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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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Notes on echolocation calls, food and roosting behaviour of the Old World Sucker-footed bat *Myzopoda aurita* (Chiroptera, Myzopodidae)

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Abstract

In 1992 one individual of the rare species *Myzopoda aurita* was captured near Fort Dauphin in southeastern Madagascar. Pellet analysis revealed that the animal had fed on Microlepidoptera before capture. The bat was observed in a flight cage. It clinged head upright to the lower leaf surface of a traveller's palm *Ravenala madagascariensis*, using its stiff tail as a prop. While readily flying in the cage, the specimen emitted FM echolocation calls which were recorded and analysed for the first time in this species: They are characterized by two to four distinct pulse elements of increased amplitude. The second of maximal four harmonics was always the strongest component. During the remarkably long call of up to 23 ms, the frequency of the second harmonic decreased from 42 to 24 kHz with a shallow sweep at the beginning and a steep sweep at its end. Most calls were emitted in pairs. Possible functions of this call structure are discussed.

Introduction

The "old world sucker-footed bat" *Myzopoda aurita* (Milne-Edward and Grandidier, 1878) is the only representative of the monotypic family Myzopodidae, endemic to Madagascar. This species shows remarkable morphological specializations like sucking disks on thumbs and feet, long ears with unique mushroom-shaped processes, elongated palate and projecting tail, all indicating a long isolated evolution (reviewed by Schliemann and Maas 1978). *M. aurita* seems to be very rare: Schliemann and Maas (1978) estimated less than 15 records of its existence, most dating before 1900. Since then, a few specimens have been recorded during expeditions by Cambridge and Aberdeen Universities and the Smithsonian Institute (Safford and Duckworth 1990 and unpublished data). Due its rarity, there is still no information about the biology of this bat. Only the use of the sucking disks in *M. aurita* is indicated by one specimen collected by Hoogstral in 1947 (unpublished data) from smooth leaves of the traveller's palm *Ravenala madagascariensis* (Musaceae), which served as a roost (Schliemann and Maas 1978). However, no further details concerning roosting behaviour have been reported.

Although echolocation calls of representatives of nearly all bat families have already been recorded (Sales and Pye 1974; Novick 1977), calls of *M. aurita* are still unknown. The same applies to nutrition. Because the dentition is of the normal insectivorous type (Thomas 1904), *M. aurita* has been assumed to feed on insects, but this has not yet been confirmed.

During an expedition in 1992, we captured one individual and collected some data about echolocation calls, food, and roosting behaviour.

Material and methods

On August 13, 1992 a female *M. aurita* was captured with mist nets at Antanifotsy, 8 km north of Fort Dauphin in southeastern Madagascar. The nets were installed at the border of a rice field near the village at the base of the coastal mountains. In the surroundings, remains of primary forest were limited to inaccessible ravines and the upper regions of mountain slopes, while the lower areas were cleared. Wide marshlands extended between the village and the coast. Traveller's palms were common in primary and secondary forests. In the following weeks no other specimen was found, although up to 6 mist nets have been set up almost every night in the surroundings and several palms have been checked for roosting *M. aurita*.

The bat was trapped at a height of 1.5 meters above ground at 18.55 h local time about one hour after sunset. The following measurements were taken: forearm length 48 mm, head-body length 62 mm, tail 48 mm, ear 33 mm. The nipples of the female were well developed. After capture it was kept in a bag for a few hours to collect fecal pellets and then in a cage of two meters side length for two nights. For roosting, *Ravenala* leaves were installed in the cage and the bat had the opportunity to feed on free-flying and hand-held mosquitoes, Microlepidoptera, and larger moths.

Echolocation calls of the flying bat were recorded in the cage with a QMC PSM3 microphone on a modified Panasonic video recorder. For evaluation, calls were recorded with a RACAL store DS tape recorder and after appropriate slow down (mostly 16×) analysed with a MOSIP-FFT-processor (Fa. MEDAV, Erlangen, Germany). Spectrograms presented in the present study are copies of the originals in which echos have been removed.

40 fecal pellets were collected after capture. They were stored dry and later analysed in ethanol (70%).

Results

Behaviour and food

Caged, the bat spontaneously used leaves of the traveller's palm *Ravenala madagascariensis* for roosting. The bat preferred to cling head upright to the surface of the leaves with help of all four sucking disks, using the stiff, projecting tail as a prop (Fig. 1). It even climbed on the lower surface with its dorsum downwards, if the leaf was bended horizontally by the bat's weight. After sunset, it performed a highly manoeverable flight but was never observed to pursue free-flying insects, nor did we succeed to feed it.

The 40 analysed fecal pellets contained only remnants of Microlepidoptera, identified by the dimensions and structure, especially of head, leg and wing fragments, with scale insertions and great quantity of scales. A more specific determination was not possible.

Echolocation calls

While flying in the cage, the bat emitted complex frequency modulated (FM) echolocation calls remarkable for each being composed of two to four distinct elements of increased amplitude and long call durations. Due to different numbers of elements and the presence of up to four harmonics, the call structure was highly variable.

Most calls (65%, n = 85) were composed of four elements (Fig. 2 a, b): The amplitudes of the four elements varied: The fourth element showed the highest amplitude in 81% and the fourth and second at nearly same levels in 13% of the calls. While the fourth element was always loud, high amplitude levels of the other elements were observed more rarely.

Frequencies decreased from the first to fourth element. Thus, the elements are characterized by different frequency ranges and maximum amplitudes at specific frequencies

Fig. 1. *Myzopoda aurita* resting on the lower surface of the leaf of a traveller's palm *Ravenala madagascariensis* in captivity.

(Tab. 1). In each element serveral harmonics could be present and the second harmonic was always the strongest component. Considering all elements, the second harmonic decreased from 42 to 24 kHz with a shallow FM sweep (about 0.6–0.9 kHz/ms) during the first three elements and a steep FM sweep (about 2 kHz/ms) during the fourth element. Due to low amplitude components between the peaks, a pulsed sweep resulted with four amplitude peaks in the second harmonic (Fig. 2 a, b). The first harmonic was much weaker and was only observed in some elements of about half of the calls (Fig. 2 a, c, Fig. 3). According to its low amplitude, it was often limited to amplitude peaks of elements. A third harmonic was found in the last element of only seven calls (Fig. 2 b) and two times in the second, while a fourth harmonic was present in nearly half of the calls in the last and more rarely in the second and third elements (Fig. 2 b). Although the frequency range above 80 kHz has been examined, a fourth harmonic was never observed in the first element.

The remainder of the analysed calls was composed of only two (9%) or three (26%) elements. In comparison to calls with four elements, in these calls the first and third elements could be absent (e. g. in the second and fourth call in Fig. 3) or elements were fused as indicated by frequency spectra. The call presented in figure 2 c, for example, shows fused second and third and barely separated first and fourth elements resulting in continuous sweeps from 20 to 18 kHz in the first harmonic and from 38 to 24 kHz in the second one. In addition, a fourth harmonic is visible in the last element.

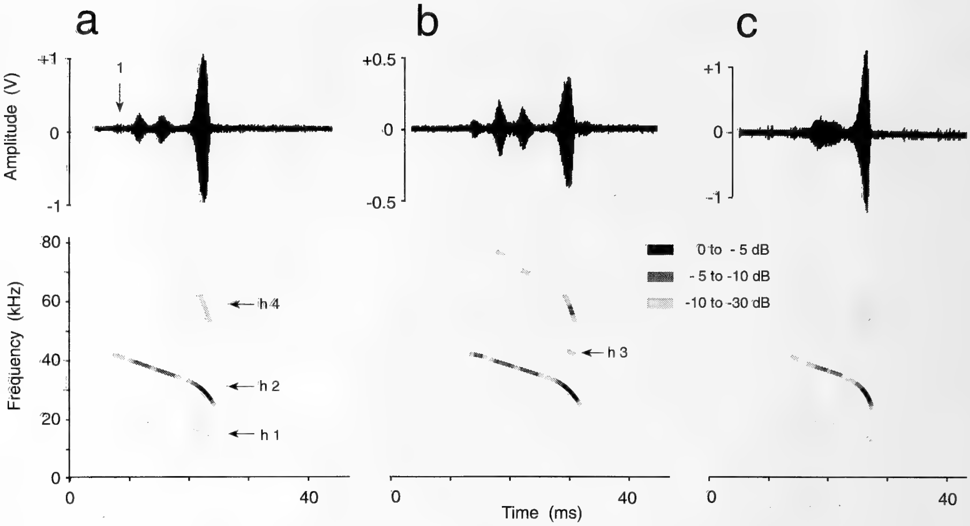

Fig. 2. Single echolocation calls of *Myzopoda aurita*. Relative sound pressure levels from 0 (= loudest) to —30 dB below maximum are shown. h1–h4: first to fourth harmonic. a: Call composed of four elements (arrow 1: hardly visible first element), with pronounced second harmonic. In the fourth element the first and fourth harmonics are visible; b: Call composed of four elements. In addition to a pronounced second harmonic third and fourth harmonics are visible. A first harmonic is not detectable; c: Call composed of three elements resulting from a call with four elements by fusion of second and third elements.

An impression of the high variability resulting from emission of different numbers of elements and different amplitudes of harmonics is given in figure 3, showing a call sequence of four calls presented in two pairs. Four elements are present in the first and third, three in the fourth and two in the second call. There are also differences concerning the presence of the first and fourth harmonics.

Durations of 85 analysed calls varied between 12 and 23 ms (Fig. 4). While durations of calls composed of two or three elements did not differ significantly ($p > 0.05$; median-test), durations of calls with four elements were shifted to longer times ($p < 0.01$; median-test). Call intervals lasted between 11 and 108 ms and showed a bimodal distribution (Fig. 5): during most of the recording time calls were emitted in pairs with only short intervals between the two calls of one pair (25 ± 5 ms, $n = 32$) and longer intervals between different pairs (69 ± 10 ms, $n = 28$).

Table 1. Peak frequencies and frequency ranges of the four elements and four harmonics in 85 analysed calls of *Myzopoda aurita*. In some elements the third and fourth harmonics were visible as amplitude peaks. Therefore, only peak frequencies are presented. *: not visible in spectrograms of analysed calls.

	elements				
	1	2	3	4	
harmonics	peak frequencies (kHz)				frequency range (kHz)
1	20	19	18	14	14-21
2	41	38	35	29	24-42
3	*	57	*	43	(43/57)
4	*	76	70	58	50-64 (70/76)

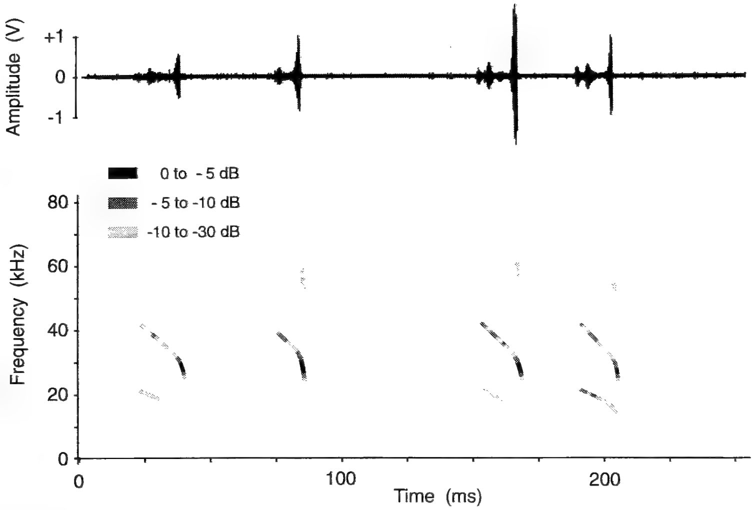

Fig. 3. Continuous call sequence consisting of four calls emitted in two pairs. Note the high variability concerning numbers of elements in calls and presence of first and fourth harmonics.

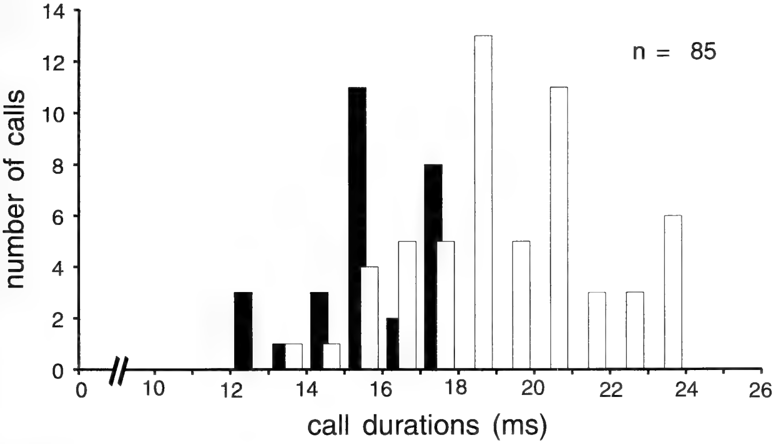

Fig. 4. Distribution of call durations in *Myzopoda aurita*. Calls composed of four elements (white) show longer durations than calls composed of two or three elements (black).

Discussion

Distribution, behaviour and food

Previous records of *Myzopoda aurita* indicate that the species is distributed mainly along the east coast of Madagascar. The locality of our record fits with this distributional pattern, for several specimens have already been captured in the northern vicinity of Fort Dauphin (Schliemann and Maas 1978 and unpublished records of Smithsonian Institute in 1989).

Roosting behaviour of *M. aurita* is indicated by one specimen collected from leaves of the traveller's palm *Ravenala madagascariensis*, but no further details have been reported

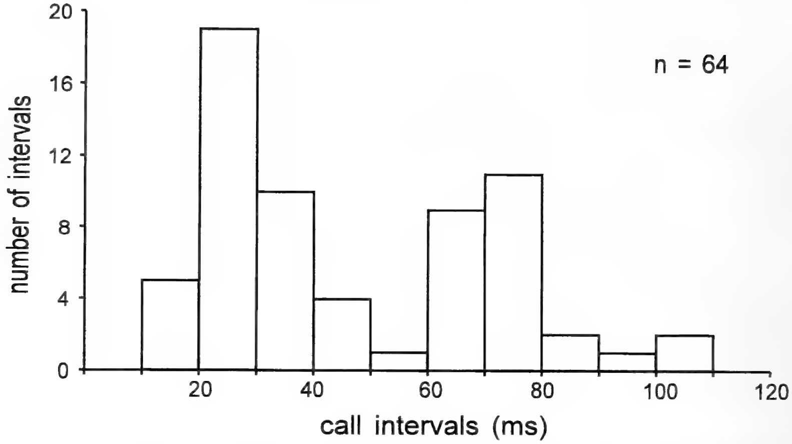

Fig. 5. Distribution of call intervals in *Myzopoda aurita*. Calls were mostly emitted in pairs causing a bimodal distribution.

(SCHLIEMANN and MAAS 1978). *Ravenala* is abundant and is possibly used as a roost in the surroundings of the capture site, but other plants providing large smooth leaves such as Araceae are also common. We observed that caged *M. aurita* uses its adhesive disks to cling to leaves of *Ravenala* and that adhesion is sufficient to carry the entire weight of the bat. A head upright roosting position as shown by the presently described individual has also been reported for the New World sucker-footed bats (Thyropteridae, NOWAK 1991). The stiff, projecting tail of *M. aurita* is used as a prop comparable to the use of the tail in woodpeckers.

The examined pellets of the captured bat contained fragments of Microlepidoptera. This confirms earlier assumptions that this species feeds on insects deduced from dental characters (THOMAS 1904). The occurrence of Microlepidoptera in the diet may be an indication of specialization or a mere result of accidental abundancy of this type of prey at that time. As most sound energy of the calls of *M. aurita* lies within the frequency range known to be conspicuous to many tympanate moths (FENTON and FULLARD 1979), the feeding on Microlepidoptera may also be explainable with the absence of tympana in most microlepidopteran families (exept e. g. Pyralidae).

Echolocation calls

The echolocation calls recorded of *M. aurita* flying in a cage show some pecularities: They are complex FM echolocation calls remarkable for long durations and for composition of two to four elements. Each element contains several harmonics and the second harmonic is always the strongest component. Frequencies decrease in the course of the call resulting in an pulsed sweep, which is shallow during the first three elements and steep during the last, mostly loudest element.

Call durations can be influenced by recording conditions: In the field, even longer durations can possibly be expected considering that in captivity a reduction of call durations has been reported for several species, probably as an adaptation to short distances (e. g. GRIFFIN 1958; NOVICK 1977; KALKO and SCHNITZLER 1989). The pulsed pattern of the calls cannot be attributed to frequency characteristics of the recording equipment: In calls of other bat species with similar frequency spectra that have been recorded with the same equipment under the same circumstances, no such effect is visible.

The long, shallow sweep and the short, steep sweep at the end of the call are appropriate for the detection of different characteristics of the target according to the optimal filter theory (Glaser 1974):

Long, shallow sweeps are interpreted to function as long-distance probes (Neuweiler 1983) and to be utilized for recognition of fluttering targets (Schnitzler 1987). A long-distance probe can be achieved by packing sound energy in a shallow sweep, if it lies within the critical band (Neuweiler 1983). Considering call durations and average frequency decrease, the calls of *M. aurita* are comparable to those of Molossidae (estimated from data presented by Fenton and Bell 1981). Molossids are assumed candidates for detection of fluttering targets. In this family an increased probability of target detection has been demonstrated, when amplitude glints originating from the moving insect are present in the echos (Schnitzler 1987). While the shallow sweep in calls of *M. aurita* can possibly be used for detection of insect wing beats, their high-amplitude modulated calls seem to be rather disadvantageous for the detection of amplitude glints.

Short, steep sweeps as emitted at the end of the call show a broader bandwidth and are therefore favourable for measuring the distance to discrete targets (Glaser 1974). The last element may also be used for target detection, because it always combines high amplitudes with low frequencies, which are less affected by atmospheric attenuation than the higher frequencies at the beginning of the call.

Complex calls composed of two elements have already been reported from other bat species. In contrast to *M. aurita*, these calls often show two amplitude maxima at the same frequency, and pulsation is caused by changes in energy distribution between different harmonics (Sales and Pye 1974). A pulsed structure as emitted by *M. aurita* has hitherto not been described. Therefore, only some hypotheses about possible functions can be presented:

The pulsations could offer time markers to measure the distances to targets, a function that is considered for the slopes of intensity envelopes (Neuweiler 1983).

Assuming a limitation of total energy disposable for one call, pulsed calls might be emitted to increase the amplitudes of specific frequencies by temporal concentration of sound energy. Thus, the distances from which echos can be recognized are increased for specific frequencies. In addition, the entire echo might be more conspicuous due to the characteristic temporal pattern of a pulsed call.

The use of pulsed calls to measure flight speeds of insects by comparing the echo delays at the distinct amplitude peaks of one call is rather improbable: During one call, movements of flying insects are short and the resulting echo delays are often shorter than minimal time differences detected by other bat species (Simmons 1973).

The pulsation of calls could also enable the bat to adapt its calls to different conditions by pronouncing different elements and therefore portions of different sweep ratios and different frequencies, as indicated by the variability of the relative amplitudes of the distinct elements. For a detailed interpretation of the function of this pulsed call structure and the echolocation abilities of *M. aurita* echolocation calls have to be recorded in the field and details about foraging behaviour should be observed.

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Zusammenfassung

Echoortungssignale, Nahrung und Gebrauch der Haftorgane von Myzopoda aurita (Chiroptera, Myzopodidae)

Ein Exemplar der seltenen Art *Myzopoda aurita* wurde 1992 bei Fort Dauphin im Südosten Madagaskars gefangen. Kotprobenanalysen ergaben, daß das Tier vor dem Fang Microlepidopteren gefressen hatte, und belegen damit erstmals die Insektivorie der Art. In einem Flugkäfig wurde beobachtet, daß sich *M. aurita* zum Schlafen mit nach oben gerichtetem Kopf an Blattunterseiten von *Ravenala madagascariensis* mit den Haftscheiben festsaugt, wobei der Schwanz als Stütze dient. Während das Tier wendig im Käfig flog, wurden erstmals Echoortungssignale der Art aufgezeichnet: Die Rufe weisen auffällige, regelmäßige Amplitudenmodulationen auf, die die Rufe in zwei bis vier Elemente gliedern. Von maximal vier sichtbaren Harmonischen ist die zweite am deutlichsten: Während der maximal 23 ms langen Rufe sinken die Frequenzen der zweiten Harmonischen von 42 bis 24 kHz. Die Rate der Frequenzmodulation ist gering, nur am Rufende tritt ein breitbandiger FM-Teil auf. Die Rufe wurden meist paarweise abgegeben. Die Signalstruktur wird im Hinblick auf mögliche Ortungsleistungen diskutiert.

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Diet of badgers (*Meles meles*) in central Switzerland: an analysis of stomach contents

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Abstract

We investigated the contents of 217 badger stomachs from central Switzerland. Overall, faunal material constituted 55%, and vegetal material 45%, of the diet. Earthworms had a higher frequency of occurrence, were more often the only prey found in a stomach, and occurred in more months of the year, than any other food type; but they were not usually eaten in large volumes. Voles, insects and maize were eaten during most of the year but never in large volumes, while wasps, cherries, plums and oats were eaten seasonally and in large volumes. Total food intake was greatest in autumn, while the diversity of foods consumed was greatest in summer. No particular type of food was preferentially consumed at any particular time of night, nor was there a significant correlation between the number of different foods consumed and the total volume of stomach contents. Composition of the diet did not differ significantly with age, sex or degree of tooth wear of the donor animals; but total volume of stomach contents, tooth wear and age were significantly correlated with one another. Faunal foods in general, and earthworms in particular, can be regarded as staple components of the diet of badgers in this part of Switzerland. However, the most conspicuous feature of badger diet is the diversity of foods consumed, not only by the population as a whole but also by individual animals during only a few hours of foraging activity.

Introduction

Many studies of badger (*Meles meles*) diet have been undertaken, in countries including the U.K., France, Spain, Sweden, Denmark, Switzerland, Italy, Ireland, the Netherlands and the former Soviet Union (for references see Vink 1993; Lüps and Wandeler 1993). It is clear from these studies that the species consumes a wide variety of foods including both faunal and vegetal material, causing most investigators to describe badgers as "omnivorous", "generalist" or "opportunistic" foragers (see review by Roper 1994). However, there is a tendency for badger diet to be dominated by earthworms in northwestern and central Europe and by other foods, especially fruits and insects, in Mediterranean regions (Pigozzi 1987). This has led to the suggestion that badgers are in fact food specialists, with any one population preferentially selecting one or at most a few particular food types from the range that is potentially available in its particular habitat (Kruuk 1986,1989; Kruuk and Parish 1981).

The "food specialist" hypothesis can be questioned on the grounds that some studies show badgers to have a broad diet, even within a single study area (Roper 1994). A more fundamental difficulty, however, arises from the fact that almost all studies of badger diet so far published have been based on the analysis of faecal remains. Such data are likely to be incomplete, because of the difficulty of estimating the volume of food eaten on the basis of whatever fragments remain in the faeces: for example, faeces analysis tends to underestimate the importance of mammalian and avian material in the diet, and to overestimate the importance of small, frequently consumed items such as insects (e. g., Liberg 1982; Reynolds and Aebischer 1991). The problem of converting faecal remains to an estimate of volume of food consumed is particularly acute for soft-bodied invertebrates such as earthworms, whose size and number have to be deduced from fragments such as chaetae or gizzard rings (Bradbury 1977; Wroot 1985). Furthermore, faeces analysis can at best give information about the relative, as opposed to the absolute, amounts of different foods ingested (Roper 1994).

Data from stomach contents constitute a superior source of information about diet because they are more accurate and yield information about the absolute amounts of different foods eaten. Furthermore, by comparing the contents of stomachs from animals killed at different times of night, it is possible to extract information about the way in which consumption of different foods proceeds over the course of a typical foraging period (Skoog 1970; Lüps et al. 1987 b). Thus, data from stomach contents can permit inferences about the foraging tactics of individual animals as well as about the overall dietary adaptation of a population. So far, however, only four studies of badger stomach contents from western European populations have been published (Andersen 1954; Skoog 1970; Stocker and Lüps 1984; Neal 1988), and one of these (Skoog 1970) only provides information about the frequency, as opposed to the volume, of different foods consumed.

In the present study we describe the contents of 217 badger stomachs from central Switzerland. Our intention in analysing the data was (a) to provide a more accurate and detailed overall picture of badger diet from this part of Europe than has hitherto been available; (b) to address the controversy as to whether badgers are best described as food specialists or generalists; and (c) to extract information about the sequence in which different foods are eaten during a single foraging period in individual animals.

Material and methods

Animals and study area

Carcasses of 217 badgers (96 males, 121 females) were collected by the Berne Natural History Museum during the period 1973 to 1992, from an area of about 650 km^2 in the region Berne-Thun-Burgdorf, in the canton of Berne, Switzerland. The area consisted of 30% forest and 57% farmland, the forests containing a mixture of deciduous and coniferous species (especially beech *Fagus sylvatica*, Norway spruce *Picea abies* and silver fir *Abies alba*). Farmland was used mainly for cattle breeding and production of potatoes, other root crops and cereals (primarily maize, wheat, barley, oats and rye). Fruit trees (apple, pear, plum and cherry) were often situated near to farms and villages.

Most of the animals were killed by road or railway traffic (N = 120) or were shot to prevent damage to crops (N = 67); a minority (N = 30) were found dead from other or unknown causes. In addition to information about stomach contents, the following data were collected whenever possible: sex of the animal, cause and time of death (date and time of day), body weight and degree of tooth-wear (see Lüps 1983, 1984; Lüps and Roper 1988 for details). 160 animals were aged by counting dentine rings in the lower canines and the remainder by other methods (Lüps et al. 1987 a). Those aged 12 months or less were classed as "young", the remainder as "adult".

Analysis of stomach contents

After removal and dissection of a stomach, the contents were washed out and stored in 4% formalin. Material was subsequently analysed by washing it with water in a 1 × 1.5 mm sieve and sorting the solid remains into the following 17 "primary" prey categories: voles, other mammals, reptiles, birds (including egg shells), gastropods (slugs and snails), earthworms, wasps, bumble-bees, other insect larvae, other insect imagos, cherries, plums, strawberries, maize, oats, seeds, and grass and other types of leaves. For further analysis, these primary prey categories were combined into four "secondary" categories (invertebrates, vertebrates, fruits and cereals) and two "tertiary" categories (faunal and vegetal material).

The volume of each primary prey category was determined to the nearest 0.1 ml using a glass measuring cylinder, by recording the volume of water displaced. A given type of prey was only recorded as "present" if its volume exceeded 0.5 ml, and stomachs were classified as "empty" (i. e., none of the contents were recorded) if they contained less than 20 ml of material.

As well as recording the volume of each prey type for each stomach, we also recorded the frequency of occurrence of different prey types (i. e., the percentage of stomachs containing each prey type, regardless of volume), prey "diversity" (i. e., the number of different prey types found per stomach), and "main prey" (i. e., the most voluminous prey type found per stomach). Stomachs were collected in every month of the year but comparisons between individual months were not possible because too few stomachs containing food were available in the months December to February. Therefore, in order to examine seasonal changes in diet, the year was divided into four three-month seasons: spring (March to May), summer (June to August), autumn (September to November) and winter (December to February). Variability in intake was assessed by calculating the coefficient of variance (sd × 100/mean) for each food type across all stomachs.

One stomach (from a female, killed in September 1989) was exceptionally full: it contained 1 235 ml of material, consisting of 1 153 ml maize, 75 ml plums and 7 ml of other items (slugs, insects, carrion, grass). Since this stomach contained more than twice as much material as any other, we excluded it from the analysis in order to avoid unduly biassing the results.

Results

Empty stomachs

105 stomachs contained <20 ml of material and were therefore classed as "empty". There were no seasonal, sex or age differences in the proportion of empty stomachs ($\chi^2 = 3.17$, df = 3; $\chi^2 = 0.85$, df = 1; $\chi^2 = 1.1$, df = 1), nor was there any relationship between the likelihood of a stomach being empty and the way in which the donor was killed ($\chi^2 = 3.21$, df = 2). Empty stomachs were therefore an unbiassed subset from the total sample, presumably deriving from animals which happened to be killed early in the night.

Effects of age and sex

Male badgers weighed significantly more than females (mean body weights = 12.62 kg and 11.23 kg respectively; Mann-Whitney test, $U = 6\,080$, $p < 0.01$), but there was no sex difference in total volume of stomach contents, diversity of stomach contents or percentage of faunal versus vegetal material in the diet (Mann-Whitney tests, $U < 3\,200$, $p > 0.8$). No significant effect of age (young versus adult) was found on either the diversity of stomach contents or the percentage of faunal material (Mann-Whitney tests, $U < 950$, $p > 0.7$). However, there were significant positive correlations between age and total volume of stomach contents (Spearman test, $r_s = 0.26$, $N = 80$, $p < 0.05$), age and degree of tooth wear ($r_s = 0.85$, $N = 80$, $p < 0.001$), and degree of tooth wear and total volume of contents ($r_s = 0.25$, $N = 109$, $p < 0.01$). Thus older animals had fuller stomachs at the time of death, despite the fact that their teeth were more worn.

Since these findings provide no evidence that the composition of the diet (as opposed to total amount eaten) was affected by either age or sex, we combined the whole sample of stomachs for subsequent analysis.

Overall composition of the diet

Table 1 summarises the occurrence of each of the 17 primary, the 4 secondary and the 2 tertiary prey categories. The most consistently consumed primary prey was grass/leaves, which had the highest frequency of occurrence, was present in every month of the year and had the lowest coefficient of variance. There was no significant correlation between the absolute volume of grass/leaves per stomach and the volume of any other primary, secondary or tertiary prey category, contrary to what might have been expected if grass/leaves were ingested accidentally whilst foraging for other prey ($r_s < 0.25$ in all cases). Nor was the volume of grass/leaves correlated with the combined volume of all other stomach contents ($r_s = 0.20$). Nevertheless, we excluded grass/leaves from subsequent analyses since it seems unlikely that badgers derive significant nourishment from such material.

Table 1. Summary of stomach contents (N = 111).

Category	Food	Frequency of occurrence (%)	Mean vol when[1] present (ml)	Mean vol(ml)[2]	Main prey (%)[3]	Only prey (%)[4]	Months present	CV (%)
1°	Voles	27	32.5	8.8	8	2	10	235
	Other mammals	12	56.4	6.6	4	1	6	588
	Reptiles	1	3.0	0.1	0	0	1	–
	Birds	2	3.0	0.1	0	0	3	–
	Slugs/snails	20	26.6	5.3	4	0	5	395
	Earthworms	76	60.2	45.5	34	13	11	170
	Wasps	13	130.8	16.5	6	5	4	366
	Bees	1	22.0	0.2	0	0	1	–
	Insect larvae	14	1.5	0.2	0	0	8	435
	Insect imagos	49	1.1	0.5	0	0	8	167
	Cherries	21	128.9	26.7	19	2	3	266
	Plums	12	123.2	14.4	6	2	3	308
	Strawberies	2	62.0	1.1	1	0	2	–
	Maize	28	85.8	24.0	18	2	9	235
	Oats	1	110.0	1.0	0	0	1	–
	Seeds	2	3.5	0.1	0	0	1	–
	Grass/leaves	93	5.9	5.5	0	0	12	103
2°	Vertebrates	40	38.1	15.5	12	3	11	276
	Invertebrates	89	76.5	68.2	44	18	12	134
	Fruits	35	123.2	42.2	26	4	4	197
	Cereals	29	83.4	24.9	18	2	9	228
3°	Faunal	95	87.6	83.6	52	21	12	111
	Vegetal	57	118.5	67.2	48	6	11	143

[1] Includes only stomachs containing the prey in question.

[2] Includes all stomachs.

[3] Number of stomachs in which the prey in question occupied a greater volume than any other prey.

[4] Number of stomachs containing only the prey in question.

Of the remaining 16 primary prey types, earthworms had a higher frequency of occurrence and overall mean volume, were more often the main prey, were more often found as the only prey in a stomach, and occurred in more months of the year, than any other food. They also had almost the lowest coefficient of variation, though this was still high (170%) by absolute standards. However, earthworms did not have an especially high mean volume when present (mean = 60.2 ml). Thus earthworms were eaten fairly consistently, year-round, but usually only in moderate volumes. This is not because it was impossible for badgers to consume large quantities of earthworms: one stomach contained 475 ml of earthworms and another 345 ml.

Table 2. Number of stomachs containing a given number of primary prey types.

Prey types/stomach*						
1	2	3	4	5	6	$\overline{X}$
15	34	35	17	9	1	2.77

* Includes all prey present in volumes > 0.5 ml

Voles, insect larvae, insect imagos and maize were eaten in at least 8 of 12 months but did not appear in a large proportion of stomachs and did not contribute greatly to overall diet. All other foods were eaten sporadically but some of them (notably wasps, cherries, plums and oats) tended to be eaten in large amounts, given that they were consumed at all.

As regards the secondary and tertiary prey categories, invertebrates were eaten more consistently and contributed more overall to the diet than either vertebrates, fruits or cereals. The same was true of faunal by comparison with vegetal material. However, fruits and vegetal material had the highest mean volumes when present. Overall, faunal material contributed 55% of the total provided by all stomachs, while vegetal material contributed 45%. To summarise, animal and plant material contributed approximately equally to the overall diet and both were eaten more or less year-round: but animal material tended to be eaten often and in moderate volumes, whereas plant material was eaten less often but in larger amounts.

The modal number of different primary prey types per stomach was 3 (mean = 2.7; see Tab. 2). Only 27 stomachs (24%) contained a single prey and in 13 (48%) of these the prey in question was earthworms (Tab. 1).

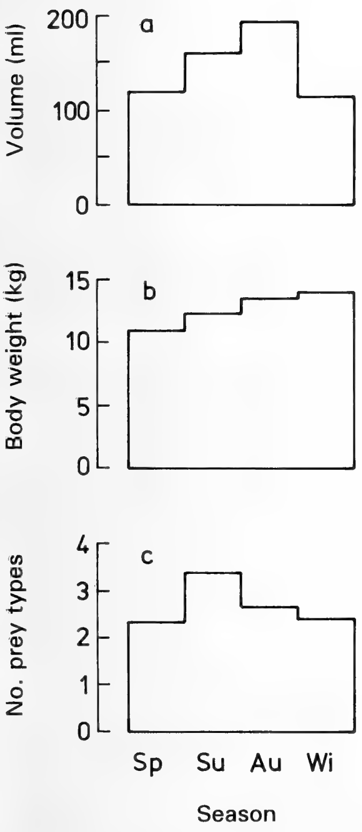

Fig. 1. Seasonal changes in (a) mean total volume of contents per stomach, (b) mean body weight and (c) mean number of primary prey types per stomach. Sp = spring (March to May); Su = summer (June to August); Au = autumn (September to November); Wi = winter (December to February).

Seasonal changes in diet

The mean total volume of stomach contents was greatest in autumn (Fig. 1 a), which was also a season in which body weight was high (Fig. 1 b). However, diversity of intake was greatest in summer (Fig. 1 c), reflecting the availability at that time of year of fruits such as plums and cherries, in addition to faunal foods, such as earthworms and voles, which were available more or less year-round.

Data on the frequency of occurrence, mean volume when present, and mean volume overall of different primary food types reveal considerable seasonal variation (Fig. 2). Only voles, earthworms and maize were eaten year-round and of these, earthworms were eaten with the highest frequency in all four seasons. Earthworms did not, however, represent an especially large volume except in spring, when they were eaten in large amounts in absolute terms (Fig. 2) and constituted 67% of the total volume ingested. Wasps, cherries, plums and mammals other than voles were eaten in only one or two seasons, and even in those seasons the frequency of

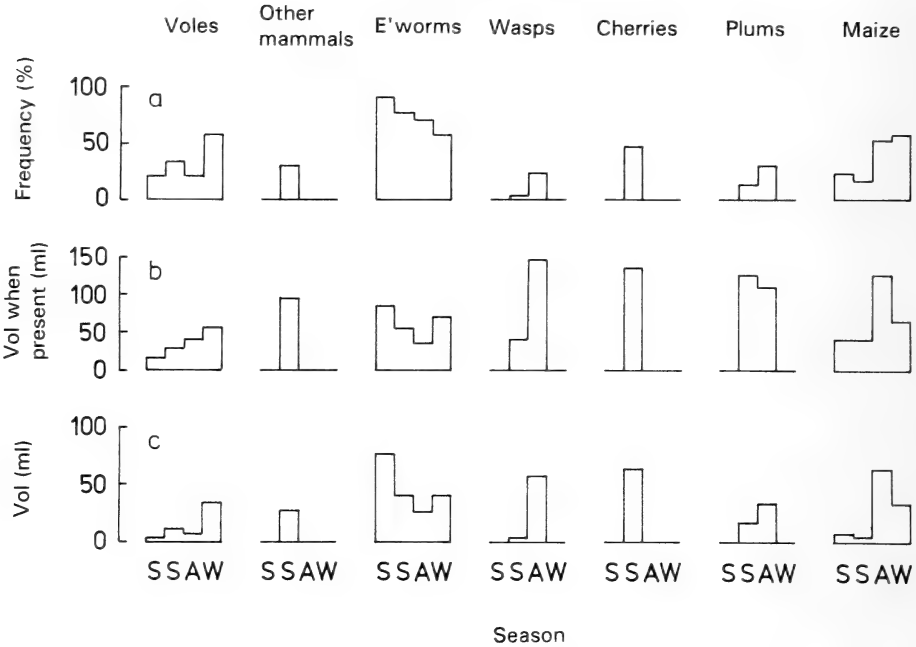

Fig. 2. Seasonal changes in the consumption of the 7 most important primary prey types. (a) Frequency of occurrence; (b) mean volume per stomach, including only stomachs that contained the prey in question; (c) mean volume per stomach, including all stomachs. SSAW: spring, summer, autumn, winter.

consumption was in all cases less than 50%. However when they were eaten, these foods tended to be eaten in large quantities. Cherries were the most voluminous food overall in summer (38% of total intake), maize in autumn (35%) and earthworms in winter (36%).

There were striking differences in the seasonal pattern of intake of faunal and vegetal foods (Fig. 3). Faunal material occurred in virtually every stomach in all four seasons and the absolute volume consumed showed relatively little seasonal variation. Vegetal foods, by contrast, never appeared in more than 75% of stomachs in any one season, and only contributed significantly to the diet in summer and autumn. In the latter seasons, however, they formed a slightly higher proportion of the diet overall than did faunal material.

Pattern of consumption within a single feeding period

In order to make deductions about the pattern of consumption of different foods from hour to hour in individual animals, using data from stomach contents, it was necessary to know when the donor animals ceased feeding. In 52 animals for which the relevant data were available, the volume of total stomach contents was positively correlated with time of death, which ranged from 1 800 to 0 600 h ($r_s = 0.64$, $p < 0.001$). The volume of total stomach contents could therefore be used as an indication of time of death in cases where the latter was not known.

It follows that if badgers preferentially consume a particular type of food early in the night, this food should be disproportionately evident in stomachs whose total contents are relatively small. To test this prediction, we plotted the percentage by volume of each primary, secondary and tertiary food category against total stomach contents, for all stomachs containing both faunal and vegetal material. (We included only stomachs containing

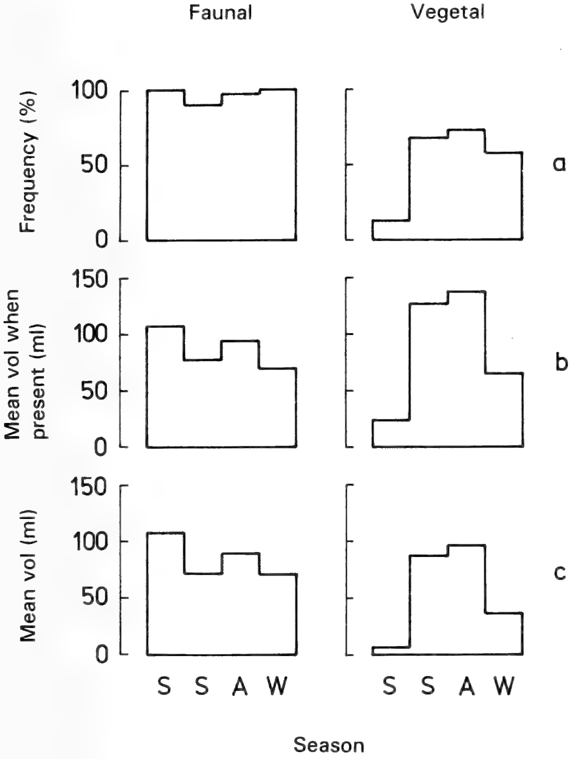

Fig. 3. Seasonal changes in the consumption of faunal and vegetal material. Conventions as in Fig. 2.

both faunal and vegetal material because only in these cases could we be sure that a range of different foods was available on the night when the animal was killed.) None of the correlations was significant ($r_s < 0.1$). Furthermore, data from stomachs whose total contents were <100 ml, and which therefore derived from animals killed very early in the night, showed no evidence of a bias towards any particular food category. Thus, there was no evidence that any one type of food was preferentially eaten at any particular stage in an individual's nocturnal foraging period.

To test whether there was an increase in the diversity of stomach contents as a function of time spent feeding, we correlated diversity (i. e., number of different prey types per stomach) with total stomach contents for all stomachs (Fig. 4). The result was not significant ($r_s = 0.168$, $N = 111$). Diversity in stomachs containing <100 ml of total contents ranged from 1 to 5 (mean = 2.62), while in stomachs containing <50 ml it ranged from 1 to 4 (mean = 2.4). Thus, even stomachs collected very early in the night usually contained more than one food type.

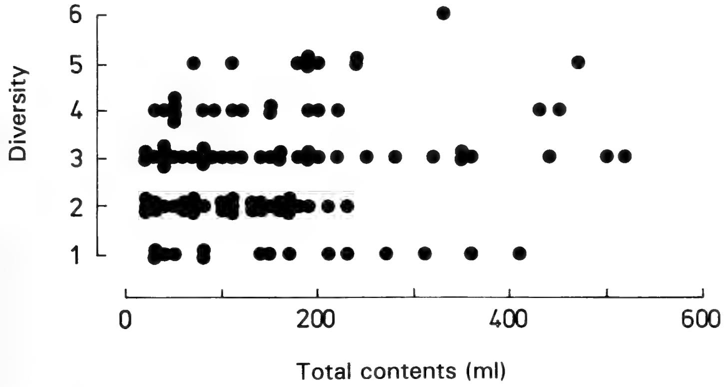

Fig. 4. Relationship between diversity (the number of primary prey types per stomach) and the total volume of food in the stomach.

Discussion

In common with almost all previous studies of badger diet (see reviews by Neal and Cheeseman 1991; Lüps and Wandeler 1993; Roper 1994), our results confirm that badgers eat a wide range of foods even within a relatively restricted geographical area. Specific foods that contributed to the diet, in descending order of overall volume consumed, were earthworms, cherries, maize, wasps, plums, voles, other mammals, slugs and snails, strawberries, oats, bumble-bees, unidentified insects (both larvae and imagos), reptiles, birds and seeds. There were no sex or age differences in the composition of the diet; but there was substantial individual and seasonal variability in the consumption of all food types, with the volume of no single food having a coefficient of variation of less than 150%. Overall, faunal and vegetal foods contributed about equally to the diet in terms of total volume consumed. However, faunal foods occurred in a substantially higher proportion of stomachs than did vegetal foods, and the total amount of faunal material eaten was subject to relatively little seasonal variation.

