nombre total d'individus dans la population considérée.

Résultats

Le tableau 1 donne la moyenne et l'écart-type des variables (= caractères) vart 1, vart 2 et vart 3 pour chacune des 18 classes définies précédemment.

Pour chaque groupe d'analyses de variance ANOVA 1, ANOVA 2 et ANOVA 3, le couple de degrés de liberté du calcul du test F de Fisher étant toujours le même (égal respectivement à 17 et 300, 9 et 180, 5 et 114), il est possible d'établir un classement entre les variables pour voir lesquelles diffèrent le plus entre les classes considérées. Ainsi, la lecture du tableau 2 illustre:

1. la diminution de l'importance au cours du temps de l'inclinaison du rhombe pitymyen dans l'évolution de la morphologie de la M1 (variable la plus significative pour ANOVA 1, la moins pour ANOVA 3);
2. L'importance croissante au cours du temps de la fermeture de la boucle antérieure et du développement de la partie antérieure dans l'évolution de la morphologie de la M1 (variable la plus significative pour ANOVA 2 et ANOVA 3).

Tableau 2. **Résultat des analyses de variance faites pour les variables vart 1, vart 2 et vart 3**

La première valeur est égale au test F de Fisher, la seconde au classement de la variable selon sa significativité par rapport à l'analyse de variance considérée. Tous les tests F calculés sont significatifs avec une probabilité $< 0{,}001$

Analyse Variables	ANOVA 1 F		ANOVA 2 F		ANOVA 3 F	
Vart 1	10,29	3	13,94	3	10,60	2
Vart 2	47,46	1	16,74	2	7,15	3
Vart 3	29,15	2	33,51	1	19,01	1

Etude du développement de la partie antérieure (vart 1)

La figure 3 donne la distribution de la moyenne (moyenne $\pm$ t $\alpha/2$*erreur-type avec α = 0,05) des classes pour la variable vart 1.

Le test de Scheffé se rapportant à l'analyse de variance ANOVA 1 (tableau 3) donne les paires de classes statistiquement différentes ($p < 0{,}05$).

Cette analyse oppose globalement les classes 6 = *M. (T.) duodecimcostatus*, S2 = *M. (A.) species* d'Atapuerca et P = *M. (T.) tarentina*, caractérisées par une longueur relative de la partie antérieure de la dent réduite (vart 1 faible), aux classes 1 = *M. (T.) subterraneus*, U2 = *M. (T.) gregaloides*, C2 = *M. (A.) nutiensis*, J2 = *M. (T.) vaufreyi* et O1 = *M. (T.) vergrannensis*, caractérisées par une longueur relative de la partie antérieure de la dent développée (vart 1 élevée).

Les classes 6, S2 et P correspondent à des espèces méditerranéennes, tandis que les classes 1, U2, J2 et O1 se rapportent à des espèces médio-européennes ou atlantiques.

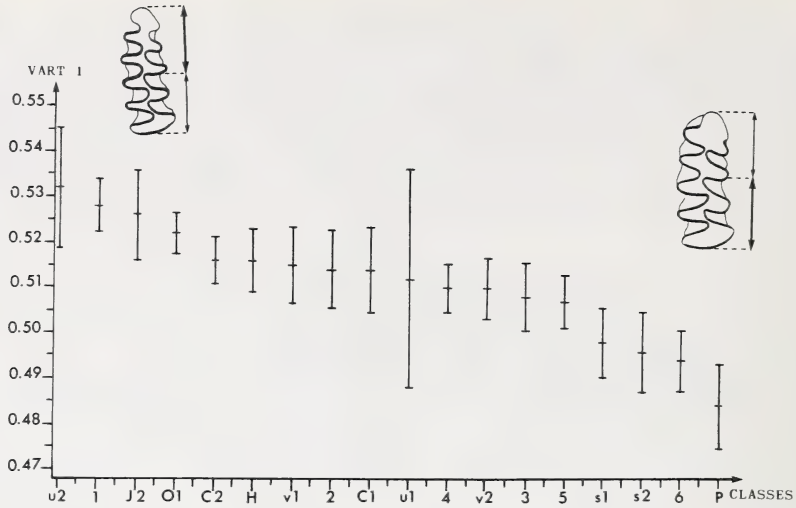

Fig. 3. Distribution du développement de la partie antérieure de la dent (vart 1) chez les différentes populations. Moyenne ± t α/2*erreur-type, avec α = 0,05. La variable est sans dimension. Légende des classes: 1 = *Microtus (Terricola) subterraneus*, 2 = *M. (T.) multiplex*, 3 = *M. (T.) savii*, 4 = *M. (T.) pyrenaicus*, 5 = *M. (T.) lusitanicus*, 6 = *M. (T.) duodecimcostatus*, U1 = *M. (T.) arvalidens*, U2 = *M. (T.) gregaloides*, V1 = Population de Villany attribuée à *M. (T.) gregaloides*, V2 = *M. (T.) hintoni*, C1 = *Microtus (Allophaiomys) pitymyoides*, C2 = *M. (A.) nutiensis*, S1 = *M. (A.) chalinei*, S2 = *M. (A.) species* d'Atapuerca, H = *M. (T.) mariaclaudiae*, J2 = *M. (T.) vaufreyi*, O1 = *M. (T.) vergrannensis* et P = *M. (T.) tarentina*

Etude de l'inclinaison du rhombe pitymyen vart 2

La figure 4 donne la distribution de la moyenne (moyenne ± t α/2*erreur-type avec = α 0,05) des classes pour la variable vart 2.

Tableau 3. **Paires des classes présentant un test de Scheffé se rapportant à l'analyse de variance ANOVA 1 pour la variable développement de la partie antérieure de la dent significatif = * (p < 0,05)**

Toutes les autres paires de classes ne sont pas statistiquement différentes (p > 0,05)

Classe	6	S2	P
1	*	*	*
U2	*	*	*
C2	–	–	*
J2	*	–	*
O1	–	–	*

Légende des classes: 1 = *Microtus (Terricola) subterraneus*, 6 = *M. (T.) duodecimcostatus*, U2 = *M. (T.) gregaloides*, C2 = *M. (A.) nutiensis*, S2 = *M. (A.)* species d'Atapuerca, J2 = *M. (T.) vaufreyi*, O1 = *M. (T.) vergrannensis* et P = *M. (T.) tarentina*.

Le test de Scheffé se rapportant à l'analyse de variance ANOVA 1 (tableau 4) donne les paires de classes statistiquement différentes (p < 0,05).

Cette analyse permet de séparer deux groupes morphologiques:

Groupe 1: Classes V2 = *M. (T.) hintoni*, C2 = *M. (A.) nutiensis*, S2 = *M. (A.) species* d'Atapuerca, C1 = *M. (A.) pitymyoides*, U2 = *M. (T.) gregaloides* et S1 = *M. (A.) chalinei*, caractérisées par un rhombe pitymyen peu ou pas incliné.

Groupe 2: Classes 2 = *M. (T.) multiplex*, O1 = *M. (T.) vergrannensis*, 1 = *M. (T.) subterraneus*, 3 = *M. (T.) savii*, 4 = *M. (T.) pyrenaicus*, P = *M. (T.) tarentina*, 6 = *M. (T.) duodecimcostatus* et 5 = *M. (T.) lusitanicus*, présentant un rhombe pitymyen incliné ou très incliné.

Les classes suivantes: V1 = population de Villany attribuée à *M. (T.) gregaloides*, J2 =

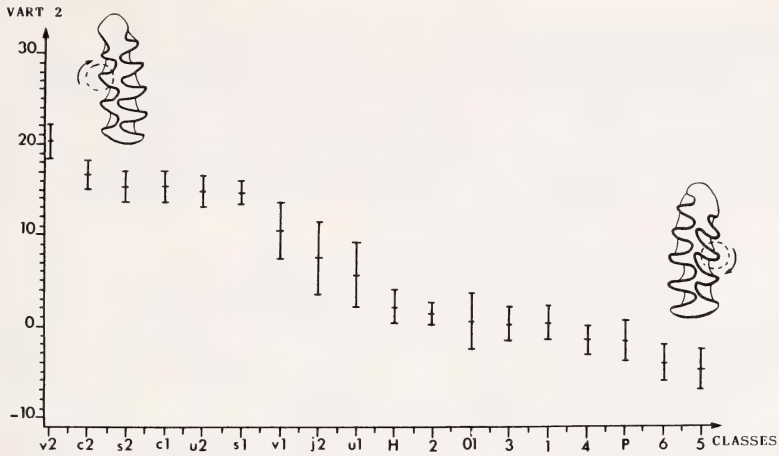

Fig. 4. Distribution de l'inclinaison du rhombe pitymyen (vart 2) chez les différentes populations, Moyenne ± t α/2*erreur-type, avec α = 0,05. La variable est exprimée en 1/100 de millimètre. Légende des classes: 1 = *Microtus (Terricola) subterraneus,* 2 = *M. (T.) multiplex,* 3 = *M. (T.) savii,* 4 = *M. (T.) pyrenaicus,* 5 = *M. (T.) lusitanicus,* 6 = *M. (T.) duodecimcostatus,* U1 = *M. (T.) arvalidens,* U2 = *M. (T.) gregaloides,* V1 = Population de Villany attribuée à *M. (T.) gregaloides,* V2 = *M. (T.) hintoni,* C1 = *Microtus (Allophaiomys) pitymyoides,* C2 = *M. (A.) nutiensis,* S1 = *M. (A.) chalinei,* S2 = *M. (A.) species* d'Atapuerca, H = *M. (T.) mariaclaudiae,* J2 = *M. (T.) vaufreyi,* O1 = *M. (T.) vergrannensis* et P = *M. (T.) tarentina*

M. (T.) vaufreyi, U1 = *M. (T.) arvalidens* et H = *M. (T.) mariaclaudiae,* caractérisées par un rhombe pitymyen moyennement incliné se situent entre les groupes 1 et 2.

Les groupes 1 et 2 forment chacun un ensemble homogène (aucune paire statistiquement différente à l'intérieur de chaque groupe), et chaque classe d'un groupe est statistiquement différente de chacune des classes de l'autre groupe.

Par ailleurs il faut noter que: les espèces du sous-genre ancestral *Allophaiomys* (Chaline 1966, 1972; Rabeder 1981) sont classées dans le groupe 1, de même que les

Tableau 4. **Paires des classes présentant un test de Scheffé se rapportant à l'analyse de variance ANOVA 1 pour la variable inclinaison du rhombe pitymyen significatif = * (p < 0,05)**

Toutes les autres paires de classes ne sont pas statistiquement différentes (p > 0,05)

Classe	V1	J2	U1	H	2	O1	1	3	4	P	6	5
V2	*	*	*	*	*	*	*	*	*	*	*	*
C2	–	*	–	*	*	*	*	*	*	*	*	*
S2	–	–	–	*	*	*	*	*	*	*	*	*
C1	–	–	–	*	*	*	*	*	*	*	*	*
U2	–	–	–	*	*	*	*	*	*	*	*	*
S1	–	–	–	*	*	*	*	*	*	*	*	*
V1	–	–	–	–	*	*	*	*	*	*	*	*
J2	–	–	–	–	–	–	–	–	*	*	*	*

Légende des classes: 1 = *Microtus (Terricola) subterraneus,* 2 = *M. (T.) multiplex,* 3 = *M. (T) savii,* 4 = *M. (T.) pyrenaicus,* 5 = *M. (T.) lusitanicus,* 6 = *M. (T.) duodecimcostatus,* U1 = *M. (T.) arvalidens,* U2 = *M. (T.) gregaloides,* V1 = Population de Villany attribuée à *M. (T.) gregaloides,* V2 = *M. (T.) hintoni,* C1 = *Microtus (Allophaiomys) pitymyoides,* C2 = *M. (A.) nutiensis,* S1 = *M. (A.) chalinei,* S2 = *M. (A.)* species d'Atapuerca, H = *M. (T.) mariaclaudiae,* J2 = *M. (T.) vaufreyi,* O1 = *M. (T.) vergrannensis* et P = *M. (T.) tarentina.*

populations types des espèces primitives *M. (T.) gregaloides* et *M. (T.) hintoni*; les espèces actuelles sont classées dans le groupe 2;

M. (T.) arvalidens, espèce d'âge ancien, mais de morphologie déjà proche de celles des espèces actuelles est classée entre les groupes 1 et 2; les quatre espèces du Pléistocène moyen sont classées, soit dans le groupe 2 (*M. [T.] vergrannensis* et *M. [T.] tarantina*) et montrent une morphologie proche de celle des espèces actuelles, soit dans l'ensemble intermédiaire entre les groupes 1 et 2 (*M. [T.] mariaclaudiae*) et présentent une morphologie encore proche de celle des espèces primitives.

Etude de la fermeture de la boucle antérieure vart 3

La figure 5 donne la distribution de la moyenne (moyenne ± t $\alpha/2$*erreur-type avec = α 0,05) des classes pour la variable vart 3.

Le test de Scheffé se rapportant à l'analyse de variance ANOVA 1 (tableau 5) donne les paires de classes statistiquement différentes ($p < 0,05$).

Cette analyse montre que:

De façon précise les classes 1 = *M. (T.) subterraneus* et P = *M. (T.) tarentina*, se différencient de la plupart des autres classes; la classe 1 = *M. (T.) subterraneus* est caractérisée par une fermeture nette de la boucle antérieure, la classe P = *M. (T.) tarentina* par une fermeture très réduite de cette boucle.

De façon plus globale, elle oppose deux groupes constitués des classes suivantes:

Groupe 1: P = *M. (T.) tarentina*, V2 = *M. (T.) hintoni*, C1 = *M. (A.) pitymyoides*, S2 = *M. (A.) species* d'Atapuerca, C2 = *M. (A.) nutiensis*, S1 = *M. (A.) chalinei* et 6 = *M. (T.) duodecimcostatus*; caractérisés par une boucle ouverte ou très ouverte.

Groupe 2: 1 = *M. (T.) subterraneus*, 5 = *M. (T.) lusitanicus*, 2 = *M. (T.) multiplex*, 4 = *M. (T.) pyrenaicus*, H = *M. (T.) mariaclaudiae*, U2 = *M. (T.) gregaloides* et O1 = *M. (T.) vergrannensis*; caractérisés par une boucle fermée ou très fermée.

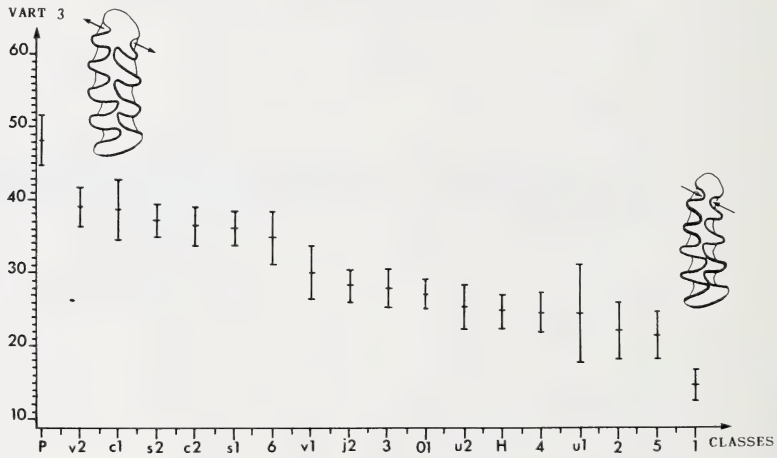

Fig. 5. Distribution de l'ouverture de la boucle antérieure (vart 3) chez les différentes populations. Moyenne ± t $\alpha/2$*erreur-type, avec α = 0,05. La variable est exprimée en 1/100 de millimètre. Légende des classes: 1 = *Microtus (Terricola) subterraneus*, 2 = *M. (T.) multiplex*, 3 = *M. (T.) savii*, 4 = *M. (T.) pyrenaicus*, 5 = *M. (T.) lusitanicus*, 6 = *M. (T.) duodecimcostatus*, U1 = *M. (T.) arvalidens*, U2 = *M. (T.) gregaloides*, V1 = Population de Villany attribuée à *M. (T.) gregaloides*, V2 = *M. (T.) hintoni*, C1 = *Microtus (Allophaiomys) pitymyoides*, C2 = *M. (A.) nutiensis*, S1 = *M. (A.) chalinei*, S2 = *M. (A.) species* d'Atapuerca, H = *M. (T.) mariaclaudiae*, J2 = *M. (T.) vaufreyi*, O1 = *M. (T.) vergrannensis* et P = *M. (T.) tarentina*

Tableau 5. **Paires des classes présentant un test de Scheffé se rapportant à l'analyse de variance ANOVA 1 pour la variable fermeture de la boucle antérieure significatif = * ($p < 0{,}05$)**

Toutes les autres paires de classes ne sont pas statistiquement différentes ($p > 0{,}05$)

Classe	C2	S1	6	V1	J2	3	O1	U2	H	4	U1	2	5	1
P	*	*	*	*	*	*	*	*	*	*	*	*	*	*
V2	–	–	–	–	–	–	*	*	*	*	–	*	*	*
C1	–	–	–	–	–	–	*	*	*	*	–	*	*	*
S2	–	–	–	–	–	–	–	–	–	*	–	*	*	*
C2	–	–	–	–	–	–	–	–	–	*	–	*	*	*
S1	–	–	–	–	–	–	–	–	–	–	–	*	*	*
6	–	–	–	–	–	–	–	–	–	–	–	*	*	*
V1	–	–	–	–	–	–	–	–	–	–	–	–	–	*
J2	–	–	–	–	–	–	–	–	–	–	–	–	–	*
3	–	–	–	–	–	–	–	–	–	–	–	–	–	*
O1	–	–	–	–	–	–	–	–	–	–	–	–	–	*

Légende des classes: 1 = *Microtus (Terricola) subterraneus*, 2 = *M. (T.) multiplex*, 3 = *M. (T) savii*, 4 = *M. (T.) pyrenaicus*, 5 = *M. (T.) lusitanicus*, 6 = *M. (T.) duodecimcostatus*, U1 = *M. (T.) arvalidens*, U2 = *M. (T.) gregaloides*, V1 = Population de Villany attribuée à *M. (T.) gregaloides*,, V2 = *M. (T.) hintoni*, C1 = *Microtus (Allophaiomys) pitymyoides*, C2 = *M. (A.) nutiensis*, S1 = *M. (A.) chalinei*, S2 = *M. (A.)* species d'Atapuerca, H = *M. (T.) mariaclaudiae*, J2 = *M. (T.) vaufreyi*, O1 = *M. (T.) vergrannensis* et P = *M. (T.) tarentina*.

Les classes V1 = population de Villany, J2 = *M. (T.) vaufreyi* et 3 = *M. (T.) savii* se situent entre ces deux groupes; la classe U1 = *M. (T.) arvalidens* se situe dans le second groupe, mais son effectif réduit ne permet de la séparer statistiquement de la plupart des classes du premier groupe.

Cette séparation en deux groupes n'isole pas, contrairement à celle obtenue avec le caractère rhombe pitymyen, les espèces anciennes des espèces récentes et/ou actuelles. Il convient de noter la présence majoritaire d'espèces ou de populations méditerranéennes dans le premier groupe (classes 6, C1, C2, S1, S2 et P), et d'espèces médio-européennes ou atlantiques dans le second groupe (classes 1, 2, 4, U2, H et O1).

Discussion

Les analyses précédentes faites sur les trois parties suivantes de la M1: l'inclinaison du rhombe pitymyen, le développement de la partie antérieure de la dent et la fermeture de la boucle antérieure, montrent que l'évolution de ces trois caractères dentaires n'a pas été constante au cours du temps:

L'inclinaison du rhombe pitymyen (vart 2) permet de séparer les espèces anciennes des plus récentes et actuelles. Cette caractéristique avait déjà été observée et figurée chez les espèces *M. (A.) pitymyoides, M. (A.) nutiensis* (Chaline 1972) et *M. (A.) praehintoni* (Rabeder 1981) dont sont issues les espèces de *Terricola*.

Le développement de la partie antérieure de la dent (vart 1) et la fermeture de la boucle antérieure (vart 3) ne séparent pas les espèces anciennes des espèces actuelles, mais permettent de mettre en évidence l'existence de deux ensembles évolutifs distincts chez les campagnols souterrains:

1. Ensemble morphologique méditerranéen: caractérisé par un développement réduit de la partie antérieure de la dent et une fermeture de la boucle antérieure faible. Cet ensemble comprend *M. (A.) chalinei* (S1), *M. (T.) tarentina* (P) et *M. (T.) duodecimcostatus* (6). *M. (T.) lusitanicus* (5), espèce génétiquement très proche de *M. (T.) duodecimcostatus*, n'appartient pas à ce groupe; cette espèce se distingue de *M. (T.) duodecimcostatus* par

une fermeture plus prononcée de la boucle antérieure (vart 3 faible). Cette différence entre les deux espèces a déjà été soulignée par ailleurs (Brunet-Lecomte et al. 1987); l'évolution morphologique de *M. (T.) lusitanicus* sans doute récente (inférieure à 80 000 BP) et rapide, peut expliquer cette différence morphologique entre ces deux espèces.

2. Ensemble morphologique médio-européen: caractérisé par un développement de la partie antérieure de la dent et une fermeture de la boucle antérieure moyens à importants. Cet ensemble comprend *M. (T.) arvalidens* (U1), *M. (T.) gregaloides* (U2), *M. (T.) mariaclaudiae* (H), *M. (T.) vaufreyi* (J2), *M. (T.) vergrannensis* (O1), *M. (T.) subterraneus* (1), *M. (T.) multiplex* (2) et *M. (T.) pyrenaicus* (4).

M. (A.) pitymyoides (C1), *M. (A.) nutiensis* (C2) de Bourgade et *M. (T.) hinoni* (V2), qui se situent entre ces deux ensembles et se différencient par ailleurs par une inclinaison du rhombe pitymyen réduite, constituent des espèces primitives caractérisées par une morphologie de certains caractères dentaires (vart 1) encore peu différenciée.

M. (T.) *savii* se situe entre les deux ensembles géographiques; toutefois la double appartenance de *M. (T.) tarentina* à l'ensemble méditerranéen et au groupe *savii* par le type morphologique de la troisième molaire supérieure, invite à rattacher *M. (T.) savii* à l'ensemble méditerranéen.

Les populations d'*Allophaiomys* (C1, C2, S1 et S2) présentent une fermeture réduite de la boucle antérieure. Cette caractéristique associée à l'inclinaison réduite du rhombe pitymyen sont les traits les plus typiques des espèces ancestrales des campagnols souterrains.

Au contraire le développement de la partie antérieure de la dent n'est pas un trait typique des espèces ancestrales analysées dans cette étude. Les populations anciennes d'Espagne (Atapuerca) montrent un développement réduit de la partie antérieure de la dent par rapport aux populations anciennes de France (Bourgade). Cette caractéristique des espèces méditerranéennes (Atapuerca), encore observée chez l'espèce actuelle *M. (T.) duodecimcostatus,* est à rapprocher de l'observation faite sur la croissance de la M1 inférieure dans une population actuelle de *M. (T.) duodecimcostatus* (Brunet-Lecomte 1988a): cette étude montre que les individus âgés de quatre semaines ont une longueur relative de la partie antérieure de la dent plus réduite que celle observée chez les individus âgés de huit semaines et plus, exprimant ainsi une allométrie de croissance de la dent à la fin de son ontogenèse au profit de la partie antérieure. Aussi peut-on dire que les espèces qui présentent un rapport longueur de la partie antérieure/longueur totale faible (*M. [A.] chalinei, M. [T.] tarentina* et *M. [T.] duodecimcostatus*) sont ancestrales pour ce caractère, et celles qui présentent un tel rapport élevé (*M. [T.] arvalidens, M. [T.] gregaloides, M. [T.] mariaclaudiae, M. [T.] vaufreyi, M. [T.] vergrannensis, M. [T.] subterraneus* et *M. [T.] multiplex*) sont évoluées pour ce caractère.