Small amounts of grass and leaves were also found in a large majority of stomachs but it seems unlikely that these yield any nutritional benefit, given the structure of the badger gut (Stark et al. 1987). Furthermore, grass and leaves recovered from stomachs showed no signs of having been digested. It is generally assumed that badgers ingest such material accidentally whilst grubbing for other prey in or on the surface of the ground (e. g., Neal 1986), but we found no correlation between the volume of grass and leaves present in stomachs and either the total volume of all other prey or the volume of any other single prey type. Thus, the consumption of grass and leaves remains unexplained.

To what extent do our results support the idea that badgers are food specialists (Kruuk 1986, 1989; Kruuk and Parish 1981)? The "food specialist" hypothesis predicts, first and foremost, that one or at most a few of the foods that are available in a particular location should predominate in the diet. This was the case in Kruuk's study areas in Oxfordshire and Scotland, where earthworms accounted for about 50% by volume of all foods eaten (Kruuk and Parish 1981; see also Neal 1988 for a similar finding); and also in two study areas in Italy, where diet was dominated by fruits and/or insects (Kruuk and de Kock 1981; Ciampalini and Lovari 1985). But several other studies of badger diet in the U.K. and Scandinavia have not shown any single type of food to be especially important (Andersen 1954; Harris 1982; Skinner and Skinner 1988; Shepherdson et al. 1990). Our results show that earthworms were the most frequently eaten food overall, were eaten in more months of the year than any other food and contributed the largest volume overall of any food. Earthworms were also most often the "main prey" (i. e., the most voluminous food in any one stomach) and, in stomachs containing only one type of food, that food was more often earthworms than anything else. On the other hand, earthworms were rarely eaten in very large quantities and they did not often constitute the only food consumed. More importantly, they only constituted 30% of the diet overall, in terms of volume. Thus while earthworms could reasonably be described as a staple food, eaten consistently in moderate amounts, they did not dominate the diet to the extent implied by the "food specialist" hypothesis.

The term "food specialist" has also been used to refer to two other perceived features of badger diet, namely that (i) intake of one particular food is immune from seasonal variation, and (ii) this food is preferred over other foods (Kruuk 1986, 1989). As regards the former point, Kruuk and collaborators found that in Scotland, badgers maintained a fairly constant year-round intake of earthworms, despite variation in earthworm availability (Kruuk and Parish 1981; Kruuk 1989). However, since the study in question was based on faeces analysis, it could only provide information about the relative, and not the absolute, intake of different foods at different times of year (Roper 1994). Contrary to Kruuk's results, we found that earthworms were virtually absent from the diet in January and February, when the main foods eaten were voles and maize. Furthermore, the absolute amount of earthworms consumed was not noticeably less variable than that of other foods, either comparing variance in intake across the whole sample of stomachs or comparing the mean volume consumed across seasons. In summer, for example, cherries were a more important food than earthworms in terms of the average volume consumed, while in autumn the same was true of both wasps and maize. We did find relatively little seasonal variation in the total amount of faunal material eaten, but this result is not shared by other studies of badger diet (e.g., PIGOZZI 1987). To conclude, there is no compelling evidence, either from our results or from other literature on badger diet, that badgers forage in such a way as to sustain a constant level of intake, either of earthworms or of any other particular dietary component.

Since badgers have not been subjected to food-choice experiments, any claims made about their dietary preferences are bound to be speculative. However, it could be argued that if badgers seek out one particular food in preference to others, this food should be especially predominant in the diet early in the night. We found no evidence to support this idea: there was no overall correlation between the percentage of any single food in the stomach and the total volume of contents, and no suggestion that relatively empty stomachs, which can be assumed to have resulted from animals killed early in the night, were especially likely to contain any particular food. Furthermore, there was no correlation between the total number of food types in a stomach and the total volume of its contents, showing that the diversity of foods eaten did not significantly increase as a function of time spent foraging. Even stomachs containing as little as 50 ml in toto could contain as many as four different types of food. Thus it seems that badgers normally consume several different prey types within a few hours of the start of their activity period.

To conclude, by far the most striking feature of badger diet is the diversity of foods consumed, not only when considering the species as a whole but also considering single stomachs whose contents represent the results of a few hours of foraging activity by one animal. The simplest and most convincing hypothesis to account for these data is the traditional one (e.g., NEAL 1948; ANDERSEN 1954; SKOOG 1970) that badgers are opportunistic food generalists. Their foraging behaviour is such that they both encounter and consume a variety of foods, rather than concentrating on a single one.

Acknowledgements

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Zusammenfassung

Nahrung von Dachsen (Meles meles L.) in der Zentralschweiz:
Eine Analyse von Mageninhalten

Untersucht wurden die Mageninhalte von 217 Dachsen in der Zentralschweiz. Insgesamt bestand die Nahrung zu 55% aus Tiermaterial und zu 45% aus Pflanzenmaterial. Regenwürmer waren häufiger und in mehr Monaten in der Nahrung vertreten und waren öfter die einzige Futterart im Magen, als alle anderen Nahrungstypen, aber sie wurden für gewöhnlich nicht in großen Mengen gefressen. Spitzmäuse, Insekten und Mais wurden die meiste Zeit des Jahres gefressen, aber nie in großen Mengen; während Wespen, Kirschen, Pflaumen und Hafer nur in den entsprechenden Jahreszeiten und dann in großen Mengen gefressen wurden. Die gesamte Nahrungsmenge im Magen war im Herbst am größten, während der Reichtum an verschiedenen Nahrungsarten im Sommer am größten war. Keine Nahrungsart wurde bevorzugt zu einer bestimmten Zeit in der Nacht gefressen. Es wurde auch keine Korrelation

zwischen der Anzahl verschiedener Nahrungsarten und dem gesamten Volumen an Mageninhalt gefunden. Die Zusammensetzung der Nahrung unterschied sich nicht signifikant zwischen Dachsen verschiedenen Alters, Geschlechts oder Zahnabnutzung; aber das Gesamtvolumen des Mageninhalts, Zahnabnutzung und Alter waren jeweils signifikant korreliert miteinander.

Tiermaterial allgemein und Regenwürmer im besonderen können als konstanter Bestandteil der Nahrung von Dachsen in diesem Teil der Schweiz betrachtet werden. Aber der auffallendste Aspekt der Dachsnahrung war die Diversität an Nahrungsarten, die gefressen wurde, nicht nur von der Dachspopulation als Gesamtes, sondern ebenfalls von individuellen Dachsen innerhalb nur weniger Stunden der Nahrungsaufnahme.

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Telemetrische Untersuchungen zur Raumnutzung und Aktivitätsrhythmik freilebender Gelbhalsmäuse *Apodemus flavicollis* Melchior, 1834

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Abstract

Range utilisation and activity of radio-collared Yellow-necked mice Apodemus flavicollis Melchior, 1834. Investigated range utilisation and activity of yellow-necked mice *Apodemus flavicollis* in an agricultural area and in a montane forest, 7 individuals were radio-tracked over a period of 5 months, and 1737 locations recorded. Mean home range for adult *A. flavicollis* measured 15,500 m^2 for males and 7,400 m^2 for females during and 3,800 m^2 respectively 3,600 m^2 outside the mating season, and they overlapped considerably. Females monopolized core areas against other females. During the breeding season males moved faster and covered longer distances than females. Outside the hiding places, *A. flavicollis'* activity is crepuscular and nocturnal. In summer, only females visited their hides, occasionally, whereas in fall a male spent extended periods resting in his hides. Up to 7 different hides were used by the same individual.

Einleitung

Die Gelbhalsmaus *Apodemus flavicollis* ist ein in Mittel- und Osteuropa häufiger und weit verbreiteter Kleinsäuger. Aufgrund ihrer verborgenen nächtlichen Lebensweise ist die Kenntnis des Raum-Zeit-Musters und der sozialen Organisation noch sehr lückenhaft. Die bisher vorliegenden Daten aus dem Freiland stützen sich fast ausschließlich auf Fallenuntersuchungen (Niethammer 1978). Im Vordergrund dieser Arbeiten standen zumeist populationsbiologische oder taxonomische Aspekte. Ziel der vorliegenden Untersuchung war es, die Raumnutzung und das Aktivitätsmuster von Gelbhalsmäusen darzustellen, und die Mechanismen der Anpasssung in einem landwirtschaftlich geprägten Lebensraum und in einer Waldlandschaft zu beleuchten. Zu diesem Zweck wurden 7 Gelbhalsmäuse mit Radiosendern markiert und ihre Ortsbewegungen über mehrere Wochen verfolgt.

Untersuchungsgebiete

Die Untersuchungen wurden an 2 Standorten in Niedersachsen durchgeführt:

Fuhrberg (52°50′ N, 9°53′ E, Landkreis Burgwedel): Die ca. 10 ha große Untersuchungsfläche (40 m NN) liegt in der naturräumlichen Region des Weser-Aller-Flachlandes am Fluß Wulbeck. Das Landschaftsbild bestimmen hier neben landwirtschaftlich genutzten Flächen vor allem stillgelegte bzw. extensivierte Grünlandflächen. Hervorstehende Geländestrukturen der Untersuchungsfläche sind ein Grasbruchdamm und ein Gehölzstreifen (Abb. 1). Im Norden, Süden und Osten ist das Gebiet von Kiefernforsten umgeben.

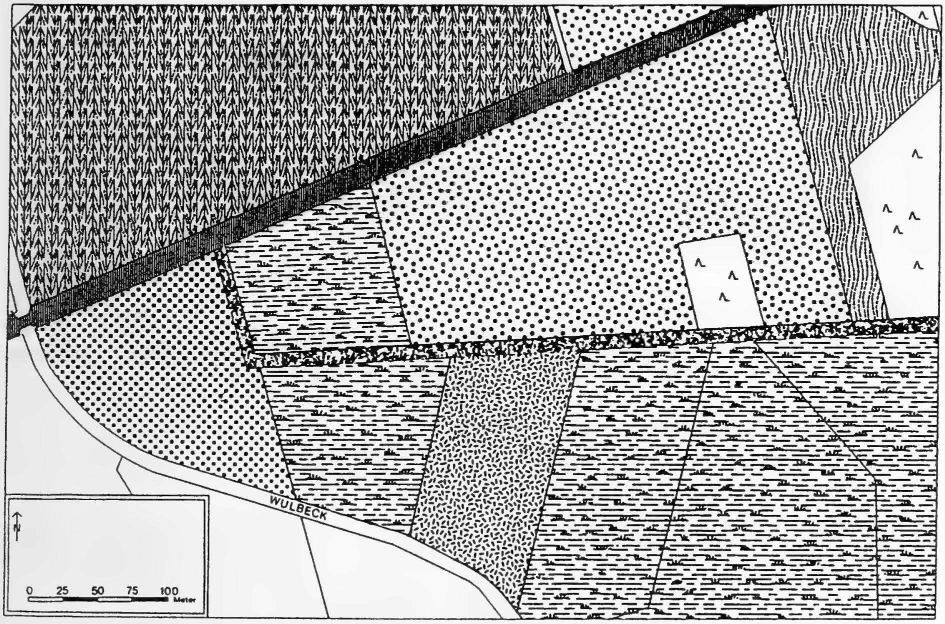

Abb. 1. Landschaftsstrukturen im Gebiet Fuhrberg.

▥	**Graben:**	Vergraste Böschungen beidseitig entlang des asphaltierten Grasbruchdamms (Weg 1), Schwarzpappel- (*Populus nigra*) und Birkenallee (*Betula pendula*), Strauchschicht mit Stieleiche (*Quercus robur*), Weißdorn (*Crataegus monogyna*) und Heckenrose (*Rosa corymbifera*), Grabensohle trocken, mit Laub bedeckt, ca. 1,5 m unter Wegniveau.
▩	**Gehölzstreifen:**	Überwiegend Schwarzerlen- (*Alnus glutinosa*) und Stieleichenbestand, z. T. beidseitig entlang eines schmalen, vergrasten Feldwegs (Weg 2), Strauchschicht mit Brombeere (*Rubus fructicosus*), Holunder (*Sambucus nigra*), Eberesche (*Sorbus aucuparia*) und Salweide (*Salix caprea*), Krautvegetation gering.
ʌ ʌ	**Wald:**	Lichter, vergraster Kiefernforst (*Pinus sylvestris*) mit Birke (*Betula pendula*) und Brombeere in der Strauchschicht.
⁘	**Kartoffelacker:**	Landwirtschaftlich genutzte Ackerfläche.
▧	**Gerste:**	Landwirtschaftlich genutzte Ackerfläche.
☰	**Grünbrache 1:**	Stillgelegte Wiesen und Weiden, deren Aufwuchs auf der Fläche belassen wird; Selbstbegrünung oder Grasansaat.
▒	**Grünbrache 2:**	Wie Grünbrache 1, hier mit flächendeckender Aussaat von Roggen aus dem Diasporenvorrat des Bodens aus der Bewirtschaftungszeit.
⁙	**Mähwiese:**	Extensiviertes Grünland, Mahdgut wird zur Heugewinnung verwendet.
▦	**Viehweide:**	Extensiviertes Grünland mit eingeschränkter Beweidung.

Oderhaus (51°42′ N, 10°34′ E, Landkreis Goslar): Das Untersuchungsgebiet liegt im Mittelharz im Nationalpark Harz. Die Landschaft ist gekennzeichnet durch Höhenzüge bis ca. 700 m NN und schmale, steile Taleinschnitte. Die an einem Westhang in der montanen Stufe gelegene Untersuchungsfläche (520–550 m NN) im Mittleren Spindeltal befindet sich im Übergangsbereich zwischen einem etwa 80jährigen Fichtenforst mit sehr schwachem Unterwuchs und einem ca. 140jährigen z. T. vergrasten Hainsimsen-Buchenwald.

Material und Methode

Von Juni bis August 1991 wurden Gelbhalsmäuse in Fuhrberg und im September und Oktober 1991 in Oderhaus mit Radiosendern markiert (Tab. 1). Die Telemetrieanlage bestand aus Halsbandsendern zweier Hersteller, einem tragbaren Empfänger und einer 4-Element Yagi-Antenne. Die Ortung erfolgte in der Regel per Triangulation von 2 oder mehreren, im Gelände festgelegten Peilpunkten. In Fuhrberg wurden Standortermittlungen von Tieren, die sich in den linearen Geländestrukturen Gehölzstreifen und Graben (Abb. 1) bzw. in ihren Verstecken aufhielten, besonders schnell und präzise mittels der „Homing-in-Methode" (WHITE und GARROT 1990) von den parallel verlaufenden Wegen aus durchgeführt. In Fuhrberg wurde 3–5mal wöchentlich die ganze Nacht hindurch von Sonnenuntergang bis Sonnenaufgang telemetriert. Die Ortung der Tiere erfolgte dabei bis Mitternacht in halbstündigen Intervallen, danach wurde stündlich gemessen. In Oderhaus wurde im Wechsel jeweils in der 1. oder 2. Nachthälfte in halbstündigem Rhythmus sowie auch tagsüber gepeilt.

Für die graphische Darstellung der Aktionsräume wurde die Konvex-Polygon-Methode (Minimum-Area-Methode, MAM) verwendet. Den Flächenberechnungen liegt eine Rasterauswertung zugrunde. Bei dieser werden alle ermittelten Standorte in chronologischer Reihenfolge durch gerade Linien verbunden und außer den tatsächlich registrierten nur die von diesen Verbindungslinien durchzogenen Quadrate in die Auswertung miteinbezogen (vgl.GEORGII 1980). In Anbetracht der Peilgenauigkeit und der Mobilität der Gelbhalsmäuse wurde die Größe der Rasterzellen auf 10 × 10 m festgelegt.

Bewertung der Habitatpräferenzen

Ein nach dem beschriebenen Verfahren ermittelter Aktionsraum besteht aus einer Anzahl von Rasterzellen. In Fuhrberg konnte jedem einzelnen Rasterquadrat ein bestimmter Habitattyp zugeordnet werden. Durch Aufsummieren der Quadrate erhält man die Flächenprozentwerte der einzelnen Habitattypen für einen bestimmten Aktionsraum – die Aktionsraumausstattung. Um einen Gesamteindruck von den artspezifischen Lebensraumansprüchen zu erhalten, wurden alle Aktionsräume in Fuhrberg zusammengefaßt. Die den Einzelindividuen zugrunde liegenden Habitatansprüche wurden dadurch graphisch „gemittelt" (BERBERICH 1988). Bei jeder Positionsbestimmung in Fuhrberg konnte der betreffende Habitattyp direkt mitprotokolliert werden. Die Nutzungshäufigkeit der Landschaftsstrukturen wurde für die Gesamtheit aller im Untersuchungsgebiet bearbeiteten Tiere berechnet. Dabei wurden ausschließlich Standortbestimmungen „aktiver" Mäuse berücksichtigt, die individuell im Abstand von mindestens 30 min aufgenommen worden waren. Für die Berechnung standen dann insgesamt 628 Ortungen zur Verfügung. Wird ein Landschaftselement proportional zu seinem Vorkommen im Aktionsraum genutzt, so ist der Präferenzindex (P.I.) = 1; Werte > 1 zeigen Präferenz, Werte < 1 Meidung (BERBERICH 1988; SKIRNISSON 1986). Die Präferenz-Indizes für die verschiedenen Landschaftsstrukturen wurden gebietsspezifisch als Summe aller Ortungen in Fuhrberg berechnet.

Tabelle 1. Telemetriedaten der 7 sendermarkierten Gelbhalsmäuse (M = ♂, W = ♀)

Gebiet	Maus-Nr.	Gew.[1] (g)	Beobachtungszeit	Tage	Ortungen
Fuhrberg	M1	40	10. 06.–01. 08. 1991	47[2]	425
Fuhrberg	M2	31	10. 07.–12. 08. 1991	34	217
Fuhrberg	M3	28	10. 07.–25. 07. 1991	16	140
Fuhrberg	W1	25	18. 06.–12. 08. 1991	53[2]	410
Fuhrberg	W2	33	25. 06.–25. 07. 1991	31	279
Oderhaus	M4	37	09. 09.–25. 10. 1991	29[2]	235
Oderhaus	W3	26	12. 09.–16. 09. 1991	5	31
					1 737

[1] zum Zeitpunkt der Erstmarkierung. – [2] durch Senderausfall verlorene Beobachtungstage wurden abgezogen.

Aktivitätsrhythmik

Der Aktivitätsstatus der Tiere wurde in Abhängigkeit von den ermittelten Aufenthaltsorten festgelegt. Aktivität wurde wie folgt registriert: Im Versteck geortete Gelbhalsmäuse wurden als inaktiv betrachtet, solche außerhalb des Verstecks als aktiv. Unter dem Begriff „Aktivität" ist daher im folgenden ausdrücklich allein der Aufenthalt einer Gelbhalsmaus außerhalb eines Nestes ohne weitere Differenzierung zu verstehen. Um den tageszeitlichen Aktivitätsverlauf zu ermitteln, wurden die individuellen Daten halbstündig zu einer Messung zusammengefaßt. Insgesamt wurden 1654 Halb-Stunden Messungen ausgewertet. Infolge von Senderausfällen beschränken sich die Auswertungen in Oderhaus auf das Datenmaterial von einem einzigen Tier, dem ♂ M4. Die Zeitangaben erfolgen in mitteleuropäischer Zeit (MEZ).

Ergebnisse

Größe und räumliche Lage der Aktionsräume

Alle sendermarkierten Gelbhalsmäuse in Fuhrberg waren fortpflanzungsaktiv. Die Aktionsräume der ♂♂ messen 3700 bis 34800 m^2, im Durchschnitt 15500 m^2. Die Aktionsräume der beiden ♀♀ sind mit 4400 bis 9700 m^2 und durchschnittlich 7400 m^2 etwa halb so groß. Die Aktionsräume von M4 und W3 in Oderhaus außerhalb der Fortpflanzungszeit waren deutlich kleiner. Standardabweichungen über 50% der mittleren Aktionsraumgröße zwischen den verschiedenen Berechnungsmethoden ergeben sich bei M1 und W2. Die MAM überbewertet dabei aufgrund der Geländetopographie in Fuhrberg vermutlich die tatsächlichen Aktionsraumgrößen. Die räumliche Lage der Aktionsräume nach MAM in Fuhrberg ist in Abb. 2 dargestellt. Die Ergebnisse der Flächenberechnungen nach den unterschiedlichen Berechnungsmethoden sind in Tab. 2 gegenübergestellt.

M1, M2, und W2 hatten während des gesamten Beobachtungszeitraumes in Fuhrberg je einen zusammenhängenden Aktionsraum (Abb. 2), anders die übrigen Tiere. W1 verlagerte zweimal seinen Aktionsraum. Dabei wurde jeweils ein angrenzendes Gebiet neu besetzt, das mit dem jeweils vorigen Aktionsraum noch überlappte. M3 wechselte nach 3 Beobachtungstagen in ein 150 m entferntes Gebiet. Dabei drang es in den Aktionsraum von M1 ein und wurde von diesem mehrfach attackiert und verfolgt.

Tabelle 2. Flächengröße der einzelnen Aktionsräume (AR) in m^2 berechnet nach Minimum-Area-Methode (MAM) und Raster-Methode. x = Mittelwert, SD = Standardabweichung

Gebiet	Maus	Ar-Nr.	Beob.-tage	Ortungen	MAM	Raster	x	SD(%)
Fuhrberg	M1		47*	425	49500	20100	34800	59,7
Fuhrberg	M2		34	217	18500	15200	16900	13,8
Fuhrberg	M3	I	3	24	8200	5000	6600	34,2
		II	12	116	2900	4400	3700	29,1
Fuhrberg	W1	I	14*	128	10100	6200	8200	33,8
		II	10	111	5200	3500	4400	27,6
		III	26	171	8500	5900	7200	25,5
Fuhrberg	W2		31	279	14200	5500	9700	62,5
Oderhaus	M4		29*	235	3700	3500	3600	3,9
Oderhaus	W3		5	31	4200	3400	3800	14,9

* durch Senderausfall verlorene Beobachtungstage wurden abgezogen.

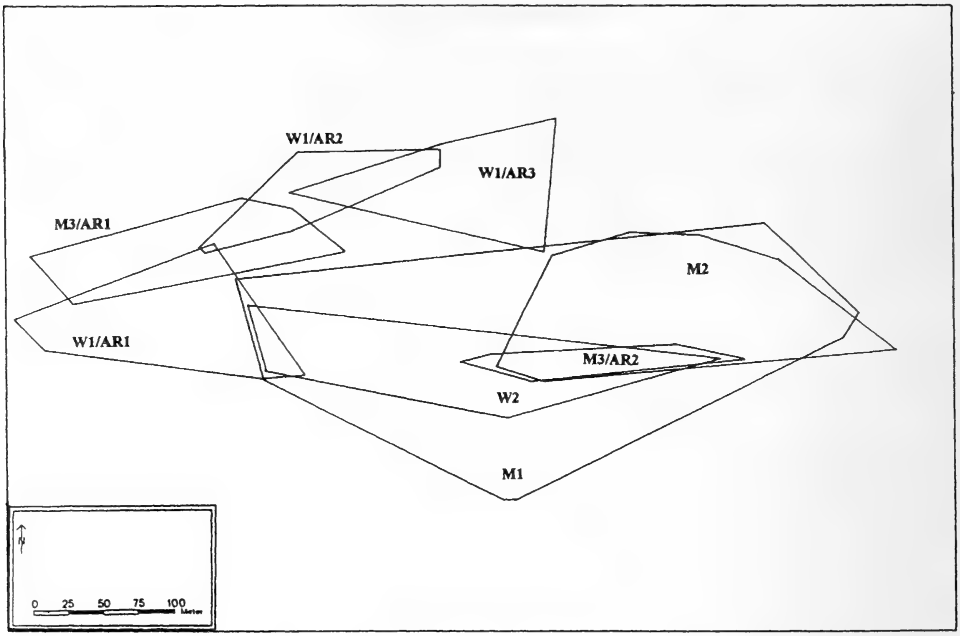

Abb. 2. Aktionsräume (nach MAM) von 5 fortpflanzungsaktiven Gelbhalsmäusen in Fuhrberg. M = ♂, W = ♀; AR = Aktionsraum.

Überlappung der Aktionsräume

Das Ausmaß der Aktionsraum-Überlappung zweier Individuen wurde nach der Raster-Methode berechnet (Tab. 3). Aktionsräume fortpflanzungsaktiver ♂♂ können sich großflächig überlappen. Der gegenseitige Flächenanteil zwischen den individuellen Aktionsgebieten der 3 ♂♂ in Fuhrberg beträgt im Mittel 54% (SD = 26,6%, n = 3 Individuenpaare). Der Überlappungsgrad dürfte größer als angegeben sein, da sich, wie bei den Fangaktionen festgestellt, weiterere ♂♂ im Gebiet aufhielten. Die sendermarkierten ♂♂ wurden jedoch während der nächtlichen Aktivitätsphase nur äußerst selten und nie über längere Zeiträume gemeinsam in einem Rasterquadrat geortet, gingen sich also offenbar aus dem Weg. Die prozentuale Überlappung der Aktionsräume zwischen den Geschlechtern beträgt im Mittel 30% (SD = 31%, n = 6 Individuenpaare). W2 hielt sich sogar ständig innerhalb der Aktionsraumgrenzen von M1 auf, mehr als 50% ihres Aktionsraumes überlappte sich auch mit den Gebieten von M2 und M3. Vor allem M1 wurde häufig und auch über längere Zeiträume in unmittelbarer Nähe von W2 geortet. Auch die gemeinsame Nutzung eines Nestes konnte, allerdings nur einmal, registriert werden. Untereinander überlappten sich die Aktionsräume der beiden ♀♀ in Fuhrberg nur geringfügig. Im gesamten Beobachtungszeitraum wurden innerhalb der Aktionsräume von W1 und W2 nur zwei weitere fortpflanzungsaktive ♀♀ gefangen.

Tabelle 3. Überlappung der Aktionsräume von fünf Gelbhalsmäusen in Fuhrberg. Dargestellt ist die prozentuale Überlappung des Aktionsraumes X durch den Aktionsraum Y

Y/X	M1	M2	M3	W1	W2
M1	–	66,2	93,7	16,1	100
M2	42,8	–	65,9	0	55,6
M3	21,8	31,2	–	0	66,7
W1	11,8	0	0	–	16,3
W2	29,2	21,5	54,5	12,9	–

Ausstattung der Aktionsräume

Mit Ausnahme der Viehweide gehören alle in Abb. 1 dargestellten Habitate zum Ausstattungsmuster der Aktionsräume der sendermarkierten Gelbhalsmäuse in Fuhrberg. Es dominiert der Kartoffelacker mit einem Anteil von 35% der insgesamt von allen Individuen genutzten Fläche. Zusammen mit dem Gerste-Areal (8%) beträgt der Anteil intensiv bewirtschafteter Anbaufläche 43%. Der Gesamtanteil stillgelegter bzw. extensivierter Grünlandfläche liegt bei 21%; am stärksten repräsentiert ist hier die Grünbrache2 (11%). Mähwiese (5%) und Grünbrache1 (5%) spielen nur eine untergeordnete Rolle. Die übrigen 36% entfallen auf die Saumhabitate Gehölzstreifen (13%), Graben (17%) und Wald (6%).

Nutzung der Aktionsräume

Der Gehölzstreifen wurde mit 54% aller Ortungen (n = 628) von den Gelbhalsmäusen am intensivsten genutzt. Alle sendermarkierten Individuen wurden in diesem Habitat angetroffen. Der Kartoffelacker (17%) wurde von allen Tieren außer W2 belaufen. Die Nutzung der Ackerfläche begann in der zweiten Juliwoche, als der Aufwuchs auf der Fläche eine Höhe von etwa 60 cm erreicht hatte und offensichtlich ausreichende Deckung bot. Betrachtet man bei der Auswertung allein diesen Zeitraum, so ergibt sich mit 32% eine deutlich höhere Nutzungshäufigkeit dieses Habitattyps. Die Gräben entlang des Grasbruchdammes (15%) nutzten W1 und M3. In der Grünbrache2 (10%) wurden mit Ausnahme von W1 wiederum alle Tiere geortet. Die individuelle Nutzungsintensität variierte zwischen 3% (M2) und 19% (W2). Das Gerstenfeld (1,6%) wurde, abgesehen von 2 kurzen Exkursionen von M3, sporadisch von W1 aufgesucht. Im Wald (1,1%) wurden nur M1 und M2 geortet. Mit weniger als 1% aller Ortungen wurden Mähwiese und Grünbrache1 nur kurzzeitig bei seltenen Exkursionen aufgesucht.

Habitatpräferenzen

Bezogen auf den prozentualen Flächenanteil der verschiedenen Habitate ergeben sich Präferenz-Indizes (Abb. 3) von +2,4 (Gehölzstreifen) bis –24,9 (Grünbrache1, nicht dargestellt). Überproportional häufig genutzt werden von den Gelbhalsmäusen allein der Gehölzstreifen und die Gräben. Die übrigen Habitate werden mehr oder weniger deutlich gemieden. Der Gehölzstreifen wird auch von allen Individuen deutlich bevorzugt. Individuelle Präferenzen zeigte außerdem W1 für die Gräben entlang des Grasbruchdammes, M2 für Grünbrache2, M3 für Grünbrache2 und den Kartoffelacker.

Verstecknutzung

Während der hellen Tagesstunden suchen Gelbhalsmäuse Verstecke auf, die sie in der Regel erst in der Abenddämmerung wieder verlassen. Die sendermarkierten Mäuse in Fuhrberg wurden an 112 Kontrolltagen in 21 verschiedenen Verstecken angetroffen. Alle Versteckstandorte waren an Gehölzstrukturen gebunden. 13 Verstecke befanden sich im Gehölzstreifen, 6 in den Grabenböschungen am Grasbruchdamm, 2 im Wald. Die 21 benutzten Verstecke im Gebiet Fuhrberg wurden 4 verschiedenen Typen zugeordnet. Am häufigsten (38% der Kontrolltage) benutzten die Mäuse Höhlungen in Bäumen bis in 1,3 m Höhe oder in morschen Baumstümpfen. Unterirdische Baue suchten sie zu 35% der Tage auf. An 21% der Kontrolltage wurden sie in oberirdischen Hohlräumen unter Astwerk, Wurzeln, Laub oder in Moospolstern angetroffen. Derselbe Unterschlupf am Erdboden wurde nur bis zu viermal benutzt, bestimmte Baumverstecke oder Erdbaue dagegen von denselben Individuen an bis zu 17 Kontrolltagen. M1 wurde an 7 Kontrolltagen

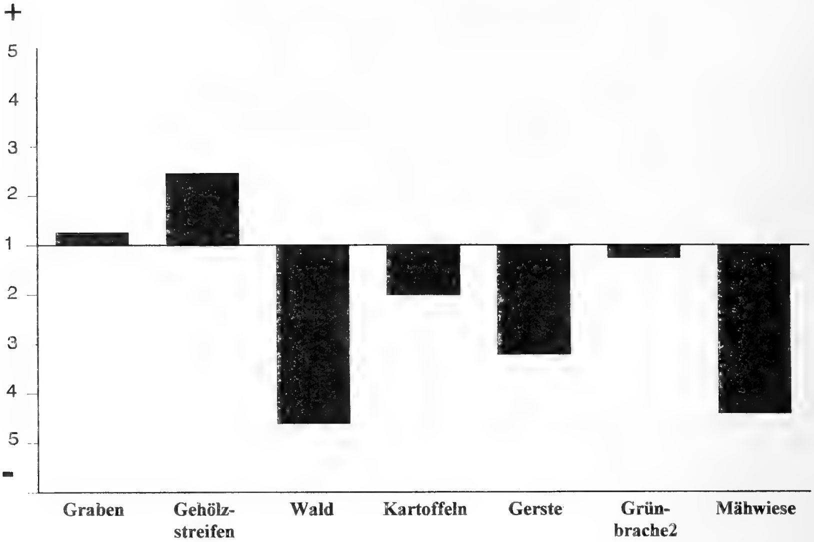

Abb. 3. Habitatpräferenzen von *A. flavicollis* in Fuhrberg (n = 628 Ortungen). Präferenzindex (P.I.) = Nutzungshäufigkeit eines Landschaftselementes / Rel. Häufigkeit des Elements im Gesamtaktionsraum. Werte > 1 zeigen Präferenz, Werte < 1 Meidung.

(6%) unter einer schwarzen ca. 3 m^2 großen Plastikplane geortet. Bemerkenswert waren die häufigen Versteckwechsel. Die einzelnen Individuen bewohnten wenigstens 2 (W2) und maximal 7 (W1) verschiedene Verstecke. M1 wechselte im knapp 7wöchigen Beobachtungszeitraum zehnmal zwischen 6 verschiedenen Verstecken. Kein Versteck wurde von einem ♂ an mehr als 7 Kontrolltagen hintereinander benutzt. Die beiden ♀♀ wurden kontinuierlich über 17 (W1) bzw. 16 (W2) Kontrolltage in einem bestimmten Versteck angetroffen, höchstwahrscheinlich hatten sie in dieser Zeit Junge. Zuvor hatten auch diese Tiere fünf- (W2) bzw. sechsmal (W1) das Versteck gewechselt.

Fortbewegung

Um die Laufaktivität der Gelbhalsmäuse zu bestimmen, wurde für jede Beobachtungsnacht die kürzeste Verbindung zwischen den jeweiligen Ortungen gemessen und dadurch die zurückgelegte Minimalstrecke pro Nacht festgelegt. Die ausgemessenen Distanzen wurden in Beziehung zum jeweiligen Zeitaufwand beim Überwinden der Strecken gesetzt. In Fuhrberg war die durchschnittliche Fortbewegungsgeschwindigkeit der ♂♂ höher als die der ♀♀ (Tab. 4). Dieser geschlechtsspezifische Unterschied ist mit einer Ausnahme (M2/W1) statistisch signifikant (Mann-Whitney U-Test). Das sexuell inaktive M4 in Oderhaus bewegte sich etwa auf dem Geschwindigkeitsniveau der ♀♀ in Fuhrberg, aber signifikant langsamer als seine männlichen Artgenossen dort während der Fortpflanzungszeit.

Fortpflanzungsaktive ♂♂ erreichen nicht nur höhere Fortbewegungsgeschwindigkeiten als ♀♀, sondern legen pro Nacht auch um 25–40% längere Laufstrecken zurück (Tab. 4). Mit Ausnahme der sehr kleinen Stichprobe von M3 konnten die Unterschiede zwischen den Geschlechtern statistisch abgesichert werden. W2 legte mit 712 m in einer Nacht die längste Laufstrecke aller Individuen zurück. Von den ♂♂ erreichte M1 mit 662 m die längste Strecke. Die höchste Geschwindigkeit erzielte M1 mit 58,3 m/min; er legte in der Morgendämmerung auf dem Rückweg in das Versteck 175 m in einer Furche des Kartoffelackers in 3 min zurück.

Tabelle 4. Fortbewegungsgeschwindigkeit und zurückgelegte Strecke pro Nacht von sendermarkierten Gelbhalsmäusen. x = Mittelwert, SD = Standardabweichung, n = Anzahl Beobachtungsnächte

		Geschwindigkeit (m/min)			Strecke pro Nacht (m)		
		x (m/min)	SD	n	x (m)	SD	n
M1	Fuhrberg	1,45	0,61	26	534,1	108,4	9
M2	Fuhrberg	1,25	0,61	17	487,5	143,6	6
M3	Fuhrberg	1,37	0,62	10	425,3	54,1	4
W1	Fuhrberg	0,94	0,42	28	303,7	139,6	12
W2	Fuhrberg	0,82	0,40	19	308,6	160,2	10
M4	Oderhaus	0,81	0,23	17	–	–	–*

* M4 wurde nachts jeweils nur abschnittweise bis zu 6 Stunden überwacht.

Aktivitätsrhythmik

Faßt man die Aktivitätswerte stundenweise über mehrere Wochen zusammen, so stellt die daraus resultierende Kurve den mittleren Tagesablauf der Aktivität im 24-Stunden-Rhythmus dar (Georgii 1980). Gelbhalsmäuse sind vorwiegend dämmerungs- und nachtaktiv. Der tageszeitliche Aktivitätsverlauf, gemittelt jeweils über die Beobachtungszeiträume für beide Untersuchungsgebiete ist in den Abb. 4 und 5 dargestellt. Das tägliche Aktivitätsmuster unterliegt saisonalen Veränderungen. In der Dunkelphase der kurzen Sommernächte halten sich die fortpflanzungsaktiven Gelbhalsmäuse in Fuhrberg nahezu vollständig im Freien auf, in den hellen Tagesstunden dagegen fast ausschließlich in ihren Verstecken (Abb. 4). Tagaktivität beschränkt sich auf einen kurzen Zeitraum vor Sonnenuntergang.

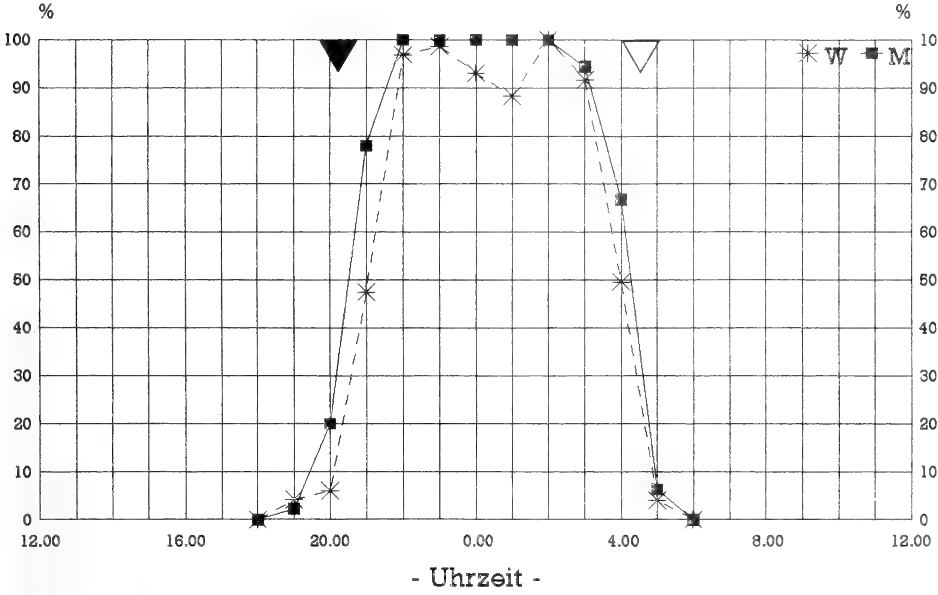

Abb. 4. Tagesaktivitätsmuster in % Aktivität pro Stunde von *A. flavicollis* in Fuhrberg, 10. 06.–10. 08. 1991; M = ♂ (n = 3), W = ♀ (n = 2); ▼ = Sonnenuntergang, ▽ = Sonnenaufgang.

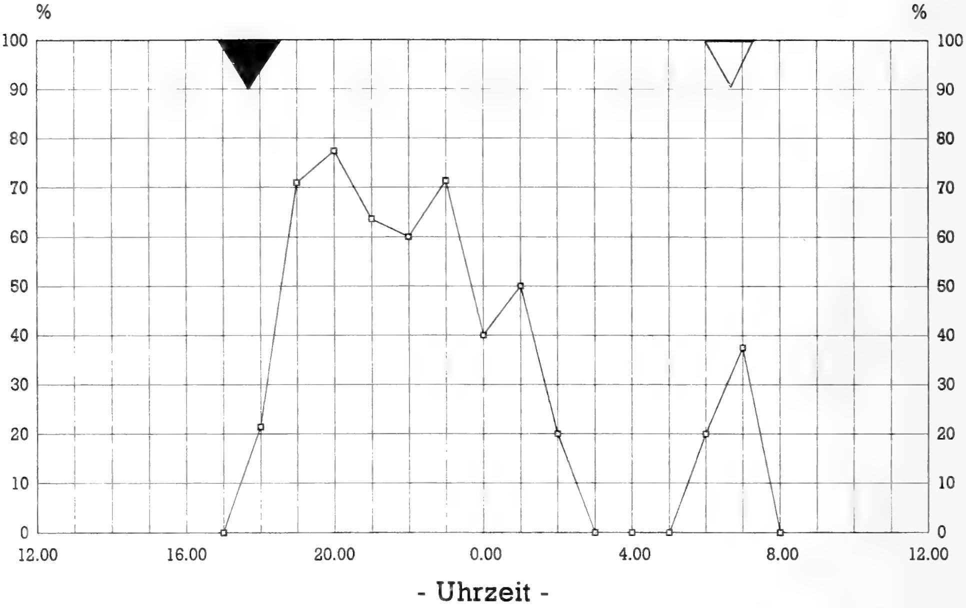

Abb. 5. Tageszeitliche Verteilung der Aktivität von M4 in Oderhaus, 19. 09.–25. 10. 1991; ▼ = Sonnenuntergang, ▽ = Sonnenaufgang.

Die Aktivitätskurve von ♂ M4 in Oderhaus verläuft im Herbst, außerhalb der Fortpflanzungszeit polyphasisch (Abb. 5). Die Aktivität erreicht in den ersten beiden Nachtstunden einen Höhepunkt, das Aktivitätsniveau ist im Herbst jedoch deutlich niedriger als in den Sommermonaten. Bereits in der ersten Nachthälfte wird der Aufenthalt im Freien häufig unterbrochen. Von 2:30 bis 5:30 Uhr wurde das ♂ immer in einem Versteck geortet. In der Morgendämmerung zeichnet sich ein weiterer Aktivitätsgipfel ab.

Im Sommer bestehen wesentliche geschlechtsspezifische Unterschiede (Abb. 4). Die Aktivitätskurve der ♂♂ verläuft monophasisch, die der ♀♀ zeitweise biphasisch. Der Grund dafür dürfte die Versorgung der Jungtiere sein; beide ♀♀ kehrten in der 2. Julihälfte wiederholt gegen Mitternacht, vermutlich zum Säugen der Jungen, vorübergehend in ihre Verstecke zurück.

Diskussion

Telemetrische Untersuchungen an *Apodemus flavicollis* wurden bisher noch nicht durchgeführt. Literaturangaben zur Aktionsraumgröße der Gelbhalsmaus basieren daher ausnahmslos auf der Fang-Wiederfang-Methode. Die von PELIKAN und ZEJDA (1962), RADDA (1969) und ZEJDA und PELIKAN (1969) in verschiedenen Wald-, aber auch Wald/Feldgebieten (RÖDL 1974) festgestellten durchschnittlichen Aktionsraumgrößen liegen zwischen 1000–2000 m^2 für ♀♀ bzw. 2000–3000 m^2 für ♂♂. KUCERA (1970) gibt durchschnittliche Aktionsraumgrößen von 4633 m^2 an, ohne dabei nach Geschlechtern zu differenzieren. Maximale Aktionsraumgrößen meist fortpflanzungsaktiver ♂♂ werden mit 10000 m^2 angegeben (ZEJDA und PELIKAN 1969; RÖDL 1974; KUCERA 1970). Alle angegebenen Werte liegen weit unter den in der vorliegenden Untersuchung ermittelten Aktionsraumgrößen fortpflanzungsaktiver Gelbhalsmäuse (15500 m^2 für ♂♂ bzw. 7400 m^2 für ♀♀), die geschlechtsspezifischen Flächenunterschiede stehen jedoch in Einklang mit unseren Befunden.