Remerciements

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Résumé

La morphologie de la première molaire inférieure (M1) des campagnols souterrains d'Europe, sous-genre *Microtus (Terricola),* a été étudiée chez différentes espèces actuelles et fossiles. Trois caractères dentaires résument l'évolution morphologique de la M1: le développement de la partie antérieure de la dent, le rhombe pitymyen et la boucle antérieure. Chacun d'eux a été comparé chez les différentes espèces par la méthode de l'analyse de variance à un facteur (ANOVA).

Le rhombe pitymyen est le caractère qui discrimine le mieux les espèces fossiles, chez lesquelles il est peu ou pas incliné, des espèces actuelles, chez lesquelles il incliné ou très incliné.

La boucle antérieure classe les *Terricola* en deux groupes géographiques: le groupe médio-européen et atlantique avec les espèces *M. (T.) gregaloides, M. (T.) vergrannensis, M. (T.) subterraneus* et *M. (T.) multiplex*, caractérisées par une boucle antérieure fermée; le groupe méditerranéen avec les

espèces *M. (T.) tarentina* et *M. (T.) duodecimcostatus,* caractérisées par une boucle antérieure ouverte.

Le développement de la partie antérieure est souvent plus réduit chez les espèces du groupe méditerranéen que chez les espèces du groupe médio-européen. Les données paléontologiques montrent que la séparation des deux groupes est ancienne, antérieure à 700 000 BP.

Zusammenfassung

Morphologische Evolution des ersten unteren Molaren bei europäischen Wühlmäusen (Arvicolidae, Rodentia)

Der erste untere Molar (M1) von Wühlmäusen der Gattung *Microtus* und der Untergattung *Terricola* (früher *Pitymys*) wurde bei verschiedenen europäischen rezenten und fossilen Arten untersucht.

Vor allem bei drei Merkmalen zeigten sich innerhalb dieser Gruppe Artunterschiede:

1. Die relative Länge des Vorderteils des Zahnes, 2. die Neigung des *Pitymys*-Rhombus und 3. der Grad der Abschnürung des Vorderlobus. Die Signifikanz der Unterschiede wurde mit der Einfaktoren-Varianzanalyse (ANOVA) überprüft.

Der *Pitymys*-Rhombus erlaubt eine Trennung der rezenten Arten (stark geneigt) von den fossilen (wenig geneigt).

Der Vorderlobus ist bei den nördlicher verbreiteten Arten *M. (T.) subterraneus, M. (T.) multiplex* und *M. (T.) pyrenaicus* (rezent), *M. (T.) gregaloides* und *M. (T.) vergrannensis* (fossil) deutlich abgeschnürt, bei den mediterranen *M. (T.) duodecimcostatus* (rezent) und *M. (T.) tarentina* (fossil) mit T6 und T7 offen verbunden. Der Vorderteil des M1 ist bei den mediterranen Arten überwiegend relativ kürzer als bei den nördlicher verbreiteten.

Mindestens 700 000 Jahre in die Vergangenheit zurück läßt sich die Zweiteilung der *Terricola*-Gruppe verfolgen.

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Reproductive cycle of *Arvicola terrestris* (Rodentia, Arvicolidae) in the Aran Valley, Spain

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Abstract

Studied the reproductive biology of *Arvicola terrestris* in the Aran Valley (Lérida, Spain). 684 specimens (304 males, 380 females) captured between July 1983 and December 1984 were analysed. The breeding season of this population starts in March and ends in October/November. Spermatozoids are present in adult individuals throughout the year, although the testicles and seminal vesicles vary in size. The minimum size is reached in December and the maximum between April and June. During the breeding season, males attain sexual maturity before females. The sexual activity in mature females varies throughout the year with a maximum between May and August/September. Pregnant females are found between March and October/November. The average litter size is 4.48 ± 1.23, n = 80.

Introduction

Although the data published on the reproduction of the northern water vole, *Arvicola terrestris* are abundant (Reichstein 1982), studies of a complete annual cycle are relatively scarce (van Wijngaarden 1954; Pelikán 1972; Wieland 1973; Morel 1981). Apart from some data given by Gosálbez (1976), there is no detailed information on the reproductive biology of *A. terrestris* from Spain. The purpose of this paper is to indicate the reproductive characteristics of this species in the northeast of the Iberian Peninsula.

Material and methods

The analysed specimens (n = 684; 304 males, 380 females) originate from monthly captures between July 1983 and December 1984 in the meadow lands on the left shore of the Garonne river between the localities of Aubert (930 m) and Arròs (900 m), in the Aran Valley (Lérida, Spain). The animals were collected after death and subsequently dissected to study their sexual state.

The body weight of each specimen was taken. To determine the stage of maturity and sexual activity in males, the following characteristics and parameters were considered: position of testicles (abdominal or scrotal), testicular cell content (Gosálbez et al. 1979), minor and major diameters of the testicle and length of the seminal vesicle (Gosálbez and Sanscoma 1976).

Three categories of males were distinguished from the testicular cell content, according to the criteria mentioned by Ventura and Gosálbez (1987): immature: specimens lacking spermatids and spermatozoids in the testicle; submature: specimens with few spermatozoids and spermatids in the testicle; mature: specimens with a large amount of spermatozoids in the testicle.

In the females, the main criterion used to determine the stage of maturity was the histological appearance of the ovaries (Ventura et al. 1989). Immediately after capturing the animal, ovaries were extirpated and kept in the fixation liquid (Bouin). Once in the laboratory, conventional histological procedures were carried out: embedding in paraffin, preparation of 5–7 μm thick sections stained with hematoxylin-eosin.

The following characteristics were also studied: status of the vulva (open or closed), stage of development and vascularization of the uterus and ovaries, and presence and number of embryos and placental scars.

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The following categories were established:

Immature: species not yet in the first oestral cycle (corpora lutea lacking in the ovary). They present closed vulva, poorly developed and vascularized uterus and lack placental scars.

Inactive mature: specimens displaying at least one ovulation (corpora lutea in the ovary). They present closed vulvae. The uterus is developed but scantily vascularized. They may present placental scars but no embryos.

Active mature: specimens displaying at least one ovulation (corpora lutea in the ovary). They present an open vulva. The uterus is fully developed and well vascularized. They may present placental scars and/or embryos.

To determine the average weight at which individuals reach sexual maturity, W_{50} was calculated. This estimate represents the body weight at which 50 % of the specimens are mature. This weight is the limit above which all individuals are considered adults (Pelikán 1972). W_{50} has been calculated according to the method described by Leslie et al. (1945) and taking into account the presence of spermatozoids in males and of corpora lutea in females.

All the specimens were distributed into six classes of relative age (0–V) according to their type of coat, stage of moult (Maximov 1959; Morel 1981) and characteristics of the skull (Kratochvíl 1974). The diagnostic traits for skull were (Ventura 1988): degree of flatness of skull case, development of the mastoid process and separation of the interorbitary crests. In the mandible, the degree of development of the condyloid tuberosity and the separation of the angular process in relation to the base of the condyloid branch.

The intervals of age and the characteristics of the coats and moults corresponding to each class are the following (Ventura 1988):

Class 0: 0–3 weeks. Specimens with the first coat and lacking melanic prints.

Class I: 3–6 weeks. Specimens with the first coat partially or totally developed and with regular prints corresponding to the ventral sequence of the first moult.

Class II: 6–10 weeks. Specimens with melanic prints corresponding to the dorsal sequence of the first moult.

Class III: 10–14 weeks. Specimens with the second coat partially or totally developed and with melanic prints corresponding to the second moult.

Class IV: older than 14 weeks, but before the end of their first winter. Specimens with adult coat. Irregular melanic prints may be present.

Class V: specimens that have wintered at least once. They have adult coat. Irregular and scattered melanic prints may be present.

Results and discussion

Reproduction in males

Fig. 1 reveals that starting at a certain body weight spermatozoids are present throughout the year, although their density undergoes seasonal variations. During December and January some specimens with few spermatozoids in correlation to their body weights are observed.

According to these observations, the November–February period has not been taken into account when determining the minimum weight of sexual maturity. During the remainder of the year, all individuals weighing less than 65 g are immature. Specimens between 65 and 95 g are at different stages of maturity, and above 95 g only mature individuals are found. The W_{50} obtained in males is 73 g (Fig. 2).

The lengths of testicles (TL) and seminal vesicles (VL) vary between 3.8–12.2 mm and 2.0–19.5 mm, respectively. Not taking into account the November–February period, spermatozoids appear in TL and VL ranging between 5.5 mm and 2.8 mm, respectively. Between 5.5–7.5 mm of TL and 2.8–7.0 mm of VL there is a noticeable variation in the stage of sexual maturity. Above these ranges, all individuals show a high density of spermatozoids in the testicular contents.

These values are clearly lower than those found in the literature. Thus, Wieland (1973) found in Eastern Germany fertile males of *A. terrestris* with TL > 10 mm. Pelikán (1972) in Czechoslovakia found VL minimum values higher than 13 mm. These differences are due to larger body size of the specimens of these populations.

Those individuals captured in December and January with a low spermatozoid density in relation to their body size also show reduced TL (4.9–6.3 mm) and VL (6.1–8.4 mm).

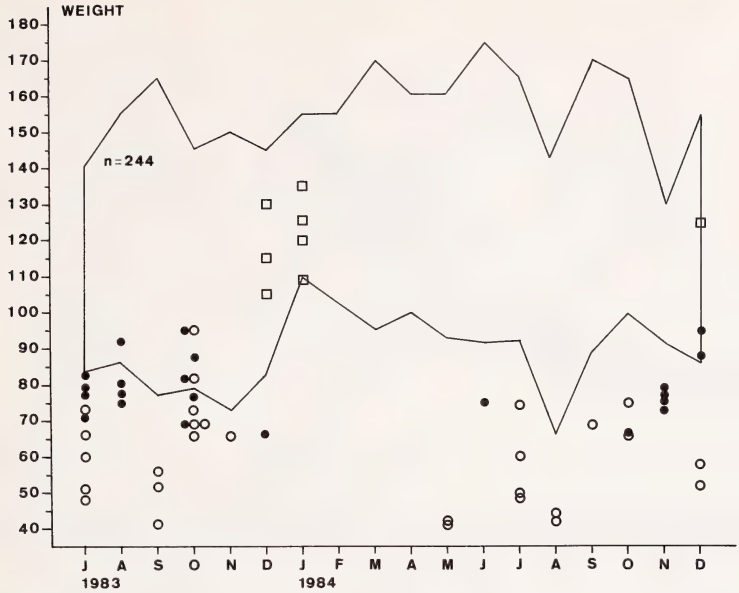

Fig. 1. Relationship between body weight (in g) and sexual status of males of *A. terrestris* from the Aran Valley, throughout the period of study. ○ = immature; ● = submature, □ = mature with few spermatozoids; solid line: remainder of mature specimens (n)

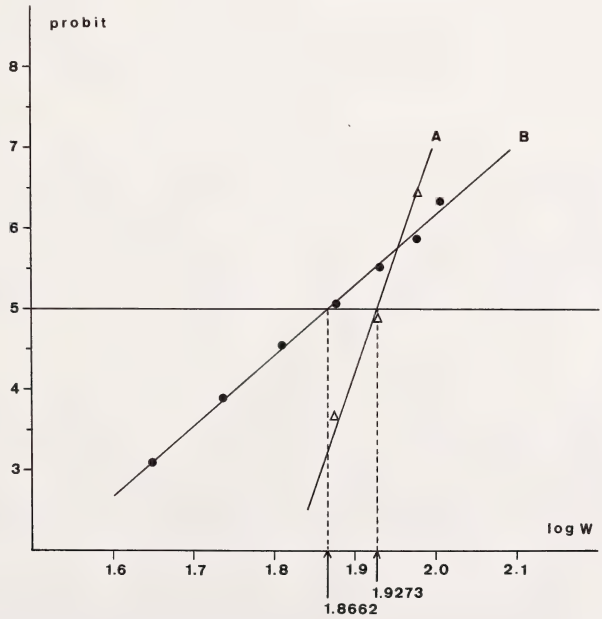

Fig. 2. Determination of 50 % of sexual maturity in *A. terrestris* from the Aran Valley. The probit corresponding to the percentage of mature specimens is plotted against the logarithm of body weight (log W). The equations for the straight lines are B: males: y = 4.9314 + 8.8188 (x − 9.8584); log (weight 50 % maturity) = 1.8662; antilog 1.8662 = 73.48 g; A: females: y = 4.8840 + 28.1679 (x − 1.9232); log (weight 50 % maturity) = 1.9273; antilog 1.9273 = 84.58 g

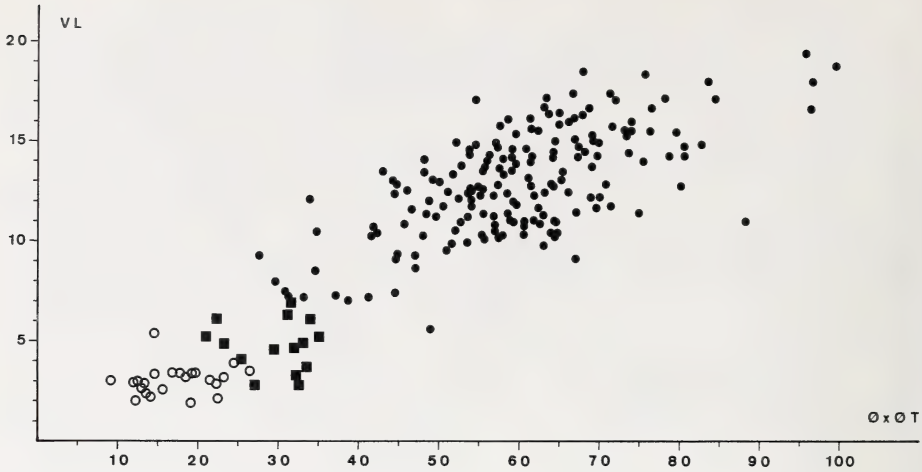

Fig. 3. Relationship between the sexual status of males and the correlation between the product of the minor and major testicular diameters (∅ × ∅ T, in mm^2) and the seminal vesicle length (VL, in mm) in *A. terrestris* from the Aran Valley. ○ = immature, ■ = submature, ● = mature

The correlation between the product of the minor and major testicular diameters (∅ × ∅ T) and VL (Fig. 3) allow us to discriminate the individuals according to their sexual stage. Only the specimens captured between March and October are taken into account. Below 25 mm^2 of ∅ × ∅ T and 4.0 mm of VL only immature specimens appear. Between these two values and 35 mm^2 and 7.0 mm, respectively, submature individuals appear, some males also being found without spermatozoids. Above these upper limits, all the specimens are sexually mature. These values are lower than those reported by Pelikán (1972) (70 m^2 ∅ × ∅ T and 9.0 mm VL), a fact due to the larger body size of *A. terrestris* in Czechoslovakia.

All males of classes 0 (n = 4) and I (n = 18) are immature. The first submature specimens are found in class II (57.14 %, n = 35). In this age class, immature (14.28 %) and mature (28.57 %) specimens also appear. In class III it is possible to find, although in small percentage, submature males (5.12 %, n = 78). These specimens were captured during the October–December period. A delay in the onset of sexual maturity in those individuals born between the end of the summer and the beginning of the autumn can be deduced. In classes IV (n = 102) and V (n = 66) only mature specimens appear. According to these results, the onset of sexual maturity in males takes place in class II.

The testicles and seminal vesicles of adult specimens (classes IV and V) undergo significant changes in size throughout the year (Fig. 4). Between June and October there is a slow but progressive decrease in the mean values of TL and VL, a process that is enhanced during November. In December and January, both parameters reach minimum values. From January on, there is an obvious size increase, which shows maximum values between April and June. A clear relationship between testicle and seminal vesicle lengths can be observed ($r = 0.90 \pm 0.04$; f.d. = 122; $p < 0.001$).

Wieland (1973) mentioned a cyclic variation of the testicle size throughout the year in *A. terrestris*. The pattern of variation that he described coincides with the observations in the Aran Valley. Likewise, Wieland (1973) indicated that the size reduction of the testicles inevitably implies sexual inactivity in males, but he did not explain precisely the causes of this alteration.

Claude (1970) and Martinet (1972) indicated that size reduction of the testicle determines a total pause or partial suppression of spermatogenesis. Therefore, the first

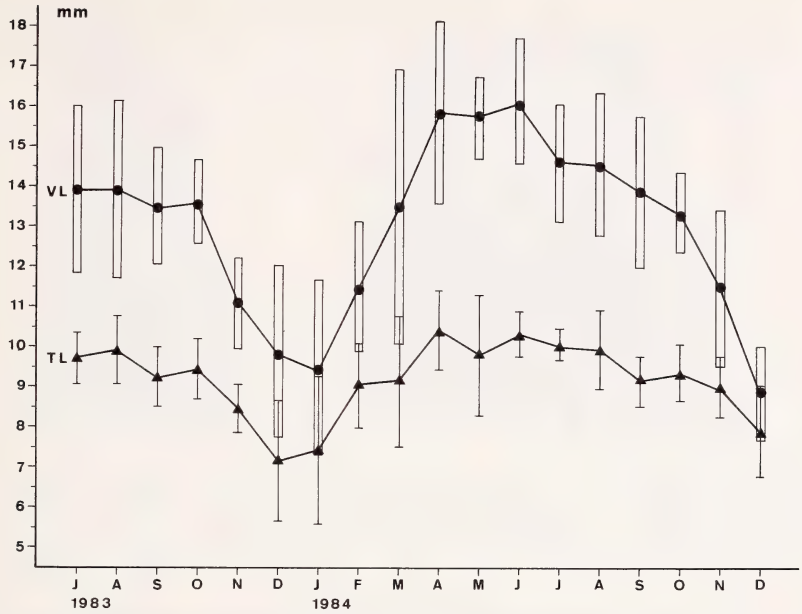

Fig. 4. Monthly variation of the average ($\bar{x} \pm s$) length of the seminal vesicle (VL) and of the testicle (TL) in adult specimens (classes IV and V) of *A. terrestris* from the Aran Valley

circumstance does not seem to have occurred in the studied population since spermatozoids in adult individuals are present throughout the year.

According to microscopic observations, the existence of a reduction in the spermatogenesis in some adult specimens during December and January can be deduced. These specimens showed especially low values of TL, even within the variation range of immature and submature males. The spermatogenic alteration seems to appear only in those mature individuals with high testicular reduction. In the remainder of the adult males, the density of spermatozoids did not show clear differences with those from individuals captured during the breeding season. However, although the adult males captured during the sexually inactive period can show a high density of spermatozoids, the testicular size reduction occurring during this period may considerably affect the reproductive potential of these individuals (Ventura and Gosálbez 1987).

Reproduction in females

Fig. 5 shows the relationship between body weight and sexual stage of females, throughout the year. During the March–October period, all specimens weighing less than 76 g are immature. Between 76 and 96 g, there is a wide range of specimens that show different stages of maturity. The lightest pregnant female weighed 86 g. All females with body weights above 96 g are sexually mature. Thus, between 76 and 96 g females reach sexual maturity.

The W_{50} obtained in females is 85 g (Fig. 2). This value is clearly higher than that found for males. Taking the body weight as an estimate of the age, the fact that males attain sexual maturity before females can be stated.

All females of classes 0 (n = 5) and I (n = 18) are immature. The first mature females appear in class II (20.41 %, n = 49). In class III the number of sexually immature individuals is still significant (15.25 %, n = 49), but in higher classes (IV = 175; V = 74) all

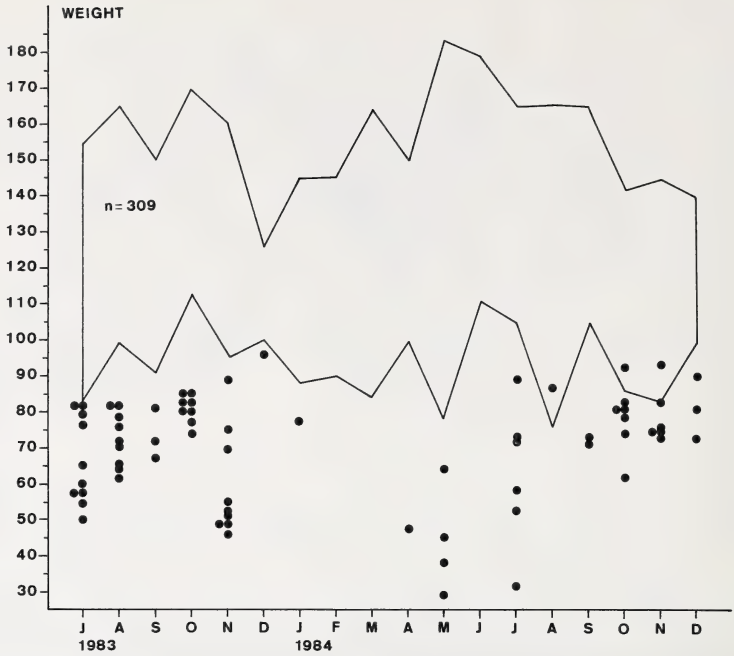

Fig. 5. Relationship between body weight (in g) and sexual status of females of *A. terrestris* from the Aran Valley, throughout the study period. ● immature, solid line: mature (n)

females have reached sexual maturity. Comparing them to the general data found for males, they seem quite coincident, although there are some particular differences. Thus, although the range of the onset of sexual maturity is also situated between classes II and III, this latter shows no immature males. These results support the observations seen previously according to W_{50}, which show that males reach sexual maturity at a lower weight than females.

The sexual stage of females according to the month of capture reveals that a relatively high percentage of the immature individuals belonging to class III (66.67 %, n = 9) were captured between November and January. This substantiates that females also show a possible delay in the onset of sexual maturity between the end of autumn and winter.

The percentage of active females referred to the total of mature females (Fig. 6) shows a cyclic variation throughout the year. Between May and August/September the level of sexual activity in females is maximum, but from September/October onward, there is a progressive decrease of activity. Between December and February the sexual activity is zero. During March this percentage shows a sharp increase lasting until May.

Pregnant females appear between March and October, despite the fact that one pregnant individual was captured during November 1983 (Fig. 6). The monthly percentage of pregnant individuals over the total of mature females shows a seasonal variation of reproductive intensity. The reproductive dynamics of the species throughout the year show a bimodal distribution with maximum values at the beginning (March) and the second half of the reproductive cycle (August). From these months onward, the relative percentage of pregnant females decreases progressively. Therefore, lower values are found in July and a total pause of reproductive activity at the end of the year.

Of 307 mature females, 80 (26.05 %) presented embryos in different stages of development. The total number of viable implanted fetuses was 359, distributed in litters of 2 to

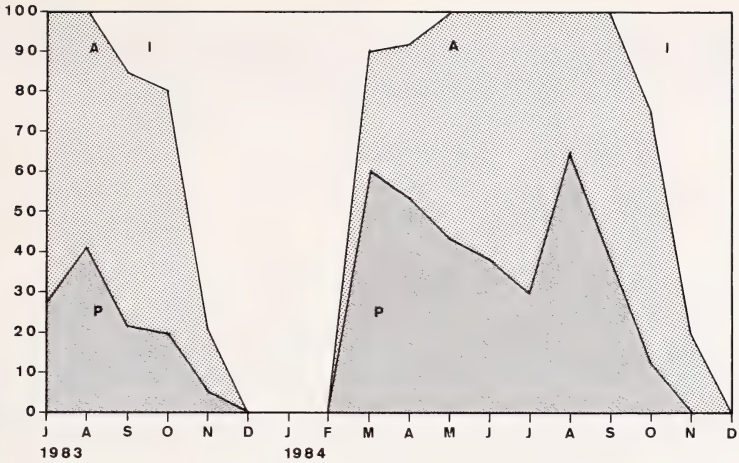

Fig. 6. Variation throughout the period of study of the percentage of active mature females with reference to the total mature females (upper line), and percentage of pregnant females over the total of active mature females (bottom line) in *A. terrestris* from the Aran Valley. I = inactive mature, A = active mature, P = pregnant

9 embryos. The average litter size is 4.48 ± 1.23 embryos/female (n = 80). This value is relatively lower than the averages registered in other populations of this species (Reichstein 1982) and coincides, approximately, with the value given by Gosálbez (1976) for northeast Iberian Peninsula.

Reichstein (1982) mentioned that the heaviest individuals of *A. terrestris* regularly show larger number of embryos. Likewise, Pelikán (1972) mentioned a geographical increase in litter size of this species from west to east of its distribution area. Regarding these observations, the two factors conditioning the low average in the analysed population could mainly be: on one hand, comparatively smaller body sizes of the individuals from the Pyrenees (Ventura and Gosálbez 1988), and, on the other, the geographical situation of the studied population.

Conclusions

According to the present results, the breeding season of *A. terrestris* in the Aran Valley extends from March to October/November. From the monthly averages of VL and TL it is possible to conclude that the period of maximum sexual activity for males is situated between April and June. Maximum activity levels for females appear between March and August. This fact is established by the large number of pregnant females during this period.

Between November/December and February a sexual resting period appears, as all adult females are inactive and males show lower averages of LV and LT. Despite the significant size reduction of both structures during these months, all males present spermatozoids in their testicles independently of the season. Therefore, it is necessary to state that although the presence of spermatozoids allows us to classify an individual as sexually active, the reproductive efficiency needs to be verified when the size reduction of the testicle and seminal vesicle size reduction is still in progress (Ventura and Gosálbez 1987). Despite the fact that spermatogenesis is not interrupted once sexual maturity is reached, an adult animal with reduced testicular and vesicular sizes may not be fertile. The sexual inactivity of males needs to be considered only as a secondary factor since females regulate the duration and reproductive intensity of the population (Pelikán 1972). Thus, the absolute inactivity of females during November/December–February determines the

pause of reproductive activity, because even if males still present some fertilizing capacity (according to the presence of spermatozoids in the genital tract), the regulating effect exerted by females controls the incidence of matings.

Acknowledgements

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Zusammenfassung

Zum Fortpflanzungszyklus von Arvicola terrestris (Rodentia, Arvicolidae) im Nordosten der Iberischen Halbinsel

An 304 Männchen und 380 Weibchen von *Arvicola terrestris*, die zwischen Juli 1983 und Dezember 1984 im Aran-Tal in Spanien gefangen worden waren, wurde das Fortpflanzungsverhalten untersucht. Die Fortpflanzung beginnt im März und endet im Oktober/November. Bei den adulten Männchen findet man ganzjährig Spermatozoen, obwohl die Größe von Hoden und Vesikeldrüsen im Jahreslauf stark schwanken. Am kleinsten sind sie im Dezember, am größten von April bis Juni. Während der Fortpflanzungsperiode erreichen die Männchen früher die Geschlechtsreife als die Weibchen. Von Mai bis August/September sind alle geschlechtsreifen Weibchen auch geschlechtstätig. Geschlechtstätige Weibchen fehlen von Dezember bis Februar. Trächtige Weibchen kamen nur von März bis Oktober/November vor. Die durchschnittliche Embryonenzahl war 4.48 ± 1.23, n = 80.

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Interspecific aggression in sympatric *Gerbillurus* species

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Abstract

Studied interspecific aggression in four *Gerbillurus* species, which are closely related and ecologically similar. Areas of sympatry between *G. paeba* and *G. tytonis, G. paeba* and *G. setzeri, G. tytonis* and *G. setzeri*, and *G. paeba* and *G. vallinus* have been identified. Interspecific agonistic behaviour was investigated by means of staged encounters between sympatric species in order to ascertain whether interference competition may influence ecological segregation.

Results showed that the ecological "specialists" *G. tytonis* and *G. vallinus* dominated the ecological "generalist" *G. paeba*, while *G. setzeri* avoided contact with *G. paeba* or *G. tytonis*. Interference competition through agonistic behaviour may result in ecological segregation of sympatric *Gerbillurus* species.

Introduction

Two or more closely-related and/or ecologically similar species of organisms coexisting in a particular habitat are likely to affect one another. If these species suffer as a result of the association, competition is said to occur, which may take the form of resource competition or interference competition (Krebs 1985).

Competitive ability evolves by animals becoming more efficient resource users, and/or by the evolution of interference mechanisms that prevent competing species from using scant resources (Krebs 1985). Thus, aggressive behaviour has evolved in many animals and forms part of resource competition in some situations.

Interference competition through agonistic behaviour has been implicated in several taxa of coexisting, ecologically-similar rodent species (Blaustein 1980; Grant 1972; Cranford and Derting 1983). Clear evidence for the dominance of one species in laboratory encounters is provided in most cases (Blaustein and Risser 1976; Ambrose and Meehan 1977; Banks and Fox 1968). Staged laboratory encounters have been criticized because of their artificial nature (Banks and Fox 1968), but nevertheless provide results which are usually consistent with field observations (Grant 1972).

Four species of the genus *Gerbillurus* inhabit the arid areas of Southern Africa and have similar diets (Boyer 1988; Erasmus in litt.). Several areas of sympatry have been identified: *G. paeba* and *G. tytonis* coexist along the eastern border of the Namib dunefield and along the Kuiseb River, Namibia; *G. setzeri* is reported to cross the Kuiseb River and enter the dunefield, which is normally occupied by *G. tytonis*, at times of high population density (de Graaff 1981); *G. setzeri* and *G. paeba* have been trapped together on the gravel plains near Rössing Uranium Mine; *G. vallinus* and *G. paeba* coexist in the northern Cape province (Erasmus, in litt.). All four species are nocturnally active and diurnally fossorial.

The ecology of *G. tytonis* in two areas of allopatry and in one area of syntopy with *G. paeba*, has been studied (Boyer 1988). Considerable dietary overlap between these two species occurs, but partial spatial separation may occur at certain seasons, since *G. paeba* prefer the dune trough and slope, and *G. tytonis* the dune crest. *G. paeba* and *G. tytonis* were found to be highly aggressive, *G. setzeri* less so, and *G. vallinus* least aggressive in

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intraspecific agonistic encounters (Dempster and Perrin 1989). In this study, interference competition by aggressive interaction was investigated in all species combinations known to be sympatric. It was predicted that interspecific encounters would reflect the levels of agonistic behaviour observed in intraspecific encounters. Dominant species in laboratory encounters would be expected to displace subordinate species in the field.

Materials and methods

Seven *G. paeba* (5 females, 2 males) were trapped near Swakopmund (23° 37′ S, 14° 34′ E) and 12 *G. tytonis* (7 females, 5 males) were trapped in the area south of Gobabeb (23° 37′ S, 15° 01′ E) during August 1984. Twelve *G. setzeri* (7 females, 5 males) were trapped near Rössing Uranium Mine (22° 31′ S, 14° 52′ E) in June 1985. Four *G. vallinus* (3 males, 1 female) and six *G. paeba* were trapped near Copperton (29° 59′ S, 22° 17′ E), Northern Cape in August 1986.

Gerbils were housed in 60 × 30 × 30 cm glass terraria provided with a layer of sand and a nest box. Food and water were provided ad lib. The light regime was 16L:8D using light supplied by a 100 W light bulb. The circadian photoperiod was reversed; temperature was maintained at 25 °C.

Agonistic encounters were staged in a terrarium provided with a 3–4 cm layer of sand. The sand was thoroughly mixed between encounters and changed after 10–15 encounters, when the tank was also washed out with soap and water to reduce possible pheromonal effects. Lighting was provided by a 40 W red light bulb positioned above the tank. All encounters were staged during the dark phase of the light cycle when the animals were most active. Individual animals were not used repeatedly over a short period of time.

A partition was used to separate the two opponents initially and to permit investigation of the tank for 5 min before the partition was removed. Ten-min encounters were videorecorded using a video camera (JVC Model TK1700EG) and recorder (National Portable VCR NV-180). The animals were weighed after the encounter. Twenty encounters including all possible sex combinations were staged in *G. paeba-G. tytonis, G. paeba-G. setzeri,* and *G. tytonis-G. setzeri* combinations. The small numbers of animals trapped permitted only 9 encounters in the *G. vallinus-G. paeba* combination.

Agonistic behaviour in intraspecific same-sex encounters consisted of attacking (AT), attack leaping (AL), chasing (CH), fighting (FI), uprights (UP), stop/freeze (ST), escape leaping (EL), fleeing (FL), and crouching (CR). The aggressive acts AT, AL, and CH and the submissive acts EL, FL, and CR were mutually exclusive, i.e., dominance was established at the beginning of an encounter. In addition, approaching (AP) and exploring

Table 1. **Mean dominance – submissive scores in interspecific encounters**
n = 5 encounters for each combination, except where indicated in parentheses

Subject	Opponent							
	G. t. ♀	*G. t.* ♂	*G. s.* ♀	*G. s.* ♂	*G. p.* ♀	*G. p.* ♂	*G. v.* ♀	*G. v.* ♂
G. tytonis ♀			25.5	32.6	63.7	66.0		
G. tytonis ♂			51.4	44.4	−68.5	35.3		
G. setzeri ♀	−30.3	−21.8			−46.1	31.8		
G. setzeri ♂	−25.7	−74.1			−54.4	−57.0		
G. paeba ♀	−76.9	65.4	53.9	46.2			26.0 (1)	−32.9 (3)
G. paeba ♂	−61.2	10.0	2.3	44.7			−17.0 (1)	−23.1 (4)
G. vallinus ♀					69.0 (1)	60.0 (1)		
G. vallinus ♂					35.3 (3)	47.7 (4)		

(EX) were significantly more frequently performed by dominant than by submissive animals ($p < 0.05$, chi-squared contingency table analysis).

A scoring system was applied to the results of all interspecific encounters in order to determine the dominance/submissive relationships. Scores were calculated for each individual in each encounter by summing the following frequencies:

Offensive behaviour: (AT, AL and CH) × 2
Exploratory behaviour: (AP and EX) × 1
Submissive behaviour: (EL, FL and CR) × −2

A mean score for each species in each class of encounters was calculated. Dominance/submissive scores were compared by means of Wilcoxon's T-test.

Results

Mean frequencies (± S.E.) of agonistic behaviours are shown in Figures 1 to 4, and dominance scores in Table 1.

Encounters between *G. tytonis* and *G. paeba* (Fig. 1) involved a high level of interaction and aggression. Males were less aggressive towards each other than females were, and females of both species dominated males of both species. Differences between dominance indices for all *G.paeba-G. tytonis* encounters were not significant, however if female *G. paeba*-male *G. tytonis* encounters were excluded, *G. tytonis* was significantly dominant over *G. paeba* ($p < 0.005$).

In *G. paeba-G. setzeri* encounters (Fig. 2), little aggressive behaviour was displayed in all classes of encounter. Male and female *G. setzeri* behaved submissively, despite the low

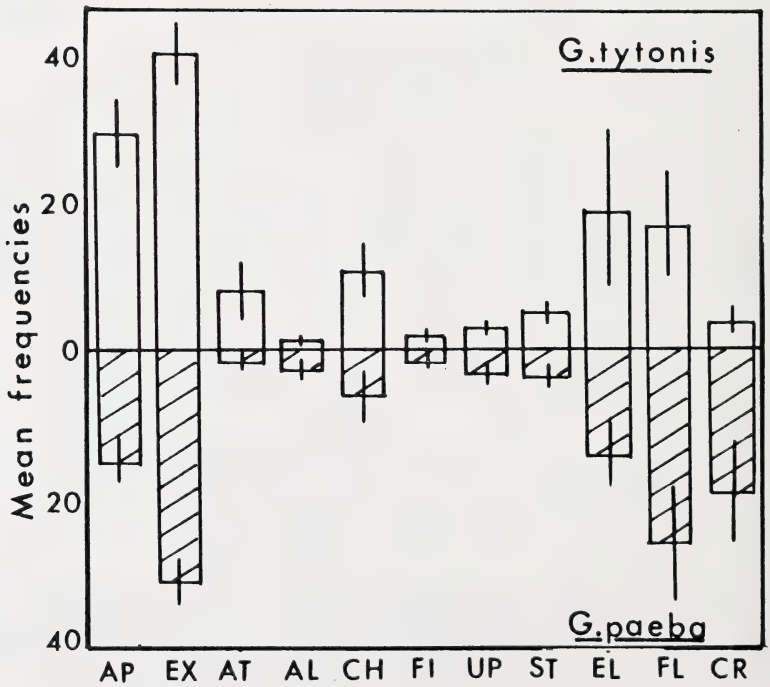

Fig. 1. Mean frequencies (± S.E.) of agonistic behaviours in *G. tytonis-G. paeba* encounters (n = 20)

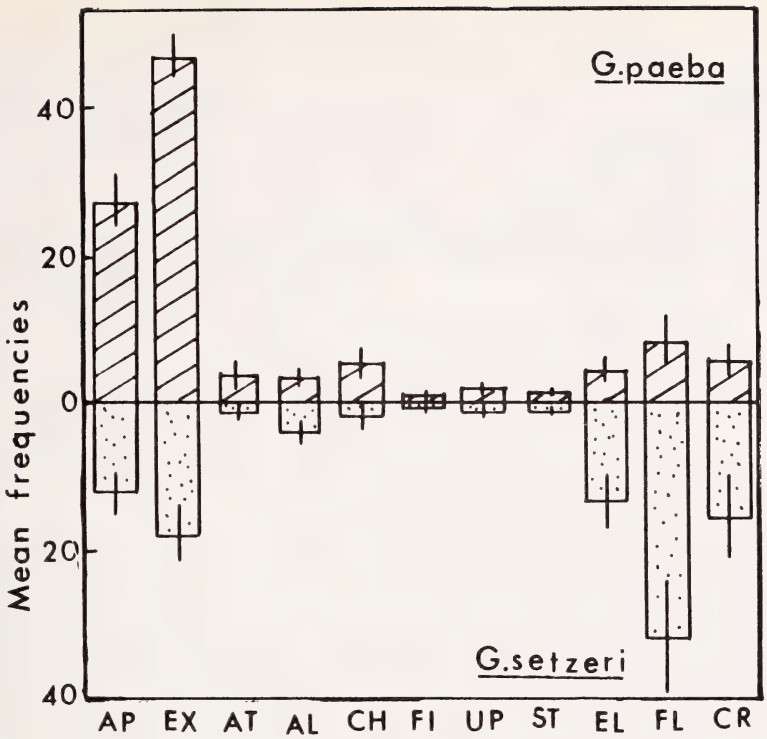

Fig. 2. Mean frequencies (± S.E.) of agonistic behaviours in *G. paeba-G. setzeri* encounters (n = 20)

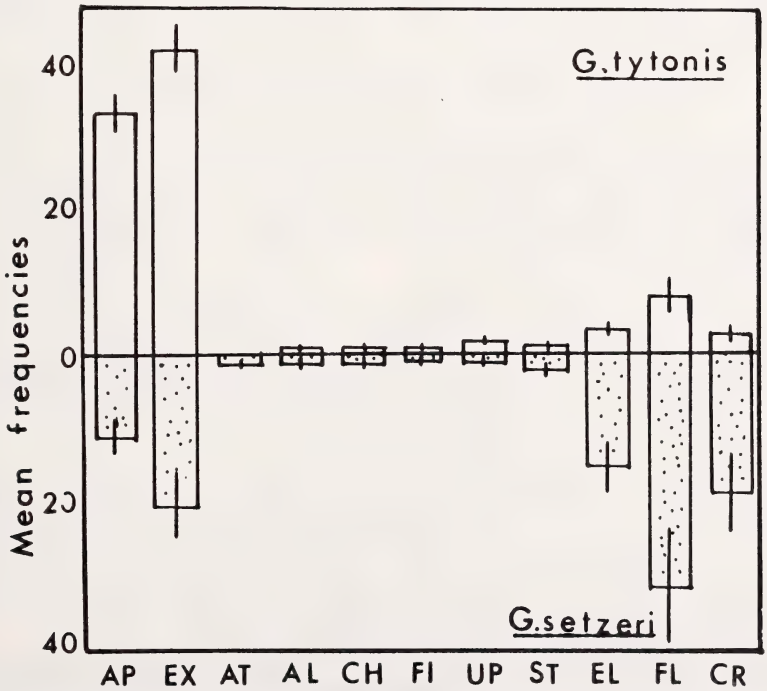

Fig. 3. Mean frequencies (±S.E.) of agonistic behaviours in *G. tytonis–G. setzeri* encounters (n = 20)

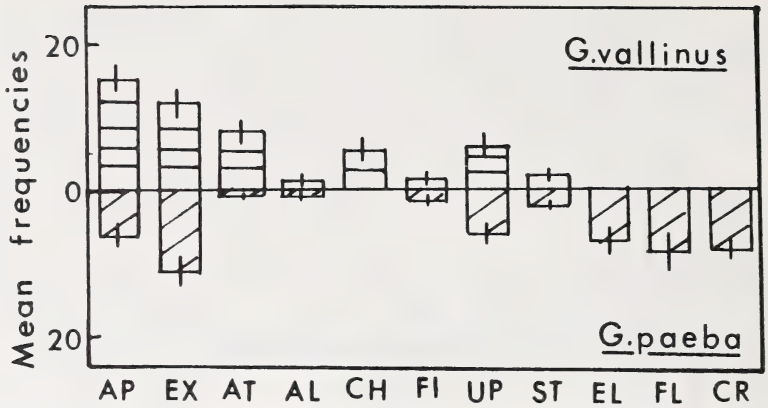

Fig. 4. Mean frequencies (± S.E.) of agonistic behaviours in *G. vallinus*-*G. paeba* encounters (n = 9)

level of aggressive behaviour displayed by their opponents. Most aggression was observed in female *G. setzeri*-male *G. paeba* encounters. Differences in dominance indices were significant for all encounters ($p < 0.01$).

Encounters between *G. tytonis* and *G. setzeri* (Fig. 3) were characterised by little aggression, and submissive behaviour performed by both species. Male and female *G. setzeri* performed more submissive behaviour than their opponents. *G. tytonis* was significantly dominant over *G. setzeri* in all encounters ($p < 0.001$).

In nine encounters between *G. vallinus* and *G. paeba* (N. Cape) (Fig. 4), *G. vallinus* performed more aggressive behaviour than *G. paeba* and no submissive behaviour, while the converse was true for *G. paeba*. Dominance indices did not differ significantly ($p > 0.1$).

Table 2. **Mean mass (g) of laboratory and wild-caught gerbils**

Species	Laboratory mean ± S.D.	n	Wild-caught	n
G. paeba	33.9 ± 10.2	19	22.0	177 (Boyer 1988)
G. tytonis	29.9 ± 4.9	16	25.0	168 (Boyer 1988)
G. setzeri	44.7 ± 10.6	14	37.6	31 (this study)
G. vallinus	40.9 ± 8.9	5	31.5	17 (this study)

Since dominance may be influenced by body size, the mean mass of laboratory and wild-caught individuals is shown in Table 2. Individual animals used in this study were generally larger than the mean mass quoted from field studies. *G. setzeri* was the heaviest species, followed by *G. vallinus*, while *G. tytonis* and *G. paeba* were the lightest species.

Discussion

The linear dominance hierarchy suggested by interspecific encounters involving *G. paeba, G. tytonis* and *G. setzeri* is: 1. *G. tytonis* females; 2. *G. paeba* females; 3. *G. tytonis* males; 4. *G. paeba* males; 5. *G. setzeri* females; 6. *G. setzeri* males.

This hierarchy reflects the results of intraspecific agonistic encounters, in which *G. paeba and G. tytonis* were identified as more aggressive than *G. setzeri* (Dempster and Perrin 1989).

Male and female *G. vallinus* dominated male and female *G. paeba* (N. Cape), however, differences were not statistically significant. This contradicts the results of intraspecific agonistic encounters, which identified *G. vallinus* as less aggressive than *G. paeba* from the Namib desert (Dempster and Perrin 1989).

Body size has been implicated in the dominance patterns of sympatric species of kangaroo rats (Blaustein and Risser 1976; Frye 1983). Grant (1972) has stated that in interspecific encounters between rodents, absolute body size is less important than size relative to the maximum for that species.

The assumption is made that all individuals used in this study were near the maximum body size for the species. However, dominance did not always correlate with body size. *G. setzeri,* the largest species, was dominated by the smaller *G. tytonis* and *G. paeba.* Body size may have influenced the outcome of encounters between the larger *G. vallinus* and *G. paeba.* Grant's (1972) statement is only partially supported by these data.

Ecological "specialist" species generally dominate ecological "generalist" species (Blaustein and Risser 1976; Ambrose and Meehan 1977; Martin 1984), however, experience may influence the outcome of encounters. Animals from areas of sympatry are more aggressive towards each other than are animals from areas of allopatry (Banks and Fox 1968; Martin 1984).

To date, little information has been published on the realized niches of the species of the genus *Gerbillurus. G. paeba* is reported to be a "generalist", with a wider habitat-niche breadth than *Rhabdomys pumilio* and *Tatera brantsii* in the southern Kalahari (NEL 1978). Pavlinov (1982) regards *G. paeba* as the most primitive of the *Gerbillurus* species, and the other three species as "specialists". *G. paeba* was dominated by the "specialists" *G. tytonis* and *G. vallinus*, supporting the hypothesis of dominance of "specialist" species.

Interactions between *G. paeba* and *G. setzeri* and between *G. tytonis* and *G. setzeri* were characterized by mutual avoidance rather than aggressive interaction. However, the "specialist" *G. setzeri* was dominated by the "generalist" *G. paeba*, and by the "specialist" *G. tytonis.* Behavioural differences resulting from differing habitats may have resulted in a reduction in interaction between the species. It is suggested that interference competition may result in the displacement of *G. setzeri* in areas of sympatry, but that mutual avoidance is more likely to occur than aggressive interaction.

Past experience may have influenced the results of encounters between *G. vallinus* and *G. paeba*, since the animals used in this study were all trapped within an area of approximately one hectare. It is suggested that the "specialist" species *G. vallinus* displaces the "generalist" species *G. paeba* in areas of syntopy. Due to the small sample size, these results are tentative.

The present study provides laboratory evidence of interspecific aggression in four *Gerbillurus species*, with clear patterns of dominance emerging in most species combinations. Field evidence is now required in order to assess more fully the role of interference competition in the ecological segregation of these species.

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Zusammenfassung

Zwischenartliche Aggression unter sympatrischen Gerbillurus-Arten

Die vier Arten der Gattung *Gerbillurus* sind nah verwandt und ökologisch ähnlich. Sympatrische Vorkommen sind gefunden worden bei *G. paeba* und *G. tytonis, G. paeba* and *G. setzeri, G. tytonis* und *G. setzeri* und *G. paeba* und *G. vallinus.* Meist sind die Arten aber allopatrisch. In Begegnungs-

versuchen in Gefangenschaft wurde geprüft, ob die Dominanzbeziehungen bei Auseinandersetzungen zwischen den Arten ihre ökologische Trennung im Freiland erklären können.

Die Versuche ergaben, daß die ökologischen Spezialisten *G. tytonis* und *G. vallinus* dem Generalisten *G. paeba* überlegen waren. *G. setzeri* wich *G. paeba* und *G. tytonis* aus. Danach könnte agonistisches Verhalten die Separation der Arten in sympatrischen Vorkommen mit bedingen.