Unserer Ansicht nach entsprechen die durch Fallenfang ermittelten Aktionsraumgrößen in den meisten Fällen wegen der geringen Größe der Fangflächen von oft nur 1 ha nicht den tatsächlichen Verhältnissen. Umfangreiche Untersuchungen von Brown (1966, 1969) an Waldmäusen *Apodemus sylvaticus* bestätigen dies. Diese Autorin legte mit Talg bestrichene Platten aus, auf denen durch Zehenamputation markierte Tiere individuell unterscheidbare Spuren hinterließen. So fand sie Aktionsräume der dominanten ♂♂ von bis zu 25 000 m^2. Die auf diese Weise ermittelten Flächen waren 5–10mal größer als die mit Fallenfang für dieselben Individuen erhaltenen Werte. Telemetrische Untersuchungen an der gleichen Art erbrachten ähnliche Flächengrößen (Attuquayefio et al. 1986: 36 500 m^2 für ♂♂, 15 800 m^2 für ♀♀; Tew 1992: 14 800 m^2 für ♂♂, 5 300 m^2 für ♀♀). Die Daten von Tew (1992) stammen aus einem landwirtschaftlich geprägten Untersuchungsgebiet nahe Oxford, das ähnlich wie in Fuhrberg von Hecken und Gehölzstreifen durchzogen ist. Die hier ermittelten Aktionsraumgrößen der Waldmaus entsprechen den Flächengrößen der Gelbhalsmaus in Fuhrberg. Ursache für die deutlich kleineren Aktionsräume von *A. flavicollis* in Oderhaus dürfte neben der hier bereits beendeten Fortpflanzungsaktivität auch die unterschiedliche Verfügbarkeit von Nahrung sein.

Über das Sozialverhalten von *A. flavicollis* ist, wie über das der meisten heimischen Muriden, wenig bekannt. Radda (1969) stellte bei *A. flavicollis* durch Fallenfang deutliche Aktionsraum-Überlappungen bei ♂♂, nicht jedoch bei ♀♀ fest. Er folgert daraus, daß sich fortpflanzungsaktive ♀♀ im Gegensatz zu ♂♂ territorial verhalten.

Auch bei den fortpflanzungsaktiven Gelbhalsmäusen der vorliegenden Untersuchung überlappten sich die Aktionsräume der ♂♂ sowohl untereinander als auch mit denen der ♀♀. Die Aktionsräume der ♀♀ überlappten sich dagegen nur geringfügig. Es liegt daher nahe, daß fortpflanzungsaktive ♀♀ zumindest in den engeren Bereichen ihrer Wohngebiete territorial sind und diese Bezirke gegen gleichgeschlechtige Artgenossen verteidigen bzw. monopolisieren.

Sehr ähnliche telemetrische Befunde ermittelte Tew (1992) an *A. sylvaticus* und leitet ein polygynes Sozialsystem durch Verteidigung von ♀♀ durch ♂♂ ab. Dieses bei Kleinsäugern weit verbreitete System evoluiert, wenn limitierende Ressourcen geschlechtsspezifisch sind; im vorliegenden Fall, wenn der Fortpflanzungserfolg der ♂♂ von der Anzahl der ♀♀ limitiert ist, jener der ♀♀ dagegen vom Nahrungsangebot abhängt (Emlen und Oring 1977).

Unsere Beobachtungen in Fuhrberg deuten jedoch eher darauf hin, daß bei *A. flavicollis* ein territoriales Fortpflanzungssystem mit einem dominanten ♂ an der Spitze vorliegt. M1, das schwerste ♂, bewohnte mit annähernd 35 000 m^2 den größten Aktionsraum im Gebiet. In den verschiedenen Bereichen dieses Areals wurde es regelmäßig, wenn auch in verschiedenen Zeitabständen, angetroffen. Die deutlich kleineren Aktionsräume der beiden anderen, vermutlich subdominanten ♂♂ M2 und M3 befanden sich zum überwiegenden Teil ihrer Fläche innerhalb des Gebietes von M1. Beide Tiere mieden jedoch auffällig die Nähe von M1. Die Tatsache, daß allein M1 über längere Zeiträume zusammen mit den beiden ♀♀ angetroffen wurde und auch in diesen Fällen erhebliche Flächenüberschneidungen vorlagen, spricht ebenfalls dafür, daß es sich bei diesem ♂ um ein dominantes Tier handelt. Ausdruck der Dominanzverhältnisse war auch der beobachtete Angriff auf das wesentlich kleinere, wahrscheinlich aus dem ersten Jahreswurf stammende ♂ M3. Solche Auseinandersetzungen sind für Gelbhalsmäuse offensichtlich nicht ungewöhnlich. Andrzejewski und Olszewski (1963) beobachteten an einer mit Infrarotlicht ausgeleuchteten Futterstelle im Freiland ein sehr starkes ♂ von 45 g, das andere Individuen häufig und besonders heftig attackierte. Nach Ansicht der Autoren ist ein solches ♂ in der Population dominant.

Ein territoriales Sozialsystem wurde auch für *A. sylvaticus* beschrieben. Nach Brown (1969) leben Waldmäuse in Großfamilien, die von einem dominanten ♂ kontrolliert werden. Das dominante ♂ jeder Familiengruppe verteidigt ein bis zu 25 000 m^2 großes Territorium, das durch Urin markiert wird. Die weit kleineren Aktionsräume der übrigen Bewohner liegen meist innerhalb dieses Gebietes und variieren in der Größe je nach Alter, Geschlecht und sozialer Stellung.

Obwohl die vorliegenden Befunde an *A. flavicollis* gut in das von Brown (1969) für *A. sylvaticus* beschriebene Sozialsystem passen, kann aufgrund der geringen Datenbasis der Nachweis nicht gesichert werden.

Nach Schröpfer et al. (1984) ist die Gelbhalsmaus stenök und im westfälischen Verbreitungsgebiet ein stetes Faunenelement des Laubhochwaldes. Als Primärbiotope nennen die Autoren Buchenwälder und Eichen-Hainbuchenwälder. Gebüschstreifen und Hecken bieten der Gelbhalsmaus immer wieder die Möglichkeit, aus den Waldbiotopen in die Ackerlandschaft einzudringen. Dies bestätigen auch unsere Ergebnisse in Fuhrberg. Bevorzugt werden auch hier die Säume der Primärbiotope. Besonders der strukturreiche Laubgehölzstreifen, der den Tieren infolge einer nur schwach ausgebildeten Krautschicht eine hohe Mobilität erlaubt und dennoch ausreichend Deckung bietet, scheint den Lebensraumansprüchen der Gelbhalsmaus im besonderen Maße entgegenzukommen. Die Anpassungsfähigkeit der Gelbhalsmaus an Agrarlandschaften wird durch die Nutzung fast aller in Fuhrberg vorkommenden Landschaftsstrukturen dokumentiert. Stillgelegte bzw. extensivierte Grünlandflächen spielen dabei mit Ausnahme der Grünbrache2 aufgrund des unattraktiven Nahrungsangebotes erwartungsgemäß keine Rolle. Vielmehr üben intensiv genutzte Anbauflächen wie der Kartoffelacker nahrungsbedingt eine große Anziehungskraft aus. Gelbhalsmäuse ernähren sich nach Drodz (1966) überwiegend von Baumsamen, deren Anteil saisonabhängig um 69–89 Vol.% schwankt. Daneben finden sich in den Mägen beträchtliche Anteile an Invertebraten (15%) und vor allem im Sommer auch grüne Pflanzenteile (10%). Grassamen spielen nur eine untergeordnete Rolle.

Über Verstecke von *A. flavicollis* liegen bisher keine Angaben vor. Für *A. sylvaticus*, konnte Brown (1966) nachweisen, daß einzelne Individuen ebenfalls mehrere Verstecke besaßen, gewöhnlich 4 bis 5, die regelmäßig zu verschiedenen Zeiten in Benutzung waren. Im Herbst wurden einige dieser Höhlen als Vorratskammern genutzt.

Die in Fuhrberg beobachteten höheren Laufgeschwindigkeiten und längeren nächtlichen Gesamtstrecken der ♂♂ bestätigen die von zahlreichen Autoren geäußerte Vermutung, daß insbesondere während der Fortpflanzungszeit festgestellte höhere ♂♂-Anteile in den Fallen als Anzeichen einer höheren Laufaktivität gewertet werden können. In der Literatur fehlen vergleichbare Freilanddaten für *A. flavicollis*. Für *A. sylvaticus* liegen dagegen telemetrische Daten vor. Wolton (1985) errechnete in einem Waldbiotop nächtliche Gesamtstrecken von im Mittel 422 m für ♂♂ und 275 m für ♀♀, die nur geringfügig unter den hier vorgelegten Ergebnissen bei *A. flavicollis* liegen. Tew (1992) ermittelte in einer Feldlandschaft bei sehr kurzen Meßintervallen (10 min) deutlich längere Strecken, ♂♂: 1 093 m, ♀♀: 402 m.

Über Aktivitätsmuster freilebender Gelbhalsmäuse und ihre Anpassung an Tages- und Jahresablauf liegen bisher keine Ergebnisse vor. In Gefangenschaftsuntersuchungen beschränkte sich die Aktivität der Käfigtiere weitgehend auf die Nachtstunden. Es wurden sowohl ein- als auch zweigipfelige Aktivitätskurven ermittelt (Gelmroth 1969; Mildner 1983).

Mit den zur Verfügung stehenden Radiosendern konnten in der vorliegenden Untersuchung lediglich Ortsbewegungen, jedoch nicht die Bewegungen im Versteck registriert werden. Die Tiere waren fast ausschließlich dämmerungs- und nachtaktiv. Nur während des Sommers verließen sie bereits vor Sonnenuntergang ihr Nest. Diese Befunde stimmen gut mit den Ergebnissen von Wojcik und Wolk (1985) überein, die im Nationalpark Bialowieza die Aktivitätszeiten der beiden Arten *A. flavicollis* und *Clethrionomys glareolus* mit Lebendfallen untersuchten. *A. flavicollis* hatte hier einen monophasischen nächtlichen Rhythmus, der sich in einem sprunghaften Anstieg der Fänge nach der Dämmerung und einem Maximum zwischen 22:00 Uhr und 2:00 Uhr äußerte. Während des Tages fanden sie *A. flavicollis* praktisch inaktiv. Mit der gleichen Methode hatte bereits Buchalczyk (1964) den Aktivitätsrhythmus der Gelbhalsmaus in Bialowieza untersucht. Im Gegensatz zu Wojcik und Wolk (1985) und in Übereinstimmung mit den hier vorliegenden Ergebnissen fand er Hinweise auf einen Wechsel von einem monophasischen nächtlichen Aktivitätsrhythmus im Juli und August zu einem zweigipfeligen Rhythmus im September mit erhöhter Aktivität in den frühen Morgenstunden.

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Zusammenfassung

In einer 5-monatigen Feldstudie in Niedersachsen wurden 1991 in einem landwirtschaftlich geprägten Gebiet bei Fuhrberg nahe Celle und in einem Bergwald bei Oderhaus im Harz telemetrische Untersuchungen zur Raumnutzung und zur Aktivitätsrhythmik von *Apodemus flavicollis* durchgeführt. 7 Tiere wurden mit Radiosendern markiert. Von ihnen liegen 1 737 Ortspeilungen vor. Für fortpflanzungsaktive Gelbhalsmäuse beträgt die Aktionsraumgröße 3 700 bis 34 800 m^2, im Durchschnitt 15 500 m^2 bei ♂♂ und 4 400 bis 9 700 m^2, im Durchschnitt 7 400 m^2 bei ♀♀. Außerhalb der Fortpflanzungszeit waren die Aktionsräume eines ♀ und eines ♂ mit 3 800 bzw. 3 600 m^2 wesentlich kleiner. Bei 2 Individuen wurden Verlagerungen der Aktionsräume festgestellt. Aktionsräume von ♂♂ und ♀♀ sowie der ♂♂ untereinander überlappten sich während der Fortpflanzungszeit z. T. erheblich. ♀♀ untereinander monopolisierten dagegen zumindest die engeren Bereiche ihrer Wohngebiete. Fortpflanzungsaktive ♂♂ erreichten signifikant höhere Laufgeschwindigkeiten als ♀♀ und legten längere nächtliche Gesamtstrecken zurück. Aktivität im Freien beschränkte sich in der Regel auf die Dämmerungs- und Nachtstunden. Die Aktivitätsphase wurde im Sommer nur von ♀♀ selten durch Versteckbesuche unterbrochen. Im Herbst wurden von einem ♂ nachts regelmäßig längere Ruhepausen im Versteck eingelegt. Die Anpassungsfähigkeit der Gelbhalsmaus an Agrarlandschaften wird durch die Vielgestaltigkeit ihres Lebensraumes in Fuhrberg dokumentiert. Neben den Saumhabitaten wurden vor allem die intensiv bewirtschafteten Anbauflächen von den Tieren genutzt, stillgelegte bzw. extensivierte Grünlandflächen in der Regel aber deutlich gemieden. Die Verstecke waren immer an Gehölze gebunden. Versteckwechsel traten regelmäßig auf.

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The effect of female distribution on male territoriality in Chinese Water deer (*Hydropotes inermis*)

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Abstract

Territoriality in the Chinese water deer (*Hydropotes inermis*) was studied in its native habitat at Poyang Lake, Jiangxi, China. Adult males held small territories of 0.5 ha on average during the mating season. The territorial grounds were located according to the ranging behavior of females. Males held clustered or individual mating territories in areas frequented by females. Male territoriality showed daily fluctuation following the change in female density within males' territories. Our findings provide strong evidence that male spatial behaviour in the mating season is primarily determined by female distribution pattern in the water deer.

Introduction

In species lacking male parental care, such as ungulates, males are selected to increase their reproductive success through increasing copulations (Clutton-Brock et al. 1982). Since the distribution patterns of receptive females construct the spatial feature of mating opportunities, mating tactics of males are determined, directly or indirectly, by female distributions (e.g., Jarman 1974; Parker 1978; Bradbury 1981; Gosling 1986; Rubenstein 1986). Therefore, the diversity and dynamics of female distribution may impose a strong effect on the form and fluctuation of male spatial behaviour. The intra- and interspecific variations in the distribution of cervid females could be one of the main reasons why spatial behaviour of males is so diversified in this group of animals. Not surprisingly, territoriality has recently been found in some populations of species which were traditionally considered non-territorial (e.g., Miura 1984; Marchinton and Atkeson 1985; Apollonio 1989; Carranza et al. 1990).

The behaviour of Chinese water deer (*Hydropotes inermis*) introduced in Europe has been described by various authors (Cooke and Farrell 1981, 1983; Feer 1982; Stadler 1988, 1991). The male deer is territorial, at least in the population in England (Cooke and Farrell 1981, 1983; Stadler 1988, 1991). The most detailed study was conducted by Stadler (1991) at Whipsnade Wild Animal Park. He reported that adult male water deer hold small permanent territories that average 0.98 ha in size and show the highest degree of territoriality in the rutting season. A similar pattern of seasonal fluctuation in male territoriality is also well reported in another small deer, the roe deer *Capreolus capreolus* (Hennig 1962; Kurt 1968; Bramley 1970; Stüwe and Hendrichs 1984; Chapman et al. 1993). None of these authors, however, has specifically probed the effect of female movement on male territoriality. Here we report on the territorial system in a natural population of the water deer in China, where males appeared to space their mating territories and showed daily fluctuation in their territoriality according to the distribution of females.

Material and methods

The research area was located at 29°10′ N and 116°03′ E at Jiniushan Hill, Yongxiu County, Jiangxi, China (Fig. 1). The mean annual temperature is 17 °C (range: –4 to 40 °C). The annual precipitation is 1 400–1 500 mm, 48.2% of which falls in April, May and June. The habitat of the water deer is the grassland and hills at the mouth of Ganjiang River. Jiniushan Hill is a low, narrow zone slightly elevated above the grassland with an area of about 1 km^2. It is submerged annually for 2–4 weeks in the summer, when all the deer take shelter in the higher Jishan Hills.

This research was conducted from May 1988 to April 1989. Most of the observations were centered on 22 individually identified deer (11 males and 11 females) on Cluster 2 (Fig. 1) from October 1988 to January 1989, a period that included the mating season of the deer. The activity of the deer during the day time was composed of two active periods (dawn to 10.00 h and 15.30 h to dusk), when the deer were in move, and one resting period (between 10.00 h and 15.30 h), when most deer were ruminating, resting or sleeping. We hence divided our daily observations into three sessions: morning (7.00 h–10.00 h), afternoon (12.00 h–13.30 h), and evening (15.30 h–17.30 h). Individuals were identified by their facial marks with a 10 × 30 NIKON spotting scope. Males (denoted by “M”) possessed tusks and thus were distinguished from females (denoted by “F”). We used the focal animal and scan sampling methods to collect observational data (ALTMANN 1974). We chose focal animals each day and alternated among these animals every 10 min. We also scanned animals four times a day (at 8.00 h, 11.00 h, 13.00 h and 16.30 h), two of which were in the active period and the other two in the resting period, and recorded their locations. To determine the relationship between male territoriality and female distribution, we defined and measured the following parameters:

1. Territory size (TSZ): defined as a defended area. We dotted the locations where a male marked or drove out invading males on a topographic map, and calculated the area using the minimum polygon method (MOHR 1947).

2. Territory stability (TST): defined as the percentage of time spent, for the holder, within his territory (see OWEN-SMITH 1975). This index is intended to show an animal’s tenacity in territory-holding. It was measured separately for the active and resting periods using the percentage of scans that an animal was observed within its territory.

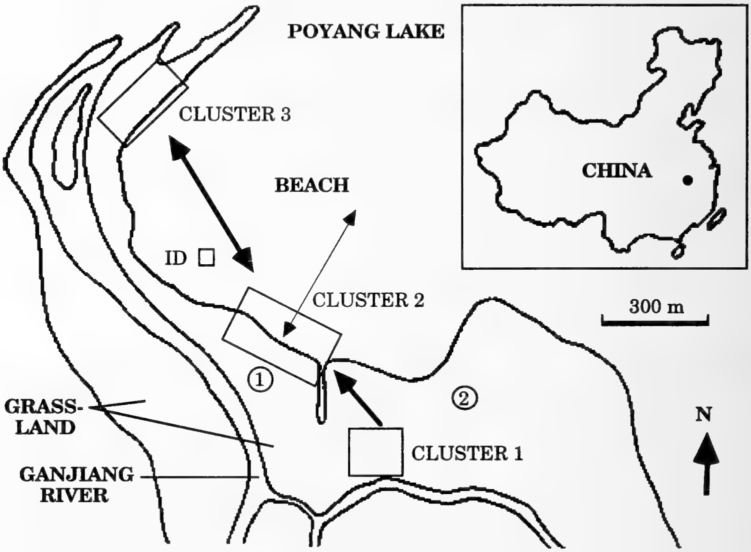

Fig. 1. The research area. Cluster 1, 2 and 3 were the approximate locations of the three territorial grounds. IT indicates the individual territory of M12. Thick arrowed lines represent the movement of males between territorial grounds. The thin arrowed line shows the movement of females, who regularly visited Cluster 2, between the resting place and feeding ground. Jiniushan Hill and Jishan Hills are marked with (①) and (②), respectively.

3. Female occurrence frequency (FOF): defined as the average number of females per scan on a territory and used for evaluating the quality of the territory.

4. Female density (FD): defined as female occurrence frequency per hectare of territory. It was obtained by using FOF divided by the territory size and multiplied by 10^4.

Also, we searched other areas regularly to monitor the direction and sequence of the movement of males and females between territorial grounds. The word "cluster" was used to indicate a territorial ground where several males spaced their territories closely (within 50 m between the nearest points of two neighbouring territories).

Results

Establishment of territories

Five females and three males were found at Cluster 1 (Fig. 1) on 25 October 1988. The females ranged over an area of 20–40 ha and intensively used a 5 ha core area for feeding and resting. Females' home ranges overlapped extensively and no areas were defended. Each of the three males, however, occupied an exclusive area of about 0.5 ha by driving out invaders and marking (see Sun et al. 1994).

On 3 and 4 November 1988, all five females moved to Cluster 2 (Fig. 1), coinciding with the onset of grass-cutting activity of local farmers at Cluster 1. The three males came to Cluster 2 two or three days later and began to set up new territories. By 12 November, nine males and six females from other areas, as a result of continued grass-cutting activity of local people, had also joined Cluster 2. Having failed to set up a territory, male M13 left Cluster 2 for Cluster 3, which had been divided into territories by six males and used as a feeding ground by seven to nine females. Male M11 deserted his territory on Cluster 2 after females previously visiting his territory had shifted to other places. Male M12 set up an individual territory of 0.5 ha on a quiet short grass area (Fig. 1) in early November. He stayed with F12, who was seldom out of the territory throughout the mating season.

Correlates of territories

During the mating season, all adult males were territorial. For the 11 territories on Cluster 2 (Fig. 2), the mean size was 4,980 $m^2 \pm 1,260$ (SD), with FOF 0.84 ± 0.48 (SD) and FD 1.64 ± 0.77 (SD). The mean TST was 96.85% in the active period and 74.14% in the resting period (Tab. 1). Positive associations between FOF and TSZ ($r = 0.699$, $P < 0.05$), FOF and FD ($r = 0.885$, $P < 0.01$), and FD and TST during the active period ($r = 0.768$, $P < 0.05$) were detected using the Pearson's product-moment correlation coefficient. The correlation between FOF and male TST at active period was marginally significant ($r = 0.558$, $P \approx 0.05$). Other correlations in the pairwise comparisons of these parameters failed to show any significance. Also, female density over the 11 territories was not differently from the uniform distribution (Kolmogorov-Smirnov goodness of fit test, $D = 0.64$, $N = 11$, $P = 0.07$). TST was significantly higher during the active period than the resting period (Wilcoxon paired-sample test, $T = 3$, $N = 11$, $P = 0.006$).

Use of territories

Females used the quiet beach of the lake as resting place and came to males' territorial grounds as feeding sites. The 11 regular female visitors on Cluster 2 came to feed at 15.30 h each day, resulting in a locally high density (from 0.13/ha on the beach to 1.64/ha on the cluster) of females on the territorial ground. They scattered across the 11 territories and could freely move between territories without interference from males. The ter-

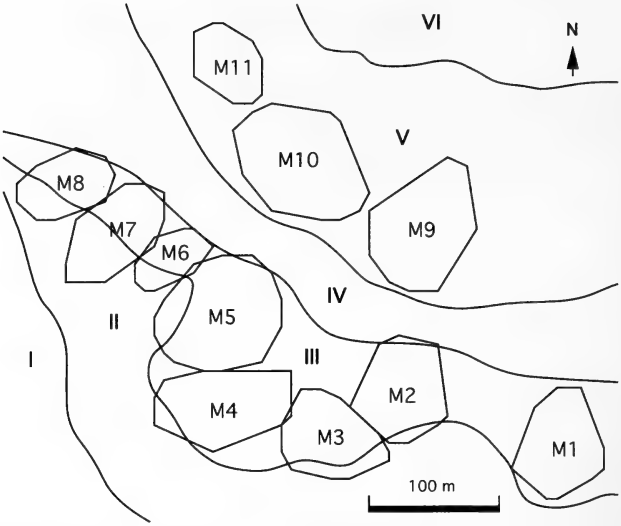

Fig. 2. The locations, shapes, and sizes of the 11 territories on the territorial ground, Cluster 2. Vegetation types are also shown: I. *Carex*-dominant zone; II. *Carex* and *Artemisia*-dominant zone; III. *Artemisia*, *Kalimeris* and *Viola*-dominant zone; IV. sparse *Artemisia* Zone; V. *Kalimeris* and *Artemisia*-dominant zone; VI. beach.

Table 1. Territory sizes, territorial stabilities, occurrence frequencies of females and female densities of the 11 territories on Cluster 2 during the mating season. (The numbers in parentheses are the number of total observations.)

Territory Holder	Territory (TSZ) (m)	Female Occurrence Frequency (FOF) (Females/scan)	Female Density (FD) (Females/ha)	Territorial Stability (TST) (%)	
				Active Phase	Resting Phase
M1	3 700	0.78(9)	2.10	100.0(6)	100.0(5)
M2	4 010	0.88(25)	2.19	100.0(17)	81.3(16)
M3	3 940	0.82(11)	2.08	100.0(9)	57.1(7)
M4	6 060	1.15(26)	1.90	100.0(17)	81.3(16)
M5	6 840	1.76(29)	2.57	100.0(19)	88.9(18)
M6	2 990	0.21(14)	0.72	100.0(10)	90.0(10)
M7	4 990	0.29(31)	0.58	86.4(22)	100.0(19)
M8	4 280	0.17(23)	0.41	88.9(9)	28.6(7)
M9	6 300	1.50(8)	2.38	100.0(6)	83.3(6)
M10	6 710	0.82(22)	1.22	90.0(20)	55.0(20)
M11	4 960	0.94(18)	1.90	100.0(6)	50.0(6)

ritories were divided into two sub-clusters of territories by a non-territorial zone, where few plants grew well (Fig. 2). Females frequently travelled through that area, but did not linger there. Also, females feeding on Cluster 2 were rarely seen outside of the 11 territories. They went back to the beach at 10.00 h the second day and rested there until 15.30 h. Activities of the deer at night were not clear due to lack of night-vision equipment. The resting place was 800–1,500 m away from the feeding ground, and the ranging area of females was estimated to be 50–120 ha. Four females rested in tall grass near Cluster 2 after they transferred from Cluster 1. They shifted their resting places to the beach after the plants used as cover were cut.

Males were rarely observed out of their own territories during the active period. When females left their feeding ground for the beach, some males vacated their territories to join the females. Males often pursued and courted females on the beach, but no matings were observed. These males always returned alone to their territories by 15.30 h, before females came back to feed on the territorial ground. Males usually marked their territories upon their return. A few males remained in their territories throughout the resting period. They were seen to court females which passed by infrequently.

From the onset of the non-mating season at the end of January, the frequencies of marking behaviour in males and chases between males during the active period both tapered from 4.0/hr in the mating season down to less than 0.5/hr in April, indicating a significant drop in male territoriality.

Discussion

Female ungulates are usually more sensitive to disturbances than males (Clutton-Brock et al. 1982, 1989; Deutsch and Nefdt 1992). In our study, the change of the territorial ground from Cluster 1 to Cluster 2 was initiated by females. The energetically costly daily travel between the beach and the feeding ground could have been avoided (like the case of F12), had there been no disturbance. Thus, grass-cutting activity of local farmers seemed to be responsible for the shift of the females from tall grass areas at Clusters 1 and 2 to the quiet beach. The time lag of the males' movement to Cluster 2 indicated that the subsequent relocation of males' territories was initiated by the change in female home range.

The density of females in some cervids appears to play a pivotal role in males' assessment of whether and where to set up territories (Bramley 1970; Miura 1984; Carranza et al. 1990). This is supported by our study. First, all the 11 territories on Cluster 2 were located in areas with a high density of females, leaving the areas not frequented by females, like the non-territorial zone between the two sub-clusters (Fig. 2), unoccupied. Second, territories may be spaced in close proximity or solitarily, but no territories were located in areas without females, even if the food was abundant (Sun 1989). Males may desert a territorial ground if they failed to obtain a turf with a high female density (like the case of M13) or if females formerly feeding on their territories shifted to other places (like the case of M11). Finally, the positive correlation between female density and territorial stability in the active period provided a strong evidence that males' tenacity in holding territories was determined by female density. When fewer females appeared in territories during the resting period, males were more inclined to leave their territory to follow females.

The positive correlation between the size and occurrence frequency of females of a territory can be explained by the moderate evenness in female density over the 11 territories on Cluster 2. That is to say a large territory may include more females, which is similar to the case in roe deer (*Capreolus capreolus*) (Bramley 1970) and other vertebrate species (see review in Davies 1991 and Stamps 1994). It follows that males should defend a territory as large as possible. This tendency, however, is counteracted by the efficiency in territorial defense, which decreases as the size of a territory increases and eventually sets the upper limit of the size (Gosling 1981). Compared with other ungulates of similar body size (e.g., Estes 1967; Walther 1972; 1978; Hofmann 1973; Dunbar and Dunbar 1974; Dubost 1980; Kingdon 1982), the territory of the water deer in our study was very small, only half of that reported by Stadler (1991). This may be due to the difference in female ranging behaviour between the two populations: females used a larger area in our study than in Stadler's study. It is suggested that large ranging areas of females make it less possible or worthwhile for males to defend large territories that include the whole ranging areas of females (Barrette 1977; Gosling 1981). A more efficient way to gain access to reproductive opportunities may be to wait at some places where females occur most frequently (Bradbury 1981). Hence, male territory clusters can be expected in areas where female densities are high, the extreme form of which is lek (Bradbury 1981). This may account for the formation of territorial grounds in the water deer. The small territory size may be a result of intense competition among males in partitioning the limited feeding ground frequented by females. In these small and clustered territories, females are easily prompted to move between the territories, which did not favour males' interfering with females (Clutton-Brock et al. 1988; 1989; Clutton-Brock 1989; Stillman et al. 1993). This may be the reason why male water deer showed no attempts to prevent females from moving freely between territories both in Stadler's (1991) study and ours. The territorial system in the water deer looks somewhat like a lek (Buechner 1961; Leuthold 1966; Schuster 1976; Fryxell 1987; Clutton-Brock et al. 1988). However, the fact that males occupied relatively large territories (compared with lekking animals), which included the main food resource, was contrary to the criteria of a lek (Bradbury 1981, 1985; Clutton-Brock et al. 1988; Wiley 1991). This territorial system resembled the mating territory in some African ungulates (Estes 1974; Gosling 1986), which is considered an intermediate form between resource defense territories and classical leks (Clutton-Brock 1989).

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Zusammenfassung

Der Einfluß der Verteilung von Weibchen auf die Territorialität der Männchen beim chinesischen Wasserreh (Hydropotes inermis)

Das chinesische Wasserreh (*Hydropotes inermis*) wurde in seinem heimischen Lebensraum am Poyang See, Jiangxi, China, studiert. Diese Studie behandelt das Territoriumsverteidigungsverhalten während der Paarungszeit von Ende Oktober bis Januar. Während dieser Zeit war der tägliche Aktivitätszyklus von Weibchen folgendermaßen: Aktivitätsperiode von Tagesanbruch bis Mitte Vormittag, Ruheperiode bis Mitte Nachmittag und Aktivitätsperiode bis Einbruch der Dunkelheit. Die Weibchen verbreiteten sich weit voneinander im Sand entlang des Sees während der Ruheperiode. Während der Aktivitätsperiode liefen sie hinüber zum Weidegelände, das in der Nähe unter Territoriumsherrschaft der Männchen gehalten wurde. Die meisten Territorien der Männchen waren eng nebeneinander, und die Männchen versuchten die Weibchen zu umwerben, während sie auf ihren Territorien grasten. Wenn alle Weibchen das Weidegelände verließen und zurückkehrten zur Sandfläche entlang des Sees um zu ruhen, folgten einige Männchen den Weibchen nach, während andere in ihren Territorien auf dem Weidegelände verblieben.

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Extensive mitochondrial-DNA differentiation among European Red deer (*Cervus elaphus*) populations: implications for conservation and management

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Abstract

To investigate genetic differentiation among populations of European red deer (*Cervus elaphus*), mitochondrial(mt) DNA of a total of 70 individuals from 15 sampling sites in Western, Central, and Southeastern Europe was digested with 16 restriction enzymes. A total of 69 restriction sites allowed us to define nine haplotypes, whereby most of the samples were monomorphic for a particular haplotype. Relationships among haplotypes were largely consistent both with the geographical distribution of haplotypes among sampled populations and with relationships among samples as inferred from allozyme electrophoresis. Given the subdivision of European red deer into several distinct gene pools, mtDNA restriction profiles will serve as a powerful tool for a number of applications in conservation and management: Regarding the alteration of native gene pools by introductions of red deer from various parts of Europe, mtDNA haplotypes allow to assess the genetic impact of introductions and to trace the origin of introduced females. Even at a comparatively small geographic scale the distribution of haplotypes is helpful in detecting isolation or hybridization among populations. Finally, mtDNA restriction profiles may contribute to shed light both on the controversial systematic position and on the geographic origin of some subspecies, such as the Sardinian red deer.

Introduction

Among all extant European ungulate species the red deer (*Cervus elaphus*) is probably the one most strongly affected by anthropogenic influences on genetic population structure. Many populations are isolated because of fragmentation of the landscape (e. g. forest clearings, fenced motorways) and being kept in enclosures (cf. Kleymann 1976 a; Hartl et al. 1990 a; Ströhlein et al. 1993). Selective hunting in favour of large and branched antlers was found to result in frequency changes of allozyme marker alleles which are associated both with antler traits (Hartl et al. 1991, 1995) and with various fitness components (Pemberton et al. 1988, 1991). A potentially very important anthropogenic influence on the genetic structure of red deer populations comes from the introduction of foreign deer into autochthonous stocks. Artificial hybridization of red deer from different source populations, either in the course of restocking operations or of attempts to breed for larger antler size, has been a common practice in several European countries for centuries (cf. Beninde 1937, 1940). Given the variety of red deer subspecies proposed to exist in Europe on the basis of morphological characters (cf. Trense 1989), such hybridization may have caused considerable alterations of local gene pools. However, whereas many red deer populations are known to have received some introductions, the exact origin of the introducted animals is usually not recorded.

Apart from a single approach based on blood groups (Kleymann 1976b), only allozymes and blood proteins have been used for assessing genetic differentiation among populations and presumed subspecies of European red deer so far (e.g. Bergmann 1976; Gyllensten et al. 1983; Dratch and Gyllensten 1985; Herzog 1988, 1990; Hartl et al. 1990a, 1991, 1993a; Herzog et al. 1991; Ströhlein et al. 1993). However, biochemical genetic differences among populations and subspecies were quantitative (variation in frequencies of ubiquitous alleles) rather than qualitative (rare, private or fixed alleles). Frequency differences of ubiquitous alleles in red deer can be ascribed to a variety of demographic factors (Ryman et al. 1981; Hartl et al. 1990a; Herzog et al. 1991) and may to a certain extent be also due to selection (Pemberton et al. 1988, 1991; Hartl et al. 1991, 1995). Thus, in this species, electromorphs alone are not very powerful markers for resolving differentiation and for detecting introgression at the population level.

Due to a smaller effective population size for mitochondrial than for nuclear genes (Birley and Croft 1986), population specific markers should be found more likely in mitochondrial(mt) DNA than in allozymes (cf. Avise et al. 1987). Indeed, in several cases restriction site analysis of mtDNA has already been successfully applied to stock identification in the context of conservation and management of fish populations (see Avise 1994, for a review). However, in red deer, data on intraspecific mtDNA differentiation are available so far only from North American elk, where no variation among populations and subspecies could be detected (Cronin 1992). It is the aim of the present study to investigate mtDNA differentiation among European red deer populations on the basis of restriction fragment length polymorphisms. Furthermore, the distribution of mtDNA haplotypes will be evaluated as to its relevance for conservation and management of this species.

Material and methods

A total of 70 red deer from 15 sampling sites in Europe were investigated (Fig. 1). Except for the samples from Vienna and Chambord, which were drawn from populations in enclosures, all other samples are from native populations. In this context, the term 'native' refers to populations, where, at least in historical times, introductions of foreign deer are neither recorded nor likely.

MtDNA analyses

Preparation of mitochondria from frozen liver, extraction and purification of mtDNA were performed according to standard methods (Hartl et al. 1993b). MtDNA was digested by a total of 16 six-base cutting restriction endonucleases purchased from Boehringer Mannheim according to protocols provided by the supplier: ApaI, BamHI, BclI, BglII, ClaI, DraI, EcoRI, EcoRV, HindIII, PstI, PvuII, SacI, SfuI, StyI, XbaI, XhoI. One gram of frozen liver yielded mtDNA sufficient for two to three digests. Fragments were separated electrophoretically in agarose gels containing EtBr and visualized under UV light (for details see Hartl et al. 1993b). Fragment lengths were determined using Lambda phage DNA digested with HindIII as a size standard. Restriction sites were mapped by the double-digestion method (Avise 1994). In order to make our data comparable to

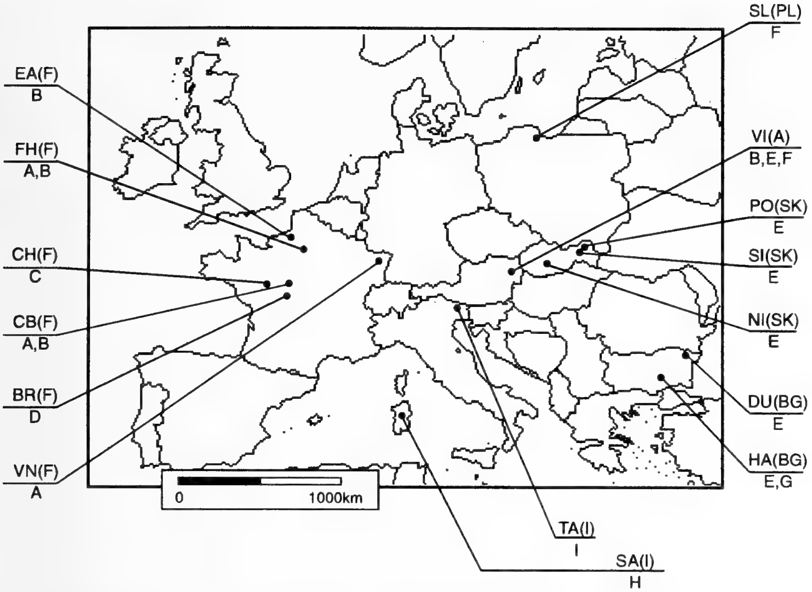

Fig. 1. Geographical distribution of sampling sites of European red deer.

those of previous studies on cervids, we attempted to adjust the starting site for mapping by comparing our data with those presented on North American elk by CRONIN (1991).

Allozyme analyses

For assessing correspondence of major groups of European red deer as revealed both by mtDNA and allozyme analyses, we used those samples, where numbers of available individuals were sufficient for obtaining reasonable estimates of allozyme allelic frequencies ($n > 25$, except for DU, $n = 13$, and for SL, $n = 10$). Data are based on 43 presumptive loci screened by HARTL et al. (1993a) in samples from SI, PO, DU, HA, and by HARTL et al. (unpubl.) in samples from Poland (SL) and France.

Statistics

Relationships among haplotypes were inferred by the following methods: Based on restriction sites (Tab. 1) we calculated the mean number of base substitutions per nucleotide (p) using formulas 10 and 8 in NEI and LI (1979). To display relationships among mtDNA haplotypes, the p-values were used to generate an unrooted tree by means of the FITCH option in FELSENSTEIN's PHYLIP-package (FELSENSTEIN 1988). This procedure was preferred to standard cluster analysis because of the possibility of differences in evolutionary rates among major mtDNA lineages. Based on NEI's (1978) unbiased genetic distance, the same method was used for inferring genetic relationships among samples as revealed by allozyme allelic frequencies. Cladistic analysis of mtDNA data was performed by using restriction sites as characters and calculating WAGNER parsimony trees by means of the MIX option (PHYLIP). Clades remaining stable in various equally parsimonious trees were separated from ambiguous ones by calculating a majority rule consensus tree (CONSENSE option in PHYLIP).

Table 1. Numerical restriction maps of 9 mtDNA haplotypes (A–I) in European red deer. 1 (0) = restriction site present (absent). Among the 16 restriction endonucleases applied, only XhoI had no cutting site. Based on the comparison of cutting sites of restriction enzymes used in both studies, the starting point for mapping corresponds to that of Cronin (1991).

Enzyme	Position	Haplotypes								
		A	B	C	D	E	F	G	H	I
ApaI	0.1	1	1	1	1	1	1	1	1	1
	3.6	1	1	1	1	1	1	1	1	1
	4.4	1	1	1	1	1	1	1	1	1
	13.4	0	0	0	0	0	0	0	1	0
BamHI	0.4	1	1	1	1	1	1	1	1	1
	7.8	1	1	1	1	0	1	0	0	0
	16.4	1	1	1	1	1	1	1	1	1
BclI	0.1	0	1	0	0	1	1	0	0	1
	2.9	1	1	1	1	1	1	1	1	1
	4.6	1	1	1	1	1	1	1	1	1
	5.4	1	1	1	1	1	1	1	1	1
	6.3	0	0	0	0	0	0	1	0	0
	7.7	1	1	1	1	1	1	1	1	1
	11.2	1	1	1	1	1	1	1	1	1
	11.9	1	1	1	1	1	1	1	1	1
BglII	0.4	1	1	1	1	1	1	1	1	1
	15.8	1	1	1	1	1	1	0	1	1
ClaI	1.2	1	1	1	1	1	1	1	1	1
	10.5	1	1	1	1	1	1	1	1	1
DraI	0.5	1	1	1	1	1	1	1	1	1
	1.1	1	1	1	1	1	1	1	1	1
	1.9	1	1	1	1	1	1	1	1	1
	3.5	1	1	1	1	1	1	1	1	1
	5.6	1	1	1	1	1	0	1	1	1
	11.3	1	1	1	1	1	1	1	1	1
	12.5	1	1	1	1	1	1	1	1	1
	13.6	1	1	1	1	1	1	1	1	1
	16.2	1	1	1	1	1	1	1	1	1
EcoRI	9.3	1	1	1	1	1	1	1	1	1
	12.1	1	1	1	1	0	1	0	0	0
	12.4	0	0	0	0	1	0	0	0	1
	15.7	1	1	1	1	1	1	1	1	1
EcoRV	2.9	1	1	1	1	1	1	1	1	1
	5.6	1	1	1	1	1	1	1	1	1
	12.8	1	1	1	1	1	1	1	1	1
	13.6	1	1	1	1	1	1	1	1	1
	15.8	1	1	1	1	1	1	0	0	1
HindIII	6.0	1	1	1	1	1	1	1	1	1
	7.8	1	1	1	1	1	1	1	1	1
	12.0	1	1	1	1	1	1	1	1	1
PstI	8.8	1	1	1	1	1	1	1	1	1
	9.5	1	1	1	1	1	1	1	1	1
PvuII	9.2	1	1	1	1	1	1	1	1	1
	9.9	1	1	1	1	1	1	1	1	1
SacI	7.5	1	1	1	1	1	1	1	1	1
	9.1	1	1	1	1	1	1	1	1	1

Results

Cutting red deer mtDNA with 16 restriction enzymes yielded a total of 69 restriction sites, representing approximately 400 bp of mtDNA sequence or 2.4% of the 16,600 bp genome generally found in cervids (cf. Cronin 1991). The restriction site data allowed us to define nine haplotypes (A – I, Tab. 1). The distribution of haplotypes among the various red deer samples studied is shown in table 2. Most single samples or groups of geographically proximate samples were monomorphic for a unique haplotype and, thus, an analysis of relationships among haplotypes corresponded to a certain extent to that of genetic relationships among presumptive populations. Pairwise values of nucleotide divergence (p) among haplotypes are presented in table 3, overall phenetic relationships among haplotypes are shown in a FITCH-tree in figure 2. Relationships among haplotypes as revealed by a character state approach (Wagner parsimony) are shown in a majority rule consensus tree (Fig. 3), calculated from the 24 most parsimonious solutions found in resolving the restriction site matrix in table 1. Both trees yielded essentially the same result: a major separation of haplotypes A-F from haplotypes E and I, and from haplotypes G and H, the latter two groups being also quite distinct from one another.

The major tree pattern obtained from allozyme data was fairly similar to that based on the geographic distribution of mtDNA haplotypes (see Fig. 4). The samples with haplotype E were generally well separated from those with haplotypes A, C, and D. Of all samples with haplotype E, the one polymorphic for haplotypes E and G (HA) was most separated from samples with haplotypes A–D. The overall rather intermediate position of samples monomorphic for haplotypes B and F (Fig. 4) conformed with relationships among haplotypes as shown in figures 2 and 3. There B and F held a linking position between haplotypes A, C, D on the one hand, and haplotypes E and I on the other.