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Home range of *Gerbillurus paeba* in a southern African coastal dunefield

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Abstract

We studied the home range of *Gerbillurus paeba* (Cricetidae) in dune slacks. Live-trapping was conducted on a fixed grid from March 1981 to July 1982. Average distance moved between captures was calculated from 542 movement records. Home range size (area of the minimum convex polygon) was calculated for all gerbils captured at least 10 times. Average distance moved was 102 m. The longest movement recorded was 577 m. Adult males in the breeding season moved significantly longer distances than adult females. There were no significant differences in distances moved by males and females in the non-breeding season, nor between male and female juveniles. Adult males moved significantly longer distances in the breeding than in the non-breeding season, while adult females moved significantly smaller distances in the breeding season. Home ranges overlapped considerably.

Introduction

This investigation of the home range of *Gerbillurus paeba* (Cricetidae) formed part of a broad ecological study of the species in the Alexandria dunefield in the eastern Cape, South Africa. Information regarding home range can be obtained from repeated recaptures of individuals on a trapping grid. It is important to note that there is no evidence that the trap-revealed home range and the true home range are identical (Hayne 1949) and that biologists measure, at best, an apparent home range.

This study utilized two methods of measuring home range. The first method gives an index of home range by measuring the average distance moved between captures (Brant 1962). This method allows maximal use of data, since only two captures per individual are required. It has been widely used (Krebs 1966; Wolfe 1968; Brooks 1974; Slade and Swihart 1983). The second method measures home range area. The smallest convex polygon which contains all of the capture points for an individual is drawn (as described by Southwood 1978), and the area of the polygon measured. Although this method has a sample size bias, it has been used by many authors (e.g. Perrin 1979; Jones and Sherman 1983). Jenrich and Turner (1969) have found the method to be reasonably statistically stable.

Statistical methods, which calculate the probability of occurrence of an individual within a given area, were avoided, since many require the a priori assumption of a particular home range shape (e.g. Hayne 1949; Jenrich and Turner 1969), while more recent models (e.g. Ford and Krumme 1979; Anderson 1982), which require no assumptions of shape have not been proven to be applicable other than in specific instances.

Study area

The Alexandria dunefield lining the shores of Algoa Bay is the largest (120 km^2) active coastal dune system in South Africa. The major part of the dunefield lies between the mouth of the Sundays River (33° 44′ S; 25° 51′ E) and Cape Padrone, 48 km eastwards up the coast. The climate is warm temperate,

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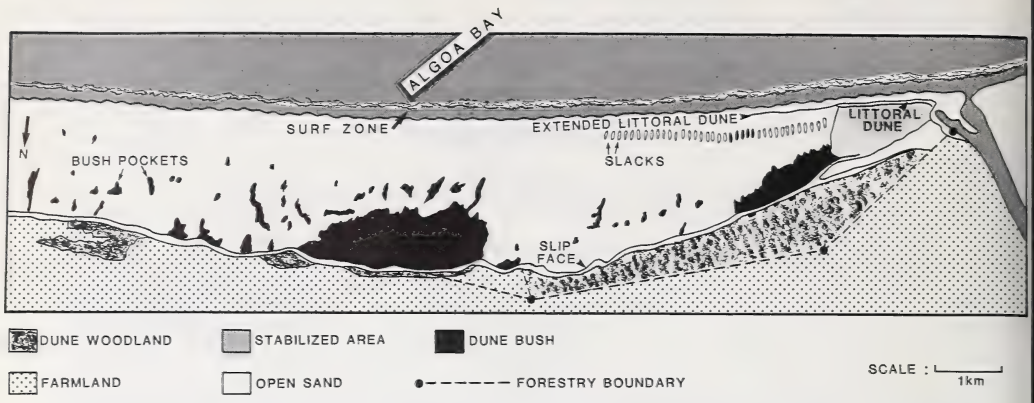

Fig. 1. Map of the western section of the Alexandria dunefield, showing the dune slack habitat. Shaded slacks indicate the study site

but variable. Rain can occur in all months of the year and averages 400–800 mm per annum along the dunefield from W to E. Mean annual temperature for the study period (1981 and 1982) was 17.7 °C. Lowest and highest temperatures recorded were 3.9 and 40.0 °C, respectively.

Fig. 1 shows the dune slack area where trapping was conducted. The area comprises a series of 36 damp hollows separated by bare dune ridges. These are known as dune slacks, i.e. valleys where the water table is close to the surface. They extend in a strip 3.5 km long, parallel to the shoreline. Five slacks were covered by the trap grid. Each slack is approximately 200 m long and 40–50 m wide. Due to the action of predominantly west winds, the slacks migrate eastwards at a rate of 7 m per year. To the south, they are bordered by the beach, to the north, by high dunes.

Vegetation in the slacks is sparse, averaging 2–10 % and rarely exceeds 0.5 m in height. Most abundant plants are two hummock forming species, *Arctotheca populifolia* and *Gazania rigens* and sandgrass, *Sporobolus virginicus*. *G. paeba* is the only rodent species permanently resident in the slacks.

Materials and methods

A mark-multiple recapture programme was carried out for 17 months, from March 1981 to July 1982. The programme is described in detail by Ascaray (1986). Sampling occurred at three-weekly intervals, yielding a total of 24 samples. A fixed grid marked with metal poles was laid out over six dunes and their five corresponding slacks, chosen as being typical of the area as well as for accessibility. Grid dimensions were 525×200 m (area: 10.5 ha). Each trapping session lasted 48 hours; data from the two trap nights were pooled.

Distance between traps was 25 m. Every six weeks, traps were placed round the outside of the grid, (10 traps per side), at distances ranging from 50–200 m from the outermost grid poles, to monitor movement outside the grid. This formed a third trap night. This additional trap information gave a more accurate picture of home ranges of individuals. Each captured gerbil was identified, weighed, its reproductive condition assessed and grid location noted.

Average distance moved was calculated for all gerbils that had been captured on the study grid two or more times, thus including the movements of transient animals. Distances moved within a sample (i.e. between the first and second night of a sample), as well as distances moved between samples were used after a preliminary analysis using Student's t-test (Zar 1984) showed no significant difference ($p > 0.05$) between using all values and using only between-sample values. The data were analysed separately for males and females, adults and juveniles and for the breeding season (September–February) and the non-breeding season (March–August). Movements spanning the boundary between the breeding and non-breeding seasons, or between juvenile and adult status, were discarded. Student's t-test was used to test for differences between the categories. A total of 542 movement records was analysed.

Since apparent home range size increases asymptotically with an increasing number of location records (the asymptote representing total home range size), an attempt was made to establish the minimum number of captures that could be used to determine an individual's home range. Home range size (area of the minimum convex polygon) was calculated for 20 gerbils that were captured 10 or more times after 4, 6, 8, 10, 12 and 15 captures. A graph of mean home range size versus number of

captures was plotted. In addition, home range size versus number of captures was plotted separately for three individuals that were captured more than 20 times.

Since the graphs revealed that approximately 20 captures are needed to disclose the home range area of *G. paeba,* and only three gerbils were captured more than 20 times during the study, an indication of the relative size of male and female home ranges was obtained as follows: home range area was calculated for all gerbils that had been captured at least 10 times (14 males and 11 females), using 10 location records for each. Student's t-test Zar 1984) was used to test for differences between the home ranges. Spatial relationships on the grid were examined by plotting location records for all gerbils captured 10 or more times over the same time period (December, 1981 – May, 1982) on maps of the study grid. Home range areas of 12 males and 10 females were plotted, using the minimum convex polygon method as described by Southwood (1978). Location records outside the study grid, obtained from six-weekly trapping sessions, were included. The number of capture records used for each individual ranged 10–15. The home range maps were examined for overlap between members of the same and of the opposite sex.

Results

The average distance moved by all classes of *G. paeba* was 102 m. The longest distances moved by a male and female in one night were 526 m and 577 m, respectively. Average distances moved by the different classes of *G. paeba* in the breeding and non-breeding seasons are summarized in the Table. Adult males in the breeding season exhibited the largest average distance moved (130 m), while adult females in the breeding season moved the smallest distances (68 m).

Data from male juveniles and female juveniles were combined for the breeding and non-breeding seasons to obtain sample sizes suitable for analysis, as breeding season sample sizes were small. There was no significant difference ($p > 0.05$) between distances moved by adult males and adult females in the non-breeding season, but during the breeding season there was a highly significant difference ($p < 0.01$) in their movements, with females moving much smaller distances (68 m) than males (130 m). There was no significant difference ($p > 0.05$) between the movements of male and female juveniles.

Intrasex comparisons showed that adult males moved signifi-

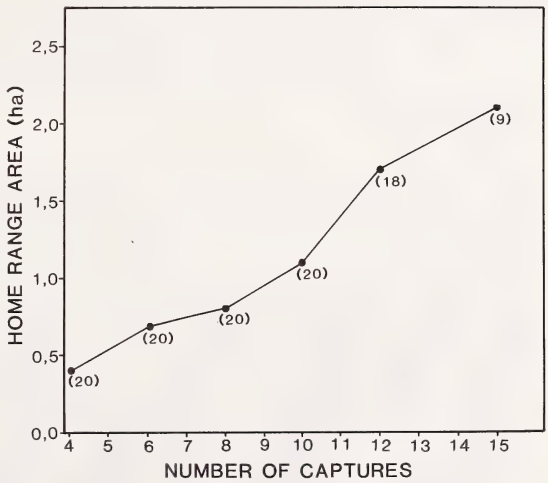

Fig. 2. Increase in home range size with number of captures. The number of individuals used to calculate each point appears in parentheses

Mean distance (m) moved by various classes of *G. paeba* in the breeding and non-breeding seasons

Class	Breeding Season n	Mean distance	SD	Range	Non-breeding Season n	Mean distance	SD	Range
Adult male	80	130	114	25–526	142	99	91	25–525
Adult female	54	68	62	25–382	137	108	115	25–577
Juvenile male	16	98	77	25–292	38	100	93	25–443
Juvenile female	13	100	73	25–269	62	90	63	25–257

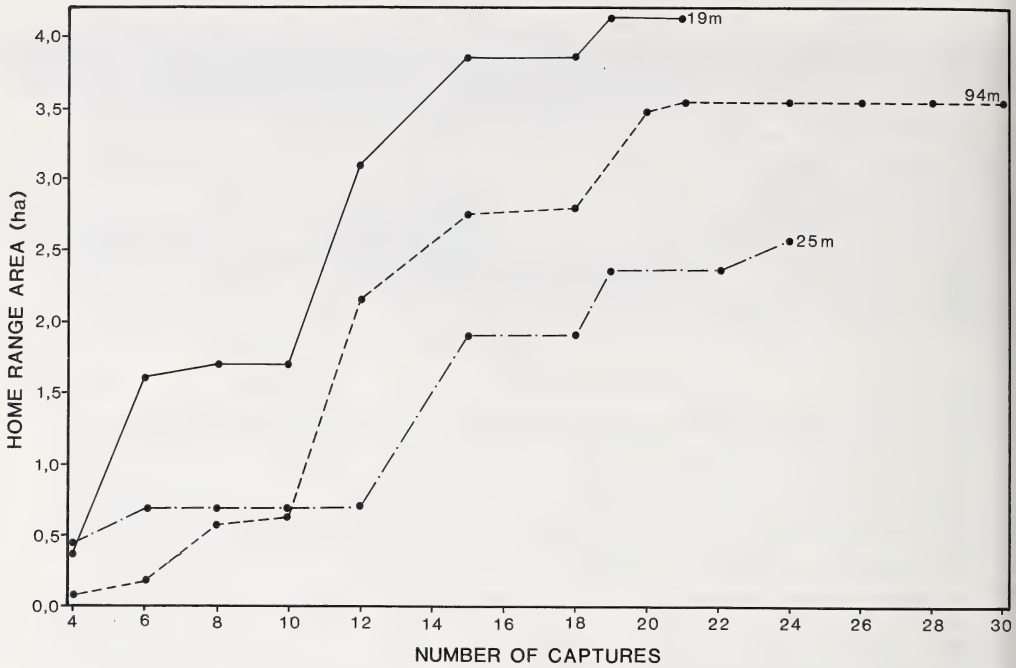

Fig. 3. Increase in home range size with number of captures for three *G. paeba* individuals captured more than 20 times

cantly larger distances in the breeding season than in the non-breeding season, but their movements were not significantly different from those of juveniles in either season. Adult females moved significantly ($p < 0.05$) smaller distances in the breeding season (68 m) than in the non-breeding season (108 m). Adult female movements (68 m) were also significantly ($p < 0.05$) different from those of juveniles (100 m) during the breeding season, but no significant difference was found between adult and juvenile females in the non-breeding season.

A plot of home range size versus number of recaptures for 20 individuals with 10 or more recaptures showed that more than 15 captures are necessary to determine the home range size of *G. paeba,* since at 15 captures the graph had not yet approached an asymptote (Fig. 2). A subsequent plot of home range size versus number of recaptures for three individuals that were captured more than 20 times indicated that the home range size of *G. paeba* is disclosed after approximately 20 captures (Fig. 3). These three individuals had range sizes of 2.56 ha; 3.54 ha and 4.13 ha.

A comparison of 14 male and 11 female home range sizes, all based on 10 location records, showed that male home range size ($x = 1.42 \pm 1.17$ ha) is nearly double that of females ($x = 0.76 \pm 0.62$ ha). However, Student's t-test indicated no significant difference ($T = 1.668$; $p > 0.05$) between male and female home range sizes. This may be due to the small sample sizes and to the great variability in the data – female home range sizes ranged 0.16 ha–1.94 ha, while male home range sizes ranged 0.25 ha–4.64 ha.

The home ranges of 12 males and 10 females captured 10 or more times over the same time period (December 1981–May 1982) are shown in Figs. 4 and 5. Home ranges of both sexes usually included dune ridges, so that most home ranges covered more than one slack. Additional data points from the six-weekly trapping showed that gerbils also visit the dunes to the north of the slacks and the beach. Home ranges generally overlapped extensively, both within, and between sexes.

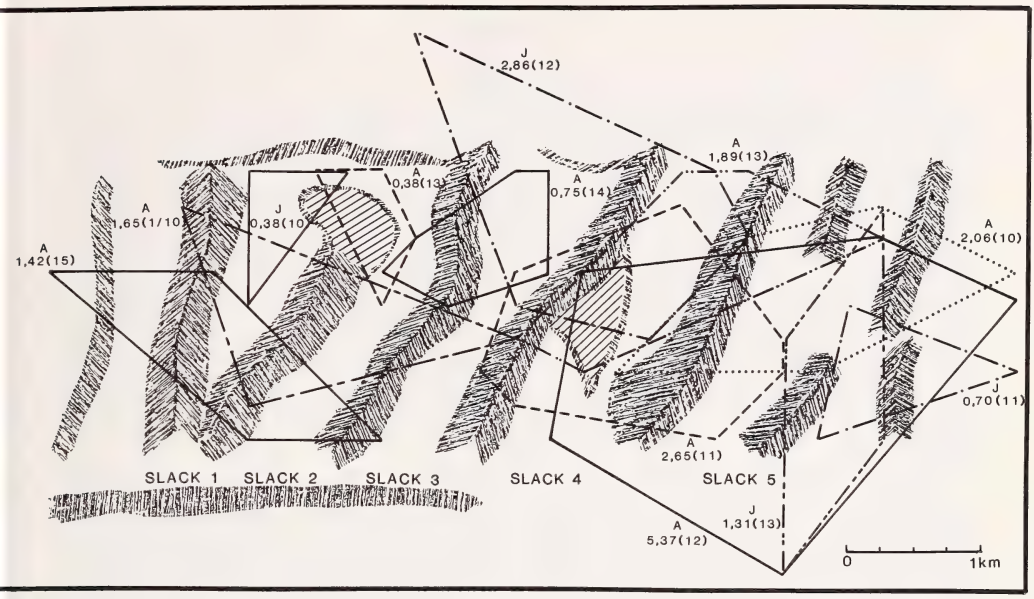

Fig. 4. Home ranges of 12 males present on the study grid from December 1981–May 1982. The age category (A = adult; J = juvenile), home range area (ha) and number of captures from which the area was calculated (in parentheses) of each individual are shown next to each home range

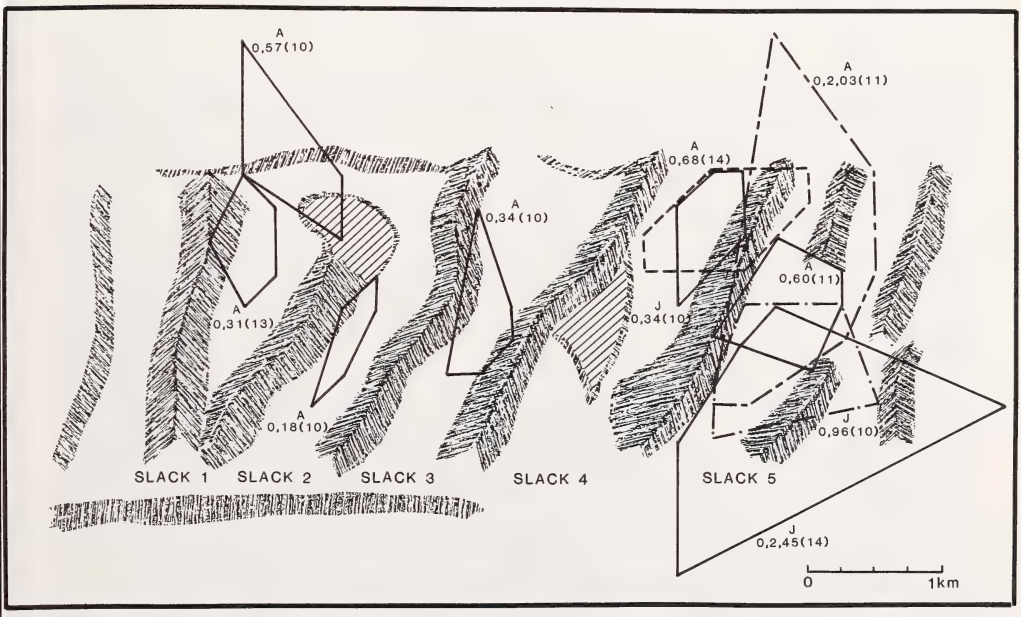

Fig. 5. Home ranges of 10 females present on the study grid from December 1981–May 1982. The age category (A = adult; J = juvenile), home range area (ha) and number of captures from which that area was calculated (in parentheses) of each individuals are shown next to each home range

Discussion

Movement

G. paeba individuals in the Alexandria dunefield move large distances of up to 0.5 km a night in their search for food and mates. LAYCOCK (1975) reports that the maximum distance moved by a marked *G. paeba* individual in the Namib desert was 75 m, but that the foraging distance, as evidenced by tracks, is much greater. Similarly large distances of approximately 350 m a night have been recorded by SCHRODER (1979) for *Dipodomys spectabilis,* a rodent inhabiting a North American desert. These distances are much greater than those reported for rodents inhabiting non-arid areas. *Rabdomys pumilio,* for example, averages movements of 14.8 m (males) and 21.5 m (females) on the Transvaal highveld during the breeding season (BROOKS 1974), while SLADE and SWIHART (1983) report that adult male and female *Sigmodon hispidus* individuals in Kansas, North America, move average distances of 30.8 m and 21.2 m, respectively. Rodents such as *G. paeba,* which inhabit sparsely vegetated areas, presumably need to travel long distances to obtain sufficient food.

There were no significant differences in male and female movements, except during the breeding season, when males moved much longer distances than females. Male rodents commonly increase their movements during the breeding season, as has been shown for *Dipodomys spectabilis* (SLADE and SWIHART 1983), *Clethrionomys glareolus* (MAZURKIEWICZ 1971), *Peromyscus maniculatus* (METZGAR 1979) and *Microtus californicus* (KREBS 1966). These longer movements presumably increase their chances of mating with females. Smaller female movements during the breeding season may be a result of the females' confinement to nest sites. *Rhabdomys pumilio* females also exhibit smaller movements during the breeding season (BROOKS 1974).

Home range area

Apparent home range size increases asymptotically with an increasing number of location records (STICKEL 1954; HAYNE 1949; VAN VLECK 1969). However, most studies of small mammals provide insufficient data to reveal the asymptote (METZGAR and SHELDON 1974). One disadvantage of the minimum convex polygon method is its dependence on sample size, since individuals with a small number of recaptures will appear to have smaller home ranges than individuals that were recaptured many times. STICKEL (1954) claims that home range size is not fully disclosed with fewer than 15 location records, while FLOWERDEW (1976) states that individuals with fewer than 10 captures are often not worth including in home range analysis. Many authors choose an arbitrary minimum number of recaptures to use in calculating home range (VAN VLECK 1969).

Analysis of results from this study showed that the home range of *G. paeba* is disclosed only after approximately 20 captures. Since only three individuals were captured more than 20 times, more data are necessary before an accurate estimate of home range size can be obtained. However, *G. paeba* conforms to the general pattern of cricetid mice in having a large home range (FRENCH et al. 1975). BLAIR (1951) has reported home range sizes of 0.79–4.31 ha for *Peromyscus polionotus leucocephalus,* a rodent which lives under conditions similar to those of *G. paeba.* Large home range sizes in these two species may be a result of the relatively poor environment in which they live.

Male home ranges appear to be much larger than female home ranges. Seasonal changes in home range size may occur, as indicated by the seasonal changes in average distances moved by both male and female gerbils.

The distribution of home ranges falls approximately into two groups, one on the eastern and one on the western side of the grid, with the centre of the grid being relatively

unoccupied. This can be explained as follows: the two slacks forming the eastern end of the grid comprised the largest area of suitable habitat on the grid, hence the greater number of gerbils occurred in that area. The two slacks forming the western end of the grid were smaller and thus offered a smaller area of suitable habitat, while the slack in the centre of the grid was characterized by the presence of a large midden of coarsely fragmented mussel shells, which could have made the substrate unsuitable for burrowing.

There was considerable overlap between male home ranges (Fig. 4) and a lesser degree of overlap between female home ranges (Fig. 5). This difference may be due to the difference in size of male and female ranges: male ranges would be more likely to overlap each other simply because they are larger, and it is more difficult for an animal to maintain an exclusive home range when the range is large. Male and female home ranges overlapped extensively (one can imagine superimposing Figs. 4 and 5). These findings agree with Nel's (1975) statement that there is a fair degree of social tolerance and interaction between *G. paeba* individuals. He reports that gerbils occur singly in burrows, but that the burrows are situated in close proximity to one another. However, since total home range sizes of the gerbils are mostly unknown, and not all individuals present on the study grid are represented on the home range maps, the distribution of home ranges should be interpreted with caution.

Gerbil home ranges were generally not confined to one slack, so dune ridges are regularly crossed. The gerbils may feed on wind-blown insects and detritus (including seeds) which accumulate on the leeward faces of the dunes. The high dunes to the north of the slacks may be visited for the same reason – there is no vegetation on these dunes to provide food. Gerbils also move on to the beach, possibly to feed on driftline debris and on other organisms feeding there. *G. paeba's* ability to travel long distances at a time thus enables it to utilize the sparse, scattered food resources the slacks and surrounding dunes and beach have to offer.

Acknowledgements

We wish to thank Dr R. Randall for his helpful suggestions; also the many people who assisted with fieldwork. This project was made possible by funds from the C.S.I.R. and the Department of Environment Affairs and Fisheries. The Directorate of Forestry is thanked for making facilities available to us.

Zusammenfassung

Der Aktionsraum von Gerbillurus paeba in einem Küstendünenfeld in Südafrika

Wir untersuchten den Aktionsraum von *Gerbillurus paeba* (Cricetidae) in Dünensenken. Von März bis Juli 1982 wurden in einem festgelegten Koordinatensystem Lebendfallen gestellt. Die zwischen den Fängen durchschnittlich zurückgelegte Wegstrecke wurde aus 542 Bewegungsaufzeichnungen berechnet. Die Aktionsraumgröße (Fläche des minimalen konvexen Polygons) wurde für alle jene *Gerbillurus* berechnet, die mindestens zehnmal gefangen wurden. Die durchschnittlich zurückgelegte Entfernung betrug 102 m, die längste 577 m. Während der Fortpflanzungszeit legten die adulten Männchen signifikant längere Wegstrecken als die adulten Weibchen zurück. Weder zwischen adulten Männchen und Weibchen außerhalb der Fortpflanzungszeit, noch zwischen juvenilen Männchen und Weibchen ergaben sich signifikante Unterschiede hinsichtlich der zurückgelegten Wegstrecke. Adulte Männchen legten während der Fortpflanzungszeit signifikant längere Entfernungen als außerhalb der Fortpflanzungszeit zurück, adulte Weibchen hingegen signifikant kürzere. Die Aktionsräume überschnitten sich erheblich.

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Eine verhaltensphysiologische Untersuchung zur Ermittlung olfaktorischer Schwellenwerte bei männlichen Ratten

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Abstract

A behavioural study for olfactory threshold detection in male rats

Investigated were the olfactory thresholds of subadult and adult male laboratory rats (Wistar) towards the odor ethyl acetate. Thresholds were established with a computerized olfactometer which allows continuous odor presentations. The olfactometer provided dilutions of the ethyl acetate vapor varying from 10^{-1} to 10^{-9} vol% of the odor. Prior to the absolute threshold tests animals were trained to respond to the odor by being rewarded with water as positive reinforcement.

A significant difference in the olfactory thresholds between subadult (7.3×10^{-5} vol% ethyl acetate) and adult (1.4×10^{-5} vol%) males was found. This difference is linked to differences in the density of the sensory cells in the olfactory epithelium between the two age groups.

Einleitung

Wie verschiedene Untersuchungen erkennen lassen, spielt bei Ratten der olfaktorische Sinn eine dominierende Rolle in vielen Verhaltensbereichen, so z. B. bei der Kommunikation oder der Nahrungssuche (Leon und Moltz 1972; Carr et al. 1979). Über die Leistungsfähigkeit ihres Geruchsorgans wie auch über die Mechanismen der Duftperzeption liegen dagegen nur vergleichsweise wenige Ergebnisse vor (Moulton 1960; Marshall und Moulton 1981). Die Kenntnis olfaktorischer Schwellenwerte ist aber eine wichtige Voraussetzung für weitergehende Fragestellungen wie beispielsweise die Klärung der Duftmolekül-Rezeptor-Interaktionen (Shirley et al. 1987). Mit der vorliegenden Untersuchung werden daher an unterschiedlich alten männlichen Laborratten die in Verhaltenstests ermittelten Schwellenwerte für den in der Geruchsforschung wiederholt verwendeten Duftstoff Ethylacetat ($C_4H_8O_2$) vorgestellt.

Material und Methode

Versuchstiere

Die olfaktorischen Schwellenwerte werden für 8 subadulte (Gruppe I) und 9 adulte (Gruppe II) männliche Laborratten (Wistar) beschrieben. Das genaue Alter der Tiere zu Versuchsbeginn und -ende zeigt die Tabelle. Die Haltung der Tiere erfolgte jeweils in Standardkäfigen zu Gruppen von je zwei oder drei Tieren; Futterpellets standen ad lib., Wasser in genau bemessenen Mengen zur Verfügung.

Versuchsanlage

Das von Slotnick (Slotnick und Schoonover 1984) entwickelte Olfaktometer (Abb. 1) eignet sich zur Ermittlung von olfaktorischen Schwellenwerten und zur Überprüfung von Diskriminationsleistungen bei Ratten. Es ermöglicht kontinuierliche, variable Duftstoffexpositionen bis in Grenz-

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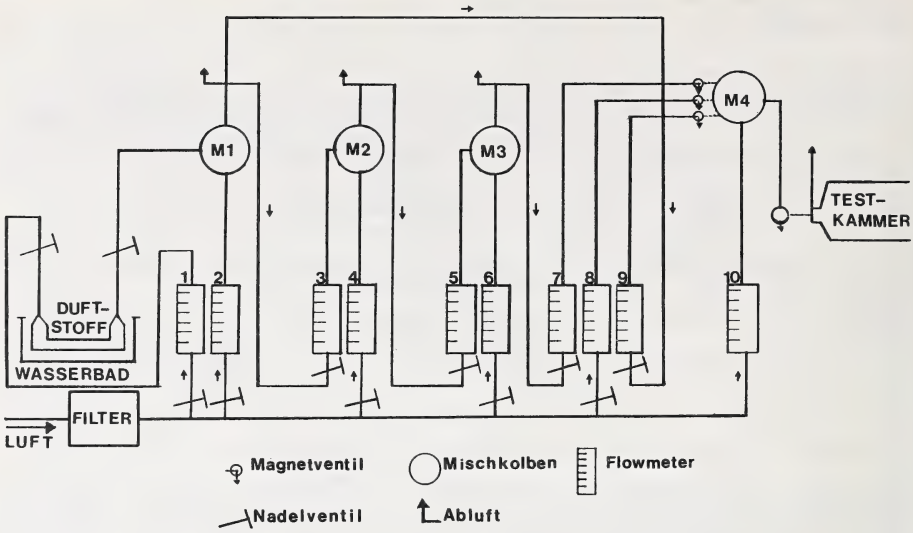

Abb. 1. Schematische Darstellung des Olfaktometers. Der Duftstoff kann mit gereinigter Luft in Mischkolben (M1–M4) variabel zwischen 10^{-1} Vol.-% und 10^{-9} Vol.-% verdünnt werden, bevor er dem Tier zur Prüfung angeboten wird

bereiche von 10^{-9} Vol.-% eines Duftstoffes und arbeitet nach dem Prinzip einer operanten Konditionierung: Im Sinne der Aufgabenstellung richtige Verhaltensantworten werden belohnt.

Der den Duftstoff enthaltende Behälter befindet sich in einem Wasserbad, wodurch die Temperatur der Luft, die über den Duftstoff strömt, etwas unterhalb der Umgebungstemperatur gehalten wird. Temperaturschwankungen und Kondensationsprozesse im Leitungssystem der Anlage werden damit verhindert. Die Bereitstellung der verschiedenen Duftkonzentrationen erfolgt in mehreren Schritten. Gefilterte Druckluft wird über den Duftstoff geleitet. Der Luftstrom läßt sich mit einem vor einem geeichten Meßrohr liegenden Nadelventil regulieren. Die mit dem Duftstoff zu über 95 % gesättigte Luft (Dravnieks 1975) wird in einem ersten Mischkolben (M1) mit einer definierten Menge gereinigter Luft vermischt und über Mischkolben M4 zur Riechvorrichtung der Testkammer geleitet, in der sich das Versuchstier befindet. Ob in die Riechvorrichtung Luft oder Duftstoff geleitet wird, wird mittels computergesteuerter Magnetventile bestimmt. Mit Hilfe des ersten Mischkolbens können Duftstoffkonzentrationen von 10^{-3} Vol.-% erreicht werden. Für geringere Konzentrationen (bis zu 10^{-9} Vol.-%) muß der Duft in nachgeschalteten Mischkolben (M2–M3) mit gereinigter Luft weiter verdünnt werden. Für eine präzise Einhaltung der eingestellten Durchströmungsraten und damit der Duftkonzentrationen ist eine Absicherung gegen Druckschwankungen im Leitungssystem erforderlich. Weiterhin müssen die Durchströmungsraten an der Riechvorrichtung konstant gehalten werden, damit das Tier keine Diskrimination aufgrund unterschiedlicher Durchflußraten vornehmen kann.

Die Testkammer besteht aus einem 27,5 × 10 cm großen Plexiglaszylinder. Das eine Ende ist durch ein Drahtgitter verschlossen, am anderen befindet sich die aus Glas gefertigte Riechvorrichtung. Diese besteht aus einem senkrechten Tubus, durch den der ankommende Duft-/Luftstrom an der Testkammer so vorbeigeleitet wird, daß kein Duft in die Testkammer gelangt. Zusätzlich wird das Gemisch über ein Abluftsystem abgesogen. Eine seitliche Öffnung am Glastubus stellt die Verbindung zur Testkammer her. Um die vorbeiströmende Duft-/Luftmischung zu prüfen, muß die Ratte ihre Nase durch diese Öffnung stecken. Sie durchbricht dabei den Strahl einer seitlich angebrachten Photozelle und startet damit einen Versuchsablauf.

Versuchsablauf und Auswertung

Wird der Lichtstrahl durchbrochen, lenkt das unmittelbar vor der Riechvorrichtung befindliche Magnetventil den zunächst reinen Luftstrom für eine zufallsgemäß variable Zeit von 0,8–2,0 sec an der Riechvorrichtung vorbei zum Abzug. Gleichzeitig wird das Luft- oder ein Duft-Magnetventil aktiviert. Wird ein Duft-Ventil aktiviert, können sich Duft und Luft in einem vorgegebenen Verhältnis mischen. Diese Mischung wird dann für 2,0 sec über die Riechvorrichtung angeboten. Das Tier muß mindestens 0,2 sec während dieser Darbietungszeit die Duft-/Luftmischung prüfen, bevor

es – nur bei Duft – an der seitlich angebrachten Belohnungsstelle für wiederum 2,0 sec als Belohnung Wasser lecken kann. Als Richtigwahl wird das Wasserlecken nach Duftpräsentation gewertet. Die Belohnungsgabe unterbleibt nach Luftpräsentation, auch wenn die Ratte an der Belohnungsstelle leckt (Falschwahl). Anschließend, nach einer Wartezeit von 2,0 sec, kann das Tier einen neuen Versuchsablauf starten. Eine Versuchssitzung besteht aus jeweils 100 Versuchsabläufen, die unmittelbar nacheinander auszuführen sind.

Alle Verhaltensantworten und Zeitabläufe (Prüfdauer bei Luft und Duft, % Richtig- und Falschwahlen) werden computergesteuert registriert, im Sinne der Aufgabenstellung bewertet und unmittelbar nach Versuchsende über einen Drucker ausgegeben. Als Riechschwelle wurde die Duftstoffkonzentration gewertet, bei der zumindest 75 % aller Verhaltensreaktionen während einer Versuchssitzung im Sinne der Aufgabenstellung richtig waren. War der Schwellenwert unterschritten, gingen die Tiere zu Zufallsreaktionen über (Abb. 3). Statistische Absicherungen erfolgten mit dem nichtparametrischen Mann-Whitney-U-Test.

Bevor mit den Schwellenwertbestimmungen begonnen wurde, wurden alle Tiere in die Anlage eingewöhnt und mit Hilfe vorgeschalteter Lernprogramme schrittweise mit der Aufgabe vertraut gemacht.

Ergebnisse

Innerhalb von nur zwei bis drei Versuchssitzungen zu je 100 Versuchsabläufen beherrschten alle Tiere die Diskrimination zwischen Luft und Duft mit über 96%iger Sicherheit bei einer Anfangskonzentration von 10^{-1} Vol.-% Ethylacetat. Altersabhängige Unterschiede in bezug auf das Erlernen der operanten Aufgabe bestanden nicht. Unterschiede ergaben sich jedoch bei der Dauer einer Versuchssitzung. Die Tiere der Gruppe I benötigten mit durchschnittlich 28 min pro 100 Versuchsabläufe signifikant mehr Zeit als die der Gruppe II (23 min; $p < 0{,}05$).

Die Prüfdauer bei Luftpräsentation war bei beiden Altersgruppen ähnlich und lag deutlich über einer Sekunde. Unterschiede ergaben sich jedoch bei der Prüfdauer der Duftmischungen. Bei der Anfangskonzentration von 10^{-1} Vol.-% Ethylacetat betrug die Prüfdauer bei Gruppe I durchschnittlich 0,38 sec, bei Gruppe II durchschnittlich 0,57 sec ($p < 0{,}035$). Mit abnehmender Duftstoffkonzentration verlängerte sich die Prüfdauer bei allen Tieren sowohl bei Duft- wie auch bei Luftpräsentation; nach Unterschreiten der individuellen Schwellenwerte entsprach die Prüfdauer bei Duftpräsentation weitgehend

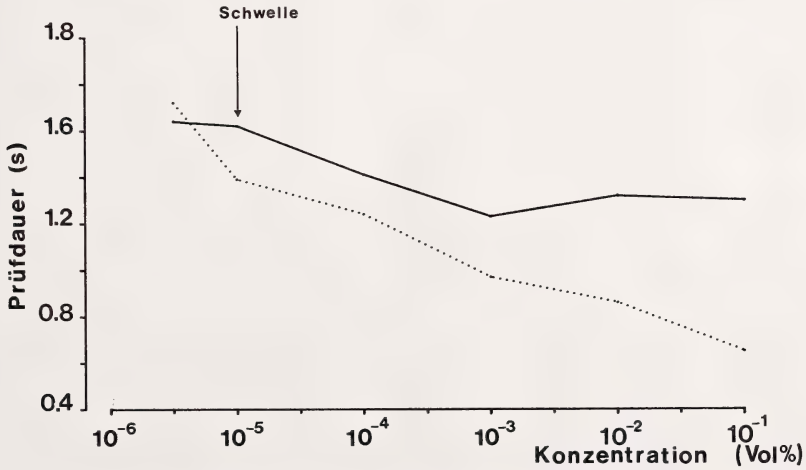

Abb. 2. Prüfdauer in Abhängigkeit von der Duftstoffkonzentration. Mit abnehmender Duftstoffkonzentration verlängert sich die Prüfzeit bei Duftpräsentation (gepunktete Linie), aber auch bei Luftpräsentation (durchgezogene Linie), was als Ausdruck eines zunehmenden Schwierigkeitsgrades angesehen wird

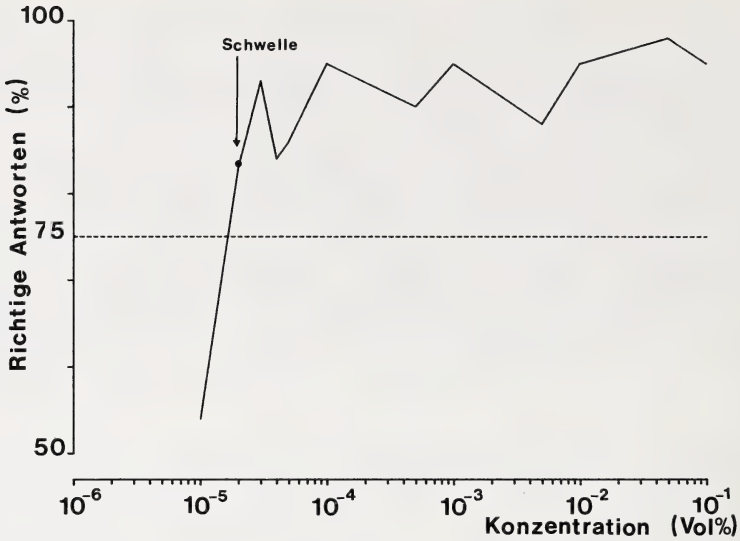

Abb. 3. Darstellung einer Schwellenbestimmung. Bei hohen Konzentrationen wird die Aufgabe mit großer Sicherheit gelöst. Kann das Tier den Duft nicht mehr von reiner Luft unterscheiden, liegen die richtigen Reaktionen im Bereich der Zufallsverteilung

der bei reiner Luftpräsentation. Einen typischen Kurvenverlauf für diese Verhaltensreaktion zeigt Abb. 2.

Bei Duftkonzentrationen zwischen 10^{-1} und 10^{-4} Vol.-% erfolgte die Diskrimination zwischen Luft und Duftstoff bei allen Tieren mit hoher Sicherheit. Mit weiter abnehmender Duftstoffkonzentration erhöhte sich die Fehlerquote zunächst leicht, um dann, nach Unterschreiten des Schwellenwertes, bis auf 50 % (Zufallswahl) anzusteigen. In Abb. 3 ist der typische Verlauf für eine Riechschwellenkurve dargestellt. Die Tabelle zeigt die individuellen Schwellenwerte aller Versuchstiere, wobei das beste Ergebnis jedes einzelnen Tieres dargestellt ist. Innerhalb von Gruppe I beträgt der durchschnittliche Schwellenwert $7{,}3 \times 10^{-5}$ Vol.-% Ethylacetat. Auffallend ist jedoch die vergleichsweise große Schwankungsbreite der Schwellenwerte innerhalb dieser Altersgruppe. Die Schwellenwerte für die Tiere der Gruppe II sind dagegen recht einheitlich und betragen durchschnittlich $1{,}4 \times 10^{-5}$ Vol.-%. Der mit 7×10^{-6} Vol.-% Ethylacetat insgesamt niedrigste Schwellenwert wurde von einem Männchen dieser Altersgruppe erreicht.

Damit ergibt sich bei den männli-

Alter (Tage) der Tiere bei Versuchsbeginn und zum Zeitpunkt der Schwellenermittlung

Tier No.	Alter bei Beginn	Alter bei Ende	Schwelle (Vol. %)
Gruppe I			
1	50	71	2×10^{-4}
2	50	75	1×10^{-4}
3	50	96	7×10^{-5}
4	50	89	6×10^{-5}
5	50	94	5×10^{-5}
6	50	113	5×10^{-5}
7	50	127	3×10^{-5}
8	50	127	2×10^{-5}
		Durchschnitt:	$7{,}3 \times 10^{-5}$
Gruppe II			
9	140	202	3×10^{-5}
10	140	202	2×10^{-5}
11	360	407	2×10^{-5}
12	140	172	1×10^{-5}
13	140	172	1×10^{-5}
14	360	411	1×10^{-5}
15	320	357	9×10^{-6}
16	360	429	9×10^{-6}
17	140	206	7×10^{-6}
		Durchschnitt:	$1{,}4 \times 10^{-5}$

chen Ratten trotz der vorhandenen interindividuellen Schwankungen ein Unterschied zwischen beiden Altersgruppen. Die Riechschwelle subadulter Tiere liegt mit $p < 0{,}002$ signifikant über der adulter Tiere.

Diskussion

Ob ein Stoff olfaktorisch wahrgenommen wird, hängt sowohl von seinen chemischen/physikalischen Eigenschaften (Amoore et al. 1964) als auch von den morphologischen und biochemischen Eigentümlichkeiten des Riechepithels und seiner Rezeptoren ab (Shirley et al. 1987). Neben der Suche nach den eine Duftempfindung auslösenden Faktoren steht die Frage nach der Empfindlichkeit des olfaktorischen Systems im Mittelpunkt verschiedener Arbeiten. Als Maß der Empfindlichkeit wird dabei üblicherweise die Riechschwelle gewertet, die je nach Duftstoff von Art zu Art beträchtlich variieren kann, z. B. zwischen Mensch und Hund bzw. Mensch und Ratte um den Faktor 10^6 (Neuhaus 1957; Laing 1975). Als mögliche Ursache für inter- und auch intraspezifische Unterschiede in der Riechschwelle wird u. a. die unterschiedliche Anzahl der Rezeptorzellen in Betracht gezogen.

Quantitativ morphometrische Untersuchungen am Riechepithel heranwachsender Laborratten lassen postnatale Reifungsprozesse an dieser Struktur erkennen. Dies betrifft sowohl die Fläche des olfaktorischen Epithels als auch die Anzahl und Dichte der Riechsinneszellen. Bei neugeborenen männlichen Ratten beträgt die Fläche des gesamten olfaktorischen Epithels (Septum nasi und Conchae) auf jeder Seite etwa 15 mm^2 und steigt bis zum 25. Lebenstag (Entwöhnen der Jungtiere) auf 120 mm^2 an (Meisami 1989). Betrachtet man nur die mit größerer Genauigkeit zu vermessende septale Fläche, so nimmt diese von der Geburt bis zum 60. Lebenstag (Eintritt der Geschlechtsreife) von 12 mm^2 auf 74 mm^2 zu; bei noch älteren Tieren wurden mehr als 106 mm^2 gemessen. Während der gleichen Zeit steigt die Anzahl der Riechsinneszellen auf der septalen Fläche von ca. 400 000 bei Neugeborenen auf über 6×10^6 bei Adulttieren an (Russ 1989).

Ohne Frage ist die Anzahl der Rezeptorzellen entscheidend für die Sinnesleistung. Uns erscheint jedoch die Dichte der Rezeptorzellen ein maßgebender Faktor zu sein, denn mit zunehmender Dichte erhöht sich die Wahrscheinlichkeit einer Duftmolekül-Rezeptor-Interaktion und senkt so die schwächste noch wahrnehmbare Duftkonzentration, die Schwellenkonzentration. Wie unsere Ergebnisse zeigen, haben 60 Tage alte Ratten mit 60 000–78 000 Riechsinneszellen/mm^2 Epitheloberfläche (Hinds und McNelly 1981; Russ 1989) trotz interindividueller Schwankungen eine höhere Riechschwelle ($7{,}3 \times 10^{-5}$ Vol.-%) als Adulttiere ($1{,}4 \times 10^{-5}$ Vol.-%), für die 80 000–85 000 Riechsinneszellen/mm^2 angegeben werden (Hinds und McNelly 1981; Russ 1989).

Für die Bewertung der Leistungsfähigkeit eines Sinnesorgans muß neben der Anzahl bzw. der Dichte der Rezeptorzellen auch die Konvergenz zwischen den Sinneszellen und den nachgeschalteten Relayneuronen berücksichtigt werden (Drongelen et al. 1978). Verschiebt sich die Konvergenz zugunsten der Sinneszellen, ist mit einer zunehmenden Empfindlichkeit der Sinneswahrnehmung zu rechnen. Solche Konvergenzstudien im olfaktorischen System liegen für Ratten bisher nur bis zum 25. Lebenstag vor (Meisami 1989). Das Verhältnis zwischen den Riechsinneszellen und den nachgeschalteten Relayneuronen (Mitralzellen) im Bulbus olfactorius ändert sich von der Geburt bis zum 25. Lebenstag von 25 : 1 (10^6 Rezeptorzellen und 4×10^4 Mitralzellen) auf 250 : 1. Eine verhaltensphysiologische Bestätigung finden diese Konvergenz-Überlegungen zur Empfindlichkeit des olfaktorischen Systems in den Arbeiten von Alberts und May (1980). Neugeborene Ratten können nach den Untersuchungen dieser Autoren sowohl natürliche (Urin) als auch künstliche Düfte (Amylacetat) riechen, allerdings nur bei hohen Konzentrationen. 15–17 Tage alte Tiere reagieren dagegen bereits auf diese Düfte, auch wenn sie in einer 10^3fach verdünnten Konzentration angeboten werden.

Ob neben der zunehmenden Dichte bzw. der zunehmenden Konvergenz auch andere Faktoren die Sinnesleistung beeinflussen, beispielsweise alters- oder hormonabhängige Unterschiede in der Rezeptorempfindlichkeit, bedarf weiterer Überprüfung.

Zusammenfassung

An unterschiedlich alten männlichen Laborratten (Wistar) wurde die Riechempfindlichkeit gegenüber dem Duftstoff Ethylacetat im Verhaltenstest ermittelt. Die Untersuchungen wurden mit Hilfe eines computerisierten Olfaktometers durchgeführt, das kontinuierliche Duftreizdarbietungen von 10^{-1} Vol.-% bis zu einer Verdünnungsstufe von 10^{-9} Vol.-% des Duftstoffes erlaubt. Die Tiere werden dabei mittels einer operanten Konditionierung mit der Aufgabe vertraut gemacht und bei Richtigwahl belohnt.

Zwischen den subadulten ($7{,}3 \times 10^{-5}$ Vol.-% Ethylacetat) und adulten ($1{,}4 \times 10^{-5}$ Vol.-%) Ratten zeigten sich signifikante Unterschiede im Schwellenwert. Diese alters-/entwicklungsabhängigen Unterschiede werden mit der unterschiedlichen Sinneszelldichte im Riechepithel in Verbindung gebracht.