Table 1. (continued)

Enzyme	Position	Haplotypes								
		A	B	C	D	E	F	G	H	I
SfuI	3.4	1	1	1	1	1	1	1	1	1
	8.2	1	1	1	1	1	1	1	1	1
	9.9	1	1	1	1	0	1	1	1	0
	11.1	1	1	1	1	1	1	1	1	1
	12.2	1	1	1	0	1	1	1	1	1
	13.5	1	1	1	1	1	1	1	1	1
	14.8	1	1	1	1	1	1	1	1	1
StyI	2.2	1	1	1	1	1	1	1	1	1
	2.6	1	1	1	1	1	1	1	1	0
	3.0	1	1	1	1	1	1	1	1	1
	3.5	1	1	1	1	1	1	1	1	1
	6.8	1	1	1	1	1	1	1	1	1
	8.4	0	0	0	0	0	0	1	1	0
	9.5	1	1	1	1	1	1	1	1	1
	10.3	1	1	1	1	1	1	1	1	1
	10.9	1	1	1	1	1	1	1	1	1
	12.6	1	1	1	1	1	1	1	1	1
	15.3	0	0	1	0	0	0	0	0	0
XbaI	1.3	1	1	1	1	1	1	1	1	1
	4.3	1	1	1	1	1	1	1	1	1
	5.8	1	1	1	1	1	1	1	1	1
	14.7	1	1	1	1	1	1	1	1	1
	15.5	1	1	1	1	1	1	1	1	1

Discussion

In the present study, covering red deer populations from Western, Central, and Southeastern Europe, we detected considerable mtDNA differentiation among local samples. Both the exclusive occurrence of particular mtDNA haplotypes in single samples or in groups of geographically proximate samples, and the extent of nucleotide divergence among haplotypes ($p =$ up to 0.4%) were unexpected in the light of previous results. The first study on intraspecific mtDNA variation in red deer was conducted by Cronin (1992), who examined four subspecies of North American elk across a sampling area comparable to ours. Except for one case, where the mtDNA of one out of 10 individuals deviated at one out of 44 restriction sites, all subspecies were found monomorphic for the same haplotype. By comparing mtDNA differentiation in elk with that in other cervid species Cronin (1992) proposed that the lack of significant variation among elk populations and subspecies may reflect founder effects following colonization of North America south of Alaska during the late Pleistocene. Our results support Cronin's hypothesis in that they show that red deer mtDNA is not generally less variable among populations than in the other species of Cervidae studied so far.

Table 2. Sampling sites of red deer in Europe (code, name, country), and distribution of mtDNA haplotypes (A – I) among samples.

Sampling site	Haplotypes								
	A	B	C	D	E	F	G	H	I
VN Vosges du Nord (F)	6	–	–	–	–	–	–	–	–
EA Eany (F)	–	6	–	–	–	–	–	–	–
CH Champchevrier (F)	–	–	5	–	–	–	–	–	–
BR Brouard (F)	–	–	–	5	–	–	–	–	–
FH Forêt de Halatte (F)	2	4	–	–	–	–	–	–	–
CB Chambord (F)	1	3	–	–	–	–	–	–	–
PO Polana (SK)	–	–	–	–	5	–	–	–	–
SI Sitno (SK)	–	–	–	–	2	–	–	–	–
NI Nitra (SK)	–	–	–	–	2	–	–	–	–
SL Slowinski (PL)	–	–	–	–	–	7	–	–	–
DU Dulovo (BG)	–	–	–	–	4	–	–	–	–
HA Haskovo (BG)	–	–	–	–	3	–	2	–	–
SA Sardinia (I)	–	–	–	–	–	–	–	3	–
TA Tarvis (I)	–	–	–	–	–	–	–	–	4
VI Vienna (A)	–	2	–	–	2	2	–	–	–

Table 3. Sequence divergence (p, in per cent) among the nine mtDNA haplotypes detected in European red deer.

	A	B	C	D	E	F	G	H	I
A	–								
B	0.04	–							
C	0.04	0.09	–						
D	0.04	0.09	0.09	–					
E	0.18	0.14	0.23	0.23	–				
F	0.09	0.04	0.13	0.14	0.18	–			
G	0.28	0.32	0.32	0.33	0.38	0.37	–		
H	0.23	0.27	0.27	0.28	0.33	0.32	0.14	–	
I	0.23	0.18	0.28	0.28	0.05	0.23	0.43	0.38	–

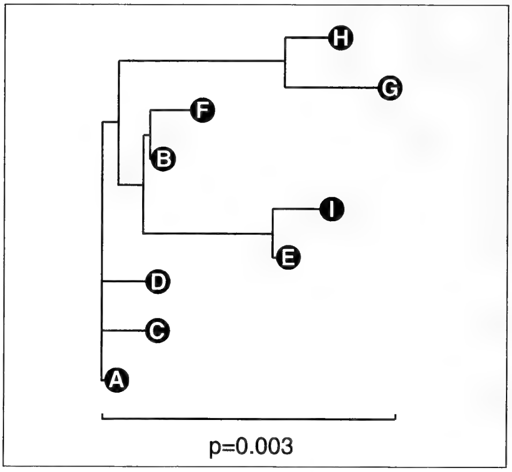

Fig. 2. Unrooted tree showing phenetic relationships among mtDNA haplotypes A – I (p, Nei and Li 1979/ FITCH-tree, PHYLIP).

Because of the lack of data on closely related outgroup species and on red deer from several important nuclei in Southwestern, Northern, and Eastern Europe our data presently are too scarce to provide a comprehensive pattern of phylogenetic relationships in European red deer. However, the distribution of mtDNA haplotypes within and among samples allows several conclusions relevant for conservation and management of this species:

In our data we found a major distinction among three mtDNA lineages (Figs. 2, 3). The "northwestern (NW) lineage" comprised several haplotypes (A, B, C, D, F) found in red deer samples from France and Poland (Tab. 2, Fig. 1). The "eastern (EA) lineage" comprised two haplotypes found in samples from Slovakia and Bulgaria (type E), and in the sample from Northern Italy (type I). The "southeastern (SE) lineage" comprised two haplotypes found in one sample from Bulgaria (type G) and in the sample from Sardinia (type H).

We are aware that evaluating subspecies status by considering a particular magnitude of genetic distance obtained from just one marker system a threshold can be seriously misleading (cf. Hartl et al. 1990b; Stüwe et al. 1992; Cronin 1992, 1993). Moreover, especially in mtDNA, separation of lineages may not always be consistent with separation of populations or subspecies (Avise 1989; Cronin 1993). However, with some exceptions discussed below (Vienna, Sardinia), the geographical distribution of haplotypes of the three major lineages may correspond to the distribution of red deer subspecies as proposed by Groves and Grubb (1987) on the basis of morphological criteria: The NW-lineage would represent *C. e. elaphus* (synonyms: *C. e. hippelaphus*, *C. e. germanicus*, Wagenknecht 1983; Gyllensten et al. 1983), and the EA-lineage *C. e. montanus.* The SE-lineage (especially type G found in sample HA from Bulgaria) may be speculated to stem from *C. e. maral*, which is described for Turkey, the Caucasus and Kurdistan, but possibly ranges also to Southeastern Europe (Groves and Grubb 1987). Separation

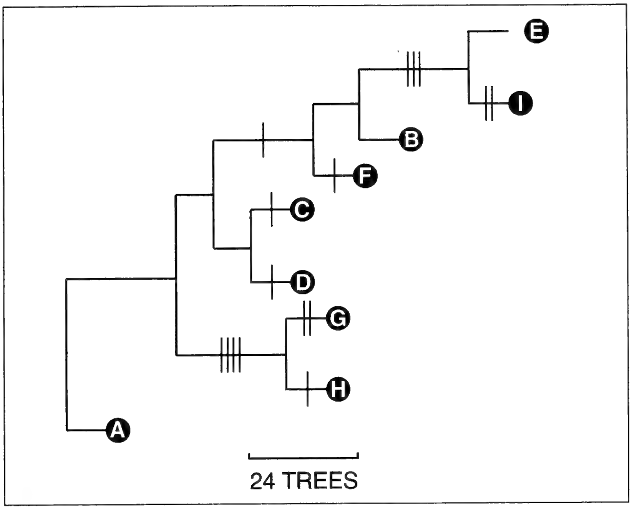

Fig. 3. Majority rule consensus tree showing cladistic relationships among haplotypes. The tree is based on 24 equally parsimonious trees obtained from Wagner maximum-parsimony analysis (MIX option, PHYLIP) of presence or absence of 69 restriction sites (Tab. 1). Both the parsimony trees and the consensus tree are basically unrooted trees, which were arbitrarily rooted at haplotype A. Distances between nodes refer to the number of trees in which the respective clusters were found. The vertical bars indicate the number of restriction site gains and losses (15 in total) for one of the parsimony trees, which was topologically largely identical to the consensus tree.

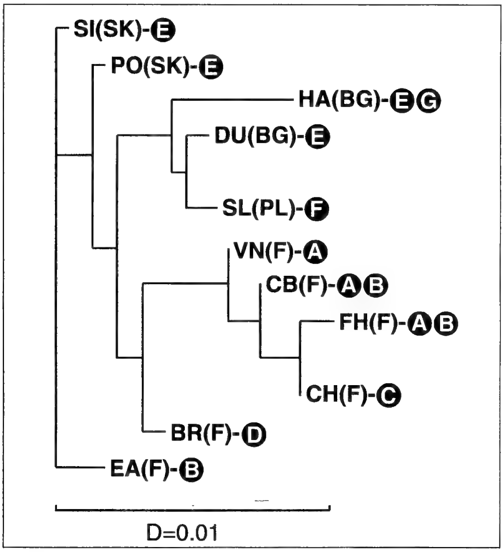

Fig. 4. Unrooted tree showing genetic relationships among 11 samples used in the present study as revealed by electrophoretic analysis of 43 allozyme loci (D, Nei 1978/FITCH-tree, PHYLIP). Haplotypes found in the respective samples are indicated by white letters following the sampling site/country code (data for SI, PO, HA, and DU are from Hartl et al. 1993 a, data for SL and the French samples are unpublished).

among the western (NW) and the eastern (EA, SE) mtDNA lineages as well as differences between eastern lineages (EA – SE) may be attributed to different glacial refugia (cf. Beninde 1937; Geist 1971). Indeed, when divergence times (t) are calculated from nucleotide divergence, assuming that p = 2% roughly corresponds to t = 1 million years (Wilson et al. 1985), separation between the NW and each of the two eastern (EA, SA) types dates back to the Riss-Würm interglacial (ranging from about 130,000 to 70,000 years before present, Haq and Van Eysinga 1987). As far as allozyme data are available, they confirm the major distinction between the northwestern and the eastern groups (especially EA) of red deer suggested by the distribution of mt DNA haplotypes (Fig. 4).

Massive changes in the genetic structure of native populations as brought about by artificial hybridization may result in the distortion of well adapted gene pools (Templeton et al. 1986). The genetic impact of introductions on red deer populations is one of the oldest and still unsettled questions in the management of European red deer (cf. Beninde 1940). Given the local restriction of major and minor lineages, mtDNA restriction profiles may serve as a powerful tool for assessing the contribution of introduced animals to autochthonous gene pools as well as for tracing their origin.

For example, the Vienna sample came from a breeding population kept in an enclosure at the Forschungsinstitut für Wildtierkunde und Ökologie for research purpose. Founder individuals of that population originated from several hunting areas in Austria. Altogether, three haplotypes (B, E, and F) were detected, which may be due to the origin of the deer from different parts of Austria. Alternatively, the polymorphism may reflect a past introduction of foreign deer into one or more of the source populations. Once a large scale screening for the distribution of mtDNA variants among as many autochthonous populations as possible is completed, questions as to the approximate geographic origin of the respective founder animals of mixed populations should readily to be answered.

Given the increasing fragmentation of habitats by fenced motorways, concreted channels, settlements, and forest clearings, formerly large and homogeneous populations of large game animals are increasingly fragmented and isolated. Within such small isolates, losses of genetic variation and, hence, of adaptability are to be expected (see Hartl and Pucek 1994). So far, isolation of populations and losses of genetic variability in the red deer have been assessed using only protein electrophoretic data (e.g. Bergmann 1976; Hartl et al. 1990a, 1991; Herzog et al. 1991; Ströhlein et al. 1993).

Due to its haploid and uniparental mode of inheritance in mammals, effective population size (Ne) for mtDNA amounts to only 1/4 of that for nuclear DNA (Birley and Croft 1986). Given the presence of polymorphism in the original population, a subdivision of that population into small isolates should be more readily detectable using mtDNA haplotypes than nuclear markers. Four out of our six red deer samples from France were found monomorphic for different haplotypes (A, B, C, D, see Tab. 2, Fig. 1), and two were polymorphic for haplotypes A and B. It is likely that the monomorphic samples represent four populations, which are genetically isolated from one another. Of the two polymorphic samples, one came from a population kept in an enclosure (CB), which is known to contain French red deer of different origin. The remaining sample (FH) may either represent a population in more ancestral condition (i.e. polymorphic) or a hybrid population of pure stocks monomorphic for type A and B, respectively. Nevertheless, although further studies are necessary for investigating the French situation in more detail, our data may be sufficient for demonstrating the power of mtDNA restriction profiles in resolving migration patterns among European red deer stocks even within a restricted geographic area. The monomorphism for haplotype E in Slovakian samples is probably the result of genetic bottlenecks. Slovakian red deer was almost completely exterminated by the end of the 18th century, and populations were restocked with red deer from adjacent geographic areas in the east and in the south (P. Hell, pers. comm.).

Given the coincidence of relationships among haplotypes and the geographic location of sampling sites where they were found (recall that haplotype F was intermediate between the NW and the EA lineage, Figs. 1, 2), the geographically very separate position of populations showing the closely related haplotypes G (HA, Fig. 1) and H (SA) is somewhat surprising. The relationship among haplotypes in a Bulgarian and the Sardinian sample may be due to a common inheritance from a remote ancestor, which cannot be tested without increasing considerably the range of populations sampled. Generally, the origin of Sardinian red deer (*C. e. corsicanus*) is still a matter of debate (Groves and Grubb 1987). Based on phenotypic resemblance, Flerov (1952) considered the deer of Sardinia, North Africa, and Southern Spain as belonging to the same subspecies. However, small body size and simple antler shape may be the parallel outcome of equally poor ecological conditions (cf. Beninde 1937; Geist 1986).

According to paleontological results, red deer had been absent from Sardinia until about 8,000 before present. The oldest red deer fossils were found in the Corbeddu Caves of the Old Neolithic together with those of mouflon (*Ovis ammon musimon*), a species that had also been absent from the island before (Sanges 1987). This date coincides with the advent of the Early Mediterranean Neolithic culture on the island, characterized by the production of Cardium ceramics (Masseti and Vianello 1991; Masseti 1993). There is already clear evidence that the mouflon was introduced to Sardinia and to other islands of the Western Mediterranean by human settlers from the Near East (Geddes 1985; Vigne 1992). The contemporary appearance of red deer on Sardinia and the similarity of its mtDNA haplotype with that found in a sample from Southern Bulgaria, possibly representing *C. e. maral* (see Groves and Grubb 1987), may suggest that the origin of Sardinian red deer is the same as in the mouflon. Compared with red deer from Southeastern Europe, the exceptionally small body size presently found in Sardinian red deer (Beninde 1937) may be attributed to a decline of body size as reported for many island forms (Soondar 1977; Damuth 1993). Further genetic studies, especially on red deer populations from Turkey and Southern Spain, are required for testing this hypothesis.

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Zusammenfassung

Ausgeprägte Mitochondrien-DNA-Differenzierung zwischen europäischen Rothirschpopulationen (Cervus elaphus L.) und deren Bedeutung für den Artenschutz und die Wildbewirtschaftung

Um die genetische Differenzierung zwischen europäischen Rothirschpopulationen (*Cervus elaphus*) zu untersuchen, wurde die mitochondriale(mt) DNA von insgesamt 70 Individuen aus 15 Probengebieten in West-, Mittel- und Südosteuropa mittels 16 Restriktionsendonukleasen verdaut. Eine Gesamtzahl von 69 gewonnenen Schnittstellen erlaubte die Definition von 9 Haplotypen, wobei sich die meisten Stichproben für jeweils den einen oder anderen Haplotyp als monomorph erwiesen. Die phylogenetischen Beziehungen zwischen den Haplotypen stimmten weitgehend mit deren geographischer Verteilung und mit den aus Alloenzymdaten abgeleiteten genealogischen Beziehungen zwischen den untersuchten Beständen überein. Nachdem sich europäische Rothirschbestände hinsichtlich des Vor-

kommens von mtDNA-Typen deutlich voneinander unterscheiden, verspricht dieses genetische Markersystem für eine Reihe von Fragestellungen im Rahmen des Artenschutzes und der Wildbewirtschaftung in der Zukunft große Bedeutung zu erlangen: Hinsichtlich einer Veränderung autochthoner Genpools durch Einbürgerungen standortfremden Rotwildes erlaubt die mtDNA sowohl eine Abschätzung des Fortpflanzungserfolges eingebürgerter weiblicher Individuen als auch eine großräumige Bestimmung deren Herkunft. Die mtDNA erweist sich aber auch kleinräumig zur Feststellung der Isolation oder der Hybridisierung von Populationen als wertvoll. Schließlich können, wie im Falle des Sardinischen Rothirsches, Restriktionsprofile der mtDNA auch zur Abklärung der systematischen Stellung von Unterarten sowie deren geographischer Herkunft beitragen.

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On the origin of sexual displays in caprids

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Abstract

Observations on the social behavior of Nilgiri tahr (*Hemitragus hylocrius*) indicated a close similarity in form between behaviors observed in mother-infant relations and sexual encounters. Specifically, the postures adopted by a Nilgiri tahr offspring toward its mother in giving behaviors termed side and rear bunts bore striking resemblance to the sexual displays termed side and rear twists. A hypothesis that the primary sexual displays of Nilgiri tahr (side and rear twist) have been derived from mother-infant behavior (side and rear bunt) yielded several predictions about the occurrence of comparable displays in related taxa, indicating that the low stretch and twists of *Capra* and *Ovis* have evolved through ritualization from behaviors similar to the side and rear twists of *Hemitragus*. This contrasts with many ungulate groups in which a close relationship between sexual and aggressive behaviors exists.

Introduction

Display behaviors are thought to arise from other already existing behaviors, often through the process of ritualization of the original behaviors or the intention movements to perform them (Huxley 1914; Daanje 1950). These original behaviors may have no element of communication (such as locomotion), they may be social acts (such as fighting or copulation), or they may be displays themselves (such as threats).

Walther (1984) presented convincing evidence of the close relationship between courtship and aggressive behaviors in many ungulate species. This relationship is particularly evident in those ungulates considered to be primitive, where the behaviors involved in sexual and aggressive encounters may be indistinguishable. Increased specialization is evident in more advanced forms, but the connection between sexual and aggressive displays is still recognizable in many species. In some of the advanced forms however, some sexual displays show no obvious connection with aggressive behavior. On the basis of the pattern discernible in other species, Walther (1984) suggests some possible means by which these displays may have arisen from aggressive behaviors. One of the taxonomic groups in this category is the sheep, goats, and their relatives. This study offers an alternative explanation for the derivation of sexual displays in these species. Specifically, that some sexual displays derive from mother-infant behavior.

Material and methods

The material presented on Nilgiri tahr is based on observations made during a two-year study at Eravikulam National Park, Kerala, India (Rice 1984, 1988 a, b, c; 1989). For this study, one subpopulation of about 120 tahr were habituated to close observation. Remarks on other species are based on published material or personal communications. Nomenclature follows Wilson and Reeder (1993).

Results

The Hypothesis: Sexual displays of Nilgiri tahr are derived from mother-infant behavior

Nilgiri tahr sexual displays included the rear twist, side twist, the foreleg kick, and tongue flicking (Rice 1988 a). The latter were usually performed in combination with the first two. In the rear twist (Fig. 1), the male stood behind the female, extended his neck and muzzle forward, and twisted the head along the long axis. The display was directed between the hind legs of the female. Depending on the distance between male and female, it terminated behind her, or with the muzzle pushing between her legs. In the side twist, (Fig. 2) the male was located further forward and slightly beside the female, so that his head was approximately level with her lumbar region. He then lowered his head, and twisted the muzzle in, usually just anterior to the hind leg of the female.

Two mother-infant behaviors of Nilgiri tahr bore a strong resemblance to the rear twist and the side twist. Although Nilgiri tahr young performed the usual bunting movements while suckling, they also performed two behaviors independent of suckling which I termed the rear bunt and side bunt. In the rear bunt (Fig. 3) the young approached the female from the rear, reached up between her hind legs, and gave a quick jab with its muzzle at the udder of the female. The side bunt (Fig. 4) was similar, but performed from the side, usually with the body of the young oriented in the same general direction as that of the female. This contrasted with the orientation of the young when suckling, which was usually in reverse-parallel position.

It should be emphasized that these rear and side bunts occurred independently of suckling and were quite different from suckling attempts, as the young executed the bunt and then turned away from the female, regardless of her reaction. Possibly, these bunts served to provide reassurance for the young. It was also clear that young were not simply

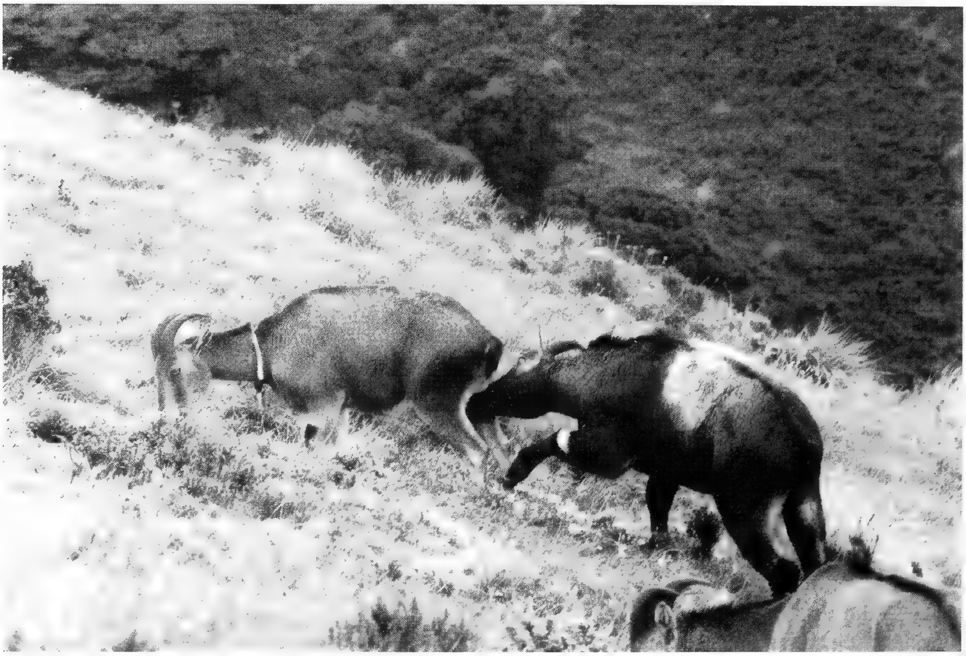

Fig. 1. To perform a rear twist, a male Nilgiri tahr extended his head and muzzle forward, and pushed the muzzle between the hind legs of the female.

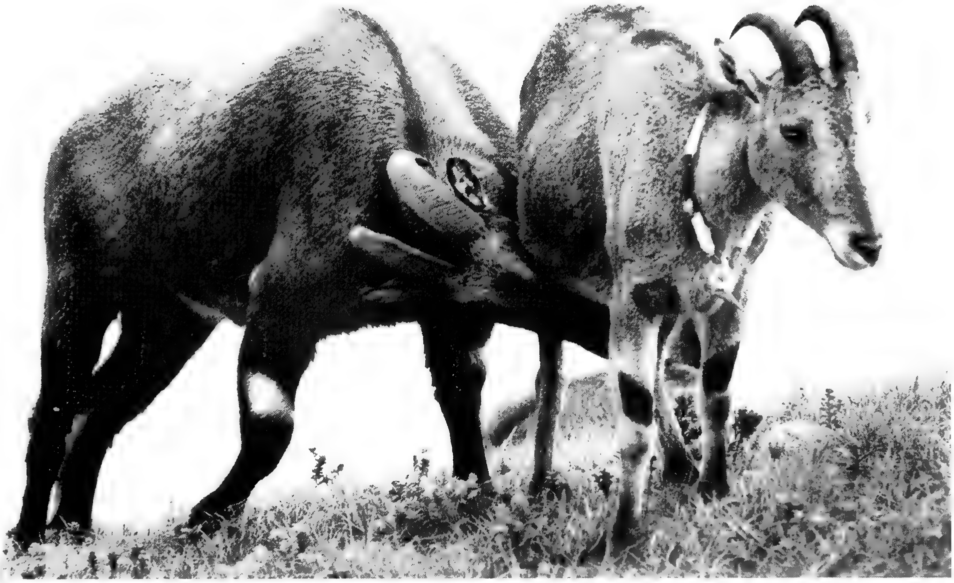

Fig. 2. In the side twist, the male turned his head just anterior to the hind leg of the female.

Fig. 3. The rear bunt was a quick poke at the udder from behind, with no apparent attempt at suckling.

Fig. 4. In the side bunt, the young turned his head in sideways to jab the udder of the female.

Fig. 5. The general orientation towards the inguinal region of the female was maintained when displays were performed in unusual positions or when the female was resting.

addressing courtship displays to females, as they showed themselves capable of normal rear and side twists in sexual play. The close similarity in form between these mother-infant and sexual behaviors suggests that the latter have derived from the former. Such a hypothesis yielded several predictions:

Prediction 1: Key elements of side and rear bunts will be evident in side and rear twists

The direction of the display in both the rear and side twists was toward the female's udder, not toward her perineum as might be expected in a posteriorly oriented sexual display. Also, when males gave corresponding displays to females which were reclining or in an unusual position, the orientation toward the udder was maintained (Fig. 5), and the neck extension and twisting were sometimes lacking. In addition, when giving the rear twist the male sometimes pushed his muzzle between the hind legs of the female to jab her udder. The orientation of both the side and rear twists toward the udder and the occasional jabbing of the udder during rear twists (as in rear bunts) is a clear indication of a close connection between these two sets of behaviors.

Prediction 2: Differences between the side and rear bunts and side and rear twists should be accountable by standard processes of behavioral evolution

There were several differences in the postures adopted by young and males in performing their respective behaviors. While the rear and side twists were oriented generally toward the udder of the female, the orientation was more specific in the rear and side bunts. That is, rear and side bunts invariably made contact with the udder, whereas the rear and side twists rarely did. Consequently, as it twisted sideways when giving the side bunt, the young had to turn its head back and in around the hind leg of the female, (Fig. 4), whereas the male merely extended his muzzle across in front of her hind leg. In the rear bunt, the young simply reached up to jab the udder (Fig. 3). An adult male, being much larger, would have to kneel or lie down to perform the same movement, but this would present obvious difficulties when displaying to a moving female. Instead, the male twisted his head sideways while lowering it slightly to achieve the orientation toward the udder of the female (Fig. 1). Also, the rear twisting male did not usually make contact with the udder, but pointed his muzzle at it, particularly if the female was moving. I made incidental note of contact in 1.5% of 2,399 rear twists. The rear and side twists of males therefore incorporated the same objective as do the rear and side bunts of the young, but the males do not usually follow through to make actual contact. The twists seem to be, in short, intention movements to the bunts, allowing for the great difference in size between young tahr and adult males.

The courting male performed his displays numerous times in succession, in contrast to the rear and side bunts which were given by the young one at a time (unlike normal bunts given during suckling). Consequently, the rear and side twists of males can be considered to have arisen through ritualization (by repetition of the intention movements) from the rear and side bunts of young.

Our understanding of the function and meaning of sexual displays in ungulates is incomplete, but probably the male gained an increased tolerance of his proximity to the female by performing actions similar to those employed by young. At the same time, courtship that was too enthusiastic was disadvantageous to the male because such courtship usually caused the female to move away. This incurred energetic costs in following and attracted the attention of other males, thereby promoting competition (and incurring further energetic costs) and risking loss of access to the female (GEIST 1971). The response of female Nilgiri tahr to being jabbed in the udder by a male was invariably to scoot away, and this explains the low frequency with which this aspect of rear twisting was employed, and the advantage of performing the intention movement rather than the complete display.

Prediction 3: If these sexual behaviors arose before Caprini diverged from the Rupicaprini, but before tahr diverged from other Caprini, more primitive related taxa will lack comparable behaviors while they will be exhibited by more advanced forms

Table 1. Occurrence of the low stretch and twist in selected ungulates (see text for references)

Species	low-stretch	twist
Tribe Caprini		
Hemitragus hylocrius	–	+
Hemitragus jemlahicus	+	+
Ovis spp.	+	+
Capra spp.	+	+
Pseudois nayaur	+	+
Ammotragus lervia	+	+
Tribe Rupicaprini		
Oreamnos americanus	+	–
Rupicapra rupicapra	+	–
Rupicapra pyrenaica	+	–
Naemorhedus crispus	–	–
Family Cervidae		
Rangifer tarandus	+	–
Cervus elaphus	+	–
Cervus eldi	+	–
Cervus unicolor	+	–

Within the Caprinae, Nilgiri tahr belong to the tribe Caprini. This tribe also includes two other tahr, the Himalayan tahr (*H. jemlahicus*) and the Arabian tahr (*H. jayakari*), as well as sheep (*Ovis* spp.), ibex and wild goats (*Capra* spp.), bharal (*Pseudois nayaur*), and aoudad (*Ammotragus lervia*). The sexual displays of the Arabian tahr have not been described, but with this exception all of these species share two displays which have a bearing on the discussion. These are the low-stretch and the twist (Tab. 1, Walther 1961; Geist 1971; Schaller 1973, 1977). To perform a low-stretch, the animal extends the neck and muzzle forward, so that the throat and the base of mandibles form a straight line, near or above horizontal. The twist is given by rotating the head, horns away from the female, while maintaining the low-stretch.

Nilgiri tahr did not give a low-stretch, but occasionally a male did not completely return to a normal posture between rear twists. Instead he left his neck lowered and muzzle extended. This posture resembled a low intensity low-stretch. The advantages of a cautious courtship have already been mentioned, and it seems reasonable that the low-stretch in other Caprini has arisen through further ritualization by intensification and 'freezing', of this interim intention movement to perform a rear twist. The twisting motion has evidently persisted, but it is done with the muzzle extended. Thus, in the parallel position, the orientation toward the udder is lost completely and the muzzle remains pointing forward.

The remainder of the Caprinae includes two tribes, the Ovibovini and the Rupicaprini, of which the Rupicaprini, with their primitive goat-like features are of primary interest. If the early stages of the low-stretch and twist are manifested in the displays of Nilgiri tahr, one would not expect to see such displays in more primitive species. The twist is indeed lacking in those species which have been studied (mountain goat, *Oreamnos americanus*, Geist 1964, 1975; north-eastern chamois, *Rupicapra rupicapra*, Krämer 1969; south-western chamois, *R. pyrenaica*, Lovari 1985; and Japanese serow, *Naemorhedus crispus*, Akasaka and Maruyama 1977; J. Berg pers. comm.), but the same cannot be said for the low-stretch. Although it is apparently lacking in the Japanese serow, it is given by both the mountain goat and chamois. In these species, the low-stretch is considered to be a submissive or appeasement posture (Geist 1964, 1971; Krämer 1969; Lovari 1985), but it is also used in courtship as the male approaches the female, especially when combined with a crouch. Lovari (1985) shows the great similarity between the extreme form of the low-stretch in south-western chamois and suckling postures of the young, and further demonstrates the relationship between the low-stretch and suckling behavior by his observation of a behavior termed the mock-suck. In the mock-suck, the courting male "inserts his muzzle under the female's udder area and delivers 2–3 blows like kids do to stimulate lactation." Therefore, it may be that the low-stretch originated in the Rupicaprini, being nevertheless derived from mother-infant relations.

Prediction 4: Comparable sexual displays will be lacking in less related taxonomic groups

The low-stretch also occurs in ungulate species outside the Caprinae (Walther 1984). This seems to contradict this prediction unless the low-stretch has arisen independently in several groups. However, this is not unlikely for the following reasons:

(1) Although it is widespread, the low-stretch is not universal (Walther 1984). Consequently, it may make as much sense to suggest separate origins for this display, as it would to suggest a common origin.

(2) In some groups, the connection between the low-stretch used in sexual contexts with aggressive displays is obvious. This is particularly true in the cervids, many of which perform a low-stretch in approaching and driving females in courtship. This is exemplified by caribou (*Rangifer tarandus*, De Vos et al. 1967), elk (*Cervus elaphus*, Geist 1966; Struhsaker 1967), Eld's deer (*Cervus eldi*, Blakeslee et al. 1979), and sambar (*Cervus unicolor*, Schaller 1967). Sambar also use the low-stretch as a threat (pers. observ.).

(3) Walther (1984) suggested that the low-stretch may have arisen from an intention movement to lick the perineal region of the female in some species. Such a separate origin would imply independent evolution of this display for those species.

Unlike the low-stretch, the twist is confined almost entirely to the Caprini, and in the few cases where it does occur in other ungulates, it is as an "aberrant or strongly reduced performance" (Walther 1984). Therefore, it seems likely that twisting has a single origin common to all Caprini. However, according to the hypothesis being suggested here, the twist and the low-stretch are closely connected. So, unless the twist was somehow "added on" to the low-stretch, this connection may indicate that both the low-stretch and the twist developed together in the manner being proposed.

Prediction 5: Comparable parallel links between mother-infant and sexual behaviors will occur in other lineages

Similar connections between sexual and mother-infant behaviors have been reported by other authors. In Indian rhinoceros (*Rhinoceros unicornis*), Schenkel and Lang (1969) interpreted the female's act of placing her muzzle in the inguinal region of the male during courtship as symbolic suckling. However, Laurie (1978) considered that she was merely sniffing his penis. Dubost (1975) reported courting African water chevrotain (*Hyemoschus aquaticus*) males licking the females' udder, and this was occasionally observed by Robin (1979) in lesser Malayan mouse deer (*Tragulus javanicus*). In mule deer (*Odocoileus hemionus*), Geist (1981) suggested that the vocalizations employed by mule deer in courtship simulate the vocalizations of infants. Horwich (pers. comm. 1983) considers the lip smacking of macaques (*Macaca* spp.) and tonguing of black howler monkeys (*Alouatta pigra*), which are used in courtship, as being derived from suckling. Ewer (1968) cites several studies reporting infantile vocalizations being used in courtship by males (i. e. in field mouse (*Microtus arvalis*), the European red squirrel (*Sciurus vulgaris*), hamsters (*Cricetus* sp.), and the raccoon dog (*Nyctereutes procyonoides*)).

One further comparison is of interest. In humans, manual and oral contact with the female's mammary glands is, in a number of cultures, a conspicuous and important component of courtship and pre-copulatory behavior. Human infants may also seek reassurance through manual and oral contact with its mother's breast. This transition from sucking to contact for reassurance to sexual behavior is directly parallel to the transition from suckling to side and rear bunts to courtship displays in Nilgiri tahr. Consequently, a relationship between mother-infant behavior and sexual behavior seems to occur in a wide diversity of mammal species.

Discussion

This study has suggested an explanation for the development of two common sexual displays in the Caprini, the low-stretch and the twist. The low-stretch occurs in many ungulate species outside the Caprini, and this is not surprising as lowering the neck and extending the muzzle is the simplest way for an animal to get its mouth or nose close to another animal. Therefore this posture may be adopted in unritualized form in all types of social interaction, be it aggression (to bite), mother-infant relations (to suckle), or sexual behavior (to sniff falling urine or the perineum of a female). In Caprini, the ritualized low-stretch has probably not developed from aggressive behavior, as biting is virtually absent in these species. Also, as the most unritualized forms of this display (mock-suck in chamois and rear and side twist in Nilgiri tahr) are directed toward the udder of the female, not toward here perineal region, the development of the low-stretch from mother-infant behaviors is strongly indicated.

There is some question as to whether the low-stretch in Caprini has its origin in the low-stretch of Rupicaprini or whether it has developed from displays similar to the rear and side twist of Nilgiri tahr. Tahr are considered evolutionary intermediaries between the Rupicaprini and the Caprini, and one would therefore expect tahr to low-stretch if this display can be traced to the Rupicaprini. Himalayan tahr do low-stretch, but Nilgiri tahr do not. On the other hand, tahr, bharal, sheep, and goats all perform a twisting courtship display, while rupicaprines do not. The close combination of the low-stretch and twist in most Caprini can be explained by considering the rear and side twist of Nilgiri tahr as precursors to these displays. One can, therefore, conclude that the low-stretch and twist employed in courtship by various members of the tribe Caprini has evolved through ritualization from behaviors similar to the rear and side twist of Nilgiri tahr. It also appears likely that the rear and side twists of Nilgiri tahr have their origins in the rear and side bunts which Nilgiri tahr young direct toward their mothers. Therefore, these sexual displays have their origin in mother-infant relations.

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Zusammenfassung

Zum Ursprung einiger sexueller Verhaltensweisen bei Capriden

Aufgrund von Beobachtungen am Nilgiritahr wird aus der Ähnlichkeit des Twists (Drehung des vorgestreckten Kopfes um seine Längsachse) – von der Seite und von hinten – als männlicher Werbegeste im Paarungszeremoniell mit einer Haltung, in der Jungtiere mitunter – von der Seite oder von hinten – zum Euter der Mutter hin vorstoßen, auf eine Verbindung in der stammesgeschichtlichen Entwicklung geschlossen. Diese Hypothese führt zu mehreren Voraussagen über die Formen dieser Verhaltensweisen und ihr Auftreten in taxonomisch verwandten Gruppen : (1) Gemeinsame Grundkomponenten sind in der besagten Werbehaltung des Bockes wie im Vorstoß des Jungtiers zur Mutter erkennbar. (2) Unterschiede der beiden sollten sich aus Vorgängen bei der phylogenetischen Verhaltensentwicklung erklären lassen. (3) Falls sich das besagte Werbeverhalten herausgebildet hat, bevor sich Caprini und

Rupicaprini voneinander schieden und auch bevor sich die Tahre von den anderen Caprini abspalteten, werden vergleichbare Werbegebärden bei primitiveren Verwandten fehlen, während fortgeschrittenere Formen sie zeigen werden. (4) Vergleichbare sexuelle Verhaltensweisen werden bei taxonomisch ferner stehenden Gruppen fehlen. (5) Vergleichbare Parallelen zwichen Verhaltensweisen in den Mutter-Kind-Beziehungen und im Paarungszeremoniell werden auch in anderen taxonomischen Einheiten auftauchen. Eine Durchsicht der verfügbaren Informationen ergab eine starke, wenn auch keine unanfechtbare Unterstützung für die hier vertretene Hypothese.

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MITTEILUNGEN DER GESELLSCHAFT

Einladung

Auf Einladung von Herrn Prof. Dr. K. Fischer, Göttingen, findet die 69. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde e. V. von Sonntag, dem 24. September, bis Donnerstag, dem 28. September 1995, an der Georg-August-Universität in Göttingen statt.

Vorläufiges Programm

Sonntag, 24. September:	Anreise 16.30 Uhr: Vorstandssitzung im Gebhards-Hotel, Goethe-Allee 22 ab 18.30 Uhr: Zwangloser Begrüßungsabend im Gebhards-Hotel, Goethe-Allee 22
Montag, 25. September:	09.00 Uhr: Grußworte und Eröffnung der Tagung durch den 1. Vorsitzenden 09.30 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Säugetiere in der Kulturlandschaft" 13.30 Uhr: Posterdemonstration 14.30 Uhr: Kurzvorträge 16.30 Uhr: Mitgliederversammlung 19.00 Uhr: Empfang im „Alten Rathaus"
Dienstag, 26. September:	09.00 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Fortpflanzungsbiologie der Säugetiere" 13.30 Uhr: Posterdemonstration 14.30 Uhr: Kurzvorträge 19.00 Uhr: Besichtigung des Deutschen Primatenzentrums
Mittwoch, 27. September:	09.00 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Chronobiologie und Aktivitätsrhythmen der Säugetiere" 13.30 Uhr: Posterdemonstration 15.00 Uhr: Kurzvorträge 16.30 Uhr: Posterprämierung 19.00 Uhr: Geselliger Abend
Donnerstag, 28. September:	09.00–17.00 Uhr: Exkursion in den Nationalpark Harz – Führung durch Forstdirektor Dr. Barth – 09.00–12.00 Uhr: Symposien/Workshops einzelner Arbeitsgruppen

Die Vorträge und Posterdemonstrationen finden in den Räumen des Fachbereichs Erziehungswissenschaften der Georg-August-Universität, Waldweg 26, D-37073 Göttingen, statt.

Alle Interessenten, Mitglieder und Nichtmitglieder, sind zu dieser Jahrestagung 1995 der Deutschen Gesellschaft für Säugetierkunde in Göttingen herzlich eingeladen. Falls eine persönliche Einladung gewünscht wird, wenden Sie sich bitte an den 1. Vorsitzenden der Gesellschaft, Prof. Dr. SCHMIDT, Zoologisches Institut, Poppelsdorfer Schloß, D-53115 Bonn (Tel. 02 28/73 54 68; Fax: 02 28/73 54 58). Das Programm mit der Vortragsfolge wird den Mitgliedern – auf Anforderung auch Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt.

Wir bitten um die Anmeldung von Tagungsbeiträgen. Außer Beiträgen zu den genannten Themenschwerpunkten werden auch dieses Mal wieder Kurzvorträge und Posterpräsentationen zu anderen Fachgebieten der Säugetierkunde angemessen berücksichtigt.

Bitte melden Sie Kurzvorträge (15 Min. + 5 Min. Diskussion) sowie Posterpräsentationen möglichst frühzeitig, spätestens jedoch bis zum 30. April (Ausschlußfrist) beim Geschäftsführer der DGS, Prof. Dr. H. ERKERT, Zoologisches Institut, Auf der Morgenstelle 28, D-72076 Tübingen (Tel. 0 70 71/29 29 58; Fax: 0 70 71/29 46 34) an. Der Anmeldung ist eine maximal einseitige informative Kurzfassung (1,5-zeilig) beizufügen. Aus ihr sollen die Fragestellung, Methoden, Ergebnisse und die daraus gezogenen Schlußfolgerungen hervorgehen. Alle Kurzfassungen werden wieder in einem Sonderheft der Zeitschrift für Säugetierkunde publiziert. Sie sind nach folgendem, schon im letztjährigen Abstractheft eingeführten Schema abzufassen: Deutscher Titel, Leerzeile, englische Titelübersetzung (kleine Anfangsbuchstaben im Text; bitte ggf. einen „native speaker“ konsultieren), Leerzeile, Initialen und Familienname(n) des/der Autors(in) bzw. der Autoren(innen) in Großbuchstaben, Adresse, Leerzeile, Text (nicht formatiert!). Aus arbeitsökonomischen Gründen bitten wir dringend darum, zusätzlich zu diesem ausgedruckten Abstract möglichst noch eine fehlerfreie Fassung auf Diskette (5.25″ oder 3.5″, IBM-kompatibler PC, DOS oder Windows) in Form eines Word- (5.0 oder 5.5) oder ASCII-Files mitzuschicken. Bitte verwenden Sie als Filebezeichnung den eigenen Namen (Initialen und Familienname, z. B. KFISCHER.TXT/DOC). Die Maße für Poster werden im Juni-Rundschreiben der DGS bekanntgegeben.

Mit Fragen zum Tagungsort und zur Organisation wenden Sie sich bitte an Herrn Prof. Dr. K. FISCHER, I. Zoologisches Institut der Universität, Berliner Str. 28, D-37073 Göttingen (Tel.: 05 51/39 54 11; Fax: 05 51/39 54 38).