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Genetic variability and conservation problems in Alpine ibex, domestic and feral goat populations (genus *Capra*)

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Abstract

Studied genetic variability in two Alpine ibex *(Capra ibex ibex)*, and in domestic and feral goat *(Capra aegagrus hircus)* populations with multilocus enzyme electrophoresis. Ibex from the Gran Paradiso National Park (Italy), the "mother" population of all the present Alpine colonies, shows genetic variability lower than the Graubünden (Switzerland) colony. Feral goats from Montecristo Island (Italy) show genetic variability higher than domestic goats. Such results have been discussed taking into account the possibility of past interbreeding between ibex and domestic goat during the first stages of captive breeding and reintroduction in Switzerland, and of repeated introductions of domestic goats into Montecristo Island. Both Alpine ibex and Montecristo feral goats have been submitted to repeated bottlenecks and founding episodes, with consequent erosion of genetic variability. The opportunity to conserve genetic variability has been discussed within the framework of ibex reintroduction plans, and of conservation projects of small island goat populations.

Introduction

Allozyme variability could be an estimate of the average genetic diversity of individual genomes or populations, if variation at different kinds of genes should be, at least in part, correlated (Soulé et al. 1973). Optimal levels of heterozygosity (Scribner et al. 1989) or linkage between particular allelic variants and other genetic systems, e.g. polygenes or regulatory genes (Pemberton et al. 1988), have been addressed as indicators of the genetic welfare of a population, and as determinants of the short-term fitness and evolutionary adaptation to varying environments (Soulé 1980). The genus *Capra* includes species of great ecological and economic importance, and offers several opportunities for biochemical and population genetics approaches to conservation problems. The geographic distribution and population size of several species have been heavily affected by the direct or indirect action of man. Goats have been domesticated before 7000 B.C. (Mason 1984). The Alpine ibex has a well documented population history (Couturier 1962; Tosi et al. 1986; Grodinsky and Stüwe 1987) of man-caused bottlenecks, which drove the species near to extinction, and of successful reintroductions started in Switzerland in 1911 and still going on. Almost all the present colonies are managed, and many areas are potentially suitable for founding new colonies in the Alps. Population genetics data have been collected on a number of colonies from Switzerland, France and Austria (Hartl 1986; Stüwe and Scribner 1989), and these data could be related to demographic and life history information to investigate the role of founder effect and genetic drift on the extent of genetic variability in the refounded colonies and its eventual relationships with their fitness.

Aims of this study are: 1. to estimate the extent of genetic variability in wild, domestic and feral populations belonging to the genus *Capra*, using multilocus protein electrophoresis; 2. to compare the genetic structure of the ibex population from the Gran Paradiso National Park, Italy, the "mother" colony of all the present Alpine ibex

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populations, with a refounded Swiss population with a documented partial origin from captive reared animals; 3. to describe the genetic structure of the feral goat population of the Montecristo Island, Italy, an ancient population, whose origins are not historically documented. The integration of the goats into the fragile ecosystem of the island, now a Natural Reserve, is problematic and management efforts are needed.

Material and methods

Heart and liver tissue samples were obtained from the following populations:

1. Ibex *(Capra ibex ibex)* from the Gran Paradiso National Park (PNGP, Italy; n = 20) and from the Piz Albris colony (Graubünden, Switzerland; n = 20). Animals were collected after incidental dead (mainly avalanches) in winter, or shooted. The PNGP has been the last colony surviving after the extermination of the ibex elsewhere in the Alps at the end of 18th century. The Piz Albris has been one of the first colonies refounded in the Swiss Alps, using some animals reared in captivity at the Peter and Paul and Harder (Interlaken) Zoological Parks (Rauch 1941; Desax 1978; Giacometti 1988).
2. Montecristo feral goat (*Capra aegagrus hircus*, n = 20); the samples were collected during a selective culling campaign planned to control population density. Montecristo is a small Mediterranean Island, about 10 square km, belonging to the Tuscany Archipelago, Tyrrhenian Sea, Italy. Probably goats were repeatedly introduced into the Island, and, although no documented historical record is available, first introductions seem to be very ancient. Some goats were probably introduced into Montecristo as a game species during the second half of last century (Bruno and Sauli 1976). Morphologic and eco-ethologic aspects of the Montecristo feral goat are described by Spagnesi et al. (1986).
3. Domestic goat (n = 20); from an Alpine rural breed (Val Chiavenna, Italian Alps), obtained from a local abbatoir.
4. An F1 hybrid male ibex × female domestic goat specimen was obtained from the French southern Alps. This individual originated from a natural crossing in the wild. Hybridization between ibex and domestic goat has been reported both in captivity and in the wild (Couturier 1962).

Tissues were homogenated in 0.01 M Tris/HCl, pH 7.5 (+0.001 M β-mercaptoethanol) buffer, centrifuged at 12.000 rpm for 15 min; supernatant was collected in Microtiter plates and stored at −80 °C until usage. Vertical polyacrylamide gel (PAGE, 7.5 % acrylamide concentration) and cellulose acetate membrane (CAM, Sartorius) electrophoresis was used to resolve 38 presumptive loci. The following electrophoretic conditions were used (multiple loci are numbered starting from the most anodal locus).

PAGE: 1. Discontinuous Tris/glycine, pH 8.3 (Davis 1964): malate dehydrogenase (MDH-1); superoxide dismutase (SOD-1, SOD-2); lactate dehydrogenase (LDH-1, LDH-2); fumarase (FUM); haemoglobin (HB-1, HB-2); albumin (ALB); non-enzymatic heart and liver proteins (H-PT and L-PT); malic enzyme (ME-1, ME-2); mannose phosphate isomerase (MPI); hexokinase (HK); glucose-6-phosphate dehydrogenase (G-6-PDH); α-glycerolphosphate dehydrogenase (α-GPDH); glutammate dehydrogenase (GLUD). 2. Discontinuous Tris/glycine, pH 8.5 (Jolley and Allen 1965): aspartate aminotransferase (AAT-1); phosphoglucose isomerase (PGI); phosphoglucomutase (PGM-2); glucose dehydrogenase (GDH-1, GDH-2). 3. Tris/borate, pH 8.9 (Studier 1973): α-naphthyl-acetate heart esterase (H-EST-1, -2, -3). 4. Lithium hydroxide, pH 8.6 (Ferguson 1980): leucyl-alanine liver peptidase (L-PEP-1, -2, -3). CAM (Grünbaum 1981): 1. Tris/maleate, pH 7.4: 6-phosphogluconate dehydrogenase (6-PGD). 2. Tris/glycine, pH 8.4: acid phosphatase (ACP). 3. Phosphate, pH 6.25: adenylate kinase (AK). 4. Citrate/phosphate, pH 7.0: isocytrate dehydrogenase (IDH-1, IDH-2). Staining recipes were adapted from Harris and Hopkinson (1976) and from Grünbaum (1981). Some serum samples (10 Montecristo goats; 10 PNGP ibexes; 1 F1 hybrid goat × ibex) were used to study serum transferrin (TF) with the Davis (1964) discontinuous PAGE system.

Genotype frequencies were obtained by scoring the gels. The percentage of polymorphic loci (P), the observed (Ho) and the expected Hardy-Weinberg (He) heterozygosity, the mean number of alleles per locus (A) were computed at each polymorphic locus, and average values were obtained for all the studied loci. The program BIOSYS-1, release 1.7 (Swofford and Selander 1989), was used to compute single locus chi-square test of Hardy-Weinberg equilibrium, F-statistics (Wright 1978), contingency analysis of heterogeneity among populations (Workman and Niswander 1972), and Nei (1978) and Rogers (1972) genetic distances.

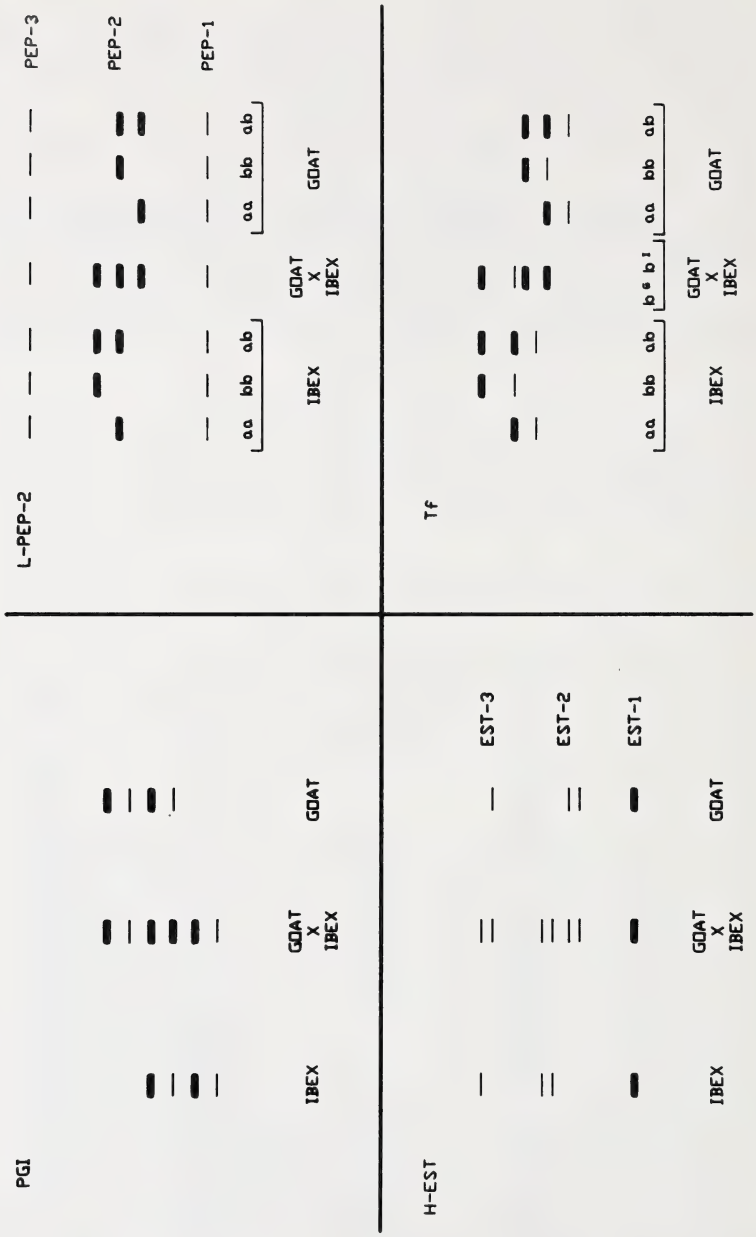
Results

Seven loci (LDH-1, PGM-2, H-PT-5, L-PT-7, L-PEP-2, ME-1, ME-2) were polymorphic in one or more populations, and four loci (PGI, H-EST-2, H-EST-3, and serum TF) showed fixed differences between ibex and goat (see Table and Fig.). Montecristo goat population showed the highest values of genetic variability (P = 13.2; $\overline{H}$ = 0.024), while Gran Paradiso ibex showed the lowest ones (P = 5.3; $\overline{H}$ = 0.009). Genetic variability was lower in the PNGP than in the Graubünden ibex. PNGP ibex showed also the lowest average number of alleles per polymorphic locus. The polymorphisms were heterogenously distributed among the four populations: LDH-1 has been found polymorphic in ibex, but monomorphic in goat. Several loci were polymorphic only in goats (PGM-2; ME-1; ME-2; L-PT-7). Leucylalanine liver PEP-2 showed a widespread polymorphism both in goat and ibex populations, but the most frequent alleles were different in the two species (Fig.). Both average FST and contingency chi-square values at all the polymorphic loci were significant. Major differences between PNGP and Graubünden ibex were observed at H-PT-5 and L-PEP-2 (χ^2 = 8.8, $p < 0.01$); between Montecristo and domestic goat at L-PEP-2 (χ^2 = 6.4, $p < 0.01$); between Montecristo and domestic goat at L-PEP-2 (χ^2 = 6.4, $p < 0.01$), ME-2 (χ^2 = 13.2, $p < 0.01$), and ME-1 (χ^2 = 18.5, $p < 0.01$). FIS values were generally low and nonsignificant, and deficiency of heterozygotes was observed only at ME-1 in the Montecristo goat and H-PT-5 in the Graubünden ibex. Expected and observed heterozygosities were similar, and chi-square tests of Hardy-

Allelic frequencies at ten loci polymorphic within populations and between ibex and goat

Locus	Allele	Populations			
		PNGP ibex	Graubünden ibex	Montecristo goat	Domestic goat
LDH-1	a	.050	.025	.000	.000
	b	.950	.975	1.000	1.000
PGI	a	1.000	1.000	.000	.000
	b	.000	.000	1.000	1.000
PGM-2	a	1.000	1.000	.974	1.000
	b	.000	.000	.026	.000
H-PT-5	a	1.000	.800	1.000	1.000
	b	.000	.200	.000	.000
L-PT-7	a	1.000	1.000	.975	1.000
	b	.000	.000	.025	.000
H-EST-2	a	.000	.000	1.000	1.000
	b	1.000	1.000	.000	.000
H-EST-3	a	.000	.000	1.000	1.000
	b	1.000	1.000	.000	.000
L-PEP-2	a	.000	.000	.950	.731
	b	.882	.559	.050	.269
	c	.118	.441	.000	.000
ME-1	a	1.000	1.000	.625	1.000
	b	.000	.000	.375	.000
ME-2	a	.000	.000	.000	.100
	b	1.000	1.000	.500	.750
	c	.000	.000	.500	.150
	$\overline{n}$	19.6	19.9	19.8	18.9
	$\overline{A}$	1.18	1.50	1.40	1.66
	P	5.3	7.9	13.2	5.3
	$\overline{Ho}$	0.009	0.021	0.024	0.023

$\overline{n}$ = mean sample size per locus; $\overline{A}$ = mean number of alleles per polymorphic locus; P = percent of polymorphic loci (0.99 criterion); $\overline{Ho}$ = observed heterozygosity.



Electrophoretic phenotypes at five loci showing diagnostic differences between ibex and goat, and phenotypes showed by an F1 hybrid goat × ibex

Weinberg equilibrium were nonsignificant for all the polymorphic loci. Serum TF was found to be polymorphic in Montecristo goat and PNGP ibex, but the alleles were different in the two species (Fig.).

Ibex and goat are well differentiated species with average Nei's genetic distance of 0.11. The genetic distances between the two ibex, as well as between the two goat populations are about one order of magnitude lower (0.01). At least four loci of the 38 screened showed clear fixed differences (PGI, H-EST-2, H-EST-3, serum TF), and L-PEP-2 showed very different allelic frequencies. The F1 hybrid ibex × goat showed hybrid (codominant) genotypes at all these loci (Fig.).

Two additional polymorphisms were found at PGM-1 and L-EST-1 loci in the Graubünden and in the two goat samples, but these loci did not stain clearly in the PNGP ibex. PGM-1 is the most anodal band we have found in our gels, and probably correspond to PGM-2 as indicated by Hartl (1986). This locus stained very faintly and was difficult to score in some specimens and in almost all the PNGP samples. For this reason we have not included PGM-1 and L-EST-1 in the comparison among the four populations.

Discussion

Wild and domestic populations of the genus *Capra* have so far been poorly investigated with biochemical genetic methods. Studies on domestic goat focused on finding genetic markers, mainly polymorphic blood enzymes, useful to the classification of different breeds, but not utilizable to obtain data of genetic variability at the population level (Fesus et al. 1983; Brabancho et al. 1984; Tuñon et al. 1987).

Some Alpine ibex populations have been studied. Stüwe and Scribner (1989) analyzed 53 ibexes belonging to 9 Swiss populations and obtained low average values of genetic variability ($\overline{H}$ = 0.007, P = 6.06, $\overline{A}$ = 1.18). Heterozygosity was lower than the value obtained by Hartl (1986) on 46 ibexes from the Piz Albris colony ($\overline{H}$ = 0.023, P = 5.30), but a partially different set of loci was resolved and included in the computations. In the present study we have obtained genetic variability estimates that confirm the data previously reported. The Graubünden sample, from the same Piz Albris colony, showed higher variability ($\overline{H}$ = 0.021, P = 7.9) than the PNGP ($\overline{H}$ = 0.009, P = 5.3), but the set of studied loci was not quite coincident. Hartl (1986) found two polymorphisms: PGM-2 (our PGM-1) and ADA; Stüwe and Scribner (1989) found polymorphic PEP-S, LDH-1, MPI, EST-2, and NP; ADA was monomorphic and PGM-2 was not scored. In the present study we have found polymorphic LDH-1, L-PEP-2 and a non-enzymatic heart protein. We did not score ADA and NP. PGM-1 (corresponding to Hartl's PGM-2) was apparently polymorphic in goats and Graubünden ibex, but impossible to score in the PNGP ibex. Different laboratories and partially different sets of loci could make it difficult to compare the data, but, notwithstanding, the Piz Albris ibex population seems to harbour a level of genetic variability higher than other Alpine ibex populations.

The PNGP ibexes constitute the "mother" population of all the present Alpine colonies (Desax 1981; Peracino and Bassano 1986; Tosi et al. 1986). This colony now counts more than 4000 individuals, but was reduced to less than 100 during the first years of the 18th century. Due to the difficulty to obtain animals from the wild, starting from 1906, captive-breeding programs with ibexes belonging to the Gran Paradiso National Park, were undertaken in Switzerland to produce the founders for new ibex colonies. Bottlenecks and low population numbers, repeated foundings of new colonies starting from few animals, contributed to cause and to maintain a low genetic variability in ibex populations, as showed by electrophoresis results.

It seems problematic to explain why the Piz Albris colony consistently shows genetic variability higher than the Gran Paradiso "mother" population. Although sampling

limitations (both specimens and number of loci) and methodological details cannot be ruled out, another explanation is possible. During the first steps of captive-breeding and during the apparently unsuccessful first attempts to release ibexes in the wild, repeated crossbreeding with domestic goats are documented in Switzerland (Grodinsky and Stüwe 1987). Although we have not found any "goat" gene in the Piz Albris specimens at the loci showing fixed differences between goat and ibex (the analysis of the F1 hybrid ibex × goat showed in the figure supported that result), there is the possibility of an increase in genetic variability as consequence of crossing. This suggestion could be supported if the polymorphism at the PGM-1 locus that is present both in goat and in the Piz Albris samples, could be definitively excluded in the Gran Paradiso population.

The domestic goat population we have studied showed a level of heterozygosity ($\overline{H}$ = 0.023) just slightly below the average value (0.029) computed for large mammals (Nevo et al. 1984). The Montecristo goats harbour higher levels of genetic variability, so it seems impossible that the population has been founded only once, starting with a few founders. The hypothesis that domestic animals were repeatedly introduced into the island (by sailors, fishermen and hunters), and that they have contributed to the present gene pool, is supported by our genetic findings.

In fact this is a closed population without gene flow, with probable natural selection acting to reconstruct a "wild" phenotype fitted to the hard environmental conditions of the island. The population is so inevitably subjected to an increase in inbreeding and to a decrease in genetic variation due to random drift (Franklin 1980). This is the only Italian feral goat population and one of the few Mediterranean (Schultze-Vestrum 1963; Nievergelt and Zingg 1986) so it has to be conserved in the island. It is therefore important to evaluate the effective population size (Ne) which has to be maintained to assure a low rate of inbreeding and a slow loss of genetic variability through the generations.

The actual population size (Na) numbers about 400–450 animals. The sex ratio is near 1 : 1. The effective number of males and of females is lower than 200, because not all the individuals will mate with the same probability (e.g. full breeding activity is reached by males not before 2–3 years). Field observations of mating behavior (Toso and Tosi unpubl.) suggest an approximate estimate of effective male number Nem = 100, and of effective female number Nef = 130. The effect of sex ratio on effective population size is computed as $Ne = 4\,(1/Nem) + (1/Nef)^{-1}$ (Lande and Barrowclough 1987), and it gives the value Ne = 227. The effects of variance in progeny number and overlapping generations are presently not evaluable, but they should lower further Ne to a value lower than 0.5 × Na. We can roughly assume that Ne is in the range from 100 to 200. If we use Ne = 100 to compute the rate of inbreeding per generation f = ½Ne, we obtain f = 0.5 %, a value half of the threshold of 1 % inbreeding per generation suggested by Soulé (1980) to permit the population to experience an eventual soft selection for inbreeding tolerance. The rate of loss of genetic variability per generation is $\Delta(\overline{H}) = \overline{H} - (1 - \frac{1}{2}Ne)\overline{H}$ (Wright 1931). Assuming $\overline{H}$ = 0.0300 (including PGM-1 and L-EST-1 polymorphisms) in Montecristo goat population, then $\Delta(\overline{H})$ = 0.0002, corresponding to a loss of about 0.7 % heterozigosity per generation.

Future conservation plans should evaluate the possibility to maintain a long-period Ne = 100 to be sure that Montecristo goat population is at low genetic risk for some 10s of generations.

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Zusammenfassung

Genetische Variabilität und Probleme ihrer Erhaltung bei Populationen von Alpensteinbock, Hausziege und verwilderter Hausziege (Genus Capra)

Durch Protein-Elektrophorese wurde die genetische Variabilität in zwei Populationen des Alpensteinbocks *(Capra ibex),* in einer Hausziegengruppe und bei den verwilderten Hausziegen *(Capra aegagrus hircus)* der Insel Montechristo geschätzt. Die Steinböcke aus dem Nationalpark Gran Paradiso in Italien zeigten eine geringere genetische Variabilität als die von ihnen abgeleiteten aus Graubünden in der Schweiz.

Die Ziegen von Montechristo sind genetisch stärker variabel als die Hausziegen, die aus menschlicher Haltung stammen. Dieses spricht dafür, daß Hausziegen zu verschiedenen Zeiten und mehrfach auf Montechristo eingeführt wurden. Eine Einkreuzung von Hausziegen in die Steinbock-Population von Graubünden konnte nicht nachgewiesen werden. Die für die Erhaltung der genetischen Variabilität auf Montechristo notwendige Mindestgröße der dortigen Population wird abgeschätzt.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Wiederfangerfolg bei Kleinsäugern mit einer neuen Markierungsmethode

Von A. Hugo

Eingang des Ms. 14. 5. 1990
Annahme des Ms. 19. 6. 1990

In einer Untersuchung zur Habitatnutzung von Kleinsäugern im Nationalpark Berchtesgaden (Hugo 1986) wurden Mäuse der Familien Muridae und Arvicolidae mit Acrylfarben individuell markiert. Mit dieser Acrylfarbmethode wurde eine preiswerte und praktikable Alternative zur gebräuchlichen Markierung durch Zehenamputation (toe-clipping) (z. B. Sykora 1978) entwickelt und getestet. Acrylfarben hatten sich bereits bei der Markierung von Fischen als geeignet erwiesen (Lotrich und Meredith 1974; Trescher und Gronell 1978; Brunken 1987), fanden jedoch bei Säugetieren bisher keine Anwendung.

Bei der Markierung werden den Kleinsäugern wasserlösliche Acrylfarben mittels Spritze und Kanüle unter die Schwanzschuppen gespritzt (Einmal-Kanüle 0.50 × 16 mm). Die Kanüle wird hierbei von caudal über eine Länge von etwa ein bis zwei Millimetern parallel zur Oberfläche eingestochen. Beim Herausziehen der Kanüle gibt man unter leichtem Druck die Farbe ab, wodurch ein länglicher Farbfleck unter der Haut zurückbleibt. Die Kanüle wird möglichst dicht unter der Oberfläche geführt, damit der Farbfleck gut sichtbar durchscheint und keine Gefäße verletzt werden. Um die Tiere ohne Betäubung und ohne fremde Hilfe kennzeichnen zu können, werden sie mit dem Kopf voran in einer Plexiglasröhre (Innendurchmesser ca. 20 mm, einseitig luftdurchlässig verschlossen) fixiert.

Die Markierungsmethode wurde in 3 Testphasen erprobt: Laborversuch (Hugo 1986), erster Freilandtest 1985 und zweiter Freilandtest von 1986 bis 1988.

Im ersten Freilandtest von Mai bis Oktober 1985 konnten 87 Gelbhalsmäuse *Apodemus flavicollis* (Melchior, 1834), 241 Rötelmäuse *Clethrionomys glareolus* (Schreber, 1780), und 5 Kurzohrmäuse *Microtus subterraneus* (de Sélys-Longchamps, 1836) markiert werden. Neben den Acrylfarben wurden auch zwei Tätowierfarben eingesetzt (Tab. 1).

Tabelle 1. **Markierungsfarben und ihre Eignung**

Hersteller	Bezeichnung	Kürzel im Text	Eignung
Schmincke	PRIMAcryl 553 „Kadmiumgrün“	Grün	**
Schmincke	PRIMAcryl 446 „Cölinblau“	Blau	**
Schmincke	PRIMAcryl 664 „Englischrot“	Rot	**
Schmincke	PRIMAcryl 771 „Schwarz“	Schwarz	*
Schmincke	PRIMAcryl 111 „Titanweiß“	Weiß	*
Schmincke	PRIMAcryl 447 „Königsblau“	Hellblau	–
Schmincke	PRIMAcryl 333 „Zinnoberrot“	Hellrot	–
Schmincke	PRIMAcryl 221 „Neapelgelb“	Gelb	–
Hauptner	Spezial-Tätowierfarbe (grün)	T-Grün	*
Hauptner	Spezial-Tätowierfarbe (violett)	T-Violett	–

**: geeignet; *: bedingt geeignet; –: ungeeignet.

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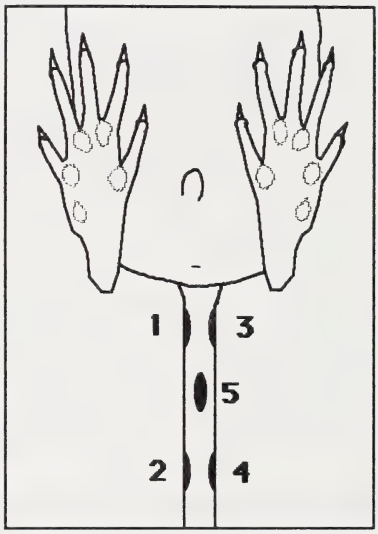
Die drei Acrylfarben Grün, Blau und Rot erwiesen sich als dauerhafte und haltbare Markierung, wenn sie unverdünnt gespritzt wurden. Die Farben Hellblau, Hellrot, Gelb, Weiß und T-Violett mußten schon nach kurzer Zeit aufgrund schlechter Sichtbarkeit oder schnellen Verblassens als ungeeignet ausgesondert werden. Schwarz und T-Grün waren zwar über kurze Zeit beständig; schwarze Farbmarken ließen sich jedoch kaum von blauen unterscheiden, und T-Grün verstopfte sehr schnell die Kanülen.

Für die Anbringung der Marken wurden 5 Schwanzbereiche unterschieden (Abb.). Die Anzahl der Markierungskombinationen bei fünf Markierungspunkten und dem Einsatz von drei verschiedenen Farben beträgt 1023; unter der Voraussetzung, daß die Anzahl der Farbmarken von eins bis fünf variieren kann, wahlweise eine, zwei oder drei Farben pro Markierung eingesetzt werden und alle Farben beliebig kombiniert werden können. Der Freilandtest zeigte, daß einzelne Markierungsmarken nach einiger Zeit verschwunden waren. Aus diesem Grunde wurden bei den Untersuchungen vom Frühjahr 1986 bis zum Herbst 1988 nur noch Drei- oder Fünfpunktmarkierungen gesetzt, wodurch verschwundene Farbmarken durch Abzählen feststellbar wurden. Die Zahl der Markierungen pro Art und Geschlecht reduzierte sich dadurch von 1023 auf immer noch ausreichende 513 Kombinationen. Eine zusätzliche Möglichkeit, Verblassungen von Farbflecken festzustellen, bot sich dadurch, daß ehemalige Markierungsmarken in der Regel eine helle Narbe oder einen haarlosen Fleck hinterließen.



Ventralansicht der 5 Markierungsbereiche am Schwanz einer Maus

Im zweiten Freilandtest über drei Jahre von 1986 bis 1988 wurden die Farben Grün, Blau und Rot als Dreipunkt- oder Fünfpunktmarkierung in beliebiger Kombination an insgesamt 627 Individuen erprobt: 205 *Apodemus flavicollis* (Tab. 2), 389 *Clethrionomys glareolus* (Tab. 2), 27 *Microtus subterraneus*, 6 *Microtus agrestis* (Linnaeus, 1761).

Apodemus flavicollis (n = 205): Insgesamt wurden 195 grüne, 216 blaue und 196 rote Marken vergeben. 172 Individuen (83,9 % der markierten Tiere) wurden mindestens einmal wiedergefangen. Dies entspricht 145 wiedergefangen grünen, 165 blauen und 154 roten Markierungsmarken. Bei 5 Individuen (2,9 % aller wiedergefangenen Individuen) wurde das Verschwinden je einer Marke registriert (1,1 % verschwundene Farbmarken von insgesamt 464 wiederentdeckten Marken). 2 Farbmarken verblaßten innerhalb der ersten

Tabelle 2. **Markierte und wiedergefangene Tiere und Anzahl der vorhandenen und verschwundenen Farbmarken**

	Apodemus flavicollis					*Clethrionomys glareolus*				
	Indiv. (Fänge)	Anzahl der Farbmarken Σ	grün	blau	rot	Indiv. (Fänge)	Anzahl der Farbmarken Σ	grün	blau	rot
Erstfänge	205 (205)	*607*	195	216	196	389 (389)	*1146*	380	414	352
Wiederfänge gesamt	172 (778)	*464*	145	165	154	278 (1227)	*833*	262	302	269
Verschwundene Marken										
1 Marke	5	5	2	2	1	11	11	5	4	2
2 Marken	–	–	–	–	–	2	4	3	1	–
gesamt	5 2,9%	*5 1,1%*	2	2	1	13 4,7%	*15 1,8%*	8	5	2
Wiederfänge im Folgejahr										
Nach über 180 Tagen	19 (174)	*61*	20	15	26	14 (181)	*40*	17	10	13
Nach über 360 Tagen	3 (24)	*11*	3	4	4	7 (39)	*22*	9	7	6
Wiederfänge im 2. Jahr										
Nach über 600 Tagen	1 (9)	5	1	–	4	– (–)	–	–	–	–

Woche, eine nach ca. 2 Wochen und eine nach etwa einem Jahr. Das Verschwinden einer Farbmarke ließ sich nicht genau datieren (zwischen einem Tag und 7 Monaten nach dem Markieren). In allen 5 Fällen konnten die Tiere trotz fehlender Marke eindeutig identifiziert werden. Das Verblassen von 2 oder mehr Marken wurde bei Gelbhalsmäusen nicht festgestellt. Mindestens 6 Monate nach Markierung konnten im Folgejahr noch 19 Individuen (174 Fänge) aufgrund ihrer Markierungen eindeutig identifiziert werden. Nach einem Jahr waren es noch 3 Individuen (24 Fänge), deren Marken (3× Grün, 4× Blau und 4× Rot) auch nach dieser Zeit noch deutlich erkennbar waren. Bei einem männlichen Tier (1× Grün und 4× Rot) lagen zwischen Markierungstag und letztem Wiederfangtag sogar 2 Winter bzw. 669 Tage!

Clethrionomys glareolus (n = 389): Insgesamt wurden 380 grüne, 415 blaue und 352 rote Marken vergeben. 278 Individuen (71,5 % der markierten Tiere) wurden mindestens einmal wiedergefangen. Das ergibt 262 wiedergefangene grüne, 302 blaue und 269 rote Marken. Bei 13 Tieren (4,7 % aller wiedergefangenen Individuen) wurden zusammen 15 verblaßte Marken (1,8 % aller wiedergefangenen Marken) registriert. Bei 11 Individuen waren je eine und bei 2 Individuen jeweils 2 Marken verschwunden. 10 der 15 Farbmarken verblaßten innerhalb der ersten Woche, eine nach ca. 5 Wochen und eine nach etwa 10 Wochen. 3 Verblassungen ließen sich nicht genau datieren (zwischen einem Tag und 2 Monaten nach dem Markieren). Alle 13 Tiere konnten trotz fehlender Marken eindeutig identifiziert werden. Mindestens 6 Monate nach Markierung konnten im Folgejahr noch 14 Individuen (181 Fänge) registriert werden, nach über einem Jahr noch 7 Tiere (39 Fänge), deren 9 grüne, 7 blaue und 6 rote Marken gut sichtbar waren und ein eindeutiges Wiedererkennen der Tiere erlaubten. Der größte Abstand zwischen Markierungstag und letztem Fangtag betrug 435 Tage bei einem weiblichen Tier (Markierung: 3× Blau).

3 Gelbhalsmäuse und 3 Rötelmäuse konnten beim Wiederfang nicht eindeutig identifiziert werden. Hier waren beim Markieren möglicherweise die Seiten vertauscht worden, oder es lagen Übertragungsfehler vor.

Bei den markierten *Microtus*-Arten betrugen die größten Abstände zwischen Markie-

rungstag und Wiederfang für einen *M. subterraneus* 347 Tage und einen *M. agrestis* 219 Tage (jeweils blaue Marken).

Während das Anbringen und Wiedererkennen der Marken an den nur schwach behaarten Schwänzen der Langschwanzmäuse (Muridae) problemlos ist, erschwert die relativ starke Schwanzbehaarung der Wühlmausarten (Arvicolidae) die exakte Anbringung und Wiedererkennung der Farbmarken, besonders bei schlechter Beleuchtung. Dies ist möglicherweise der Grund für die etwas höhere Verblassungsrate bei *C. glareolus* gegenüber *A. flavicollis*. Zur sicheren Beurteilung der Markierung bei Wühlmäusen empfiehlt es sich deshalb, den Schwanz bei der Kontrolle anzufeuchten, wodurch die Schwanzhaut besser sichtbar wird.

Ein negativer Einfluß der Markierung auf den Zustand der Tiere konnte nicht festgestellt werden. Ein Vergleich der Gewichte von markierten und unmarkierten Tieren, getrennt nach Geschlecht und Altersgruppen ergab keine statistisch signifikanten Differenzen. Der Vergleich des allgemeinen Zustandes zwischen Erstfängen und markierten Wiederfängen ergab ebenfalls keine erkennbaren Unterschiede.

Eine krankhafte Veränderung an den Markierungsstellen wurde nur einmal festgestellt. In diesem Falle war die Schwanzbasis einer wiedergefangenen Rötelmaus, offensichtlich durch die Markierung ausgelöst, entzündet und dick. In anderen Fällen waren die Markierungspunkte, vermutlich aufgrund der injizierten Farbmenge, zwar verdickt, aber nicht entzündet.

Die geringen Verblassungsraten und die lange Haltbarkeit der Acrylfarben zeigen, daß die Markierungsmethode für mehrjährige Untersuchungen an Kleinsäugerarten der Gattungen *Apodemus, Clethrionomys* und *Microtus* geeignet ist. Anwendungen dieser Methode von Jacobs (1989), Tempel-Thederan (1989) und Heydenreich (mündl. Mitt.) bestätigen dies auch für die Arten *Apodemus sylvaticus, Microtus arvalis* und *Microtus nivalis*.

Frau Katharina Tempel-Thederan und Herrn Dr. Heiko Brunken danke ich für die kritische Durchsicht des Manuskripts. Die Arbeit ist Teil eines Forschungsprojekts der Nationalparkverwaltung Berchtesgaden, finanziert vom Bayerischen Staatsministerium für Landesentwicklung und Umweltfragen.

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Histological structure of the abdominal gland and other body regions involved in olfactory communication in Pine martens *(Martes martes)*

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In pine martens *(Martes martes)*, two types of specialized glands have been described: 1. the anal glands, common to all mustelids, having their outlets into two pouches just within the anus (Stubbe 1969) and 2. the abdominal or ventral glands located on the ventral surface of the abdomen in an elongated depression of the skin (Hall 1926). Previous observations on the behaviour of captive animals (de Monte and Roeder 1990) clearly showed that martens exhibit mostly abdominal marking, associated with a particular body posture. No such behaviour suggesting anal marking was observed. Although histological studies have been undertaken on anal glands, no similar work has been carried out on abdominal glands or on other body regions (cheek, neck, flank) being also involved in olfactory contact and rubbing movements. The aims of the present study were to describe the histological structure of the abdominal glands in both sexes and to determine whether the densities of sebaceous glands were identical in the three main body regions implicated in nasal contacts.

Skin samples were collected from two adult martens (one female and one male) immediately after death. Four samples from the abdominal gland were collected from each animal, one from the frontal region, two from the central and one from the caudal region of the gland. Skin samples were collected from the cheek, neck and median flank on the left side. After fixation for 5 days in Bouin's fluid, tissue blocks were embedded in paraffin and sections cut at a thickness of 7–10 μm. Sections of the skin and taken from samples tangent to the surface were stained with hematoxylin and eosin. They were analysed with an image analysing computer (Ibas 1, Zeiss) coupled with a camera microscope system (magnification from microscope to graphic screen giving a value of 151 for 1 mm). Data concerning regions involved in body rubbing were recorded from 11 to 36 histological sections from each body area. The parameters recorded were: the total number of sebaceous glands shown on the screen (density) and the mean area of the sebaceous glands on each section. The densities of sebaceous glands in the different body regions were compared using the Mann Whitney U Test with 15 histological sections from the neck (each section involving a mean of 20 acini), 17 from the cheek and 20 from the median flank in the male; 20 from the neck and from the flank and 11 from the cheek in the female. The different sections were randomly chosen for each region. For the analysis of areas, results were analysed only in relation to their correlation with densities.

Abdominal glands occupy an area on the ventral surface of the abdomen, measuring 8.0 × 4.0 cm, being located in front of the penis in the male, and 1.0 × 6.4 cm, situated behind the caudalmost nipples in the females. Histological examination shows that abdominal glands are exclusively composed of holocrine sebaceous acini (Fig. 1A). Structurally, they consist of two well-circumscribed glandular regions in the outer skin. These two regions are limited exteriorly by a layer of keratinized cells, and internally by

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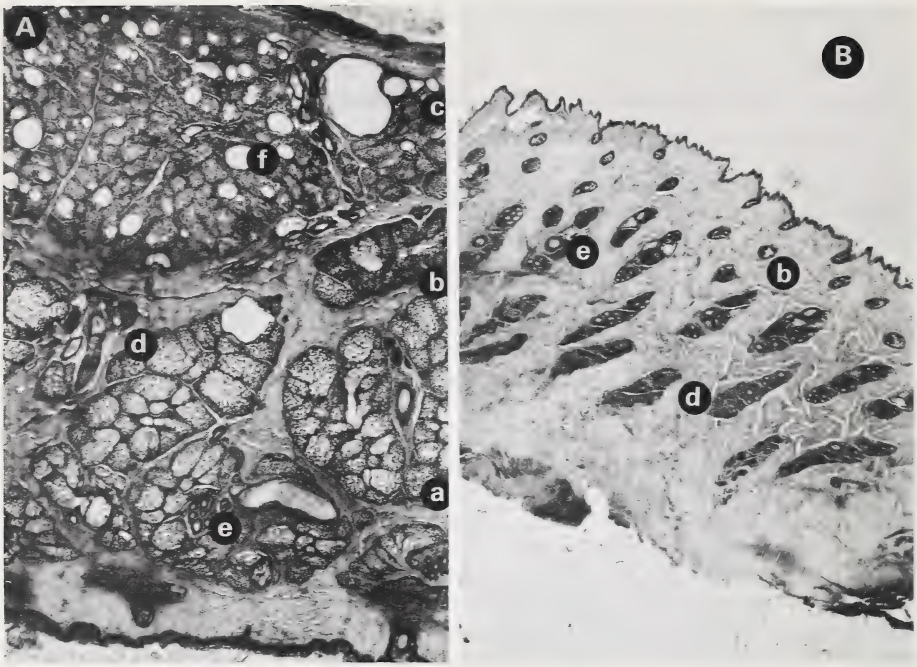

Fig. 1. Histological section (×40) of the abdominal gland (A) and from the skin of the cheek (B) in the male marten. a = external zone, b = connective tissue, c = internal zone, d = acini, e = hair shaft, f = liposome

connective tissue. The outmost zone consists of a loose collection of sebaceous acini embedded in connective tissue; each glandular group is associated with several hair follicles. The deep zone (separated from the exterior zone by a layer of connective tissue) consists of dense tissue formed almost exclusively of glandular groups. Each group is associated with only one hair follicle. This zone is very rich in liposomes. No structural differences were observed either between the male and the female, or between the different regions of the abdominal gland.

No specialized glands were found in the different regions of the skin sampled (cheek, neck and median flank). Histological examination revealed sebaceous glands in association with hair follicles and embedded in abundant connective tissue (Fig. 1B). The highest densities are found in the cheek area (see Table): they differ significantly from those found in flank areas in both sexes, and from those found in the male's neck area only in the male. The only statistically significant difference between neck and flank was found in the female. Generally, the areas are larger from cheek to flank, whereas the densities increase in the reverse order, although we found no significant correlation between densities and areas ($r = -0.65$, $p = 0.15$, Spearmann correlation test).

The ventral gland discharging through the abdominal skin anterior to the genital orifice is typical of some subfamilies of mustelids (MacDonald 1985). Its external structure has been described by Hall (1926), who found a glandular area marked externally by shorter hair in the American marten *(Martes americana)* and the wolverine *(Gulo gulo)*. Pocock (1925) described such a gland in the male of *Taxidea*. Histological studies of these glands have never been undertaken. Our study shows that in pine martens, the abdominal gland is composed exclusively of sebaceous acini in contrast to the anal glands which are composite, consisting of sebaceous glands and tubular apocrine cells (Stubbe 1969). The

Densities and sizes of sebaceous acini from different body regions in both sexes

Body region	Male		Female	
	Density	Mean areas	Density	Mean areas
Cheek	16.67 ±2.77 *	488.9 ±88.0	10.13 ±2.55	530.2 +106.4
Neck	9.44 ±1.33	* 661.4 ±109.5	* 8.05 ±1.77	* 502.8 +100.5
Flank	8.43 ±1.36	667.5 ±182.2	6.06 ±1.56	836.4 ±249

* $P < 0.05$, Mann-Whitney test.

histological structure of the gland did not differ between the male and the female. The histological study of skin samples shows decreasing densities of sebaceous glands from cheek to flank in both sexes. These results are in accordance with the decreasing frequencies of contact involving these body regions: 42.5 % of all contacts by females on males are directed to the face, reaching 41 % between two females. Sniffing frequencies decrease from the head to the hindquarters of the animals. Sniffing by males on females is essentially directed to the anogenital region (52 %). However, the face contacts reached 23 %, but only 19 % when contacts were directed to the flank (de Monte and Roeder 1990).

Cheek, neck and flank are also involved in body rubbing movements. Such rubbing movements have been described in many species of carnivores and have generally been defined as scent rubbing (Rieger 1979). In martens, body rubbing cannot be considered as scent rubbing because it is never oriented towards odoriferous substances (chemical, food or scent marks). However, the high density of sebaceous glands and the high frequency of nasal contacts with these regions involved in body rubbing suggest the existence of an olfactory message. Therefore, it would be interesting to know what kind of information may be conveyed both by such behaviour and by abdominal marking.

We are very grateful to E. Vogel for technical assistance and to Dr. J. R. Anderson for correcting the English.

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BEKANNTMACHUNGEN

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e.V. am 24. September 1990 im Hörsaal des Zentrums für Biologie der Universität Osnabrück

Der 1. Vorsitzende, Herr Kulzer, eröffnet die Versammlung um 17.30 Uhr.

1. Die Tagesordnung wird angenommen.
2. Herr Schmidt verliest den Bericht über das abgelaufene Geschäftsjahr 1989. Im Berichtsjahr erschien der 54. Band der „Zeitschrift für Säugetierkunde" in sechs Heften mit 408 Seiten. Zusätzlich wurde allen Mitgliedern das Sonderheft mit den Kurzfassungen der Vorträge und Posterbeiträge der Tagung in Lausanne zugesandt.
   Auf Einladung der Herren Vogel und Meylan fand die 63. Hauptversammlung der Gesellschaft vom 10.–14. September 1989 in Lausanne statt. Themenschwerpunkte waren „Endokrinologie und Neurohormone der Säugetiere", „Einsatz der telemetrischen Methoden in der Säugetierforschung" und „Wildlife Management und Ökologie". Erstmals wurden herausragende Poster durch Buchprämien ausgezeichnet, welche die Verlagsbuchhandlung Paul Parey dankenswerterweise gestiftet hatte.
   Aufgrund der politischen Entwicklung ist unsere Gesellschaft nunmehr auch wieder für Mitglieder aus dem Osten Deutschlands offen. Dieser Personenkreis entrichtet bis 31. 12. 1992 einen ermäßigten Mitgliedsbeitrag (z. Zt. DM 65,–).
   Durch den Tod verlor die Gesellschaft folgende Mitglieder:
   Rolf Nöhring, Berlin,
   Prof. Dr. K. Holldach, Velbert.
   Im Jahre 1989 hatte die Gesellschaft 641 Mitglieder.
3. Frau Kühnrich erläutert den von ihr vorgelegten ausführlichen Jahresabschluß unter dem dankbaren Beifall des Auditoriums.
4. Die Kassenprüfer Bohlken und Schliemann haben keinen Anlaß zu Beanstandungen gefunden.
5. Die Anträge zur Entlastung des Schatzmeisters und des Vorstandes werden einstimmig angenommen.
6. Als Kassenprüfer für das Geschäftsjahr 1990 werden die Herren Bohlken und Schliemann wiedergewählt.
7. Der Vorstand sieht keine Veranlassung zur Veränderung des Mitgliedsbeitrages für das Jahr 1991. Er beträgt DM 95,– für Vollmitglieder, DM 60,– für Studierende und DM 10,– für Ehepartner. Die Versammlung schließt sich dieser Auffassung mit 4 Enthaltungen an.
8. Die Mitglieder nehmen die Einladung von Herrn Schliemann an, die 65. Hauptversammlung vom 22.–26. September in Hamburg abzuhalten. Als Schwerpunktthemen werden „Systematik und Stammesgeschichte der Säuger", „Domestikation" und „Anpassung an aquatische Lebensräume" gewählt. Die Einladung von Frau Braun (Prof. Dr. S. Rietschel), 1992 in Karlsruhe zu tagen, wird durch Akklamation angenommen.
9. Die Versammlung wird auf die Kongreß-Berichte einer Fledermaus-Tagung hingewiesen, die in der Tschechoslowakei stattgefunden hat. Aufgrund der wirtschaftlichen Situation in Osteuropa werden die Mitglieder nachdrücklich um die Übernahme von Patenschaften gebeten.
10. Die Sitzung endet um 18.30 Uhr.

Prof. Dr. E. Kulzer 1. Vorsitzender	Prof. Dr. U. Schmidt Geschäftsführer	Dr. H. Frädrich Schriftführer

Ausschreibung des Fritz-Frank-Preises
Förderpreis der Deutschen Gesellschaft für Säugetierkunde

Die Deutsche Gesellschaft für Säugetierkunde schreibt diesen Förderpreis in Höhe von DM 3000,– als Anerkennung für hervorragende wissenschaftliche Leistungen junger Forscher/innen aus.

Voraussetzung ist eine im Druck vorliegende Arbeit oder eine hervorragende Dissertation aus den Gebieten Phylogenie und Systematik, Verbreitung, Ethologie, Ökologie und Populationsbiologie der Säugetiere. Die Arbeit muß in den drei vorausgehenden Kalenderjahren erschienen oder als Dissertation begutachtet worden sein. Die Bewerber/innen dürfen beim Erscheinen der Arbeit bzw. bei ihrer Promotion nicht älter als 33 Jahre sein.