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The reproductive biology of the Greater kudu, *Tragelaphus strepsiceros*

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Abstract

The reproductive biology of the greater kudu *Tragelaphus strepsiceros* was examined in the Eastern Cape Province of South Africa in relation to season, social organization and the biology of other Tragelaphines. Macroscopic and microscopic methods were employed to examine the reproductive condition of bulls and cows. Kudu bulls attained puberty at eighteen months of age while fifty percent of cows produced their first calf when two years old. Specific conception rates of 100% were realized and maintained. The foetal sex ratio did not differ significantly from parity. It was inferred that kudu cows were seasonally polyoestrous, with no prolonged lactational anoestrus but with a post-partum oestrus. Breeding was strictly seasonal and the incidence of conceptions suggested that kudus are short day breeders. The strict seasonality of reproduction is discussed in relation to that of other Tragelaphines.

Introduction

Although general information exists concerning the reproductive biology of kudus, much of it is anecdotal or non-quantitative. Consequently, it has been difficult to summarise the life history of kudus in relation to that of other Tragelaphines.

Seasonal breeding in mammals has evolved to ensure that conditions are optimal for the survival of both mother and young, and such conditions are referred to as the ultimate cause of the timing of breeding (Sadlier 1969). The most common ultimate factors influencing ungulate reproduction are rainfall and nutrition (Spinage 1973) but are difficult to separate (Sadlier 1969). Lactation, the period when the energetic demands of the mother are greatest (Sadlier 1972), usually occurs when plant growth is significant and the plane of nutrition is high.

Here we report on the reproductive biology of the greater kudu, *Tragelaphus strepsiceros* Pallas, 1776 (Bovidae), from a study population in the eastern Cape Province of South Africa.

The main aims of the study were to (a) quantify the reproductive parameters of kudus, (b) account for the seasonality of breeding, and (c) compare the results with data for other southern African Tragelaphines of different body mass, occupying different habitats, and over a range of latitudes. Information on the reproductive biology of kudus has significance for their conservation and management, and an understanding of their social and spatial organization (Perrin and Allen-Rowlandson 1993, 1994).

Material and methods

Reproductive organs from shot kudus were collected during the hunting seasons (June–August) of 1976 to 1979 on farms adjacent to the Andries Vosloo Kudu Reserve (33 °8′ S, 26°39′ E), eastern Cape Province, R.S.A. The vegetation of the reserve and farms consists of valley bushveld, which Acocks (1975) described as Fish River scrub. The vegetation comprises eight principal communities which range from near desert conditions, through almost pure grassveld, succulent and non-succulent bush, to non-succulent forest.

Paired testes were weighed to the nearest 0.1 g, and Kerr's (1965) smear technique was adopted for the detection of spermatozoa. Foetuses were weighed to the nearest 1.0 g and when possible (>50 g) sexed; ovaries of non-pregnant cows were sectioned sagittally at 2 mm. Each was examined microscopically for corpora lutea or corpora nigra and mean follicle diameter (two diameters at right angles) was recorded. Follicle diameters larger than 5 mm, indicative of ovulation, indicated adulthood. Lactation was recorded in shot cows, and in live cows captured to fit identification collars for behavioural research (Allen-Rowlandson 1980). Young animals (< 3 years) were categorized by horn development, and tooth eruption and replacement criteria (Simpson 1966). Rutting and calving periods were determined during field observations (>1 000 hours; Allen-Rowlandson 1980).

Seasonality of conception and births

Foetal age was determined using the Huggett and Widdas (1951) formula,

$$W = a(t - t_0)$$

where W = foetal mass, a = specific foetal growth velocity, t = foetal age and $t_0 = 0.2\times$ gestation period (for animals with a gestation length of 100–400 days).

Mean birth mass and gestation period were used to calculate a (Anderson 1978). Few records of the mass of kudu neonates have been published (Vice and Olin 1969) and data on the duration of gestation show considerable variation (Dittrich 1972). Consequently, the mean birth mass (15.3 kg) and mean gestation period (251 days) were determined from captive animals (Allen-Rowlandson 1980). When entered into the Hugget and Widdas (1951) equation, these data yielded an a value of 0.0123.

Foetal age was determined, $t = \dfrac{W + a \cdot t_0}{a}$

To determine conception date, foetal age (days) was subtracted from the culling date, while birth (calving) date was predicted by adding the length of gestation (days) to the conception date.

Results

Birth dates

Ninety-seven percent of foetuses (n = 62) had a predicted birth date between December and February, with a peak (52%) in January (Figs. 1, 2). Five pregnant yearlings shot in 1976 had birth dates in February or March. The predicted mean calving date of 22 non-lactating cows was 13 January (± 17 days).

Age at attainment of puberty

Bulls: twenty (95%) of the eighteen-month-old bulls examined had spermatozoa in the testes and epididymides, with a mean paired testes mass of 64.9 (± 10.0) g. The only prepubertal bull of this age had a combined testes mass of 41.6 g. All bulls less than one-year-old (n = 9) showed no evidence of spermatogenesis. Twenty-eight (96%) of two-year-old bulls examined possessed spermatozoa.

Cows: six (46%) eighteen-month-old cows were pregnant. A further two had large corpora lutea (indicating that ovulation had occurred), and three others had mature Graafian follicles (indicating conception). Therefore only two (15%) were prepubertal.

Material was not available for cows under one year of age. Seventy-six (99%) of cows two or more years old were sexually mature.

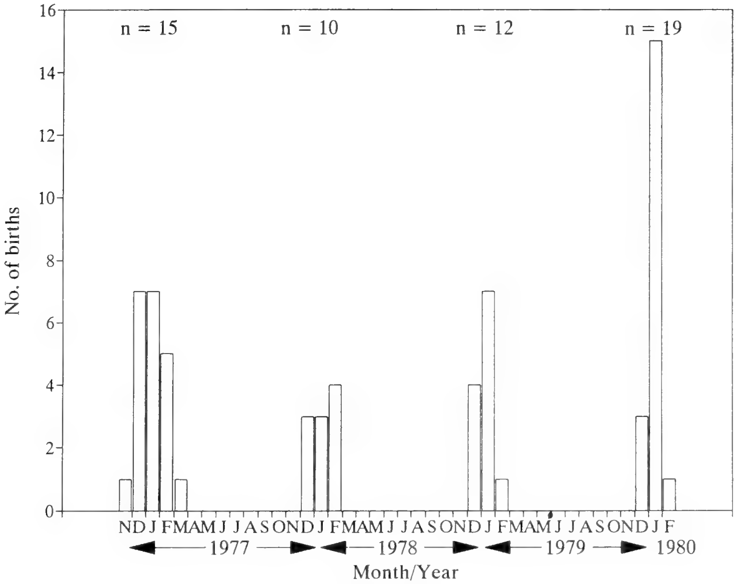

Fig. 1. Parturition dates of kudus in the Fish River Valley area, determined from foetal age.

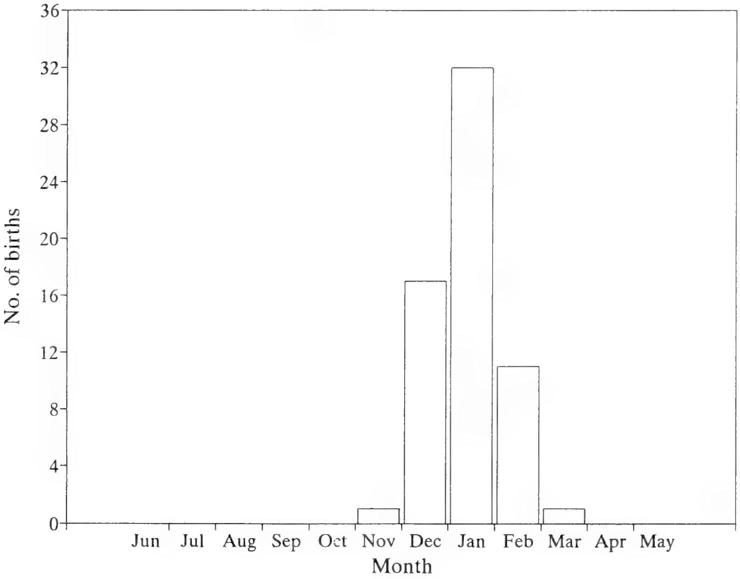

Fig. 2. Accumulated parturition dates of kudus in the Fish River Valley area determined from foetal age. (Data from 1976–1979 summed, n = 62).

Fertility

Bulls: ninety (97%) bulls older than eighteen months possessed spermatozoa (92% of samples were collected between June and August). The three exceptions were two 3.5-year-old bulls (shot in February and August) with paired testes masses of 24.6 g and 62.6 g respectively, and a 2.5-year-old bull (shot in July) with a paired testes mass of 60.5 g. One other bull, at least 5-years-old, had testes of unequal size (77.8 g and 27.6 g); spermatogenesis was only evident in the larger testis.

Cows: seventy of the 83 uteri examined contained a foetus indicating a crude conception rate of 84 percent. All adult cows (>2 years: n = 64) shot during June, July and Au-

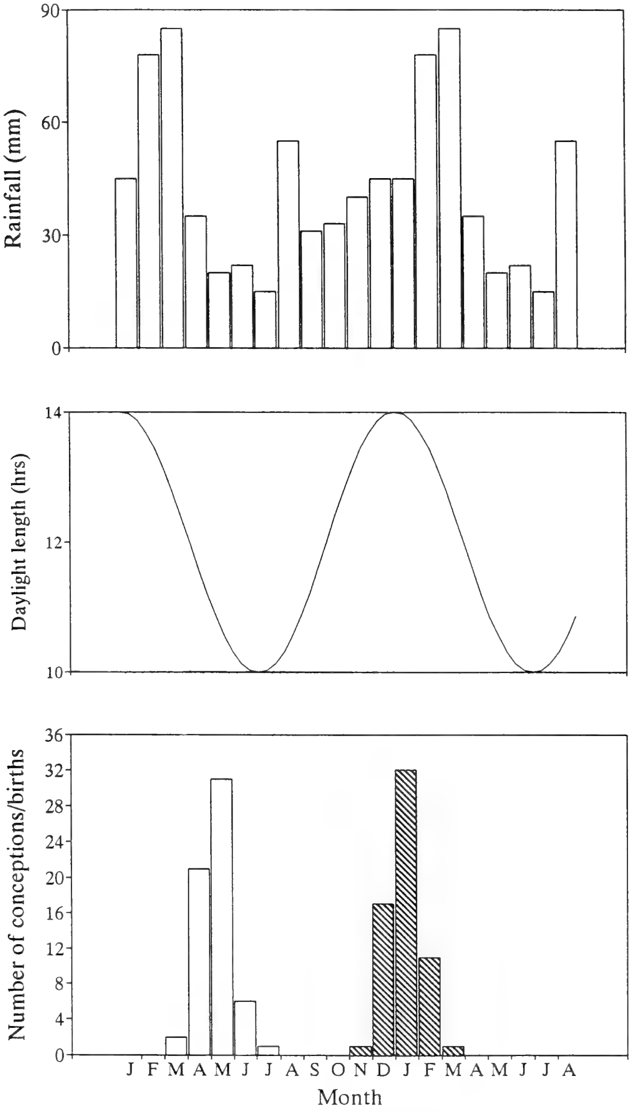

Fig. 3. The distribution of kudu conceptions (open) and births (striped) in the Fish River Valley area in relation to rainfall and photoperiod.

gust were pregnant, as were 46% of the yearlings collected at this time. Thirty-three (91%) lactating cows shot early in the year were pregnant.

Foetal sex ratio

Of the 51 foetuses sexed, 30 were bulls and 21 were cows (1 : 0.7). This ratio does not differ significantly from parity. No incidence of twinning was recorded.

Lactation

The udders of 51 adult cows shot during June, July and August (1976 to 1979) were examined and 65% of these were lactating. During August (7 months after parturition) 62% of (13) adult cows were still producing milk. Of the seven cows captured in April 1978 and recaptured in April 1979, 43% were lactating on both occasions.

Field observations

Adult bull : adult cow associations were most frequently observed from April to July, and although copulation was never witnessed in the field, bulls were seen attempting to mount cows on six occasions (April–June). Flehmen (Walther 1958, 1964) was observed during April (n = 3), May (n = 4) and June (n = 1).

Twenty-two (82%) of adult cows captured during April and June were in oestrus, as determined by vaginal smears. None of the sixteen adult cows examined in January showed this condition.

Four calves with portions of their umbilical cords still attached were caught in January or the first week of February, whereas mothers with calves were only seen regularly from March onwards.

The distributions of kudu births and monthly rainfall in the Fish River Valley area (Fig. 3) show that most calves were born just prior to the months of maximum and most predictable rainfall (February and March).

Although early accounts suggested that kudus breed throughout the year (Ansell 1960; Asdell 1964) more recent reports indicate that calving occurs from January to April (Tab. 1).

Discussion

Methodology

The accuracy of foetal age estimation depends on the accuracy of the mean birth mass and mean gestation time used to determine the specific foetal growth velocity, a. Early re-

Table 1. Gestation periods quoted for kudus

Species	*T. angasi*	*T. spekei*	*T. scriptus*	*T. strepsiceros*	*T. oryx*
Gestation (w)	1	–	26–32	32–36	37–39
Age at first parturition (m)	18–24	18–24	17–19	24–28	38–40
Birth season	Aug–Oct	year round	Apr–May Oct–Nov	Jan–Apr	Jul–Nov
Sex ratio	1 : 0.88–1.22	1 : 1.75–4.18	1 : 0.88–1.50	1 : 1.36–2.40	1 : 3.06–6.10
Longevity (y)	–	14–19	9–13	11–15	12–20

w = weeks, m = months, y = years

ports of gestation cited durations of 210 to 214 days (Stevenson-Hamilton 1912; Jennison 1927; Wilhelm 1933; Asdell 1964) but more recent records suggest 271 days (Allen-Rowlandson 1980). Since, (a) the length of gestation is rarely influenced by environmental conditions (Sadlier 1969), and (b) gestations of 210 to 220 days are known for nyala (Anderson 1978) and captive lesser kudu (Dittrich 1972), both of which are considerably smaller than the greater kudu, and (c) the length of gestation is closely correlated with the mass of the adult (Sadlier 1969, 1972), a longer duration of gestation in the greater kudu is probable. However, known parturition intervals of 259 and 266 days (Allen-Rowlandson 1980) infer that gestation is unlikely to be much longer than the 251 days used here. Entering these values in to the Huggett and Widdas (1951) equation yields a value similar to those determined for other Tragelaphines (Anderson 1978). Field observations corroborate the accuracy of the technique, and adult kudu bulls were most frequently seen associating with cows during May and June (Allen-Rowlandson 1980).

Reproduction in the bull

Kudu bulls achieved puberty (spermatozoa in the epididymides) and were sexually mature by eighteen months of age. Under natural conditions, however, young bulls (<5 years old) are prevented from mating by older, dominant bulls that have reached sociological as well as sexual maturity, which occurs at 6 years of age (Owen-Smith 1984).

Spermatogenesis likely continued throughout the year, but fluctuated according to season (Skinner and Huntley 1971; Skinner 1971). Sexual senescence was not evident in kudu bulls, but 3% of the bulls examined during this study were infertile.

Reproduction in the cow

Kudu cows reached puberty by eighteen months of age, and 50% of two-years-old produced a calf; similar results have been reported for Zimbabwean populations (Dasmann and Mossman 1962; Simson 1968). At two years of age, specific conception rates of 100% were realized and maintained, so fecundity was not age-specific. Simpson (1968) reported that cows over 30 months of age have a specific birth rate of 80% and that fecundity decreases with age. However, there was no evidence of sexual senescence in the present study.

Results indicated that kudu cows in the Fish River Valley population calved consecutively each year. However, the seasonal changes in the proportion of cows lactating suggested substantial calf mortality.

The high conception rate suggests that the kudus were seasonally polyoestrous, since, like the congeneric nyala, they are receptive for a few hours only (Owen-Smith 1984). The mean interval of 45 days between parturition and conception (Allen-Rowlandson 1980) indicates that kudus have a post-partum oestrus.

Data suggest that primiparous cows came into oestrus slightly later than multiparous cows. A similar trend has been reported in other kudu populations (Simpson 1968), in eland (Underwood 1975), and in red deer (Mitchell and Lincoln 1973).

Foetal sex ratio

The foetal sex ratio recorded here is equivalent to the published ratios of 1 male : 0.7 female (n = 34) and 1 male : 1 female (n = 20) (Simpson 1968). The preponderance of males in each of these ratios is not statistically significant. Kudus born in captivity exhibit a sex ratio closer to unity (1 male : 1.1 female, n = 490) (Allen-Rowlandson 1980).

Kudu bulls experience vastly elevated mortality rates compared with cows, generating a sex ratio of 1 male : 12 females in the Kruger Park (OWEN-SMITH 1984). The ratio of 1 male : 2.2 females for adult kudus in valley bushveld may be attributable, *inter alia*, to the absence of large predators (ALLEN-ROWLANDSON 1980).

Seasonality of reproduction in kudus

Predicted conception and parturition dates clearly demonstrated that breeding in the kudu is strictly seasonal in valley bushveld. The calving season may occur slightly later in the eastern Cape than elsewhere in the subregion, but its duration remains short.

Photoperiod is often the proximate factor initiating seasonal breeding in mammals. Since ninety-eight percent of all kudu conceptions occurred during days with decreasing and short photoperiod, they are short day breeders.

Since seasonal fluctuations in protein and water content are less severe in browse than graze (LEUTHOLD and LEUTHOLD 1975 a), and growing seasons are long in dicotyledonous plants (JARMAN 1974), seasonality of breeding is usually more marked in grazers than in browsers (LEUTHOLD and LEUTHOLD 1975 b). The marked seasonality of breeding in kudus, which are almost exclusively browsers, is therefore surprising and remains unexplained.

Acknowledgements

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Zusammenfassung

Über die Reproduktionsbiologie des Großen Kudu Tragelaphus strepsiceros

An Kudus, die während verschiedener Jagdzeiten in der östlichen Kapprovinz Südafrikas erlegt wurden, konnten Daten über den Reproduktionsstatus erstellt werden.

Kudubullen werden mit 18 Monaten fortpflanzungsreif, während 50% der Kühe in einem Alter von 2 Jahren ihr erstes Kalb zur Welt bringen. Die Geschlechtsverhältnisse der Foeten entsprechen 1 : 1. Kudukühe waren scheinbar jahreszeitlich polyöstrisch und zeigten Postpartumöstrus ohne ausgedehnten Anöstrus während der Laktationsperiode. Wenige Daten lassen vermuten, daß primipare Kühe geringfügig später im Jahr brünstig wurden als diejenigen, die mehrfach geboren hatten. Die Fortpflanzung war streng saisonal und entsprechend dem Zeitpunkt der Konzeption ist zu vermuten, daß sie bei Kudus unter Kurztagbedingungen stattfindet.

Diese Saisonalität der Reproduktion wird in Beziehung zu anderen Vertretern der Tragelaphini diskutiert.

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Rumen morphology and volatile fatty acid production in the Blue duiker (*Cephalophus monticola*) and the Red duiker (*Cephalophus natalensis*)

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Abstract

Blue duikers and red duikers have very similar rumen anatomy. In both species the rumen is a simple, plesiomorphic, sacculated S-shaped tube, while the ostia are large and the ruminal pillars weak. These specialisations facilitate rapid digesta passage. The rumens are densely papillated, and the fungiform papillae are highly vascular to aid absorption. Many of the adaptations are characteristic of concentrate selectors. Total concentrations of numeral fatty acids are lower in the red duiker than the blue duiker. Propionic and butyric acid concentrations are higher in the blue duiker than the red duiker while acetic acid concentration are greater in red duikers. Caecal concentrations of volatile fatty acids (especially acetic acid) are greater than those in the rumen of the blue duiker, but likely contribute less energy to metabolism because of the small size of the caecum relative to that of the rumen.

Introduction

Blue duikers (*Cephalophus monticola*) and red duikers (*Cephalophus natalensis*) are amongst the smallest antelope species, and are classified as concentrate selectors based on diet selection, and the morphology of the digestive tract, especially the rumen (Hofmann 1973). Both species have a diet of mainly freshly fallen leaves, and to a lesser extent fallen fruit (Faurie 1990; Bowland 1991). The aim of this study was to compare the morphology and histology of the rumen of the two closely related, sympatric, forest duikers and to correlate structure with function. Function was determined largely by quantifying volatile fatty acid (VFA) production in the rumen.

Hofmann (1973, 1983) characterised the concentrate selectors as a group of bovids having certain morphological features in common, *i. e.*, a simple, small rumenoreticulum; rapid passage of food due to wide ostia; extensive rumen papillae providing a large absorptive area; a relatively large reticulum; a small omasum for transporting and straining food partictes; relatively large salivary glands; a relatively short intestine, and with the caecum and colon forming a distal fermentation chamber.

Langer (1974) has indicated that foregut fermenters probably evolved in regions where adequate quantities of low quality food were available, such as tropical forests. Small forest artiodactyls, of the family Tragulidae, have a 'primitive' rumen in the form of an S-shaped tube that reveals the ancestral arrangement of the foregut (Hofmann 1968; Langer 1974). Forest duikers and other small African antelope (Bovidae) possess a stomach with a similar anatomy (Hofmann 1973) for rapid passage of food.

For small duikers, the most important source of energy is the volatile fatty acids (primarily acetic, propionic and butyric), the major metabolizable end products of microbial anaerobic fermentation (Kreulen and Hoppe 1979; Hume and Warner 1980), which represent 21–75% of digestible energy intake (van Hoven and Boomker 1981; Robbins 1983). Recent research has estimated the bacterial and fungal numbers in ruminal and caecal contents of the blue duiker (Dehority and Varga 1991).

Material and methods

Animals

Four red duikers (2 males (R1 and R3) and 2 females (R2 and R4)) and four blue duikers (2 males (B1 and B4) and 2 females (B2 and B3)) were used to examine rumen morphology and histology and to quantify rumen VFA concentrations. All the duikers were adult animals. With the exception of the one captive blue duiker, all the animals were shot in their natural habitats. The captive blue duiker (male B1) had been fed an experimental diet of Hunters horse cubes (14% protein, 10% fibre), fresh fruit (apples and carrots) and *ad lib.* water for three weeks prior to death. All four red duikers as well as blue duikers B1 (captive male) and B2 (female) were transported to a laboratory within 10 minutes to one hour after death. The remaining two blue duikers (B3 and B4) were frozen whole shortly after death and rumen fluid only was collected after the animals had been unfrozen.

Morphology

Stomachs (rumen, reticulum, omasum, and abomasum) were collected and preserved in four percent buffered formalin. A dissecting photomicroscope was used for gross morphological examinations. Compartments and structures of the red duiker and blue duiker stomachs were measured and photographed, while the papillae occupying various regions of the rumen were counted and measured to determine the surface area enlargement.

Histology

For histological examination, small portions of tissue were taken from the different stomach compartments within one hour after sacrifice. Tissues were fixed in Bouin's fixative for 12–18 hours, dehydrated in a series of alcohol concentrations, cleared in xylene and embedded in paraffin wax. Sections were cut on a microtome at 7 µm, and stained with Ehrlich's haematoxylin and eosin. Photographs of histological sections (10 × and 40 × magnification) were taken through a Zeiss photomicroscope.

Physiology

Rumen pH was measured, body mass determined, and rumen fluid samples were taken to determine the concentrations of the individual VFAs. Fluid from the caecum of blue duiker B2 (female) was also collected and analysed for individual VFA concentrations.

In the laboratory, samples were left to equilibrate at room temperature (20 °C). To 5 ml of the rumen fluid 1 ml of 25% metaphosphoric acid solution was added and allowed to stand for 10 minutes. The solution was centrifuged at 8 000 RPM for 20 minutes, and in a high speed centrifuge at 18 000 RPM for 20 minutes at 4 °C. The supernatant was analysed on an HP 5970 A gas chromatograph with a flame ionisation detector and N_2 as the carrier gas. The chromatograph was equipped with a 2 × 4 mm glass column, packed with 10% S–P 1 200 + 1% H_3PO_4 on chromosorb W–AW 80/100 mesh.

Standard curves were constructed for acetic, propionic and butyric acids by injecting known amounts of standard solution, over the approximate range of 0–150 nmoles of acetic acid (and proportional amounts of the other two acids). The rumen fluid samples were injected into the chromatograph and the elution times compared with those of the standard (Kellog 1969) to identify the VFA present, and its concentration.

Results

Morphology

Figure 1 shows the ruminant stomach of the blue duiker to be a blind-ending S-shaped tube. The rumen was divided into dorsal and ventral sacs by rumen pillars, the ventral sac being the larger. The ruminal pillars were simple wall duplications, only very slightly thickened but densely papillated, making them relatively inconspicuous. The bisected stomach (of the captive blue duiker) showed an evenly and very densely papillated rumen. The papillae were widespread, thereby enlarging the absorptive area of the rumen. The food retaining structures, the ruminal pillars and ostia, were very poorly developed, while the opening between the rumen and reticulum was very large. The coronary pillars were generally poorly developed while the dorsal one was absent. The rumeno-reticular opening and pillar were also covered with papillae. The ostium connecting the reticulum and omasum was relatively large, while the omasum was very small and had few laminae (6–8) with spatulate papillae.

In the captive blue duiker fed pellets, rumen fungiform papillae were short, broad (3 × 1 mm), and very densely packed (Fig. 2) while the whole rumen was covered by papillae of similar shape and density. Figure 3 shows that the rumen of a free ranging blue duiker fed on a natural diet possessed fewer papillae than that fed on a high protein, artificial diet. The foliate (vallate) papillae were thinner, longer and less regular in shape. The rumen papillae of the red duiker were very similar to the fungiform papillae of the free ranging blue duiker. The papillae approximated 5 × 2 × 2 mm in size and the entire rumen was very evenly covered by papillae of similar size and shape. There were about 90–100 papillae/cm^2 which gives a surface enlargement in the order of 15–20 ×. On the rumeno-reticular pillar and the opening between the rumen and reticulum, the papillae were longer and more slender (Fig. 4). The

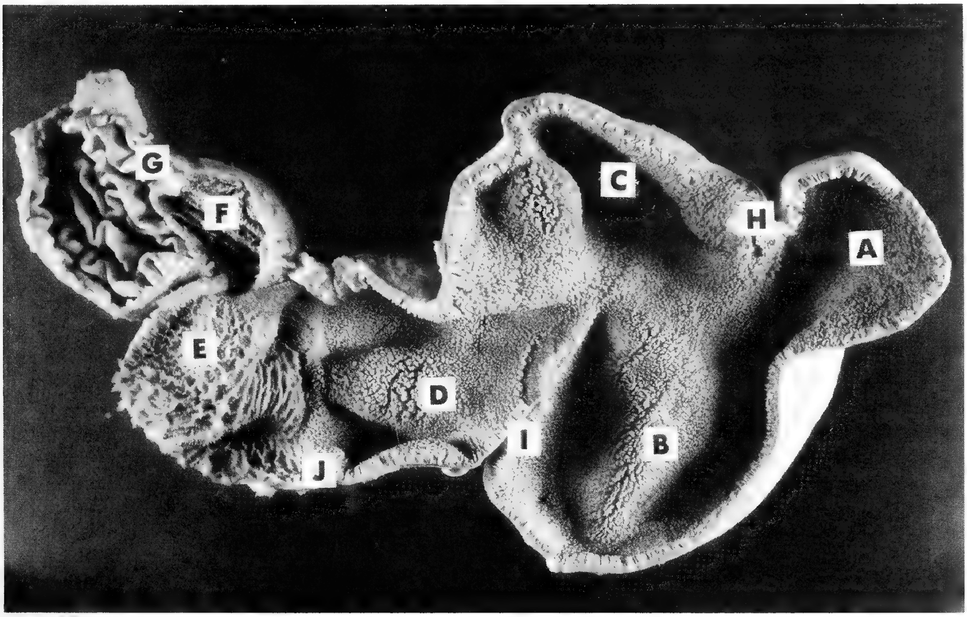

Fig. 1. Bisected stomach of captive blue duiker. A – ventral blindsac; B – saccus ventralis; c – dorsal blindsac; D – atrium ruminis (dorsal sac); E – reticulum; F – omasum; G – abomasum; H – caudal pillar; I – cranial pillar; J – rumeno-reticular fold.

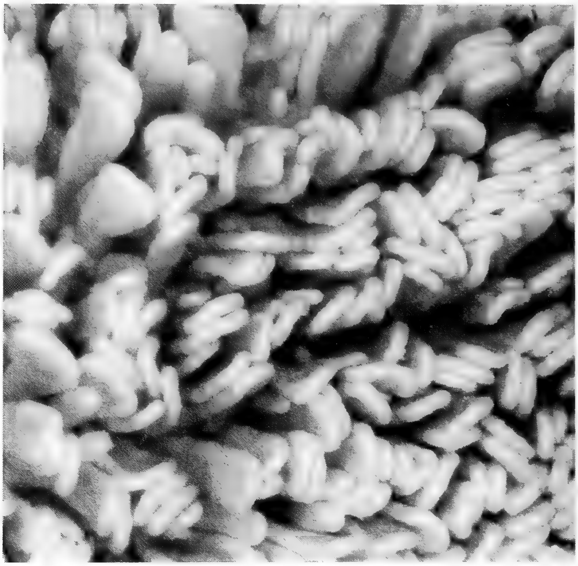

Fig. 2. Fungiform rumen papillae of the captive blue duiker fed a high protein/low fibre pelleted diet.

reticular mucosae of the red duiker and the blue duiker were very similar, and consisted of a honeycomb pattern with low bordering ridges. It was much more rigid and keratinized than that of the rumen and omasum. In the captive blue duiker, the cornified epithelial crests of the cells became very densely packed. The omasum in each species was small, and consisted of only six to eight leaflets, with spatulate papillae covering the entire epithelium.

Histology

The forestomach mucosa is the main medium of absorption from the stomach lumen into the vascular system (e. g. papillae in the rumen, and interpapillary mucosa of the omasal laminae and the reticulum) but it also serves a mechanical, protective function. Forestomach epithelium with an absorptive function is characterized by primary and secondary swelling of the epithelial cells, which are separated by a barrier layer of dense flattened cells. The papillae of the rumeno-reticulum consisted of epithelium, connective tissue and a central system of branched blood vessels. There was no histological difference between atrial papillae and those of the dorsal and ventral blindsacs of blue duikers and red duikers. The rumen epithelium comprised the stratum germinativum, stratum spinosum, stratum granulosum and the stratum corneum; the latter tissue was not highly cornified however, and consisted of a thin barrier layer with balloon cells (Fig. 5). Balloon cells are parakeratoric cells commonly found in concentrate feeders, and were clearly evident in both duiker species. Marginal arteries and venules (Fig. 5) were evident. Capillaries from the former were located within the papillae occulte. Basal epithelial cells between the papillae occulte established contact with the vascular system and venules characterized the epithelium of the absorptive papillae. In papillae with relatively thin epithelia, that consisted of only a few layers, the stratum spinosum was not very extensive. In the absorptive mucosa the nuclei of these cells were well defined in contrast to those in the protective mucosa.

The abomasum was connected to the omasum through the ostium omasoabomasicum. The abomasum was lined with spiral pillars of varying height. These pillars were formed by mucosal duplications underlain by a vascular submucosa in both duiker species; the abomasum had 10 to 14 pillars lined with fundic glandular mucosa.

Physiology

Rumen pH, molar proportions of the individual VFAs, and the acetic : propionic acid ratios for each species are given in table 1. The pH values were very similar for both species, although that of the captive blue duiker was slightly lower. The molar proportions,

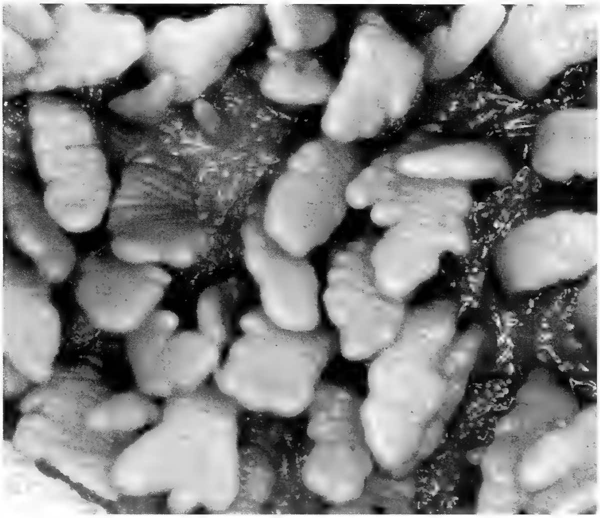

Fig. 3. Foliate (vollate), ruminal papillae of a blue duiker that had been feeding on natural vegetation.

Fig. 4. Absorptive papillae on the rumeno-reticular pillar and ostium of a red duiker.

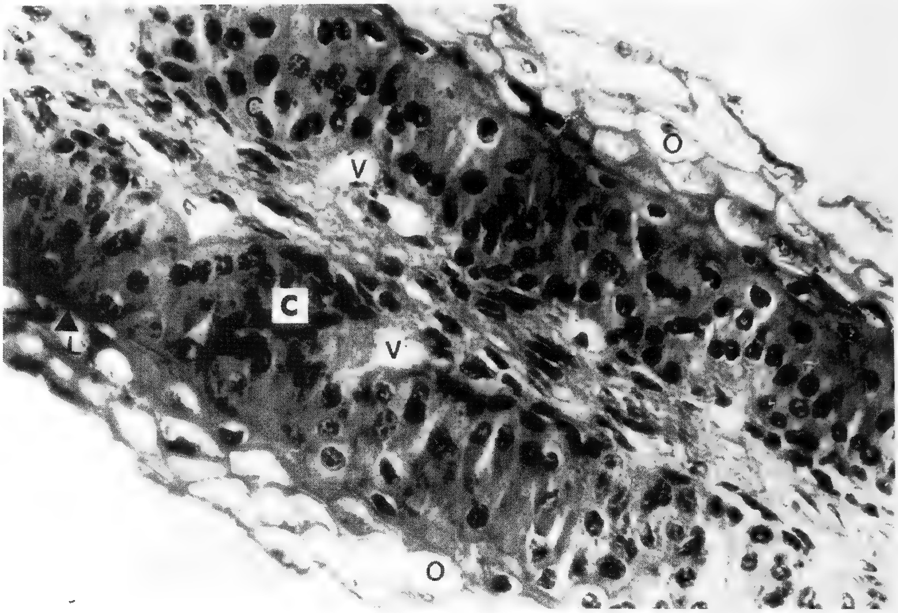

Fig. 5. Section of a ruminal papilla of a blue duiker. O – balloon cells; C – epithelial plug; L – barrier layer; V – venule.

Table 1. Relative volatile fatty acid (VFA) composition of the rumen fluid of blue duikers and red duikers.

Blue duikers	pH	Percentage VFA			A : P Ratio	Total (mM/l)
		Acetic (A)	Propionic (P)	Butyric		
B1 (captive)	5.9	52	32	16	1.6 : 1	60
B2	6.1	60	32	8	1.9 : 1	62
B3	–	64	28	8	2.3 : 1	–
B4	–	56	37	7	1.5 : 1	–
Mean	6.0	58	32	10	1.8 : 1	61
Red duikers						
R1	6.1	72	21	7	3.4 : 1	60
R2	6.0	74	20	6	3.7 : 1	70
R3	6.2	76	21	3	3.6 : 1	74
R4	6.2	74	23	3	3.2 : 1	74
Mean	6.1	75	21	5	3.6 : 1	70

and thus the acetic : propionic ratios were equivalent intraspecifically, but differences between species were evident. Sample sizes, however, were too small for reliable statistical analysis.

The (relative) composition of ruminal VFAs in red duikers and blue duikers were lower than but comparable to those of other small bovids (Tab. 2), particularly with species feeding on similar diets (*e. g.* suni, *Neotragus moschatus* and grey duiker, *Sylvicapra grim-*

Table 2. A comparison of the volatile fatty acid (VFA) composition of the rumen fluid of several small bovid species.

Species	Percentage VFA			A:P Ratio	Total	
	Acetic	Propionic	Butyric		(mM/l)	Ref.
Impala (*Aepycerus melampus*)	75	16	9	4.7:1	150	B
Grant's Gazelle (*Gazelle granti*)	78	17	5	4.6:1	141	A
Thomson's gazelle (*G. thomsoni*)	79	15	6	5.3:1	143	A
Grey duiker (*Sylvicapra grimmia*)	75	18	7	4.2:1	115	B
Harvey's duiker (*Cephalophus natalensis harveyi*)	77	18	5	4.3:1	144	B
Suni (*Neotragus moschatus*)	77	17	7	4.5:1	90	B
Dikdik (*Madoqua kirkii*)	72	20	8	3.6:1	109	B

References: A = Hoppe *et al.* (1977); B = Hoppe (1984).

mia). The low acetic:propionic ratio in the red duikers, was even more pronounced in the blue duikers (Tab. 1). In the captive blue duiker, acetic acid contributed only 52% of the VFAs with propionic and butyric acids accounting for the remainder.

Table 3 reports some data on the pH and VFA concentrations in the abomasum of the captive blue duiker, and the caecum of a wild blue duiker. The concentration of VFAs in the caecum was high.

Table 3. pH and volatile fatty acid composition of the abomasal and caecal fluid of the blue duiker.

	Abomasum (Captive)	Caecum (Wild)
pH	2.5	–
Total VFA (mM/l)	4	90
Acetic (%)	83	82
Propionic (%)	6	15
Butyric (%)	11	3
Acetic: Propionic ratio	13.8:1	5.5:1

Discussion

Morphology

It has been postulated that the structural components of the stomach that regulate food passage and intake, are so firmly established that they remain unaffected by dietary change, and, therefore, determine the limits of the adaptability of a species (Hofmann 1973; von Engelhardt 1981). Concentrate selectors are recognized as being less adaptable than grazers (Hoppe 1984). These parameters include the capacity of the rumen, the size of the ostia between the chambers, the type of contraction mechanism, and the anatomical structures (including pillars) that serve as a contracting mechanism to delay food passage. Blue duiker and red duiker have a simple stomach which facilitates a fast passage rate, and, rapid fermentation and absorption. This simple structure of the rumeno-reticulum, the poorly developed ruminal pillars, and the large ostium are characteristic of concentrate selectors (Hofmann 1973).

The very poorly developed ruminal pillars and large ostia of the rumenoreticulum indicate a fast passage rate in the two duiker species. Passage rate in the two subject species approximates 18 to 24 hours (Faurie 1990), similar to that of the suni, *Neotragus moschatus*, which has a passage rate of 12 to 22 hours (Hoppe and Gwynne 1978). *Parra* (1978) and Demment (1982) postulate that maximum rumen capacity and energy demands determine retention time. Thus, concentrate selectors with small rumens and high energy demands must have rapid passage rates.

Langer (1974) points out that only in the Pecora does the proximal part of the hindstomach help to form the omasum. The omasum delays digesta passage and is involved in the absorption of water, inorganic compounds, and VFA (Langer 1974). The size of the omasum and the differentiation of the laminae differs considerably between the different feeding guilds. In concentrate selectors, the omasum is small and has very few laminae, indicating mainly a transport and strainer function. This is evident in the red duiker and blue duiker which have an average of six to eight primary laminae, and only in the case of the red duiker a few leaflets of the second order. In both species the laminae are densely studded with spatulate papillae. Hofmann (1973) points out that this type of omasal lamina reflects the mechanical function of the omasum, as a strainer, and muscular suction pump.

In red duikers and blue duikers all areas in the rumen are papillated. There is some spatial variation in the size and density of ruminal papillae of free-living blue duiker and red duiker, *e. g.* smaller papillae occur on the rumen pillars than on the dorsal sac, but longer, more slender papillae occur near the rumeno-reticular pillar of the red duiker. The rumen papillae of Harvey's red duiker, *Cephalophus natalensis harveyi* and grey duiker, *Sylvicapra grimmia* exhibit similar local variation (Hofmann 1973). The rumen papillae of the captive blue duiker, however, showed total uniformity, with no variation present.

Histology

Under changing feeding conditions, and a lowered pH, the barrier layer cells of rumen papillae change into flat balloon cells or parakeratoric swollen cells (Houpt 1970). These swollen cells are indicative of increased absorption and are usually accompanied by an extensive subepithelial vascular system. Evidence for a faster rate of solute absorption with increased vascularisation of papillae is given by Dobson (1970). Extremely thin barrier layers are usually associated with animals feeding on rapidly fermentable food, *i. e.* concentrate selectors, or intermediate feeders feeding on lush food in the rainy season (Hofmann 1973).

Most long papillae of wild ruminants have no central artery, but two vertically ascending marginal arteries that supply the lateral edges of the papillae with capillaries (Vollmerhaus and Schnorr 1968, in Hofmann 1973). This arrangement is also seen in the red duiker and blue duiker. The capillaries ascending from the marginal artery are situated in the papillae occultae, reaching out towards the free surface of the papilla. Epithelial plugs and crests are thus formed between the capillaries, establishing intimate contact between basal cells and the blood system (Hofmann 1973). Thus the effective thickness of the epithelium is greatly reduced in the forest duikers.

The arrangement, number, and development of subepithelial venules change with food quality, and hence differing fermentation and absorption rates (Vollmerhaus and Schnorr 1968, in Hofmann 1973). In the rumen papillae of red duiker and blue duiker, the venules form pouches around which the basal cells are arranged in a radiating manner, facilitating contact between the vascular wall and many epithelial cells.

Hofmann (1973) found that concentrate selectors have a relatively large reticulum and that mucosal relief of the reticulum is dependent on food habits, and can vary extensively between species. There is a stepwise transition from absorptive papillae to reticular crests (Langer 1974). The reticular mucosa of both red duikers and blue duikers with their characteristically low mucosal crests and spatulate cornified papillae therefore exemplified the grasping-protective, non-abrasive mucosa of the concentrate-selector reticulum (Hofmann 1973).

Physiology

Although acetic acid is the predominant VFA in all ruminants (Hoppe 1984; van Hoven and Boomker 1985), relative proportions of VFA vary with diet composition. High concentrations of acetic and butyric acids are characteristic of extensive cell wall fermentation, while high propionic acids are characteristic of soluble carbohydrate fermentation. Concentrate foods thus lower acetic acid concentration relative to propionic and butyric acids (Eadie and Mann 1970; Prins and Geelen 1971). This is correlated with pH, since acetate production is inhibited below a pH of 6.2 (Owens *et al.* 1984; Hoppe *et al.* 1983). Very low methane levels characterize small concentrate selectors, and a resulting low metabolizable energy loss. Thus high acetate : low propionate levels suggest higher proportions of energy lost as methane (van Hoven and Boomker 1981). Unsaturated fatty acids, commonly found in browse, inhibit methanogenic bacteria while favouring propionate production (Hoppe *et al.* 1983; Boomker 1981, 1983, 1984; van Hoven and Boomker 1985). High concentrations of propionic acid in small ruminants inhibit methane production by channelling carbon and hydrogen into propionate. Thus, propionic acid is more efficiently utilized than acetic acid (Blaxter 1967).

Very high relative levels of propionate were recorded in both duiker species; the blue duikers had significantly higher levels than the red duikers. Allo *et al.* (1973) found that with increased grain fractions in the diet, acetic acid concentration decreased relative to that of butyric acid. This explains the high butyric acid levels found in the captive blue duiker fed on pelleted grains. Although lower acetic : propionic ratios, and thus higher propionic acid concentrations are found in concentrate selectors (Giese and van Gylswyk 1975; Hoppe 1977 *a, b*), the results obtained, especially for the blue duikers', are very high compared to other selective (and intermediate) feeders. Hoppe (1977 a, b) and Hoppe *et al.* (1977) found that smaller species of antelope select rich diets and the high concentrations of propionic acid is indicative of low microbial cellulolytic activity.

Concentrate selectors have high fermentation rates (Hoppe *et al.* 1983; Hoppe 1984; van Hoven and Boomker 1985), and those of the blue duiker and the red duiker approximate those of the suni (Hoppe and Gwynne 1978) and dik dik (Hoppe *et al.* 1983). Because of the highly papillated rumen in blue duikers and red duikers, absorption rate is fast.

The caecum provides a constant temperature and pH for the maintenance of complex microbial populations (Ulyatt *et al.* 1975). Since caecal volume relative to rumenoreticular volume is high in concentrate selectors, Drescher-Kaden (1977) and Hoppe (1984) hypothesized that caecal digestion is important in selective feeders. Prins *et al.* (1984) and van Hoven and Boomker (1985) claim that ruminal VFAs are less important in satisfying the energy requirements of concentrate selectors than nongeneralist feeders, concentrate selectors must absorb nutrients from the gastro-intestinal tract beyond the rumen to satisfy energy demands. The concentration of VFAs present in the caecum of blue duikers is higher than that in the rumen, but the volume of the caecum is much smaller than that of the rumen, making it less important overall but not insignificant. The relative composition of VFAs in the caecum and rumen indicates greater fibre utilization in the caecum, and parallels the results obtained by Boomker (1983) for grey duiker. Because of the high fermentation rates in the small selectors, protein and carbohydrates that are easily fermentable will be more rapidly absorbed than fibre, and thus fibre not utilized in the rumen will be digested in the hindgut (Boomker 1984; Kay *et al.* 1980; Maloiy *et al.* 1982).

Recently, Dehority and Varga (1991) have demonstrated the presence and density of bacterial and fungal members in the ruminal and caecal contents of blue duikers, which aid digestion. Total bacterial numbers differed in the caecum between diets, *i. e.* 1,064 × 10^6 bacteria/g for animals fed high-forage diet compared with 166 × 10^6 for those fed high-concentrate diet. Ruminal cellylolytic bacterial numbers were considerably higher than in impalas, *Aepycerus melampus* and springbok, *Antidorcas marsupualis* (Giese and van Gylswyk 1975), which may be associated with folivory in the blue duiker.

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Zusammenfassung

Morphologie des Pansens und Produktion von flüchtigen Fettsäuren bei Blauducker (Cephalophus monticola) und Rotducker (Cephalophus natalensis)

Die Anatomie des Pansens ist bei Blauduckern und Rotduckern sehr ähnlich. Bei beiden Arten ist der Pansen ein einfacher, plesiomorpher, mit Blindsäcken versehener, S-förmiger Schlauch, dessen Ostien groß und bei dem die Pansensäulen schwach ausgebildet sind. Diese Spezialisierungen erleichtern den schnellen Durchgang des Nahrungbreies. Bei beiden Arten sind die Pansen dicht mit pilzförmigen, hochgradig durchbluteten Papillen besetzt, um die Absorption zu erleichtern. Viele Anpassungen sind charakteristisch für Verwender energiereicher Nahrung.

Die Gesamtkonzentration flüchtiger Fettsäuren ist beim Rotducker niedriger als beim Blauducker. Die Propionsäure- und Buttersäurekonzentration ist jedoch beim Blauducker höher, während die Essigsäurekonzentration wiederum beim Rotducker höher ist. Im Blinddarm des Rotduckers ist die Konzentration flüchtiger Fettsäuren (besonders Essigsäure) höher als beim Blauducker, trägt jedoch wahrscheinlich weniger Energie zum Stoffwechsel bei, wegen der geringeren Größe des Blinddarms im Vergleich zum Pansen.

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A new species of the Puna mouse, genus *Punomys* Osgood, 1943 (Muridae, Sigmodontinae) from the Southeastern Andes of Perú

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Abstract

The puna mouse, *Punomys* Osgood, 1943, is a poorly known and rather enigmatic taxon in regard to its phyletic relationships within the Sigmodontinae. Since the discovery of the type species *P. lemminus* Osgood, 1943, the genus was considered monotypic and known from few specimens. We describe a second species here based on collections made by Carl B. Koford in Puno Department, Peru, in 1951 and 1970. The discovery of this new species supports the hypothesis of a generalized biogeographical subdivision in the southern Andes along both sides of the Lake Titicaca Basin. We also summarize available data on natural history, habitat, reproduction, and systematic position.

Introduction

The puna mouse, genus *Punomys*, is a rather enigmatic Andean taxon whose phylogenetic position within the Sigmodontinae is debatable (reviewed in Steppan 1993). Since the description of the type species, *P. lemminus*, by Osgood (1943), the genus has been considered monotypic in the literature. We have been studying the few available specimens of this taxon in search of information regarding its remarkable morphology, phyletic relationships, and natural history. During the course of these investigations, we realized that a series of specimens from Abra Aricoma and the head of the Limbani Valley in the Cordillera Carabaya of northern Puno Department, Perú, shared constant characteristics in external and cranio-dental morphology that, although subtle, distinguish them from members of the species from the Cordillera Occidental in southwestern Perú. We believe that these differences are sufficient to identify a new taxon, and we name this new species below.

Material and methods

Nearly all available museum specimens (preserved skin with skull) of the puna mouse, *Punomys*, were examined in the course of this study. Standard cranial measurements were taken with digitial calipers; external measurements were those taken by the preparator as recorded on the specimen tag. The 22 known specimens of this genus come from but seven localities; 11 specimens each of *lemminus* (four localities) and the new species described below (three localities; Fig. 1). Locality records and museum repositories are as follows (MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; MCZ, Museum of Comparative Zoology, Harvard University; AMNH, American Museum of Natural History, New York; and FMNH, Field Museum of Natural History, Chicago):

Punomys lemminus. (1) Arequipa: Huaylarco, 55 mi ENE Arequipa, 15,300 ft (N = 1, MVZ). Puno: (2) San Antonio de Esquilache, 16,000 ft (N = 1, FMNH; holotype); (3) Caccachara (about 5 mi SW crest of the western Cordillera, approximately 50 mi SW Ilave, 16,000 ft (N = 8, MCZ). (4) Tacna: 20 km NE Tarata, 14,600 ft (N = 1, MVZ).

Punomys new species. Puno: (5) Lago Aricoma, 13 mi ENE Crucero, 15,000 ft (N = 1, MVZ); (6) Abra Aricoma, 15 mi ENE Crucero, 15,500 ft (N = 1, MVZ); (7) 8 mi SSW Limbani, 15,000 ft (N = 7, MVZ; N = 2, AMNH).

Results and discussion

We consider that the specimens of *Punomys* from the vicinity of Lago Aricoma and the head of the Limbani Valley in the Cordillera Carabaya of northern Puno Department, Perú, are sufficiently distinct from the type species, *P. lemminus* Osgood, to warrant recognition as the second species of this poorly known genus. We name this new species with pleasure as:

***Punomys kofordi*, new species**

Holotype

Adult female, Museum of Vertebrate Zoology (MVZ) 139588, from 13 mi (20.8 km) ENE Crucero, Lago Aricoma, Department of Puno, Perú, 15,000 ft (4,550 m), approximately 14°17′S, 69°47′W (Fig. 1). Collected by Carl B. Koford on 15 July 1970, original number 4 418. The holotype is a well-made skin with skull and mandibles in excellent condition.

Paratypes

MVZ 114757 male (skin with skull), MVZ 114758 female (skin with skull), MVZ 116190 female (skin only), MVZ 116191 male (skin only), MVZ 116192 male (skin with skull), MVZ 116193 female (skin with skull), MVZ 116194 female (skin with skull), AMNH 256780 female (originally MVZ 114759; skin with skull), and AMNH 256781 male (originally MVZ 116195; skin with skull) from 8 mi (12.8 km) SSW Limbani, Department of Puno, 15,000 ft (4,550 m); and MVZ 139589 male (skin with skull) from 15 mi (24 km) ENE Crucero, Abra Aricoma, Department of Puno, 15,500 ft (4,700 m).

Distribution

Known only from the high elevations of Abra Aricoma and the adjacent Limbani Valley above 4,500 m in the Cordillera Carabaya of northern Puno Department, southern Perú (Fig. 1).

Etymology

This taxon is named in honor of the late Carl B. Koford, who collected the only known specimens while engaged in his studies of vicuña population biology in the upper Limbani Valley (Koford 1957).

Diagnosis

Large vole-like mouse with long and lax fur, dark brown above with underparts buffy-gray and not sharply contrasting with dorsal coloration. Tail short, averaging 34% of the total length; hind foot absolutely shorter than *lemminus.* Cranial conformation (Figs. 2 and 3) similar to *lemminus* but distinguished by parallel as opposed to more anteriorly convergent zygomatic arches; anterior root of zygoma squared; zygomatic plate narrow

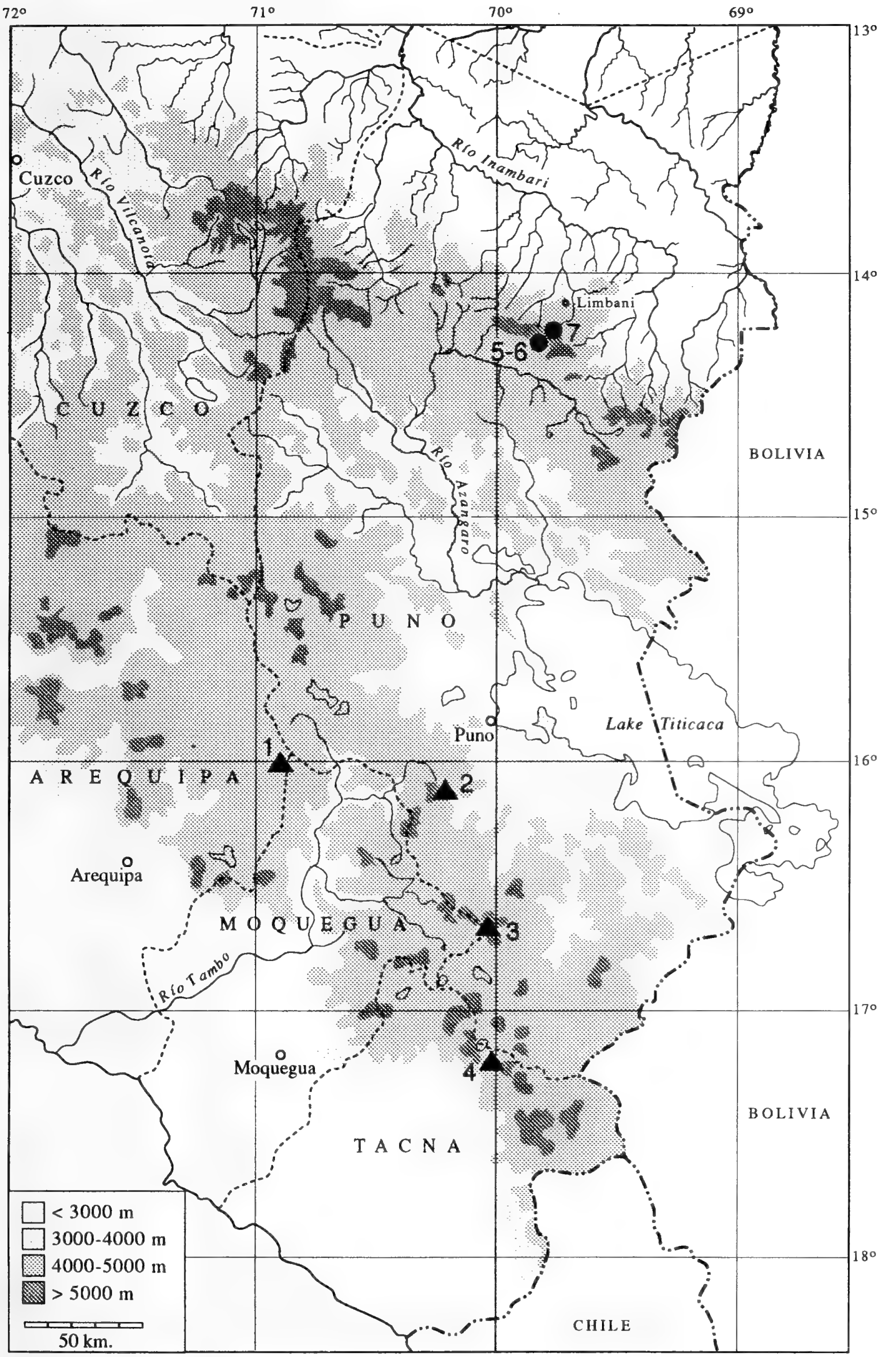

Fig. 1. Map of distribution of the puna mouse, *Punomys*, in southern Perú. Localities are numbered as in the Method and materials; localities 1–4 are of *P. lemminus*, 5–7 are of *kofordi*, new species.

Fig. 2. Dorsal, ventral, and lateral views of the cranium of the holotype of *Punomys kofordi*, new species, MVZ 139588.

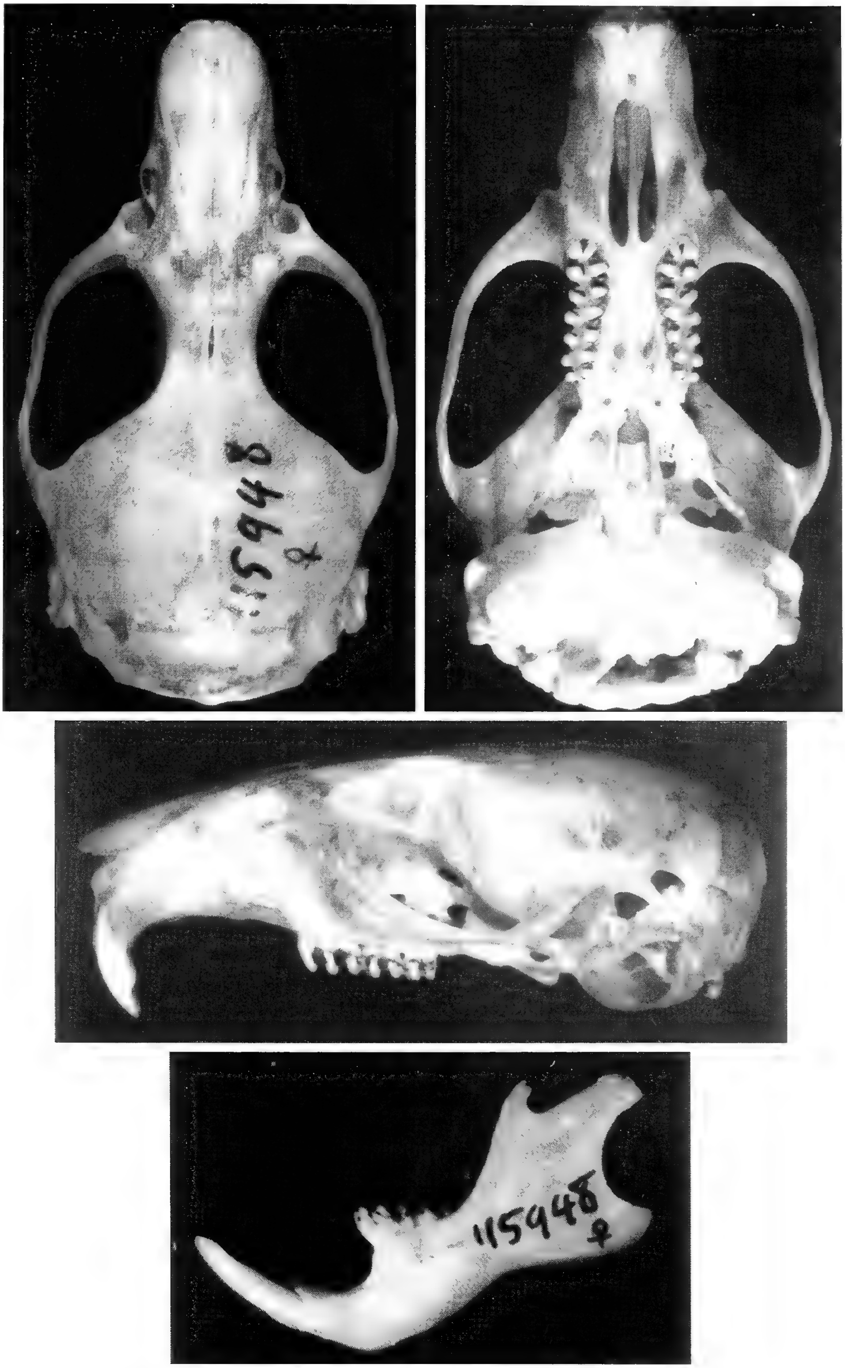

Fig. 3. Dorsal, ventral, and lateral views of the cranium of *Punomys lemminus* Osgood from 20 km NE Tarata, Tacna, 14,600 ft (MVZ 115948).

with frontal edge straight, as opposed to a broad and more posteriorly slanting edge; spine of zygomatic notch angled laterally rather than directed anteriorly, particularly in ventral view; zygomatic notch broad but shallow in comparison to *lemminus*. Nasals not abruptly expanded anteriorly, with posterior v-shaped notch. Palatal bridge short; anterior opening of alisphenoid canal small; and procingular conules of first upper molar subequal in size (Fig. 4).

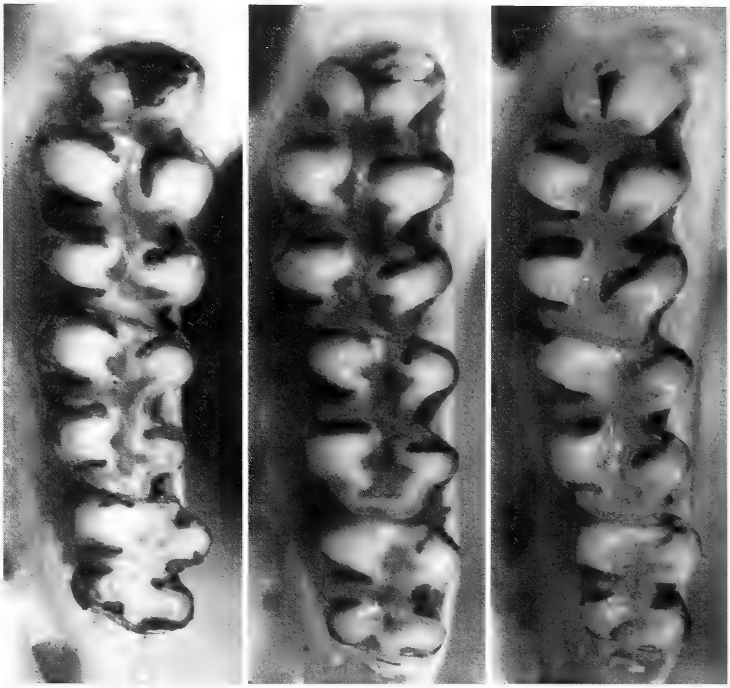

Fig. 4. From left to right, left maxillary tooth rows of *Punomys kofordi*, new species, holotype, MVZ 139588; paratype, MVZ 114758; and of *Punomys lemminus* MVZ 115948.

Measurements of the holotype

Linear measurements are in millimeters and mass (weight), in grams: Total length (ToL), 215; tail (TaL), 74; hind foot (HF), 26; ear, from notch (E), 23; greatest length of skull (GSL), 33.26; condyloincisive length (CIL), 31.50; zygomatic breadth (ZB), 17.64; breadth of braincase (BB), 14.75; least interorbital breadth (IOC), 4.44; diastema length (DL), 8.42 ; maxillary tooth row length (MTRL), 6.72; incisive foramen length (IFL), 6.92; palatal bridge length (PBL), 6.58; rostral breadth (RB), 7.01; breadth of palate, between first molars (BP), 2.51; breadth of first upper molar (M1B), 2.09; breadth of zygomatic plate (ZPB), 3.19; mass, 82.

Additional measurements

Comparisons between *lemminus* and *kofordi* in selected mensural characters are given in table 1. With available samples, *kofordi* averages larger in four external and craniodental dimensions (HF, IOC, IFL, and PB, all significantly so [$p < 0.05$]), *lemminus* in 13 measurements (ToL, TaL, E, GSL, CIL, ZB, BB, DL, MTRL, PBL, RB, M1B, and ZPB, five significantly so).

Table 1. Measurements of adult *Punomys lemminus* (combined from localities 1, 2, and 4) and of *P. kofordi*, new species (localities 5 through 7). Values are in millimeters and are the mean followed by the range (in parentheses). A * identifies those measurements that are significantly different ($p < 0.05$).

Measurement	*P. lemminus* (N = 3)	*P. kofordi* (N = 6)
Total length	194.7 (185–203)	203.3 (191–215)
Tail length*	53.0 (46–61)	69.2 (65–77)
Hind Foot length*	28.7 (28–29)	27.2 (26–28)
Ear height*	24.0 (23–25)	24.7 (23–27)
Greatest length of skull	33.3 (32.5–34.1)	32.9 (31.4–33.9)
Condyloincisive length	31.8 (31.0–32.2)	30.9 (28.8–31.9)
Zygomatic breadth*	18.9 (18.6–19.3)	17.6 (16.2–18.8)
Braincase breadth	15.2 (14.7–15.5)	14.7 (14.5–15.2)
Interorbital breadth*	4.2 (4.0–4.3)	4.4 (4.3–4.5)
Diastema length	8.3 (8.0–8.7)	8.0 (7.4–8.4)
Maxillary tooth row length	7.0 (6.5–7.5)	6.9 (6.7–7.2)
Incisive foramen length*	6.8 (6.7–6.9)	7.0 (6.9–7.2)
Palatal bridge length*	7.4 (6.5–8.0)	6.6 (6.4–6.8)
Rostral breadth	7.2 (7.0–7.6)	6.9 (6.4–7.3)
Palatal bridge width	2.2 (2.1–2.3)	2.3 (1.8–2.9)
First upper molar breadth	2.1 (2.0–2.2)	2.1 (2.0–2.2)
Zygomatic plate breadth*	3.6 (3.5–3.6)	3.2 (2.8–3.4)

Description and comparison

Pelage similar to *lemminus* (as described by Osgood 1943 and Pearson 1951), but *kofordi* is overall darker and underparts do not contrast as in *lemminus*. Specimens of *kofordi* are grayer and darker on the back, the feet and hands are duskier above, the ears darker, the tail less distinctly bicolored, and the belly considerably darker gray with a distinct buffy wash (Pearson 1957). The generally more dark coloration is typical of many other taxa that occur in the more humid eastern and northern Altiplano (for example, see Pearson 1958 for discussion of *Phyllotis* and Sanborn 1947 for *Chroeomys*). Tail absolutely and relatively longer in *kofordi* than *lemminus* (34% of total length versus 27% on average); hind feet absolutely shorter (Tab. 1).

Skull rather heavy, shorter and less broad across the braincase and zygoma than *lemminus* (Figs. 2, 3; Tab. 1). Nasals long, well developed but anterior end not abruptly expanded as in *lemminus*, tapering slightly posteriorly to end as a deep notch in most specimens. Lacrymals reduced in size, but larger than in *lemminus* and set mostly anterolateral to the maxillo-frontal suture. Interorbital region narrow, but averaging broader than *lemminus*, with edges rounded, not beaded; incipient postorbital processes are present at the frontal margin of the fronto-parietal suture in *kofordi* but are lacking in *lemminus*. Zygomatic arch rather robust, sides almost parallel rather than convergent anteriorly, so that maxillary root is more squared than *lemminus*. Zygomatic notch more shallow and broad in *kofordi*, with the spine more obvious due to more vertical, less rounded anterior edge of plate, and projecting more laterally than in *lemminus* (particularly evident when viewed from below). Parietals reduced and restricted to cranial cap, but interparietal well developed and pentagonal in shape.

Incisive foramina long and narrow, with slightly rounded posterior ends extending to the procingulum of first upper molar. Palate complex, dissected by two long and deep sulci that run divergently from incisive foramina to the postero-palatal pit region, usually deeply perforated or excavated at level of the second upper molar. Mesopterygoid fossa relatively deep, nearly extending to posterior margin of third molar in *kofordi* but not in *lemminus*; wider and more parallel sided, not narrow and divergent posteriorly as in *lemminus*. Sphenopalatine vacuities moderately large. Parapterygoid plates deeper and shorter than in *lemminus*, somewhat flared and smoothly divergent at their posterior end. The posterior opening of the alisphenoid canal is larger in *lemminus* than *kofordi*. The tympanic bullae are large and inflated. Carotid circulation of Pattern 1 (following Voss 1988), with both inferior and superior branches of the stapedial and the internal carotid arteries present, as evidenced by the enlarged carotid canal and stapedial foramen and presence of a squamosal-alisphenoid groove, spheno-frontal foramen, and groove on the posterolateral margin of the parapterygoid plates (Voss 1988; Carleton and Musser 1989).

Upper incisors strong and orthodont, with nasals extending slightly in front of the level of upper incisors. Zygomatic plate narrower in *kofordi*, front edge straight to slightly slanting posteriorly rather than strongly curved posteriorly as in *lemminus*. The sphenofrontal foramen is partially coalesced with the orbital fissure and the alisphenoid strut is absent. The trough for the masticatory-buccinator nerve is more well developed in *kofordi*, and the performation in the squamosal resulting from the squamosal-alisphenoid groove is larger. Subsquamosal fenestra fairly open; hammular process of squamosal moderately developed although usually slender with posterior end expanded and curved upward. The tegmen tympani is well developed and overlaps the squamosal. The mastoid is large; the mastoid fenestra is present but small and round in *kofordi*, larger and more irregular in shape in *lemminus*.

Molars combine coronal hypsodonty and high, sharp-angled individual cusps in the unworn dentition (Fig. 4). The molar toothrows exhibit a strong tendency to divergence posteriorly, less so in *kofordi* than in *lemminus*. The first molar appears strongly curved, with the procingulum divergent anteriorly. Anterolabial and anterolingual conules in first upper molar of more nearly equal size in *kofordi*; in *lemminus*, the anterolabial conule is more developed, so that the first upper molar is more strongly divergent. Main cusps in first molar are well developed, the lingual cusps more anteriorly placed than labial ones. Occlusal surface of molars complex due to presence of both labial and lingual styles, with the lingual styles more developed. Parastyle and mesostyle on the labial side and protostyle and enterostyle on the lingual side well developed. Posteroloph and a "lingual posterostyle" (the metaconule of Osgood 1943) distinct although not well developed. Anteroloph and posteroloph of second upper molar usually distinct but not well developed; enterostyle and mesostyle well developed. Third upper molar with the four main cusps still distinct; anteroloph and enterostyle present; mesostyle is minute or absent; posteroloph appears more distinct in *lemminus* than in *kofordi*. Occlusal view of the lower molars show same complexity of structure as the upper molars, with the labial styles more developed than those on the lingual side.

Habitat range

The genus *Punomys* has the highest elevational range (above 14,600 feet [4,400 m] in the Cordillera Occidental and above 1,5000 ft [4,500 m] in the Cordillera Oriental) than any other species of mammal. *Punomys kofordi* is known from only three closely adjacent localities in the Cordillera Oriental north of the Lake Titicaca Basin, and *P. lemminus* has been recorded from four, widely spaced localities in the Cordillera Occidental to the southwest of this Basin (Fig. 1 and Pearson 1951, 1957). The two general areas of distribution share a common high elevation and are apparently closely related floristically (Molina and Little 1981), but are quite different in available moisture. A single wet season occurs sometime between October and April, and supplies an annual average precipitation above 400 mm in the Cordillera Oriental, but only between 100 to 400 mm in the Cordillera Occidental (Cabrera 1968). This difference is the basis for the recognition of the Wet Puna versus Dry Puna ecosystems, respectively, by Tosi (1960) and Troll (1968).

Pearson (1951, 1957) summarized the habitat range of the 11 known specimens of *P. lemminus* (including the holotype) in the Cordillera Occidental. Here, *P. lemminus* was always encountered among rocks in barren, broken areas near yareta (*Azorella compacta*) and clumps of its favorite food plants, the tola shrub *Senecio adenophylloides* and the ground rosette herb *Werneria digitata*, and not far from water. It was commonly seen during the day, "... feeding or scurrying from the shelter of one rock to another" (Pearson 1951, p. 150). At Caccachara (a high valley about 5 miles southwest of the crest of the western Cordillera [16°41′S, 70°04′W], approximately 50 miles southwest of Ilave, Puno Department; Pearson 1951), the eight specimens taken were collected with other typically high elevation rodents, including "*Akodon*" *andinus* (see Patton and Smith 1992), *Chroeomys jelskii*, *Calomys lepidus*, *Phyllotis xanthopygus* (listed as *P. darwini* by Pearson 1951), *Auliscomys* (= *Maresomys* following Braun 1993) *boliviensis*, *A. sublimis*, *Chinchillula sahamae*, *Neotomys ebriosus*, *Lagidium peruanum*, and *Abrocoma cinerea*.

In the region of Abra Aricoma in the Cordillera Carabaya (of the Cordillera Oriental) in northern Puno Department, Carl Koford records the habitat and habits of *P. kofordi* as follows (fieldnotes in MVZ archives; see also Pearson 1957): individuals were found in holes under mossy rocks, under rocky piles, or at the base of steep slopes and cliffs, usually close to *Senecio* bushes. Individuals were seen both during the day and at night, and several animals were observed to use a common burrow opening. Suitable microhabitats were recognized by the presence of cuttings or flowers of *Senecio* layering the floor of holes. At or near the type locality of *kofordi*, other mice collected included *Chroeomys jelskii*, *Phyllotis xanthopygus*, *Auliscomys pictus*, *Neotomys ebriosus*, and *Chinchillula sahamae*; *Lagidium peruanum* was seen but not collected. This is generally the same assemblage of species that occurs with *P. lemminus* in the Cordillera Occidental, with the exception that *Auliscomys pictus* is replaced by *A. sublimis* and that "*Akodon*" *andinus*, *Auliscomys boliviensis*, and *Calomys lepidus* were not recorded.

Pearson (1982) distinguished a Southern Altiplano Group of rodents, restricted to the areas south of the Río Acarí in the southern Altiplano region of Peru (see Fig. 2 in Pearson 1982, p. 282). This group is comprised of various species or subspecies of *Phyllotis*, *Auliscomys*, *Chinchillula*, *Punomys*, *Chroeomys*, *Akodon*, *Bolomys*, and *Galea*, and the area includes the northern distributional limit of tuco-tucos, *Ctenomys*. However, a previously unrecognized biogeographical subdivision of the southern Andes on both sides of the Lake Titicaca Basin is also apparent at either the species or subspecies level. In the dry, mountainous zones to the south of Lake Titicaca are *Phyllotis osilae osilae*, *Auliscomys sublimis*, *Auliscomys boliviensis*, *Punomys lemminus*, "*Akodon*" *andinus*, *Akodon berlepschii*, *Akodon boliviensis*, *Akkodon subfuscus arequipae*, *Bolomys amoenus*, *Chroeomys jelskii pulcherrimus*, and *Galea musteloides*. In contrast, the wetter puna of the Cordillera Oriental contains a rodent assemblage consisting of *Phyllotis osilae phaeus*, *Punomys kofordi*, and *Chroeomys jelskii cruceri* and *inambarii*, as well as other species with wider distributions that do not occur in the Cordillera Occidental, such as *Auliscomys pictus*, *Oxymycterus paramensis*, *Akodon puer*, *Akodon subfuscus subfuscus*, and *Oligoryzomys* sp. B (sensu Carleton and Musser 1989). The Dry Puna of the Cordillera Occidental appears to contain a larger assemblage of rodents than does the Wet Puna, but sample efforts in both areas have been rather minimal. The relative distinctness of the rodent faunas of these two regions is especially noteworthy, given the likelihood that the cordilleras on both sides of the Lake Titicaca Basin would have been capped by glacial ice repeatedly throughout most of the Pleistocene (Clapperton 1983; Mercer 1984).

Reproduction

Nowak (1991) states that *Punomys lemminus* breeds during the wet season, which is from November to April in the Altiplano of southern Perú. This is presumably based on the record of a pregnant female with two embryos taken at Caccachara, Puno, on 7 November, while three individuals taken in earlier months (September and October) contained no embryos (Pearson 1951) and no juveniles were collected during these months. A second female specimen of *lemminus* taken by Pearson (MVZ 115948) at 20 km NE Tarata, Tacna, on 28 January 1952, also contained two embryos. However, within the series of *kofordi* from the Cordillera Carabaya, four females taken from June to September carried embryos or were post-lactating, with a litter size ranging from 2 to 3, and juvenile specimens were also obtained. While data are sparse, it appears that the two species may breed at different times of the year, *lemminus* in the wet season, *kofordi* in the dry. Females of both species have four pair of nipples in pectoral, axillary, abdominal, and inguinal positions.

Remarks

Punomys is a poorly known and rather enigmatic taxon of incompletely understood biogeographic affinities. As currently understood, the two species now recognized come from widely separated regions in southern Perú, although potentially suitable high elevation habitat connects the Cordillera Oriental and Cordillera Occidental along the border of Puno and Cusco departments (Fig. 1). Although this area has been very poorly sampled biologically, the two species would have been geographically separated for much of the Pleistocene by the expanded glacier of the Quelccaya Ice Cap in the Cordillera Vilcanota (Kessler 1984).

The phylogenetic relationships of the puna mouse are equally obscure. Vorontzov (1959) placed the genus in the tribe Phyllotini, an action to which Olds and Anderson (1989) and Braun (1993) agreed, based on morphological criteria. However, Hershkovitz (1962) and Reig (1980, 1984) did not affiliate *Punomys* with the phyllotines; rather they suggested the genus be maintained as incertae sedis to emphasize its unique combination of morphological attributes. Steppan's (1993) cladistic analysis of 96 craniodental, skeletal, external, and soft anatomical characters supports the position of Hershkovitz (1962) and Reig (1980, 1984). His analysis indicates that *Punomys* lies outside the phyllotines, near the base of the phyllotine-akodontine-scapteromyine radiation. Steppan (1993, p. 190) also argues that "... putative synapomorphies supporting the definition of Phyllotini are the moderate to large ears (>0.16 head and body length), the parapterygoid fossa being broader than the mesopterygoid fossa (narrower in *Punomys*), the very open sphenopalatine vacuities (partially constricted in *Punomys*) and the complete loss of a mesoloph (present in *Punomys*)." However, *Punomys* does have ears of moderate size (>0.16 head and body length), the ratio of parapterygoid fossa to mesopterygoid fossa width (sensu Olds and Anderson 1989, p. 60) is greater than 1, and the sphenopalatine vacuities, while partially constricted in *lemminus*, are more open in *kofordi* (see also Olds and Anderson 1989). These statements may indicate a closer relationship between *Punomys* with (or included within) the Phyllotini than previously suggested. Reig (1986) proposed that *Punomys* may represent an early descendent of a protophyllotine stock.

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We thank Carl B. Koford (posthumously) for collecting the only known specimens of *P. kofordi*, and Oliver P. Pearson for both reading a draft of this paper and sharing his substantial knowledge of the Altiplano rodents with us. Bruce D. Patterson (Field Museum of Natural History) and Guy G. Musser (American Museum of Natural History) kindly allowed us to examine specimens in their respective care.

Zusammenfassung

Eine neue Art der Punamaus, Gattung Punomys Osgood, 1943 (Muridae, Sigmodontinae) aus den südöstlichen Anden von Peru.

Die Punamaus, Gattung *Punomys* Osgood, 1943, ist ein wenig bekanntes und in bezug auf ihre verwandtschaftliche Stellung innerhalb der Sigmodontinae recht rätselhaftes Taxon. Seit der Entdeckung der Typusart *P. lemminus* Osgood, 1943, von der nur wenige Exemplare bekannt sind, wurde die Gattung als monotypisch angesehen. Die Autoren beschreiben hier eine zweite Art auf der Grundlage von Aufsammlungen, die Carl B. Koford 1951 und 1970 im Puno District in Peru gemacht hat. Die Entdeckung dieser neuen Art stützt die Hypothese einer grundsätzlichen biogeographischen Unterteilung der südlichen Anden auf beiden Seiten des Titicaca-Sees. Verfügbare Daten zu Naturgeschichte, Lebensraum, Fortpflanzung und systematischer Stellung werden mitgeteilt.

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Social dominance and bodily conditions in small groups of male and female laboratory rats of known familiarity

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Abstract

Studied was the significance of relationships between characteristics of behaviour, competition and bodily conditions for the social dominance rank in rats. Adult virgin male and female rats of the inbred strain DA of known familiary membership were studied. In groups of three rats 6 behavioural categories per animal were registered on 6 test days and the competition success in water, food and runway tests was determined. The body and 6 organ masses were measured and the levels of 3β-hydroxysteroid dehydrogenase (HSDH) and 5α-reductase (REDU) activity in the liver and corticosterone were determined in blood. In females, significant correlations existed between the parameters appeasement behaviour, successful food competition and low corticosterone and HSDH levels. Aggressive activity occurred between females to almost the same extent as between males, but was not correlated to the other characteristics. By contrast, in males high aggressive behaviour, successful water and food competition were closely related. In addition, high body and organ masses influenced the experimental outcome to a greater extent than behavioural gestures. Only males showed significant familiary differences in body mass and organ masses of heart, kidneys and adrenals. In females, appeasement behaviour and successful coping against stress proved to be prerequisites for achieving high dominance ranks whereas a good bodily condition and aggressiveness was the case for males.

Introduction

Functionally, social dominance is preferentially defined as the acceptance of priority distribution between animals in a number of goals (Hand 1986; Adams and Boice 1989). Conceptually, dominance is increasingly understood as a property of a relationship and not as an individual character of a certain animal (Barrette 1993; Bernstein 1981; Moore 1993). Drews (1993) defined social dominance operationally as a complex relationship between individuals, which cannot be adequately described by individual terms such as aggressiveness, bodily strength or stress resistance. According to Drews (1993), agonistic interactions however represent a particularly major dominance factor.

Because male rats are considered to be more highly motivated towards aggressiveness and sexuality than females (Matuszczyk and Larsson 1993; Poole and Fish 1976; Timmerman 1978), dominance tests were preferentially carried out on these. The frequencies of aggressiveness and submissive behaviour and copulation were often recorded as the decisive and quantifiable dominance measures. Such behavioural contrasts do not only determine the social structures between the animals, but also their physiological condition (Holst 1990).

As yet, however, only few comprehensive studies for intact female rats exist, which, apart from social parameters (Blanchard et al. 1984; Zook and Adams 1975) have also included somatic and biochemical characteristics at the same observation time. Such intercorrelations, however, are necessary in order to differentiate between the effects af bodily conditions, stress and agonistic activity on dominance ranks. The aim of the present study is to investigate under laboratory conditions whether aggressive behaviour as well as other social or competitive gestures are significantly correlated with somatic characteristics. In addition, it was of interest whether the decisive dominance factors are equal in male and female rats. The extent to which the definition of dominance according to Drews (1993) is generally applicable, can only be assessed after obtaining such information.

Studies on genetically defined animals are also expected to produce results as to whether the complex correlations between behavioural arousal and activation of the sympathic-adrenal axis (e. g. Henry and Stephens 1977; Holst 1990; Korz 1991, 1993; Sachser 1994) can be demonstrated in a similar manner in male and female rats.

Also, the family membership of animals in this study was known, allowing first orientating results on individual genetic effects to be presented, as previously demanded by Barrette (1993) and Dewsbury (1990).

Material and methods

Animals

Nine virgin male and female agouti-coloured DA-ZTM-rats (Breeder: Laboratory Animal Science Unit, Medical University of Hannover, Germany), 78 days old on arrival, were used. The animals originated from 7 different families (A, B, C, Af, Bf, Cf, Df) with identical birth dates and were ear-marked individually for identification.

From the time of arrival to the end of training (Fig. 1), the animals were kept singly in polycarbonate (Makrolon) cages type III (39 × 23 × 15 cm). During the entire period of the experiment, rats were maintained in groups in Makrolon type IV cages (55 × 33 × 20 cm) and kept under standardized conditions (room temperature: 21 ± 2 °C; relative humidity: 50 ± 5%; feed: pellets type 1324, Altromin Lage/Lippe, Germany) and water ad lib. under an inversed light cycle (artificial light 19.00–8.00 h; 40 W dimmed red-light during the dark).

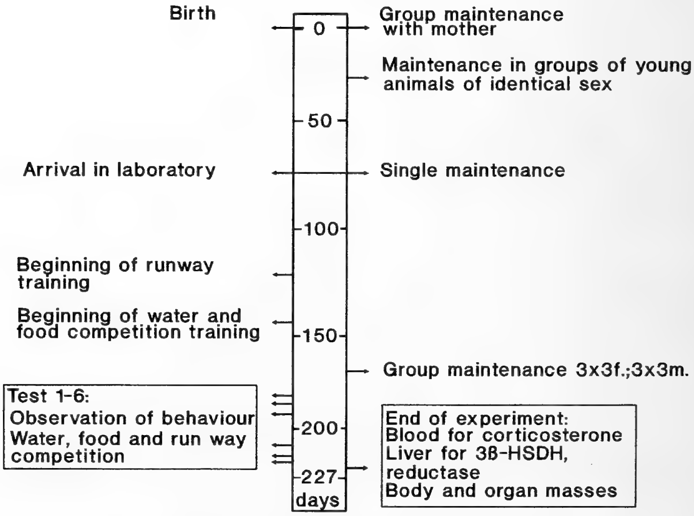

Fig. 1. Experimental design – In relation to age of rats in days, conditions of maintenance, training period, dominance tests and post-mortem evaluations (m. = male, f. = female).

All studies were carried out between July 1985 and February 1986 in accordance with the regulations of the German Animal Protection Law, 1972. Some findings for male rats, especially on sexuality, have already been published (MILITZER et al. 1984).

Training procedure

During this time the animals were kept individually in order to learn the competition tests without external influence. Training for the competitive experiments was carried out during the dark phase 8.00–13.00 h. Runway training was initiated 55 days after arrival of the rats (Fig. 1). Each of the rats, starved for 22 h, was allowed to acquaint itself with the runway, whose gates were open, in the first 3 days for 4 min per day. The rats were then trained by allowing them to hurry into the alley after opening the start box gate and to wait for 3 sec at the central gate. Upon opening, animals ran into the goal box opposite, where they were rewarded with a food pellet.

Seventy days after arrival, the conditioning of the rats to the food and water competition test box (Makralon type IV, 55×33×20 cm) was initiated. Ten times within 35 days, the animals were placed separately into the testbox. Through a 3.2 cm diameter hole in the small side of the box they were able to drink for a maximum of 2 min from an externally positioned water bottle.

Subsequently, food in the form of powder diet (type 1321, Altromin Lage/Lippe) was affered contained in a 7 cm high metal case (diameter 2.7 cm) fastened vertically to the floor in the middle of the cage. For each training time, the animals individually had 3 min time to take up food (for types of the test cages, see: MILITZER et al. 1984).

At the end of the training, at 183 days af age, the rats were individually marked by colouring the hair and divided into groups of three of the same sex, i. e. 3 female and 3 male groups. These groups remained unchanged throughout the experiment. The first rank test was carried out on the following day.