Bewerbungen der Vorschläge erbitten wir an die Geschäftsstelle der Gesellschaft, Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, W-5300 Bonn 1, unter Beifügung von 5 Sonderdrucken bzw. Kopien der Dissertation bis zum 31. 3. 1991.

Der Jury gehören Wissenschaftler verschiedener Universitäten oder Museen und Mitglieder der Gesellschaft an.

Der Preis wird bei der Eröffnung der Jahresversammlung der Gesellschaft in Hamburg (22.–26. 9. 1991) überreicht.

The Institut de Recherche sur les Grands Mammifères (I.R.G.M.) is convening a major International Congress

Ongulés/Ungulates 91

on 2–6 september 1991 in Toulouse (France).

The purpose of this congress is to bring together researchers and wildlife biologists and managers who are directly or indirectly related to the knowledge, management or protection of free or captive *wild Ungulates* (individuals, social groups and populations).

Papers (in English or French) are invited on all aspects of Ungulates study: conservation, ecology, ecophysiology, ethology, evolution, genetics, management, paleontology, parasitology, pathology and systematics.

For further information please contact: G. Gonsalez, Institut de Recherche sur les Grands Mammifères, Centre de Recherche Agronomique de Toulouse, B.P. 27, F-31326 Castanet-Tolosan Cedex, France.

BUCHBESPRECHUNGEN

SCHNEIDER, E.; OELKE, H.; GROSS, H. (eds.): **Die Illusion der Arche Noah.** Gefahren für die Arterhaltung durch Gefangenschaftszucht. Göttingen: Echo-Verlag 1989. 340 pp., Abb., Tab. ISBN 3-926914-06-8

Vom 10. 3.–13. 3. 1988 veranstalteten die Umweltschutzverbände Komitee gegen den Vogelmord e. V., Deutscher Naturschutzring und BUND in Gießen ein Symposium zu den „Gefahren für die Arterhaltung durch Gefangenschaftszucht". Die dort gehaltenen Vorträge sind im vorliegenden Band zusammengefaßt. Es ist in der Tat wichtig, einmal einen Überblick über Erfolge, Mißerfolge, und Risiken zu gewinnen, die mit der Haltung in der Natur aussterbender Arten in Gefangenschaft verbunden sind: Betrachtet werden hier ausschließlich Vögel und Säugetiere. Als wichtigste Gefährdungsursachen für diese Arten werden der Mangel an Gelegenheit in der Gefangenschaft, sich mit der natürlichen Umwelt (Futterquellen, Feinden) auseinanderzusetzen und die Beschränkung der genetischen Vielfalt angesehen. Die Funktion des Freßfeindes erörtert REICHHOLF, unbewußt negative züchterische Einflüsse WEGNER, die Frage, wie weit die Gefangenhaltung das Gehirn beeinflußt, KRUSKA, die Einschränkung der genetischen Variabilität durch Haltung in kleinen Gruppen HARTL oder die morphologischen und ethologischen Veränderungen bei Vögeln in Gefangenschaft OELKE. PECHLAHNER erörtert Anforderungen an die Haltungsbedingungen im Zoo. Über wichtige Artbeispiele berichten H. SCHULZ (Weißstorch), ZUROWSKI (Biber in Polen), STÜWE und NIEVERGELT (Steinbock in der Schweiz), PUCEK (Wisent) und Ehepaar BOUMAN (Przewalski-Pferd).

VAN BREE schildert den Standpunkt der IUCN, SOJKA glaubt, daß bereits die bestehenden Artenschutzgesetze eine Aussetzung aus der Gefangenschaft stammender Tiere ausschließen. Der Bezug anderer Beiträge zum Thema ist weniger eng: Entstehen und Vergehen von Arten in der Evolution (HÖLDER), Rückbildung der Augen bei Höhlenfischen (PETERS), Umfang des Aussetzens von Fasan und Hase zu Jagdzwecken, die zuvor gezüchtet wurden (SCHNEIDER) oder die Bedeutung von Streuobstwiesen (LEMB).

In der Mehrzahl sind die Beiträge sachgerecht und beleuchten wichtige Teilfragen. Folgendes Fazit drängt sich bei unvoreingenommenem Lesen auf: Die Zucht in Gefangenschaft von bedrohten Wirbeltierarten ist nur ein Notbehelf, der mit zahlreichen Risiken verknüpft ist, die vielfach unterschätzt wurden. Trotzdem muß der rigorosen Folgerung der Herausgeber widersprochen werden, Gefangenschaftszucht als Mittel der Artenerhaltung sei generell abzulehnen. Dies Urteil folgt aus der Einschätzung, Arten seien schon nach wenigen Generationen Gefangenschaftshaltung zerstört und nicht mehr überlebensfähig. Dem liegen zugrunde ein zum Teil mißverstandener Artbegriff, die nur bedingt zulässige Übertragung von Befunden an Haustieren auf in Gefangenschaft gehaltene Wildtiere und der Wunsch, den Artenschutz durch die Erhaltung natürlicher Vorkommen zu betonen und zu unterstützen. So sehr dem Ziel der Erhaltung der Tier- und Pflanzenarten in ihrer natürlichen Umwelt zuzustimmen ist: Die Rolle der Tierhaltung wird zu einseitig negativ dargestellt. Ohne Gefangenschaftshaltung gäbe es heute z. B. keinen Milu und keinen Wisent mehr.

Von der Polemik abgesehen, eine lesenswerte Sammlung überwiegend fundierter Grundlagen zur Diskussion des Einflusses der Gefangenschaftshaltung auf Säugetiere und Vögel.

J. NIETHAMMER, Bonn

SMIT, C. J.; WIJNGAARDEN, A. VAN: **Threatened Mammals in Europe.** Hrsg.: European Committee for the Conservation of Nature and Natural Resources – Council of Europe. Ergänzungsband zum Handbuch der Säugetiere Europas (Hrsg.: J. NIETHAMMER und F. KRAPP). Wiesbaden: Akademische Verlagsgesellschaft 1981. 259 S., 43 Verbreitungskarten. DM 84,–. ISBN 3-400-00438-3

Dieser Ergänzungsband zum Handbuch der Säugetiere Europas befaßt sich mit 36 ausgewählten, in unterschiedlichem Maße bedrohten europäischen Säugerarten. Es handelt sich zumeist um Großsäuger, doch finden neben einigen Rodentiern auch der Pyrenäen-Desman und die Großhufeisennase Erwähnung. In die der Bearbeitung zu Grunde liegenden Gebiete sind nordafrikanische Länder (vor allem Tunesien, Algerien und Marocco) ebenso mit einbezogen wie Ostgrönland, Spitzbergen, Anatolien und die europäischen Teile der UdSSR. Leitlinien bei der Auswahl der Formen waren u. a. Art und Umfang der Bedrohung und das Bestreben, bedrohte Arten aus möglichst allen Lebensräumen zu erfassen.

Die Einzeldarstellung der bedrohten Arten erfolgt nach einem durchgehenden Schema. Auf eine vorangestellte Verbreitungskarte folgen eine kurze morphologische Charakterisierung jeder Art, Angaben zur Biologie, zur weltweiten, zur ehemaligen und jetzigen Verbreitung, insbesondere letztere sind zumeist recht detailliert. Informationen über die Gründe des Rückganges, bereits durchgeführte Schutzmaßnahmen und neu vorgeschlagene beschließen den jeweiligen einer Art

gewidmeten Abschnitt. Eine tabellarische Erfassung der europäischen Säuger gibt, gesondert für die einzelnen Länder, Auskunft über den jeweiligen Bedrohungsstatus und erforderliche Schutzmaßnahmen. Eine nach Arten aufgeführte Literaturliste bildet den Abschluß dieses Buches, das auch bei spät erfolgender Rezension für eine rasche Orientierung über einzelne Fragen des Naturschutzes der behandelten Formen für das Bücherregal jedes Mammalogen empfohlen werden muß.

H. Schliemann, Hamburg

Gittleman, J. L. (ed.): **Carnivore Behavior, Ecology, and Evolution.** New York: Cornell University Press 1989. 620 pp., £ 17.95. ISBN 0-412-34360-6

This book contains 19 articles written by 30 authors and is focussed on several aspects of carnivore biology. Following a general introduction to the Carnivora by J. F. Eisenberg, the contributions are grouped in three parts, namely, behavior, ecology and evolution. Each part has its own introductory remarks given by the editor. Concerning the topics of the articles this volume covers a broad area of research results. In addition to general overviews attributed to certain biological phenomena, also rather specialized contributions on species or groups of species can be found. The following fields of research are dealt with: behavior (7 articles): acoustic and olfactory communication; behavioral development; behavioral ecology of hyaenids and canids; modes of solitary living and group living; ecology (6 articles): feeding ecology of Giant panda and Asiatic black bear; adaptations for aquatic living; ecological constraints on predation by felids; consequences of small size in mustelids; basal metabolism and food habits; reproductive output; evolution (6 articles): morphological constraints on locomotion; dentition and diet; physiology of delayed implantation; molecular and morphological approaches to phylogeny; fossil record. A classification of recent species of Carnivora is given in an appendix.

Editor and contributors do not intend to replace the well known and excellent book on carnivores written by R. F. Ewer. Instead, they aim at an enlargement and modernisation of specific knowledge. This volume can serve as a current synthesis of biological aspects in carnivores and as a good resource for special future research.

D. Kruska, Kiel

Anderson, P. K.: **Dispersal in rodents: A resident fitness hypothesis.** The American Society of Mammalogists. Special Publication No. 9. Bezug durch: H. Duane Smith, Dept. Zoology, Brigham Young University, Provo, UT 84602, U.S.A. 141 S., 4 Tab., 2 Abb. ISBN 0-935868-40-2

Bisher herrschte die Ansicht vor, daß Nager ihren Geburtsort zum Teil deshalb verlassen, weil sie dadurch an Fitness gewinnen. Die Neigung einiger Tiere zum Abwandern ist mit einem genetischen Polymorphismus innerhalb der Population verknüpft. Sie wird mit günstigeren Ressourcen in einer neuen Umgebung, besseren Möglichkeiten der Fortpflanzung, Vermeidung von Inzucht und anderen Vorteilen belohnt. Dieser "Emigration fitness hypothesis (EFH)" stellt der Autor seine "Resident fitness hypothesis (RFH)" gegenüber. Danach ist es wesentlich vorteilhafter, am Geburtsort zu bleiben. Einen Fitness-Gewinn erzielen diejenigen Tiere, die sich in vertrauter Umgebung gegenüber Artgenossen behaupten und bleiben. Jungtiere und Unterlegene wandern ab, weil sie dazu von den dominanten Individuen gezwungen werden, nicht, weil sie eine besondere genetische Disposition dazu veranlaßt.

Der Autor bespricht Befunde aus etwa 700 Arbeiten, um zu zeigen, daß die bekannten Daten überwiegend mit der RFH in Einklang stehen, oft aber zu EFH in Widerspruch geraten. An experimentellen Resultaten zu diesem Thema hat sich inzwischen eine kaum noch überschaubare Fülle vor allem in Nordamerika angesammelt, die aber oft für eine Entscheidung der vorgelegten Fragen noch nicht ausreichen. Dies beruht besonders auf der Schwierigkeit, Wandernde nach Herkunft, Ziel, sozialem Status, Zustand und späterem Ansiedlungserfolg zu beurteilen. Für Ortstreue wäre es wichtig, nahe Verwandte so weit wie möglich zu dulden und ihren Verbleib zu fördern. Dazu müssen sie aber Verwandte und Nichtverwandte unterscheiden können. Wie hoch ist das Ausmaß von Inzucht, welche Vor- oder Nachteile hat sie in der Realität?

Bei näherem Hinsehen ist das Thema höchst kompliziert und führt zu zahlreichen Fragen über die Demographie, das Verhalten und die Populationsgenetik. Es ist der Verdienst des vorliegenden Buches, diese Fragen zu formulieren und für sie Antworten zu suchen. Die Fakten sind oft widersprüchlich, und nicht selten weicht die Bewertung von der in der Quelle ab. Die Beweislage erscheint am Ende lückenhaft, die Gewichte neigen sich aber zugunsten der RFH. Das Buch liest sich mühselig, weil es für das Auge wenig gegliedert und sehr theoretisch ist. Es wimmelt von Zitaten, die allenfalls Bruchstücke aus dem Inhalt der zugrunde liegenden Arbeiten wiedergeben.

Auf der anderen Seite ist es hilfreich, mit diesem Buch eine Einführung in die Vielfalt der Arbeiten

zur Demographie der Nagetiere zu erhalten, die einheitlich geordnet sind. Wer übersieht schon, wo etwas über die Qualität des neuen Habitats von Emigranten gegenüber dem Geburtsort gesagt wird, vom Ansiedlungs- und Fortpflanzungserfolg am neuen Ort? Welche Belege gibt es für Panmixie oder Aufsplitterung in genetisch unterschiedliche Kleingruppen bei Nagern? Für die Orientierung in der englischsprachigen Literatur ist das Buch eine Fundgrube. Die ohnehin wenig zahlreichen Beiträge zum Thema aus Frankreich oder Deutschland fehlen dagegen fast völlig. Trotzdem: Vor allem denjenigen, die sich für die Soziobiologie bei Mäusen, Zieseln und Murmeltieren interessieren oder gar zu diesem Gebiet Untersuchungen vorhaben, wird das Buch eine unschätzbare Hilfe sein.

J. Niethammer, Bonn

Niethammer, J.; Krapp, F. (Hrsg.): **Handbuch der Säugetiere Europas.** Bd. 2/II: Paarhufer – Artiodactyla. Wiesbaden: Aula-Verlag 1986. 463 S., 119 Abb., 120 Tab. DM 328,–. ISBN 3-89104-026-1

In Band 2/II des Handbuches der Säugetiere Europas werden die Paarhufer-Familien Suidae, Cervidae und Bovidae abgehandelt. Als Autoren dieses Bandes zeichnen neben den Herausgebern verantwortlich H. Bohlken, W. Bützler, M. Delibes, H. Engländer, G. Heidemann, W. Herre, E. von Lehmann, B. Nievergelt, K. F. Nygren, Z. Pucek, E. Pulliainen, M. Röhrs, H. Sägesser, S. Sulkava und R. Zingg.

Die bewährte Gliederung wurde auch für diesen Band beibehalten und trägt sehr zu seiner Übersichtlichkeit bei. Auf einen kurzen Einführungsteil (im wesentlichen Erläuterungen zu Körper- und Schädelmaßen) folgt der Hauptteil, in dem die Ordnung Artiodactyla und dann jeweils folgend die Familien mit einer Diagnose, Angaben zur Verbreitung, zur Morphologie und Systematik sowie mit einem Bestimmungsschlüssel vorgestellt werden. Naturgemäß nehmen die Darstellungen der einzelnen Arten den größten Teil des Bandumfanges in Anspruch; hierbei finden auch die nach Europa eingeführten Formen Berücksichtigung. Innerhalb der den Arten gewidmeten Abschnitte findet der Leser nach einer einleitenden Diagnose und Beschreibung Informationen u. a. zur Verbreitung, zur Merkmalsvariation, zu paläontologischen Befunden, zur Ökologie und dem Verhalten; instruktive Abbildungen (Zeichnungen zu Einzelheiten des Körperbaues, Verbreitungskarten, Grafiken) und zahlreiche Tabellen insbesondere zur Dokumentation der Variabilität einzelner Maße und Merkmale ergänzen den Text in einprägsamer Weise. Zu jeder Artdarstellung gehört ein gesondertes Literaturverzeichnis. Werke umfänglicherer Bedeutung sind in einem allgemeinen Schriftenverzeichnis am Ende des Bandes zusammengefaßt. Diesem folgt noch ein Register der wissenschaftlichen und Trivialnamen der behandelten Arten sowie ein Adressenregister der Autoren dieses Bandes.

Herausgebern, Autoren und dem Verlag ist für die sowohl in wissenschaftlicher Hinsicht als auch ausstattungsmäßig hervorragende Zusammenstellung unseres Wissens über diese Großsäuger Europas zu danken. Sie wird nicht nur Wissenslücken interessierter Leser füllen, sondern gerade auch dieser Band wird für viele Fragen der wissenschaftlichen Arbeit und des Naturschutzes eine unverzichtbare Informationsquelle darstellen.

H. Schliemann, Hamburg

Jürgens, K. D.: **Allometrie als Konzept des Interspeziesvergleiches von physiologischen Größen.** Schriftenreihe Versuchstierkunde 15. Berlin und Hamburg: Paul Parey 1989. 136 S., 29 Abb., 4 Tab. DM 38,–. ISBN 3-489-76518-4

Die Allometrie beschreibt die Abhängigkeit struktureller und funktioneller Variablen von der Körpergröße eines Lebewesens. Sie hat große praktische Bedeutung, z. B. bei der Übertragung von Versuchsergebnissen, die an kleinen Labortieren gewonnen wurden, etwa auf den menschlichen Organismus. Hier werden die Grundlagen und Grenzen der Allometrie an eindrucksvollen Beispielen dargestellt und kritisch bewertet. Im ersten Teil erfolgt die Begriffsentwicklung der Allometrie. Gezeigt wird sodann die Möglichkeit einer mathematischen Beschreibung der Zusammenhänge (Potenzfunktion als Ähnlichkeitskriterium). Als Beispiele dienen die Stammquerschnitte und die Stabilität von Bäumen, die kortikale Dicke und die Gehirnmasse sowie der Ruheumsatz bei Normothermie und Torpor. Im zweiten Teil werden statistische Methoden vorgestellt, die zur Ermittlung allometrischer Potenzfunktionen geeignet sind (Korrelationskoeffizient als Gütekriterium). Im dritten Teil werden schließlich drei physiologische Variablen (Ruheenergieumsatz, Sauerstoffhalbsättigungsdruck des Blutes, maximale Lebensdauer und Ruheenergieumsatz als Funktionen der Körpermasse) zur Analyse empirischer und kausaler Ähnlichkeitskriterien benützt. Für alle, die sich mit diesen Problemen befassen müssen, wurde hier eine wichtige Grundlagenarbeit geleistet.

E. Kulzer, Tübingen

Deutsche Gesellschaft für Säugetierkunde: Referate, Vorträge und Posterdemonstrationen der 64. Hauptversammlung 1990

Ein Hauptziel der Deutschen Gesellschaft für Säugetierkunde ist, auf ihren Jahrestagungen über Säugetiere arbeitende Wissenschaftler verschiedenster Fachrichtungen zusammenzuführen, den Gedanken- und Erfahrungsaustausch anzuregen, um so Erkenntnisse aus den einzelnen Forschungsgebieten zu integrieren. Die Kurzfassungen der Vorträge und Posterdemonstrationen von der 64. Hauptversammlung, die in diesem Jahr in Osnabrück stattfand, liegen wiederum als Sonderheft der »Zeitschrift für Säugetierkunde« vor. Die Tagung war durch drei Themenschwerpunkte gekennzeichnet, die ökologische, ontogenetische und ernährungsphysiologische Fragestellungen behandeln. Zusätzlich wurde eine große Zahl freier Beiträge angeboten. Diese auch in der Vergangenheit geübte Art der Themendarbietung soll die Breite der aktuellen Säugetierforschung widerspiegeln. Die säugetierbiologische Arbeit war in der Ethologie von Anfang an ein Forschungsschwerpunkt. Im Vordergrund stehen Projekte mit öko-ethologischer Fragestellung. Da sich dafür stenöke Säugetiere besonders eignen, werden bevorzugt silvicole und ripicole Arten in Gehegen und im Freiland beobachtet. Eine intensive Freilandarbeit, auch auf Exkursionen, förderte die Untersuchung von Kleinsäugetiergemeinschaften.
Die Kurzfassungen der Vorträge und Posterdemonstrationen der Deutschen Gesellschaft für Säugetierkunde sind ab der 58. Hauptversammlung 1984 in Göttingen noch lieferbar. Zu beziehen durch jede Buchhandlung. ★ **Deutsche Gesellschaft für Säugetierkunde, 64. Hauptversammlung in Osnabrück, 23. bis 27. September 1990.** Kurzfassungen der Vorträge und Posterdemonstrationen. Herausgegeben von Dr. Christel Schmidt, Bonn, und Prof. Dr. Rüdiger Schröpfer, Osnabrück. 1990. 55 Seiten. Kartoniert 24,– DM
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Z. Säugetierkunde 55 (1990) 6, 361–432

Mit zwei Beilagen des Verlages Paul Parey

Willy Mosimann / Toni Kohler

Zytologie, Histologie und mikroskopische Anatomie der Haussäugetiere

Herausgegeben von Prof. Dr. Willy Mosimann, ehem. Direktor des Instituts für Tieranatomie der Universität Bern, und Prof. Dr. Toni Kohler, Institut für Tieranatomie der Universität Bern.

Unter Mitarbeit von Dr. Achmed Abou-Elmagd, Prof. Dr. Armin E. Friess, Prof. Dr. Hermann Goller, PD Dr. Dr. Herbert Hees, Prof. Dr. Gerhard Hummel, PD Dr. Clemens Knospe, Prof. Dr. Toni Kohler, Prof. Dr. Erich Künzel, Prof. Dr. Rudolf Leiser, Prof. Dr. Willy Mosimann, Prof. Dr. Jürgen Schlüns, Prof. Dr. Dr. Fred Sinowatz, PD Dr. Peter Tschudi, und Prof. Dr. Dr. Karl-Heinz Wrobel.

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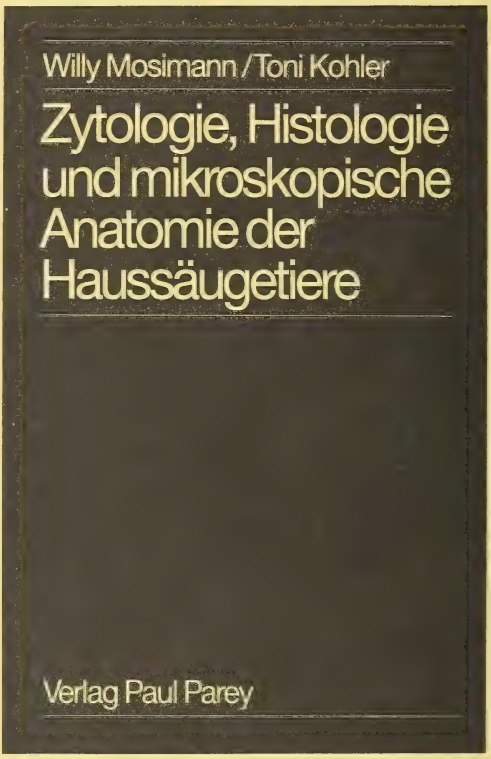

Mit Beiträgen von 14 Autoren vermittelt dieses Werk den Studierenden der Tiermedizin die heutigen, grundlegenden Kenntnisse über die Mikrostruktur des Körpers der Haussäugetiere. In didaktisch einprägsamer und konzentrierter Form bietet es mikromorphologische Informationen zur Zytologie, Histologie und mikroskopischen Anatomie, wobei besonders diejenigen biologischen Zusammenhänge verdeutlicht werden, die zu einer Gesamtschau, zu einem besseren Verständnis und zu einer vertieften medizinischen Allgemeinbildung beitragen. Darüber hinaus werden Hinweise auch zu fachübergreifenden Wissensgebieten wie Makroanatomie, Embryologie, Physiologie, Biochemie und Klinik gegeben.

Aus dem Inhalt: Zytologie – Epithelgewebe – Binde- und Stützgewebe – Muskelgewebe – Nervengewebe – Das kardiovaskuläre System – Blut und Knochenmark – Das Immunsystem und die Organe der Abwehr – Atmungsorgane – Verdauungsorgane – Endokrine Zellen und Organe – Harnorgane – Männliche Geschlechtsorgane – Weibliche Geschlechtsorgane – Bewegungsapparat – Haut – Milchdrüse – Nervensystem – Auge – Ohr – Literatur – Sachverzeichnis.

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