Test design

With the exception of the runway test, the behaviour observations and the competition tests were always carried out in the home cage. For each group of rats on the same day the following 4 test methods were carried out 6 times at intervals of 5 days to two weeks (Fig. 1). The sequence of tests remains constant, although the test was always started with another group.

a) Observation of social behaviour

During the first 10 min under dark phase conditions, the behaviour of the 3 rats in each cage was tape-recorded, always by the same observer (8.00–9.30 h). The frequency of 34 distinct behavioural elements per animal were registered and combined in major categories (LEHMAN and ADAMS 1977; SILVERMAN 1978).
Aggressive behaviour: bite and kick, full aggressive, offensive upright and sideways postures,
Submissive behaviour: defensive upright and sideways posture, submission,
Social exploration: nose, back, anal and tail sniffing,
Autogrooming: face, side, anal grooming, scratching,
Allogrooming: kick or comb body fur of another rat,
Threat behaviour: teeth exposed, turn of head towards to another rat,
Escape behaviour: retreat, fleeing and crouching.

b) Water and food competition test

The thirsty animals (28.5 h water deprivation) were offered water for 3 min. Only one rat could reach the water bottle through the wall hole at any time. Before the beginning of the food test, the container with powder diet was fixed in the centre of the home cage and the entrance to food was opened for 5 min by means of a pole operated from the outside. The drinking and feeding time per rat and test was recorded by 2 observers using a stop clock. These times were converted to their natural logarithms and evaluated. The tests were repeated after 1.5 h (from 10.00—13.00 h).

c) Runway test

Two animals from each group were tested for 2 min in an alternative and randomized order. Simultaneously from both start boxes, the rats were released into the runway. The animals met at the central gate and attempted to push each other off the alley. The rat that pushed the defeated animal back into its start box was the winner. With a single repetition 1.5 h after the first test, 6 runs per group and day were conducted. The mean time required to oust the rat starting from the opposite side was determined (from 14.00–17.00 h).

d) Morphology and biochemistry

One day after the last rank test the rats were sacrificed by decapitation (8.00–9.30 h). The animals were bled no later than 100 sec after the first cage contact. Blood serum (0.5 ml) was collected and stored at –20 °C. Corticosterone was determined fluorimetrically (Stahl et al. 1963). The corpses were autopsied and the following organs were dissected and weighed: thymus, heart, liver, spleen, kidneys, and adrenals. The activity of 3β-hydroxysteroid dehydrogenase (HSDH) and 5α-reductase (REDU) was determined in cold perfused liver tissue (Lax et al. 1976; Schriefers et al. 1971).

e) Biostatistical analysis of data

The main interest focussed on the presentation of the relations between the characteristics for the overall experiment and not on the description of individual rank relations. Since no normal distribution was to be expected above all in the behavioural data, only the coefficients of variation were calculated for all characteristics. Thus, no SD's are shown in figures 2 and 3. In the first step, means and coefficients of variation for each characteristic and sex were calculated from the absolute frequencies. Correlations (Spearman's r) between the observed characteristics irrespective of group from the overall experiment were evaluated. In accordance with others (Aspey and Blankenship 1977) a principal-component factor analysis with rotation of factors by the Varimax procedure was included.

Finally, the morphological data of individually known animals were grouped according to their family membership. They were checked by Student's t-test because they are distributed normally in contrast to the ethologic data.

Results

The major characteristics during the course of the tests are exemplified in figures 2 and 3. An increase in behavioural activities was observed for up to 2 weeks after group combination, after which no differences are seen at the various test days. The means for drinking time and food uptake show a similar pattern (Fig. 3). For trained rats, the passage times in the runway are roughly similar over the experimental period. Apart from the expected sex difference, body mass shows regular increases except during the initial test week. From the course of the curves in figures 2 und 3, the summary of data for the overall experimental period appears justified (Tab. 1).

An examination of the group means shows only slight differences between the average behavioural activities of males and females. They differ merely in the longer duration of food uptake in the case of females in the competition tests although the differences are not statistically different. For behavioural and competition parameters, aggressive behaviour in both sexes shows the largest variance with variation coefficients of 95 and 100%. In females submissive behaviour and allogrooming with threat are also characterized by large coefficients. In addition, the larger spread in competition test results in males is indicative of considerable individual differences.

The known sex and body mass dependent differences are apparent from the morphometrical data in table 1. Thus, body mass and the organ masses of heart, liver, kidneys and spleen are considerably larger in males than in females. By contrast, the heavier adrenals and thymi are found in females. The coefficients of variation for body and organ masses are less than 12%. In males, the larger coefficient of variation for body mass at the start of the experiment differs from that of the females by 10%. Sex differences are also seen in the higher corticosterone and reductase levels in females and higher liver HSDH activities in males. The coefficients range between 3.4 and 129.5%. The latter extreme value is explained by the fact that the reductase activity was below the level of detection in 7 male rats.

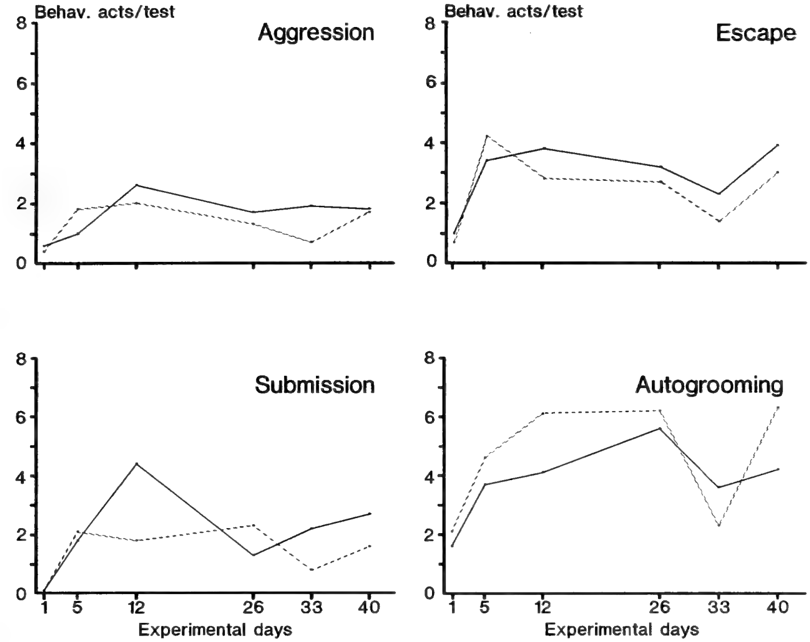

Fig. 2. Means of behavioural acts per experimental day and sex group for male (——) and female (----) DA rats on the 6 test periods

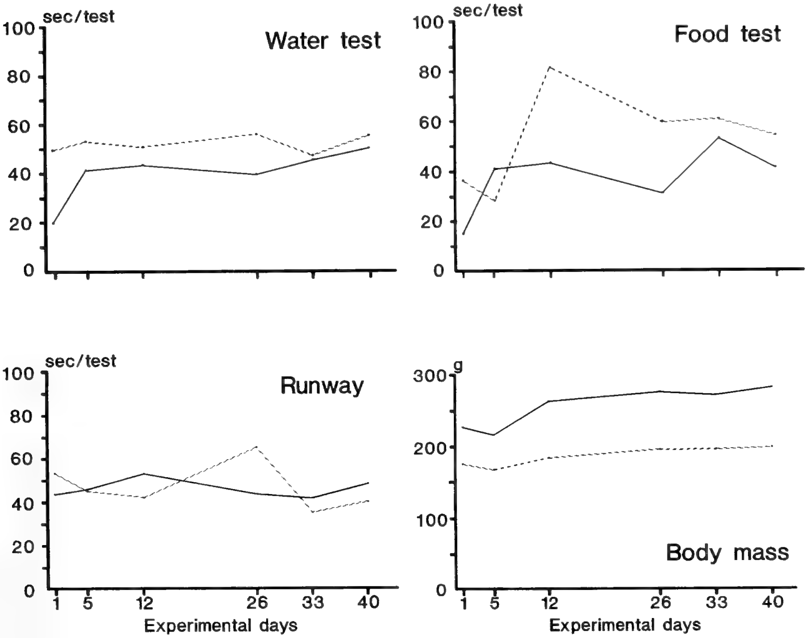

Fig. 3. Means of the competition test results per experimental day and sex group and development of body mass (details see figure 2)

Table 1. Group means and coefficients of variance of all behavioural, competitive and somatic characteristics

No.	Terms/Abbreviation	Dimension	Group means ($\bar{x}$)		Variation coefficients in %	
			Female	Male	Female	Male
	Behaviour					
1	Aggression = AGGR	Behav. frequency/test	1.3	1.6	100.0	95.0
2	Submission = SUBM	Behav. frequency/test	1.4	2.1	71.4	52.4
3	Social exploration = SOEX	Behav. frequency/test	6.4	5.6	25.0	34.4
4	Autogrooming = AUTO	Behav. frequency/test	4.6	3.8	43.5	52.4
5	Allogrooming/threat = AGOO	Behav. frequency/test	1.4	2.1	71.4	52.5
6	Escape = ESCA	Behav. frequency/test	2.4	2.9	46.2	45.7
	Competition test results					
7	Water test = WATE	Success in s/test	51.6	45.1	66.9	71.4
8	Food test = FOOD	Success in s/test	63.6	36.4	51.4	61.5
9	Runwaytest = RUNW	Runtime in s/test	46.8	46.0	47.4	65.0
	Morphometry					
10	Body mass at start = BMAS	g	66.5	72.7	8.7	18.7
11	Body mass at end = BMEN	g	198.9	282.4	2.8	8.2
12	Heart mass = HERT	mg	633	857	5.3	8.2
13	Liver mass = LIVE	mg	6 097	10 144	7.2	8.3
14	Kidney mass = KIDN	mg	1 310	1 788	5.2	7.9
15	Adrenal mass = ADRE	mg	48	34	11.6	8.8
16	Thymus mass = THYM	mg	151	111	12.3	9.9
17	Spleen mass = SPLE	mg	327	398	5.9	9.3
	Biochemistry					
18	Plasma corticosterone = CORT	µg/ml	0.49	0.28	42.3	39.1
19	5α-reductase = REDU	nmol/min/mg microsomal protein	29.7	7.29*	3.4	129.5*
20	3β-hydroxysteroid-dehydrogenase = HSDH	nmol/min/mg microsomal protein	2.79	9.33	15.0	9.7

Note: Number of animals n = 9, * n = 2

From the total of 9 behavioural and competition characteristics studied, 10 significant correlations are found for females, but only 2 for males. In females, social exploration is negatively correlated with allogrooming, escape and drinking time in the water competition test ($F = 16$, $r = 0.73$–0.90, $p < 0.05$). Success in water competition is correlated with long runway times i. e. failure in runway test ($F = 16$, $r = 0.78$, $p < 0.05$). Female rats successful in food competition often show defensive behaviour such as submission, allogrooming and escape behaviour ($F = 16$, $r = 0.72$–0.74, $p < 0.05$). Males only show significant positive correlations between aggression and water competition as well as the latter and food competition ($F = 16$, $r = 0.73$ and 0.77, $p < 0.05$).

Vice versa, there are only 5 significant correlations between the morphological and biochemical data and the results of the competition tests in the case of females, but 8 for males (Tab. 2). The organ masses of heart, kidneys and spleen are correlated with the initial body mass of males and those of heart, kidneys, liver and spleen among themselves (Tab. 2: No. 1 to HERT, KIDN, SPLE; No. 3, 4 to KIDN and SPLE; No. 5 to SPLE). Females only show a positive correlation between body mass at the beginning and end of

Table 2. Correlation coefficients of the absolute data for body and organ masses, biochemical and competition test results in female and male rats

No.	Abbr.*	Sex	Morphometry							Biochem.			Competition			
			BMEN	HERT	LIVE	KIDN	ADRE	THYM	SPLE	CORT	REDU	HSDH	WATE	FOOD	RUNW	No.
Morphometry																
1	BMAS	f.	*.68*	–.19	–.29	–.36	–.28	.54	–.02	*.90*	–.04	–.03	–.60	.35	–.51	1 f.
		m.	.17	*.70*	.53	*.83*	.25	.42	*.74*	–.11	–	–.14	–.15	–.08	.27	m.
2	BMEN	f.	–	.36	–.20	.09	–.26	.39	.35	*.79*	.03	.59	–.26	.19	–.19	2 f.
		m.	–	.59	–.08	.36	.57	.17	.32	–.09	–	.50	–.07	.19	–.25	m.
3	HERT	f.		–	–.13	.24	–.39	–.32	.28	–.01	.53	.66	.41	–.06	.21	3 f.
		m.		–	.49	*.88*	.64	.38	*.72*	–.13	–	–.12	–.16	.15	–.02	m.
4	LIVE	f.			–	.54	.11	–.47	.11	–.21	–.22	–.16	.42	.16	.42	4 f.
		m.			–	*.77*	.38	.38	*.85*	–.31	–	.21	.61	.61	.59	m.
5	KIDN	f.				–	.53	–.66	.62	–.05	–.24	–.04	.63	–.26	.64	5 f.
		m.				–	.63	.49	*.89*	–.28	–	–.06	.16	.27	.35	m.
6	ADRE	f.					–	–.29	.32	–.08	–.24	–.53	.41	–.01	.59	6 f.
		m.					–	.22	.49	–.53	–	–.02	.26	.27	–.08	m.
7	THYM	f.						–	–.08	.29	–.29	.27	*–.69*	.12	*–.73*	7 f.
		m.						–	.33	.41	–	–.55	–.01	.15	.64	m.
8	SPLE	f.							–	.17	–.36	.26	.39	–.17	–.06	8 f.
		m.							–	–.41	–	–.07	.42	.49	.35	m.
Biochemistry																
9	CORT	f.								–	.12	.14	–.37	.39	–.18	9 f.
		m.								–	–	–.18	–.52	–.06	.08	m.
10	REDU	f.									–	.19	.23	.49	.37	10 f.
		m.									–	–	–	–	–	m.
11	HSDH	f.										–	–.17	–.16	–.24	11 f.
		m.										–	.13	.20	–.29	m.

Note: Significant coefficients with $p \geq 0.05$ (*italique*); * abbreviations see table 1 the experiment; both characteristics are positively correlated with the corticosterone level. A low thymus mass is seen in females successful in the water test and those defeated in the runway test (Tab. 2: No. 1 to BMEN, CORT; No. 7 to WATE, RUNW).

The results of factor analysis shown in table 3 are not biased by triangular correlations, e. g. between the body mass and the other somatic characteristics as are the linear correlations in table 2.

Factor I exclusively describes the behavioural characteristics in females and is positively loaded through submission, allogrooming and escape as well as the outcome of food competition. As in males, social exploration is negatively loaded and thus opposite to the defensive behavioural activities in females. In males, characteristics of bodily condition such as body mass at start, masses of kidneys and spleen are positive in Factor I while the frequency of social exploration is negative (Tab. 3: No. 3, 10, 14, 17). The total variance in the experiment for both sexes can be mainly explained by factor I.

Factor II contains the result of water competition and autogrooming for males and females. In addition, the kidney mass and runway time are positively loaded for females, while body mass at start, thymus mass and corticosterone level are negative in this factor (Tab. 3: No. 4, 7, 9, 10, 14, 16, 18). For males, factor II becomes positively loaded by the parameters aggressive behaviour and autogrooming, the result of water and food competition and liver mass.

In factor III for females, aggression is negatively loaded while heart mass and the HSDH activity are positive. Defensive categories of behaviour such as submission, allogrooming/threat and escape are found in the case of males. Of the three factors, III possesses the least significance tor the total variance in the experiment and is in no way correlated with the competition results in both sexes.

Table 3. Results of the orthogonal factor analysis (Varimax) for all test characteristics, separately evaluated for female and male rats

No.	Characteristics	Factor I		Factor II		Factor III		No.
		Female	Male	Female	Male	Female	Male	
1	Aggression	–.13	–.24	.25	*.63*	*–.71*	–.07	1
2	Submission	*.93*	.41	.11	–.20	–.06	*.69*	2
3	Social exploration	*–.81*	*–.83*	–.51	.23	.08	–.03	3
4	Autogrooming	.21	.11	*.62*	*.70*	.04	–.19	4
5	Allogrooming/threat	*.93*	.41	.11	–.20	–.06	*.69*	5
6	Escape	*.83*	–.14	.04	–.58	–.25	*.68*	6
7	Water competition	.47	–.05	*.84*	*.95*	.20	–.08	7
8	Food competition	*.89*	–.04	–.24	*.77*	–.06	.09	8
9	Run way competition	.43	.46	*.74*	.42	–.02	–.26	9
10	Body mass at start	.19	*.92*	*–.84*	–.05	–.02	.13	10
11	Body mass at end	.14	.20	–.55	–.17	.56	.55	11
12	Heart mass	.11	.35	.23	.01	*.95*	.29	12
13	Liver mass	.23	.58	.36	*.72*	–.27	.13	13
14	Kidney mass	.04	*.85*	*.66*	.28	.10	.42	14
15	Adrenal mass	.16	.30	.53	.29	–.48	.56	15
16	Thymus mass	–.20	.60	*–.77*	–.05	–.02	.03	16
17	Spleen mass	.13	*.72*	.22	.46	.27	.31	17
18	Corticosterone	.37	–.08	*–.67*	–.53	.12	–.26	18
19	5α-reductase	.55	–*	.01	–*	.42	–*	19
20	3β-HSDH	–.16	–.41	–.29	.60	*.79*	–.08	20

Note: High factor loadings ≥ .60 (*italique*); n = 9, * n = 2

Table 4. Means of the absolute body and organ masses in families of female and male rats

No.	Characteristics		FEMALES			MALES				
			Family Bf (n = 4)	Sign. a)	Family Cf (n = 3)	Family A (n = 3)	Sign. a)	Family B (n = 3)	Sign. a)	Family C (n = 3)
1	Body mass at end	g	197	n. s.	201	271	n. s.	305	*	271
2	Heart mass	mg	629	n. s.	625	805	*	936	*	830
3	Liver mass	mg	6 376	n. s.	5 935	10 201	n. s.	10 340	n. s.	9 891
4	Kidney mass	mg	1 310	n. s.	1 301	1 740	n. s.	1 925	*	1 698
5	Adrenal mass	mg	47	n. s.	48	33	*	36	n. s.	34
6	Thymus mass	mg	143	n. s.	167	103	n. s.	119	n. s.	112
7	Spleen mass	mg	325	n. s.	336	397	n. s.	424	n. s.	374

Note: n = number of rats; a) t-test: n. s. = no significance, * = $p \geq 0.05$

Since in the case of females there was only one representative from family Af and Df, only the 2 families Bf and Cf with at least 3 rats will be compared. Furthermore, since only 3 family groups could be studied in the case of males, these findings are only of an orientating nature. Table 4 shows the body and organ masses at the end of the experiment for the different families. It thus becomes clear that there are no familiary differences in body and organ masses in these females. By contrast, males from families B and C show significant differences in body mass as well as heart and kidney masses. Significant differences are only seen for heart and adrenal masses between family A and B.

Discussion

Instead of the usual large collectives, where comparatively few characteristics were registered (Gärtner et al. 1991), as many of these as possible were studied in only small groups of rats of both sexes. Priority was given to the study on the significance of correlations in behaviour compared with other competitive and somatic characteristics. These data could only then be strictly compared and temporally evaluated in parallel in one experiment, if the number of animals was restricted to 9 per sex. Here, the significance and orientation of different characteristic relationships were tested and not the assignment of individually known social dominance ranks to somatic data. It was also important for later assessments of comparable rat groups that all studies were carried out under typical laboratory conditions. Thus, adult but sexually inexperienced rats were included in unisexual groups. All major burdens arising from prolonged deprivation, hormone injections or organectomy, usual in investigations on aggressive behaviour (Albert et al. 1989, 1991), were excluded. The present studies thus represent a first step towards assessing highly interwoven relations between behaviour, sex and genetics even in small laboratory animal collectives.

Sex-specific behaviour and competition in relation to social dominance

Most importantly these results show that aggressive behaviour in these female rats does not correlate with characteristics that also should reflect high dominance ranks. For example, priority of access to restricted resources is achieved by the females without correlation to agonistic activities. This is in contrast to males, where a positive correlation between aggressive behaviour and other competitive test results exists. Aggressive behaviour in females is only seen in factor III, which is the least involved in total variance of dominance in this study. This confirms the finding that aggressiveness has less decisive effects in female rats (Seward 1945), although no differences in the absolute frequencies of agonistic and competitive behaviour between male and female groups were seen here (Zook and Adams 1975). In addition, the only other investigation on social dominance in non-burdened female rats, where other rivalry fields apart from aggressive behaviour were studied, showed no correlation between aggression, food and water competition in high ranking females (Blanchard et al. 1984).

The female response in the different test situations consists of frequent defense (submission, escape) and intensive appeasement behaviour through social body contacts (allogrooming). More frequent defensive behaviour in females compared to males has already been described (Swanson et al. 1982). These findings are also in agreement with other reports, describing the more pronounced exploration and escape behaviour (Archer 1975) and lower aggressive behaviour with increasing social exploration (Thor and Holloway 1982) as being typical of female rats. Females reacted with a stronger inquisitive behaviour than males. After receiving a shock treatment, they were thus more willing to reinspect the site (Primus and Kellog 1990; van Hest et al. 1987). Even in the present study, the females could not be prevented from endeavouring to achieve access to food despite competition. They were apparently more successful in accomplishing this through frequent appeasement behaviour than the more aggressive male rats.

By contrast, strong aggression in male rats has always been suspected to be a prerequisite for a high ranking position and successful competition for limited resources (Francis 1988). In the present study, this relationship was substantiated experimentally based on the significant positive correlation between aggression and competition success (factor II). A positive but only weak significant relation between food competition and aggression has also been described for male colony rats (Blanchard et al. 1984). The pronounced aggressive male behaviour thus corresponded closely to the original concept of social dominance, the "peck order" (Schjelderup-Ebbe 1922). Even today this is considered particularly suitable because of its high descriptive value (Drews 1993).

Apart from care of body surface in rats and primates, allogrooming, of the types of behaviour additionally determined, is thought to carry out appeasing functions following successful contact behaviour (Bolles 1960; Beagley 1976). This correlation is underlined by the similarly orientated factor loadings for allogrooming, submission and escape in factor I and III for both sexes. Allogrooming and threat behaviour can thus be considered as signs that the access to the restricted resources in a group is not determined primarily by aggressive acts. Thus, in the case of females, the mutual food uptake occurs under socially relaxed conditions although actually rivalry ought to rule. Even among non-kin animals allogrooming is considered to be tension-reducing and bond-establishing (Spruijt et al. 1992).

In addition, non-social behaviour such as autogrooming, scratching and digging are considered to be signs of arousal as a result of social demands (de Boer et al. 1990; Korz 1991). Such activation of the hypophysis-adrenal-system through the competition tasks could also be seen in some of rats studied here. In any case, the significant correlations between autogrooming and the results from water and food competition would appear to justify this interpretation. Allo- and autogrooming are never found as common loadings in factor analysis from this experiment and should thus be carefully differentiated in the evaluation of dominance tests.

Somatic, biochemical and familiary dominance factors

The greatly diverging results on dominance testing in rats frequently seen by many authors can be explained by changing contextual factors (Francis 1988). Such effects arise not only through methodologically different external test conditions but also through the non-uniform internal situation of the animals.

In the present study, an attempt was made to ascertain different somatic and physiological influences on social behaviour involving quantifiable characteristics. Thus, a positive correlation between metabolically active organs in terms of kidney mass in females or liver in males and the duration of water and food uptake during competition becomes apparent even in groups of three rats. However, the opposite effect, i. e. a negative correlation between liver mass and food competition has also been described in stress-burdened groups of 10 males (Snel 1982). Nevertheless, both observations indicate that not only typical patterns of behaviour but also the metabolic situation affect the success of competition.

In contrast to Albert et al. (1992), the present study did not concern itself with the easily affected gonadal hormones, but instead for the first time with the hepatic microsomal enzymes, 3β-hydroxysteroid dehydrogenase (HSDH) and 5α-reductase (REDU) involved in their metabolism. Both show a sex-specific pattern. Thus, HSDH is higher in the males and shows a reversible reaction to loss of androgens. Oestradiol acts in an anti-androgenic manner, thus lowering the activity of HSDH. REDU is not dependent on the continuous presence of androgens, so that REDU-activities are many times higher in females than in males (Lax 1987; Lax et al. 1983). REDU shows no recognisable effect in either sex with respect to aggressive, submissive or competitive characteristics studied. However, above all, the low HSDH activity in females is an expression of an anti-androgenic predominance, so that aggressiveness is reduced, but the bodily activity as measured by heart mass is not affected.

In this study, the corticosterone level shows significant relations to body mass and success in water competition only in the females. Also the correlation of runway results to thymus mass shows that female rats achieve access to limited resources without becoming seriously stressed. Apparently they preferred those behaviours that avoided a stress induced activation of the hypophysal-adrenal axis ("behavioural release mechanism" according to Conner et al. 1971).

Effects of stress on the adrenal and thymus masses as well as the level of corticosterone related to the social situation of rats have been frequently studied (Selye 1973; Henry 1993). Up to now, a negative relation between "thymico-lymphatic tissue" and the adrenal mass was considered to be typical of stress (Snel 1982; Stern and Hartmann 1972). Further findings on male rats confirmed the relationship between heavy thymus, low cortictisterone level and dominance (Raab et al. 1986). Higher corticosterone levels occur in stressed females than in males; in this case the activity of the hypothalamus-pituitary-adrenal axis is enhanced (Aloisi et al. 1994).

In the case of males, a good bodily condition due to large body and organ masses is the first and aggressiveness is the second prerequisite for the taking up of a dominant relationship. Social behavioural gestures apparently do not decisively influence the dominance position of male rats.

The possibility of "inheritance of dominance" has recently been intensely discussed based on investigations on cockroaches, deer mice and macaques (Barrette 1993; Dewsbury 1993). It was agreed that social dominance as a relationship between individuals cannot itself be inherited. Genetic differences, i. e. in aggressiveness (Drews 1993), between individual animals, however, can influence behaviour characteristics in such a way that higher social ranks are frequently achieved above average. One then speaks of a "quasi-inheritance of dominance".

These evaluations of suitable somatic data for a few, individually known genetically uniform rats thus represent only a first attempt to register the effect of family membership and somatic characteristics on dominance. Indeed, it could be shown in the inbred males that there are significant familiary differences in the body mass and organ masses of heart, kidneys and adrenals. The animals are thus organically fit to different extents and reach differing dominance ranks and finally variously high Darwinian fitness, e. g. via copulatory efficiency (Gärtner et al. 1981, 1989; Militzer and Reinhard 1982). By contrast, the isogenetic females from only 2 families showed no significant differences in organ masses. Since several males always commonly compete for a female in heat, such familiary differences should be significant only in males with respect to reproductive success. These differences cannot be explained by chromosomal inheritance in the stringently bred isogenic DA animals. Rather, they must be an expression of very early ontogenetic variations in the embryonic plasmatype genome (Gärtner et al. 1991; Baunack et al. 1986).

The present study indicates that there is a number of combinable factors of varying context affecting social dominance behaviour in different ways between male and female rats. It is thus understandable that there is no generally accepted biological concept up to now despite an overwhelming number of studies on dominance in laboratory rats. At least two sex-specific behaviours to achieve more dominant position, however, emerge to explain these findings: Coping in stress-burdened social situations can be alleviated by behaviour minimising increased arousal (Korz 1991, 1993; Sachser 1994). This is the preferred method of choice in our female rats and explains the low significance of aggressiveness as dominance component. Despite stress burden, social dominance is reached through bodily superiority and aggressiveness (Henry 1993). This applies mainly to male rats in this study. However, aggressive behaviour is only one of many factors determining dominance in males.

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Zusammenfassung

Soziale Dominanz und körperliche Kondition in kleinen Gruppen weiblicher und männlicher Laborratten bekannter Familienzugehörigkeit

In jeweils 3 individuell bekannten Dreiergruppen von weiblichen und männlichen Laborratten wurden Merkmalskombinationen ermittelt, die soziale Dominanzbeziehungen charakterisieren können. Die Ratten waren adulte, nicht verpaarte Tiere des Inzuchtstammes DA aus bekannten Familien. An 6 Testtagen wurden 6 Verhaltenskategorien je Tier und der Konkurrenzerfolg im Wasser-, Futter- und Laufgang-Test erfaßt. Am Versuchsende wurden Körpermasse, die Masse von 6 Organen, 3β-Hydroxysteroid-dehydrogenase (HSDH) sowie 5α-Reduktase (REDU) in der Leber und Kortikosteron im Blutplasma bestimmt. Verglichen wurden nicht individuelle Dominanzränge, sondern der Zusammenhang zwischen allen Merkmalen mittels Korrelations- und Faktorenanalyse. Bei den Weibchen fanden sich gesicherte Korrelationen zwischen häufigem Beschwichtigungsverhalten, erfolgreicher Futterkonkurrenz und niedrigen Kortikosteron- und HSDH-Spiegeln.

Aggressionen wurden zwischen Weibchen zwar im gleichen Umfang wie zwischen Männchen beobachtet, zeigten jedoch keinen gesicherten Zusammenhang zu anderen Merkmalen. Dagegen ließ sich bei den männlichen Ratten häufiges aggressives Verhalten und erfolgreiche Futter- und Wasserkonkurrenz als gemeinsamer Faktor beschreiben. Nur bei den Männchen bestanden signifikante Familien-

unterschiede in der Körpermasse und der Organmasse von Herz, Nieren und Nebennieren, die auch unterschiedliche Dominanzränge erklären können.

Beschwichtigungsverhalten und Stressvermeidung erwiesen sich bei den Weibchen, körperliche Überlegenheit und Aggressivität bei den Männchen als Voraussetzung für das Erreichen höherer Dominanzpositionen.

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The possibilities of scent marking in the Mouse-eared bat *Myotis myotis* (Borkhausen, 1797) and the Noctule bat *Nyctalus noctula* (Schreber, 1774) (Mammalia, Chiroptera)

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Abstract

Studied were sebaceous glands on the cranial integument of *Myotis myotis and Nyctalus noctula* by using microanatomical methods. Both species are provided with normal sebaceous glands on the whole snout. Slightly enlarged sebaceous glands, where secretions emerge by pressing the head against an object, are restricted to the lips and the chin in *M. myotis*, and to the rostral part of the snout in *N. noctula*. In enlarged sebaceous glands secretion delivery is caused by contraction of the subcutaneous musculature. In *M. myotis* one of these glands exists on each side of the head and opens into a brush-like hair tuft. Three rows, alltogether consisting of 10 enlarged glands, lie on each side of the snout of *N. noctula*. Only *M. myotis* is equipped with an extremely enlarged sebaceous gland on each side of the snout. This gland expands through the whole dermis into the subcutaneous musculature and opens into a brush-like hair tuft. Although both species are provided with enlarged sebaceous and sudoriferous glands, the microanatomy, number and arrangement of these glands as well as the amount of enlargement diverge. Combined with the different application structures, this shows two completely divergent systems of secretion delivery, application, and distribution.

Introduction

Many studies exist on the olfactory communication in mammals as reviewed in Eisenberg and Kleiman (1972), Johnson (1973), Adams (1980), and Brown and Macdonald (1984). While in the past grossmorphological and microanatomical investigations described a large variety of integumentary glands, recent biochemical studies proved that enlarged sudoriferous and even some enlarged sebaceous glands produce scent (Bereiter-Hahn et al. 1986). In bats, for example, the purpose of a scent gland described by means of histology is often as unclear as is the context of scent marking behaviour. Glands on the head were investigated by means of histology in many vespertilionid bats (Schaffer 1938, 1940; Werner and Dalquest 1952; Dalquest and Werner 1954; Sisk 1957; Fenton 1985; Haffner 1987, 1989; Schmidt et al. 1989; Haffner and Ziswiler 1990) but literature on scent marking behaviour in bats is rare (Buchler 1980; Müller-Schwarze 1983; Lundberg and Gerell 1986; Hoeller and Schmidt 1993).

To fill in some gaps in the knowledge resulting from describing histology I have chosen *Myotis myotis* and *Nyctalus noctula* whose marking behaviour and preening I often had the opportunity to observe, and I used functional morphology on their scent glands.

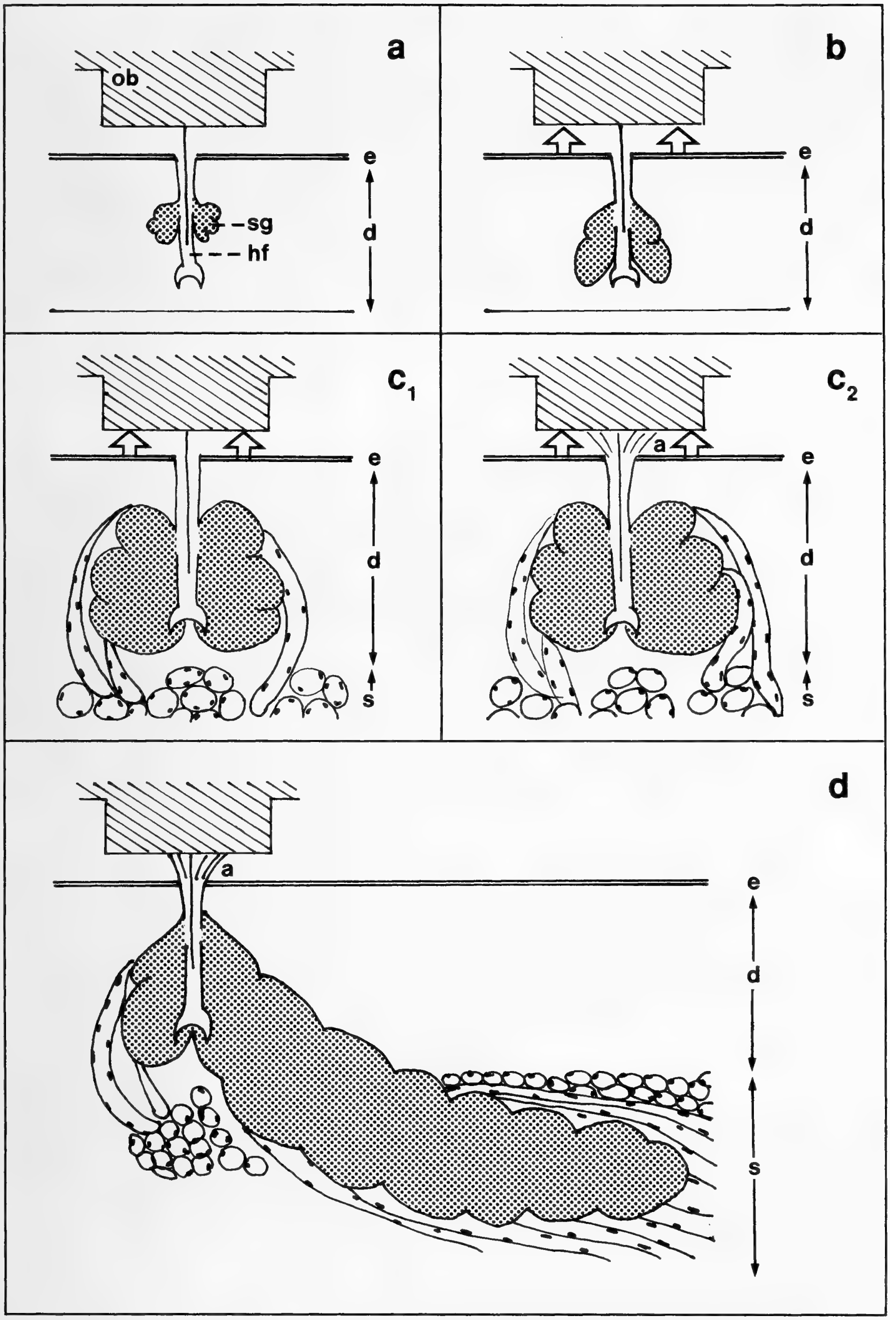

Fig. 1. Four types of sebaceous glands and their secretion. **a)** normal gland / "passive" secretion, **b)** slightly enlarged gland / pressure against object, **c_1)** enlarged gland / contraction of subcutane muscle, pressure against object, **c_2)** enlarged gland with application structure / contraction of subcutane muscle, pressure against object, **d)** extremely enlarged gland with application structure / contraction of subcutane muscle
application structure (a), epidermis (e), dermis (d), the hairfollicle (hf) contains hair, object (ob), subcutis (s), sebaceous glands (sg, dotted), pressure against the object (arrow)

Material and methods

The bats were donated by different people to the Zoological Museum. They had been found either dead or badly hurt and had to be killed; they were conserved in 70% alcohol or 10% formalin. 7 adult *M. myotis* (4 males, 3 females) and 37 adult *N. noctula* (21 males, 16 females) were investigated by means of grossmorphology. Ventral or dorsal and lateral views of the snout and chin region were drawn with a WILD drawing apparatus for the binoculars.

4 *M. myotis* (2 males, 2 females) and 7 *N. noctula* (4 males, 3 females) were prepared for histological investigations. For this purpose the skin of the head was dissected and embedded in paraffin, cut in 7–15 µm thick slices and stained with Haemalaun-Eosin using conventional methods (Romeis 1968). From these consecutive slice series the three-dimensional histoarchitecture of integumental structures was reconstructed by using a ZEISS drawing apparatus for the microscope. Based on these investigations a model for secretion delivery, application and distribution was established.

Results

The snout and chin region of both species is sparsely haired. Most of the hairs are thicker than normal body hairs and all of them are connected to sebaceous glands. These glands can be assigned to four types depending on their size, arrangement and relation to muscles:

1. Normal sebaceous glands are proportionally correlated to the thickness of the hair; they do not reach the base of the hairfollicle (Figs. 1 a, 2 a).
2. Slightly enlarged sebaceous glands surround the hairfollicle; their diameter is not much larger than the hairfollicle (Figs. 1 b, 2 b).
3. Enlarged sebaceous glands embed the hairfollicle completely; their diameter is much larger than the hairfollicle, and striated muscle fibres, connected with the subcutaneous musculature, surround the gland like a basket and attach themselves onto its connective tissue covering (Figs. 1 c_1,c_2, 2 c).
4. Extremely enlarged sebaceous glands do not only surround the hairfollicle, but they expand through the whole dermis into the subcutaneous musculature. Near the orifice of the gland the arrangement of muscle fibres is similar to type 3 (Figs. 1 d, 2 d, e).

On each side of the snout of M. myotis a brush-like hairtuft rises up between the rostral Vibrissae mystaciales (Fig. 3 a). The hair in the middle of these hairtufts is supplied with sebaceous glands of type 4 which spread within the integument from the hairtuft to the eye. Another more sparse hairtuft with sebaceous glands of type 3 is situated more dorsad. Except for some slightly enlarged sebaceous glands of type 2 near the lips, all other sebaceous glands are of normal size. On the chin two swellings occur composed of numerous slightly enlarged sebaceous glands and above the symphysis lies a hairless protuberance. Except for the sebaceous glands, nearly all hairs on the snout and only some on the chin are supplied with sudoriferous apocrine glands in the shape of a simple sac which is straight or loosely wound. All these apocrine glands are surrounded by myoepithelial cells.

Based on the histoarchitecture of the glands of *M. myotis* we can distinguish three types of secretion delivery to the orifice of the sebaceous glands:

- "passive" secretion delivery by overflow of the produced secretion: normal sebaceous glands (Fig. 1 a)
- secretion delivery caused by pressure against an object: slightly enlarged sebaceous glands on the chin and near the lips (Fig. 1 b)
- secretion delivery caused by contraction of subcutaneous muscle, probably supported by pressure against an object: sebaceous glands in the minor hairtuft (Fig. 1 c_2). In extremely enlarged sebaceous glands in the larger hairtuft contraction of the subcutaneous musculature, in which the caudal part of the gland is embedded, has the effect of pressing out secretions as if from a tube (Fig. 1 d).

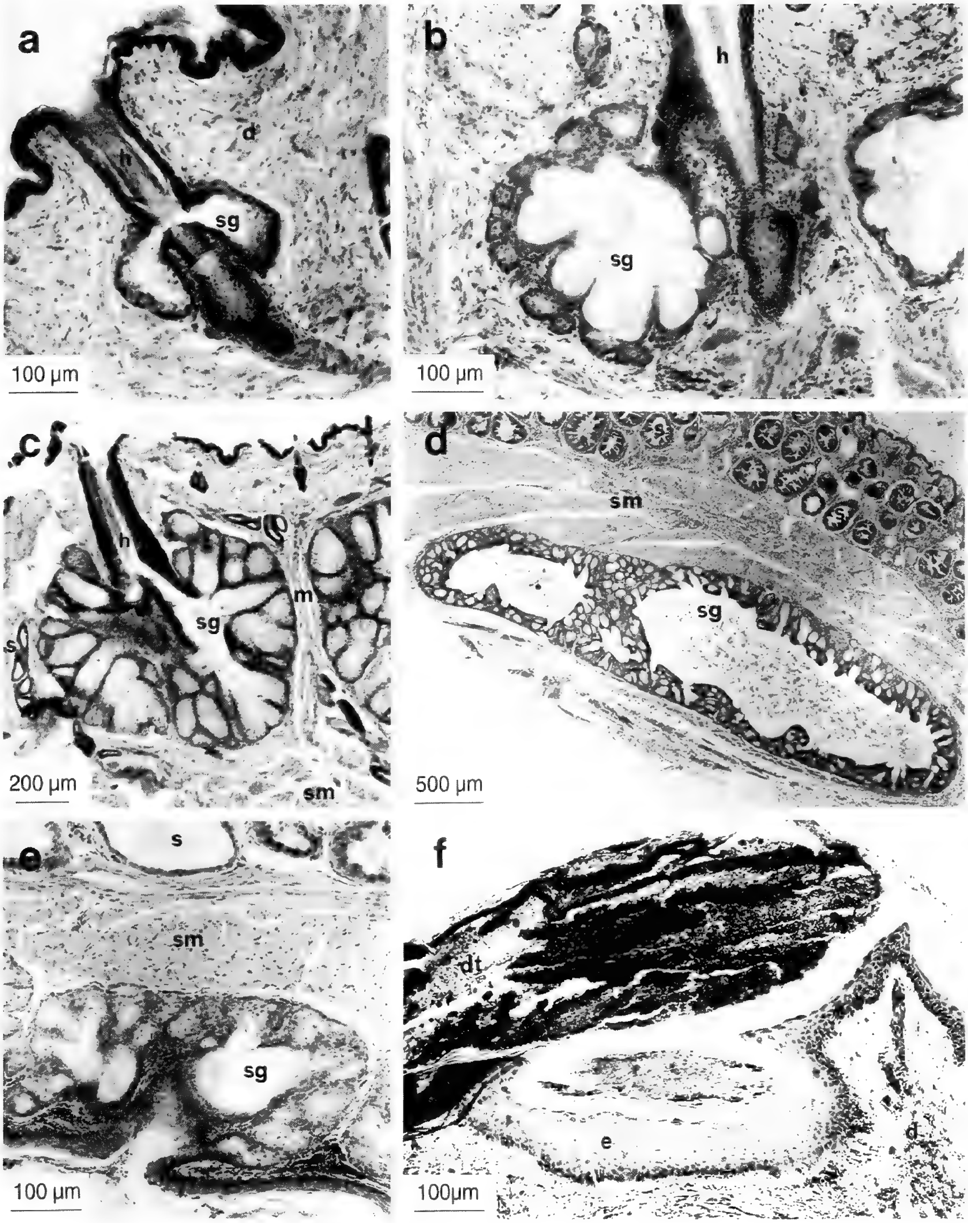

Fig. 2. Micrographs illustrating **a**) a hair with normal sebaceous glands (*N. noctula*), **b**) a hair with sligthly enlarged sebaceous glands (*N. noctula*), **c**) a hair with enlarged sebaceous glands (*N. noctula*), **d**) an extremely enlarged sebaceous gland (*M. myotis*),) a part of an extremely enlarged sebaceous gland (*M. myotis*), **f**) wound healing on the chin of *N. noctula*.
d – dermis, dt – damaged tissue, e – epidermis, h – hair, m – musculature, s – sudoriferous gland, sg – sebaceous gland, sm – subcutaneous musculature

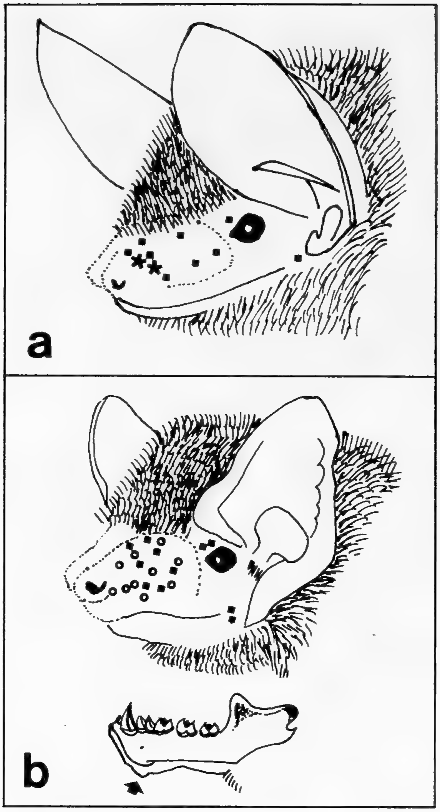

Fig. 3. Schematic drawings of the heads of *Myotis myotis* (**a**) and *Nyctalus noctula* (**b**) and lower jaw of *Nyctalus noctula* with protuberance. Vibrissae mystaciales, V. angulares and V. superciliares (squares), brush-like hairtufts (stars), orifices of sebaceous glands (rings), protruberance (arrow)

The secretion can be applied and distributed directly from the orifice of the gland to the aiming point (Fig. 1 a, b) or indirectly via the application structure, the brush-like hairtuft, as is the case in the four sebaceous glands on the snout (Fig. 1 c_2, d). By means of these hairtufts, secretions applied from other glands onto an object can also be dispersed.

There are three rows of three, five and two hairs, respectively, with enlarged sebaceous glands on each side of the snout between the vibrissae of *N. noctula* (Fig. 3 b). On the chin, four swellings composed of numerous enlarged sebaceous glands are developed. The caudal sebaceous glands are the largest, while the rostral ones are the smallest in both chin and snout. Although all nuances of enlargement can be seen in *N. noctula*, no extremely enlarged sebaceous glands exist, such as those found in *M. myotis*. Exactly above the highest part of the symphysis is a hairless protruberance which is, in contrast to *M. myotis*, often the most prominent part of the chin (Fig. 3 b). The epidermis of this protruberance is thickened, and wounds at different stages of healing can be seen (Fig. 2 f). Nearly all hairs on the snout and a few on the chin have, except for the sebaceous glands, sudoriferous apocrine glands in the shape of a loosely wound or narrowly coiled tube. These glands are smaller in the chin than in the snout but all are surrounded by myoepithelial cells.

Based on the histoarchitecture of the glands I postulate the same two types of secretion discharge for *N. noctula* as described for *M. myotis* (Fig. 1 a, b). In extremely enlarged sebaceous glands secretion delivery is caused by contraction of subcutaneous muscle, probably supported by pressure against an object (Fig. 1 c_1). There are no application structures such as hair tufts found near the orifice of the glands in *N. noctula*. The secretion can be applied and distributed directly from the orifice of the gland (Fig. 1 a–c_1) to the aiming point or indirectly via the application structure, the hairless protruberance on the chin (Fig. 2 f).

Discussion

Most terrestrial mammals can reach almost any part of the body with their extremities or head and therefore take secretions which are produced at any part of the body and distribute them practically anywhere. However, the extremities of bats are integrated into the flying membrane which would be a handicap for the purpose of secretion distribution. So if secretion is to be distributed over the body including the wings and to the nearby surroundings of these flying mammals, it is advantageous to concentrate the glands on the head, which is, due to its movement, best suited for a surface-efficient secretion-dispersion. The high density of enlarged sebaceous glands in the integument of the head of *Myotis myotis* and *Nyctalus noctula* described in this study is typical for many other vespertilionid bats (Schaffer 1938, 1940; Werner and Dalquest 1952; Dalquest and Werner 1954; Sisk 1957; Fenton 1985; Haffner 1987, 1989; Schmidt et al. 1989; Haffner and Ziswiler 1990).

On the one hand both species are able to distribute secretion onto a smooth surface, for example onto the wing membranes, simply by pressing the head into the wings and dragging the flying membrane over the snout. This pressure causes secretion of small and slightly enlarged sebaceous and sudoriferous glands. Sebaceous and sudoriferous secretions probably combine two functions: the grooming and scenting of the flying membranes which could act as a large fan, spreading scent during flight. On the other hand aimed distribution of secretions onto hard surfaces, for example in roosts, is done in a completely different way by each of the two species. As Kulzer et al. (1985) have shown in *Rhinopoma hardwickei*, sudoriferous secretions are produced in large amounts when the animal is excited. The same can be observed in agitated *M. myotis* and *N. noctula*. If these secretions are to be distributed onto a distinct surface it is practical to place the orifices of glands between the organs of orientation to the nearest surroundings, the vibrissae, as is the case in both species. However, if the surface is hard, rubbing the head against it would cause abrasion of the sensitive vibrissae and the orifices of the glands. For this purpose application structures are advantageous to distribute the secretion after it is pressed onto a hard surface. *N. noctula* can, for example, distribute the secretion with the hairless spot on its chin onto the border of a tree hole, and *M. myotis* can spread secretion with the brush-like hairtufts on the snout onto a wooden beam in an attic. By spreading secretions with application structures, products of the sudoriferous and sebaceous glands are mingled. Thereby the sebum could act as a carrier substance for scent produced by the a-glands as postulated by Starck (1982).

Both *M. myotis* and *N. noctula* have enlarged sebaceous and sudoriferous glands. However, the microanatomy, number and arrangement of these glands and the amount of enlargement diverge in the two species and show us, combined with the different application structures, two completely divergent systems of secretion delivery, application, and distribution. These differences in closely related species can be seen as adaptations to different functions.

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I wish to thank the following persons of the Zoological Museum in Zurich: Prof. Dr. Vincent Ziswiler for encouragement and commenting on an earlier draft of this manuscript, Barbara Andrew and Anita Bailly for the revision of the English version, Dr. Hans-Peter B. Stutz for the photographs, and Alfred Stätzler for staining the histological slides.

Zusammenfassung

Die Möglichkeiten der Duftmarkierung beim Großen Mausohr Myotis myotis (Borkhausen, 1797) und beim Großen Abendsegler Nyctalus noctula (Schreber, 1774) (Mammalia, Chiroptera)

Bei Fledermäusen ist die Verbreitung von Duftdrüsen über die Körperoberfläche durch die Integration von Extremitäten und Schwanz in die Flughaut eingeschränkt. Anhand von vergleichenden mikroanatomischen Untersuchungen am kranialen Integument zweier Fledermausarten wurden Ausscheidung, Auftragung und Verteilung von Sekreten als ein Funktionskomplex interpretiert. Die Talgdrüsen konnten vier Typen zugeordnet werden. Neben normalen haben beide Arten wenig vergrößerte Talgdrüsen.

Bei Kontraktion der subkutanen Muskulatur werden die vergrößerten Talgdrüsen ausgepreßt. Während *N. noctula* pro Schnauzenseite 10 solche Drüsen aufweist, mündet bei *M. myotis* je eine vergrößerte und eine extrem vergrößerte Talgdrüse in einen Haarpinsel. Während beide Arten ein Gemisch aus Sekreten der Talg- und a-Drüsen auf die Flughaut auftragen können, verteilen sie Sekrete auf harten Oberflächen, wie sie in den Tagesschlafquartieren vorkommen, auf unterschiedliche Weise. *N. noctula* verstreicht sie mit dem Kinn und *M. myotis* mit den Haarpinseln auf der Schnauze.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Coyote home range size in Durango, Mexico

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Home range sizes of coyotes (*Canis latrans*) are generally known (Laundré and Keller 1984). However, most of the data derive from individuals within the northern parts of this widely distributed species. Nearly nothing has been published on individuals from Mexico, except for reports on feeding habits (Delibes et al. 1989; Servín and Huxley 1991). The aim of this study is to determine home range size of coyotes at the Michilia Biosphere Reserve (MBR). MBR is 420 km^2 in surface, located 154 km southeast of Durango City between 23°51′ and 23°30′ N latitude, 104°15′ and 104°21′ W longitude, at approximately 2 450 m elevation. Dominant vegetation is oak-pine forest (*Quercus* spp. and *Pinus* spp.), grasslands (*Bouteloua* sp., *Mulhembergia* sp.), and plains mainly covered with *Cistus* sp. (Gonzalez-Elizondo et al. 1993). Climate is subhumid temperate with a 11 °C annual mean temperature and 76 cm annual average precipitation. Rainy season occurs from June to September, dry season from February to May, and occasional snowfall may occur in January.

Snares and foothold traps (Victor No. 3) were used to capture nine (6 male, 3 female) adult coyotes. They were immobilized with a ketamine and xilazine mixture (Servín and Huxley 1992), weighed, sexed, and measured. A 150–152 MHz Telonics radiocollar was attached to each animal in good physical condition. All coyotes were released at the capture site a few hours later. In the study area, a total of 75 stations aligned at 0.5 km intervals along roads were used to obtain two or more radiotelemetry bearings for each location. The study was conducted from September of 1986 to December of 1987. Locations were plotted on a 1 : 10,000 map of the study area. The 95% minimum convex polygon method was used to obtain coyote home range shape and size (Mech 1983). Data samples, related to coyotes' activity in this area, were grouped into four biological seasons: breeding (January 1 to March 15), gestation (March 16 to April 30), pup rearing (May 1 to August 31) and pup independence (September 1 to December 31). For each individual, a minimum of 58 fixes for each season were obtained to estimate individual seasonal home range size. Home range sizes during seasons were compared between males and females by means of a "Student t" test (Sokal and Rohlf 1981).

A total of 2 585 fixes for the 9 radio-collared adult coyotes were obtained over a period of 16 months. Average annual home range size was 9.1 km^2 [$n = 9$; range 8–18 km^2; $sd = 3.3$]. Average annual home range size of males [$n = 6$; 10.6 km^2; $sd = 2.2$] was larger than for females [$n = 3$; 6.1 km^2; $sd = 2.2$] ($t = 3.91$; $df = 7$; $p < 0.025$).

During the breeding season, average home range size for all individuals was 6.1 km^2 [$n = 8$, range 2.9–12 km^2]. Males occupied a mean area of 9.0 km^2 [$n = 5$, range 5–12 km^2] and females of 3.6 km^2 [$n = 3$, range 2.9–4 km^2]. During this season, mean male home range size is larger than for females ($t = 2.85$; $p < 0.025$). During the gestation period, the average for all coyotes is 8.3 km^2 [n = 6, range 2.9–13 km^2]. Males inhabit a larger area of 9.9 km^2 [n = 4, range 6.5–13 km^2] compared to 3.2 km^2 [n = 3, range 2.9–3.6 km^2] for females. However, during pup rearing season, average home range size is larger (12.6 km^2) than in the other three seasons. Female home range size is 18.4 km^2 which is larger than that of males 11.5 km^2 [n = 5, range 7–17 km^2]. During pup independence season, the average home range size was 11.7 km^2 [n = 7, range 5–20 km^2]. Males traveled within a 13.5 km^2 area, whereas, females occupied a 7.3 km^2 area [n = 2, range 5–9.7 km^2].

The results indicated the average home range size of the coyote in Mexico is smaller (9.1 km^2) than the average of 22.8 km^2 reported for Canada (Messier and Barrette 1982), and most studies in temperate [11.3 km^2 to 35.8 km^2] North America. In contrast, the average home range size in the semiarid zones of Texas was 4.5 km^2 (Andelt 1985). During the breeding period, adult males patrol their home range and display aggressive behavior to outside coyotes (Bekoff and Wells 1986). During the gestation season, male coyotes were observed moving around the denning (rearing) site, transporting prey to the lactating females and newborn pups. During pup rearing season, females are very active. Data from direct observation and radiotracking suggest females travel with their pups across the home range. Meanwhile, males supply prey to feed the pups. During the pup independence season, males had the largest home range size while the females show a smaller home range size than that of the preceding season. Home range size changed in shape and size throughout the year reflecting animals needs and related responses.

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Z. Säugetierkunde **60** (1995) 121–123

Weight and external measurements of Red foxes (*Vulpes vulpes*) from SW Spain

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Red foxes (*Vulpes vulpes*) show a high variability in body size, in parallel to their widespread distribution, which was used as an example or as a deviation (Davis 1977; Kolb 1978) of ecogeographical rules (Mayr 1963). Nevertheless, this tendency was evaluated in relatively small areas, compared to the whole geographical distribution of the species. In spite of being one of the most well-studied carnivore species in most aspects of their ecology and behaviour, no reliable information is available on red fox body size for most of its complete range. In the present report, we present the weight and external body measurements of one of the southern-most populations of *Vulpes vulpes.* Our results provide basic information upon which geographic variation on a continental scale could be investigated.

Foxes were captured in the Doñana area in Southwestern Spain (37°00′ N, 06°30′ W) during the course of fox control programs from 1988 to 1992. The climate is Mediterranean with Atlantic influence, with mild and wet winters and hot and dry summers. Body weight and five external measurements were taken: (1) Maximum body length (maximum length from the tip of the snout to the dorsal edge of the perineum was recorded); (2) Tail length (from the dorsal edge of the perineum to the tip of the tail, excluding fur); (3) Hindfoot length (from the edge of the calcaneum to the tip of the third phalange, with the phalanges extended); (4) Ear length (from the base of the tragus to the tip of the pinna); and (5) Shoulder height (from the top of the withers to the tip of foreleg).

The age of foxes was determined by counts of cementum annuli in premolars and by cursory examination of complete dentition, which was sufficient for young foxes. Only foxes older than about seven months were included in the study. For each sex, juveniles (from seven to twelve months) and adults (older than one year) were considered separately. Weights of pregnant or lacting females were not considered. We were not able to perform all measurements in all individuals. Sexual dimorphism was evaluated through the ratio male measurement/female measurement. For weight we used the cube roots of original values. For all comparisons we used the Student t-test (Zar 1984). Significant differences were considered when $p < 0.05$.

A total of 161 red foxes was measured. Adult males were significantly larger and heavier than vixens in all the measurements (Tab. 1). The juvenile class showed a similar pattern, but significant differences were observed only in hindfoot length and shoulder height (Tab. 1). Adult males were significantly heavier ($t = 4.19$, $p < 0.01$) and larger than juvenile males for head and body length ($t = 4.81$, $p < 0.01$) and hindfoot length ($t = 2.85$, $p < 0.01$). There were no significant differences between adult and juvenile females for all body measurements or weight.

Table 1. External body measurements and weights for juvenile and adult red foxes from Donãna National Park. Mean value (X), standard deviation (SD), sample size (n), and the significance level (p) of mean differences between male and female measurements for both age categories.

	Males			Females			
	Juveniles (7–12 month old)						
Measurements	X	SD	n	X	SD	n	p
Weight (g)	5051	1199	18	4706	642	22	–
Head and body (mm)	659	45	18	648	29	23	–
Tail (mm)	382	36	18	377	25	22	–
Shoulder height (mm)	385	36	18	366	14	20	*
Hindfoot (mm)	151	9	18	145	8	23	**
Ear (mm)	97	5	18	96	5	22	–
	Adults (> 1 year old)						
Weight (g)	6330	968	64	5124	854	60	**
Head and body (mm)	708	36	65	659	29	57	**
Tail (mm)	392	32	65	375	28	59	**
Shoulder height (mm)	401	22	59	370	16	60	**
Hindfoot (mm)	157	7	65	145	6	61	**
Ear (mm)	100	7	58	94	6	54	**

Significance levels: –: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$

Sexual dimorphism was significant only in adults for all measurements ($p < 0.01$ in all comparisons), with an average sexual dimorphism of 1.08, quite similar to that obtained from the data provided by Kolb and Hewson (1974) for Scottish (1.05) and English (1.07) red foxes, and by Lund (1959) for Norwegian specimens (1.05). Following Ralls' (1976) criterium, this sexual dimorphism would be small and typical for mammalian species exhibiting long-term pair bonding, like the red fox (Kleiman 1977). The absence of sexual dimorphism in the juvenile class, together with the absence of size differences between juvenile and adult females, suggest that females reach their adult body size in their first year of life, while males continue to grow, a fact that is typical in mammals where males are larger than females (Ralls 1976).

Red foxes from Doñana are larger than predicted by Bergmann's rule (Mayr 1963), based only on a geographical basis. Male and female red foxes are lighter than Swiss equivalents (Lüps and Wandeler 1983; Wandeler and Lüps 1993) (7080 and 5930 g for Swiss males and females, respectively). The same is true for Scottish foxes (Kolb and Hewson 1974) (7300 and 6200 g for males and females, respectively). Nevertheless, Doñana foxes are larger in body measurements but rather similar in weight compared with their conspecifics from England (Kolb and Hewson 1974) (head and body length: 671 and 627 mm, weight: 6700 and 5400 g, for males and females respectively). These results provide additional evidence on size variability in the red fox, not fully explainable by single causes (Kolb 1978).

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Z. Säugetierkunde **60** (1995) 124–127

Taxonomic status of *Delomys dorsalis collinus* Thomas, 1917 (Rodentia, Cricetidae) and description of a new karyotype

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The genus *Delomys* has two known extant species, *Delomys sublineatus* (Thomas, 1903) and *Delomys dorsalis* (Hensel, 1872), sympatrically distributed in some localities of highland habitats, along the southeastern coast of Brazil, from Rio Grande do Sul to Espírito Santo States (Zanchin et al. 1992). Thomas (1917), on the basis of molar size and upper molar row length, suggested that *D. dorsalis* had two morphotypes, *D. d. dorsalis* and *D. d collinus*, whereas Moojen (1952) considered the latter form a valid species (*Delomys collinus*). Voss (1993) recognized only two monotypic species (*D. sublineatus* and *D. dorsalis*), although be proposed that further studies were needed for analysing populations captured in localities of São Paulo State.

Previous data in the literature mentioned only two different karyotypes, *D. sublineatus* with 2N = 72, FN = 90, and *D. dorsalis* with 2N = 82, FN = 80 (Zanchin et al. 1992), while the karyotype described by Yonenaga (1975), referring to *D. collinus*, actually corresponds to *D. dorsalis.*

In this study, we present new karyological data on *Delomys* specimens collected in the states of Rio de Janeiro and Minas Gerais.

We collected 65 specimens of *Delomys* in Parque Nacional de Caparaó (20°19′ S 41°48′ W), Minas Gerais and Espírito Santo States, and five from Brejo da Lapa, Itatiaia (22°23′ S 44°43′ W), and Rio de Janeiro State.

Figure 1 shows part of the distribution of *D. dorsalis* and *D. sublineatus*, and our collecting localities. The plotted localities are: 1. (Parque Nacional do Caparaó, 1,800–2,400 m), and 2. (Itatiaia, 1,750 m) from this study; 3. (Engenheiro Reeve, Espírito Santo State, 20°46′ S, 41°285′ W, 400–600 m), 4. (Santa Tereza, Espírito Santo State, 19°55′ S 40°36′ W, 900 m), 5. (Conceição do Mato Dentro, Minas Gerais State, 19°01′ S 43°25′ W, 771 m), 6. (Itatiaia, Rio de Janeiro State, 22°23′ S 44°38′ W, 1,385 m), 7. (Teresópolis, Rio de Janeiro State, 22°26′ S 42°59′ W, ca. 800 m), 8. (Alto da Serra, São Paulo State, 23°47′ S 46°19′ W, ca. 800 m), 9. (Boracéia, 22°38′ S 45°52′ W, 800–900 m and Casa Grande, 23°37′ S 45°57′ W, 800 m, São Paulo State), 10. (Piquete, São Paulo State, 22°36′ S 45°11′ W, 600–900 m) according to Voss (1993); and locality 11. (Monte Verde, Espírito Santo State, 19°53′ S 41°57′ W) according to Zanquin et al. (1992).

One male from Caparaó (Museu Nacional 31 948) and all five specimes from Itatiaia (males: MN 33 698, 33 700; females: 33 699, 33 701 and 33 702) were karyologically analysed. Chromosome preparations were obtained from bone marrow as described by Ford and Hamerton (1956), and G-banding was performed using a modified procedure of Seabright (1971). Skins and skulls of the specimens collected in Itatiaia were deposited in the Museu Nacional (MN), Rio de Janeiro and those collected in Parque Nacional de Caparaó in the Field Museum of Natural History (FM), Chicago.

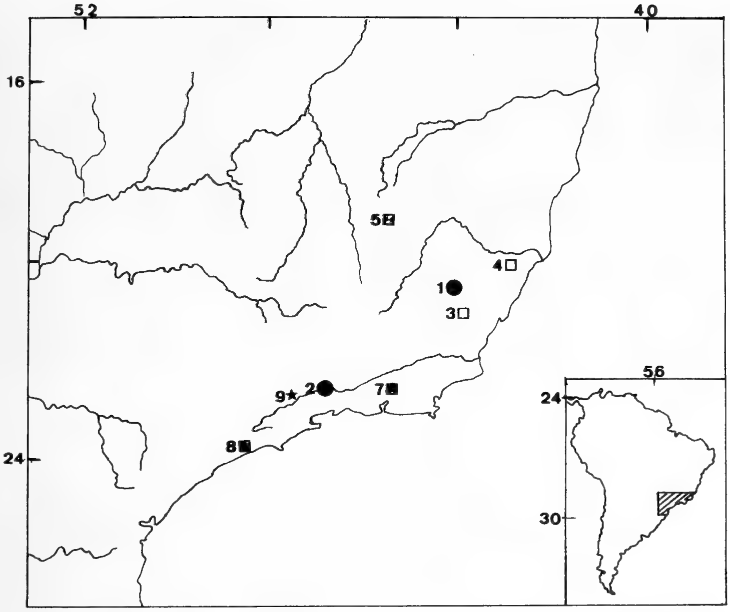

Fig. 1. Localities of occurrence of ✶ *Delomys sublineatus*, ☐ *D. dorsalis*, and ● *D. collinus*. See text for names of locality. The map scale is 1 : 5,000,000.

Chromosome analyses showed 2N = 82, FN = 86 in all studied specimens. The autosomal complement is composed of 3 pairs of biarmed chromosomes and 27 pairs of acrocentrics. Each of these groups is ordered in decreasing size in figure 2. The X chromosome is large-sized submetacentric, and the Y chromosome is a small metacentric. G-banding (Fig. 3) allows the unequivocal identification of each homologue.

Although previous data on *D. dorsalis* (Zanchin et al. 1992) show the same diploid number as specimens herewith reported, karyological differences are evident. This is due to the presense of three biarmed pairs in our specimens, while the *D. dorsalis* karyotype is exclusively composed of acrocentric chromosomes. Consequently, *D. dorsalis* has FN = 80 against FN = 86 of our specimens; this difference presumably being due to three pericentric inversions.

Our biogeographic data show that the studied populations have a disjunct distribution. Ecological data show that our specimens are endemic to vegetations that occur only at high altitudes, captured at or above 1,750 m. In Parque Nacional do Caparaó, with sampling areas as low as 1,000 m and as high as 2,700 m, we captured specimens only at altitudes equal or higher than 1,800 m, corresponding to areas of mountain scrub and mountain forest vegetation. In Itatiaia, specimens were collected at 1,750 m, also in mountain forests.

Both localities where our specimens were collected are about 400 km apart, being the two highest sites in southeast Brazil. Between these localities Voss (1993) and Zanchin et al. (1992) observed *D. dorsalis* and *D. sublineatus*.

Karyological, biogeographical, and ecological data show that our specimens, *D. dorsalis*, and *D. sublineatus* comprise three different taxa. Morphological analysis also corroborates these data, showing three different groups. Our specimens are endemic to mountain forest and mountain scrub, a reason why they are part of noncontinuous and vicariant populations. Karyological data show a discontinuous variation between them, without heterozygotes for the chromosome rearrangements reported here and for the karyotypes

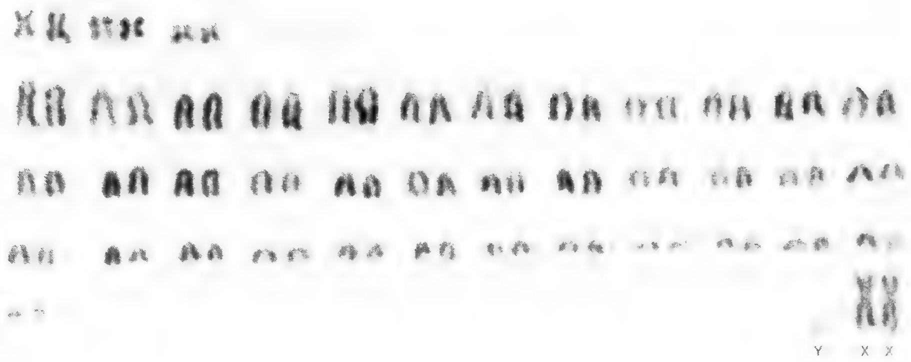

Fig. 2. Karyotype of *Delomys collinus* (conventional staining).

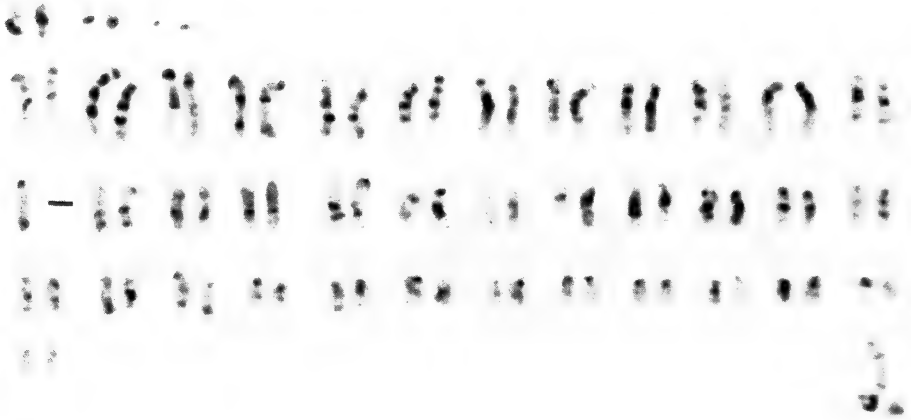

Fig. 3. G-band karyotype of *Delomys collinus.* The illustrations lacks one homologue chromosome (–).

reported for *D. dorsalis* in the literature (ZANQUIN et al. 1992; YONENAGA 1975). It is therefore likely that these groups are reproductively isolated from one another. Our results suggest that Itatiaia and Caparaó populations belong to the same taxon, which is karyologicaly different from *D. dorsalis* and *D. sublineatus*. The name that can be considered for this specimens is *D. collinus*, since we collected our Itatiaia specimens near the type locality of *D. dorsalis collinus* (THOMAS, 1917).

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Buchbesprechung

Tembrock, G.: **Verhaltensbiologie.** 2., überarbeitete Auflage. Jena, Stuttgart: Gustav Fischer Verlag 1992. UTB 1664. 386 S., 130 Abb. DM 48,80. ISBN 3-8252-1664-0.

Dieses Buch, dessen 1. Auflage 1987 erschien, liegt nun in 2. und überarbeiteter Auflage vor. Es gliedert sich in folgende Kapitel: Die Wissenschaft vom Verhalten; Methoden der Verhaltensforschung; Allgemeine Kennzeichen des Verhaltens; Physiologische Grundlagen des Verhaltens; Motiviertes Verhalten; Verhalten und Anpassung; Die verhaltensbestimmenden Umweltansprüche; Funktionskreise des Verhaltens; Die Umwelt und ihr Wirkungsspektrum; Funktionen des Verhaltens; Angewandte Verhaltensforschung; Verhaltensbiologie und Humanwissenschaften. Das Buch ist als Einführungstext in die Verhaltensbiologie konzipiert.

Es zeigt in seinem didaktischen Aufbau, teilweise auch in den thematischen Schwerpunkten sowie den erläuternden Fallbeispielen die persönliche ‚Handschrift' des Autors; viele Beispiele sind aus eigenen Untersuchungen oder solchen seiner Arbeitsgruppe gewählt. Der Text ist durchweg übersichtlich gegliedert und die geschilderten Sachverhalte sind nach Möglichkeit begrifflich klar gefaßt und voneinander abgegrenzt. Das operationalisierende Vorgehen verleitet Tembrock allerdings an einigen Stellen zur Bildung von wirklichen Begriffs-‚Ungetümen', wie er teilweise auch selbst bemerkt, und man fragt sich, ob es im Rahmen eines solchen Buches wirklich sinnvoll ist, z. B. über mehrere Seiten (S. 29 ff.) alle möglichen begrifflichen Differenzierungen für unterschiedliche räumliche Haltungen eines bzw. räumliche Anordnungen zweier Tiere zueinander aufzuführen. Auf einen inhaltlichen Gesichtspunkt möchte ich noch kurz eingehen. Wenn Tembrock in den Ausführungen zur Homologie von Verhaltensweisen auf S. 194 ff. relativ ausführlich sog. Erwerb- bzw. Traditionshomologien schildert, so wäre es nach Auffassung des Rezensenten geboten, darauf hinzuweisen, daß die Verwendung des Begriffszusatzes -homologie für die so klassifizierten Verhaltensmerkmale bzw. Merkmale generell durchaus nicht unumstritten ist. Die Verwendung des Begriffs homolog auch für Verhaltenselemente ‚gleicher Struktur', die wie im gegebenen Beispiel eine Lautäußerung eines Menschen und deren Nachahmung durch einen Papagei durch völlig verschiedene Organe (Larynx bzw. Syrinx) erzeugt werden, höhlt meines Erachtens letztlich das gesamte Konzept der Homologie in seiner phylogenetischen Verankerung aus.

Das Buch gibt insgesamt einen breiten und stellenweise weitreichenden Überblick über die Verhaltensbiologie und ihr benachbarte Wissenschaftsfelder, die teilweise in vergleichbaren Büchern kaum oder nicht so ausführlich berührt werden. Es hat allerdings den Mangel, daß wesentliche Bereiche bzw. Modellvorstellungen, die für die aktuelle Theorienbildung, daraus sich ergebende Ansätze für experimentelle Forschung sowie für die Interpretation bisher nicht sinnvoll deutbarer Beobachtungen in dieser Disziplin und der Evolutionsbiologie allgemein eine wesentliche Rolle spielen, wie z. B. Ökoethologie, Soziobiologie, ‚ESS', ‚life history strategies' oder Evolution von Signalverhalten, in seinen Ausführungen nur einen recht geringen Raum einnehmen. Generell darf man feststellen, daß es für Studenten, die sich eher peripher mit der Ethologie befassen wollen bzw. müssen und kein tiefergehendes Interesse für diese zoologische Disziplin hegen oder nicht über entsprechende Vorkenntnisse verfügen, als zu umfangreich und stellenweise in seinen Ausführungen auch zu detailliert und kompliziert erscheint. Hier wäre dann nur eine selektive Lektüre einzelner Kapitel angebracht. Bei eingehender Beschäftigung mit der Ethologie sei es aber durchaus empfohlen, da es sich in der Art der Darstellung, seinem didaktischen Konzept und auch in einigen inhaltlichen Schwerpunkten von anderen auf dem Markt befindlichen Büchern zur gleichen Thematik doch deutlich unterscheidet und so insgesamt das Verständnis erweitert und schärft. Damit kann Tembrocks Text also im wesentlichen als zusätzliche, ergänzende Lektüre neben anderen Lehrbüchern der Ethologie empfohlen werden. Dem steht allerdings als deutliches Hindernis sein Preis entgegen. Es sei dem Rezensenten gestattet, dies näher auszuführen: Im Vergleich zur 1. Auflage ist der der 2. um nahezu 150% erhöht; jede Seite der neuen Ausgabe mit einem Format von wenig mehr als DIN A6 kostet damit umgerechnet 12,6 Pfennig! Studenten, für die dieses Buch sicherlich primär geschrieben wurde, werden – zusätzlich zur übrigen erforderlichen Fachliteratur – kaum in der Lage und wohl auch nicht gewillt sein, einen so hohen Preis dafür zu zahlen. Verlage brauchen sich nicht zu beklagen, wenn solche Bücher dann von großen Teilen des potentiellen Kundenkreises nicht gekauft, sondern eher komplett oder in Teilen kopiert werden – und das zu deutlich geringeren Kosten!

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HERRE, W.; RÖHRS, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.
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ZEITSCHRIFT FÜR
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Automatic registration of bat activity through the year at Mønsted Limestone Mine, Denmark

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Abstract

Bat activity was recorded automatically the year round with a double light barrier at the exit of the mine. The method yields quantitative data without interference on the natural behaviour of the bats. Four periods are defined: 1) Hibernation period (November–late March), with very low activity. 2) Departure period (late March–mid May), with a marked peak in April, and a second small period of departure in the first half of May, representing the departure of *Myotis brandtii.* 3) Summer activity period (mid May–mid June), when a large number of *M. daubentoni* males use the mine as some sort of transitional roost. 4) Arrival period (late July–November), consisting of two periods with a gradual transition: End of July through August with a balance between in- and outflights, and September–November with a net flux into the mine indicating the start of hibernation. The species could not be separated, but this was a minor drawback as the gross number and behaviour of the different species was known in outline, studied by other methods. 80–90% are *M. daubentoni.*

Introduction

Mønsted Limestone Mine in Jutland, Denmark, is used for hibernation by 4,000–6,000 bats. Five species are found: *Myotis daubentoni* 3,500–5,000 (Baagøe et al. 1988), *M. dasycneme* 500–1,000 (Nielsen et al. 1995), *M. brandtii* 100–200 (Degn 1989), *M. nattereri* 50–100, and a few individuals of *Plecotus auritus.*

This makes Mønsted Limestone Mine one of the largest and most important hibernation sites in Northern Europe, and detailed knowledge of how and when the bats use the mine is important for conservation and management purposes. The aim of the present study was to present a year round picture of the bat activity.

Traditional counts of hibernating bats always include the risk that bats are disturbed (Stebbings 1988). Besides, in Mønsted Limestone Mine counts are impossible because most of the bats hide away (Baagøe et al. 1988). Catches at the entrance definitely cause great disturbance. Therefore the use of automatic registration is a good solution and has been used in a number of studies (Thomas and Laval 1988). One drawback is that species identification is not possible. But in the present study this was considered a minor problem because our main goal was to get an overall impression of the activity, and because the species composition and the gross number of each species was already known.

Materials and methods

Mønsted Limestone Mine consists of several kilometers of galleries of varying dimensions. The only permanent entrance to the mine for bats is through a hole in a wooden gate (for details see Baagøe et al. 1988).

Bat movements through the hole (25×28 cm) in the gate were recorded. The recording system covered the flight route so that a passing bat interrupted two arrays of infra-red beams 25 cm apart. Each array consisted of 8 infra-red light emittors (diodes) and 8 receivers (phototransistors). The light was chopped with a frequency of 1 kHz to minimize influence of ambient light-levels. A pass was recorded when the two arrays were interrupted within a minimum and maximum time calculated to fit the distance between the arrays and the flight speed of the bats.

The system was set up on 13. December 1977, and registration ended on 5. July 1982. Reliable data were sampled for 900 nights, which is 55% of the time. Non-function periods were due to unstable mains supply, light beams blocked by insect pupae, condensed water on the emittors, and break-down of electronic components.

For the first three years data were recorded on waxed paper on a Miniscript-Z event recorder. The last two years data were also stored on tape. A Memodyne data logging system stored date, time, and number of out- and inflights for 20-minute periods.

Visual counts of passing bats revealed that some bats were not recorded automatically. The data can only be regarded as a relative index of activity. The most important sources of error are: 1. Bats with a longer (or shorter?) passing-time than the time-constant are not recorded. 2. One bat circling outside and another one circling inside breaking the beams within the time-constant could cause a false recording. 3. Condensed water on the emittors dispersed the light, and the reliability decreased.

Results

Although 5 species use the mine, *M. daubentoni* make up 80–90% of the hibernating population. The data therefore largely represent the activity of this species, except when otherwise stated. Catches (e.g. BAAGØE et al. 1988; DEGN 1989) and observations at different times through the year confirm this.

Because of technical problems continuous recordings from one particular year could not be produced. So the activity throughout the year is composed of representative periods from different years, when the apparatus was in full function (Fig. 1). The following presentation is divided according to the bats' activity pattern.

Activity through the year

In winter the activity through the exit is very low until mid February. After that time it increases a little, but even in the first part of March there is no net outflux from the mine.

From mid March the activity starts increasing, and the number of departures greatly exceeds the number of arrivals per night. Departure is intensive from the end of March

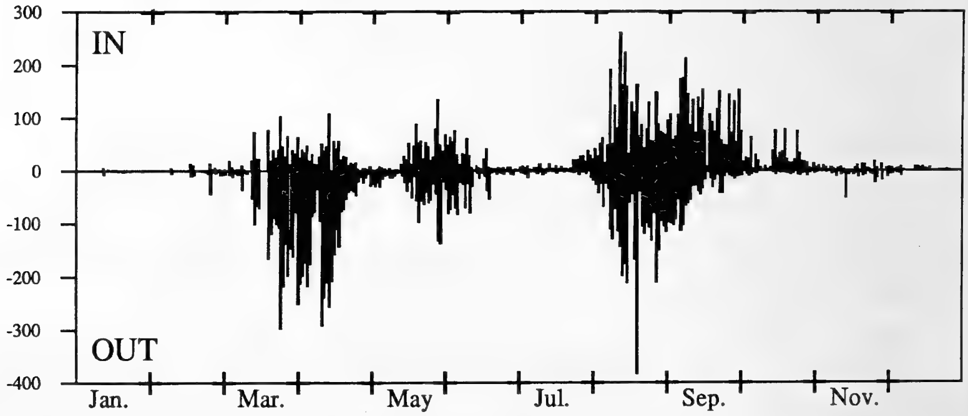

Fig. 1. Bat activity at Mønsted Limestone Mine through the year. Columns above the x-axis indicate number of inflights per night, and below the axis outflights are indicated. This also applies to figures 2–5.

towards the end of April without a sharply defined maximum, but with great variations from night to night. During the last 1–2 weeks of April the activity decreases rapidly.

In the first half of May a second period of departure is found, but involves only a small number of bats.

The departure comes to an end around the middle of May. After this time no bats were expected to use the mine, but a new activity period of about 5 weeks begins after the middle of May. The number of registrations in both directions is about equal calculated over the whole period, indicating no net in- or outflux.

During the first three weeks of July the activity is low, but starts rising around the turn of the month. The number of registrations increases until the middle of August, when a rather high level of activity in both directions is reached and maintained until about 1. September.

From then the net flux of bats into the mine is increasing, and the number of outflights per night begins to decline steadily until near zero about 1. October. The number of inflights remains high during the whole of September, and many hundred bats arrive also in October. In November and the first part of December the number of inflights becomes very small.

Activity in separate nights

In order to get a detailed description of bat activity during different periods of the year, the activity through separate nights was analysed.

An example of the activity during one night in the departure period in spring is shown in figure 2. The departure starts about 1 hour after sunset and comes to a maximum 1.5–3 hours after sunset. Already at midnight the activity is again very low and remains so for the rest of the night.

In early summer (mid May to mid June) a maximum outflight is often recorded during the night after a night with a maximum inflight. The coefficient of correlation between the number of bats arriving one night and the number leaving on the next night is high (r = 0.91). Figure 3 shows an example of the activity pattern during two successive nights, preceeded and succeeded by a night with very low activity. The first night (31. May) about

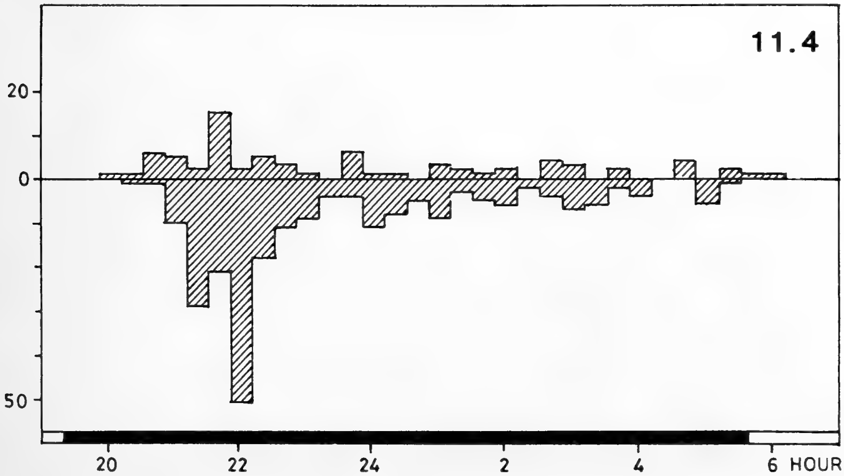

Fig. 2. Bat activity during a night in the departure period (April 11.). The period from sunset to sunrise is indicated by a black bar on the time scale. This also applies to figures 3–5.

90 bats arrive the mine around 01–02 h. The bats do not leave again the same morning but stay in the mine the following day. The next night they fly out before midnight, and bats return later in the same night.

The activity during a representative night in the beginning of the arrival period is shown in figure 4. Most bats leave the mine before 22 h. After midnight arrivals predomi-

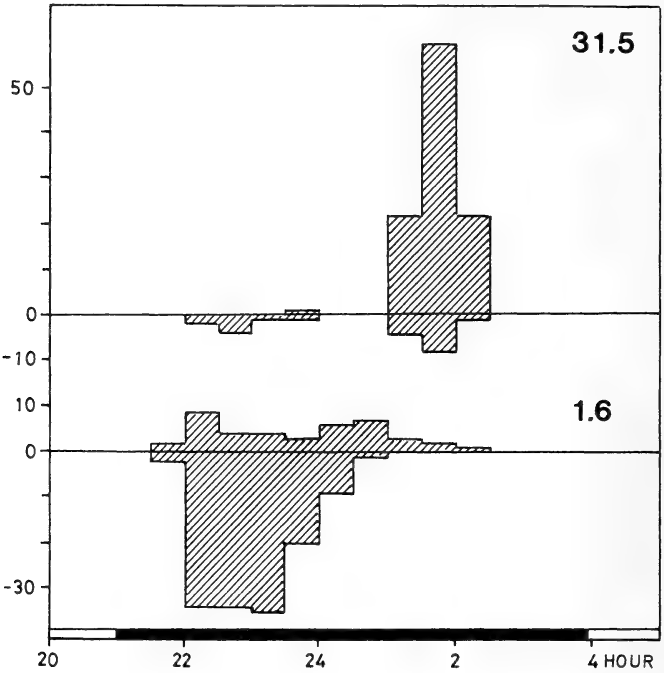

Fig. 3. Bat activity on two successive summer nights, May 31. and June 1.

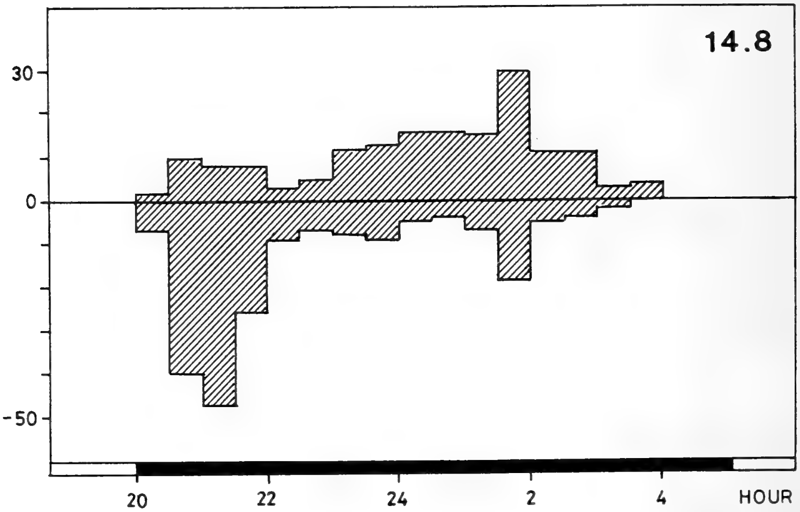

Fig. 4. Bat activity during a night in the first part of the arrival period (August 14.).

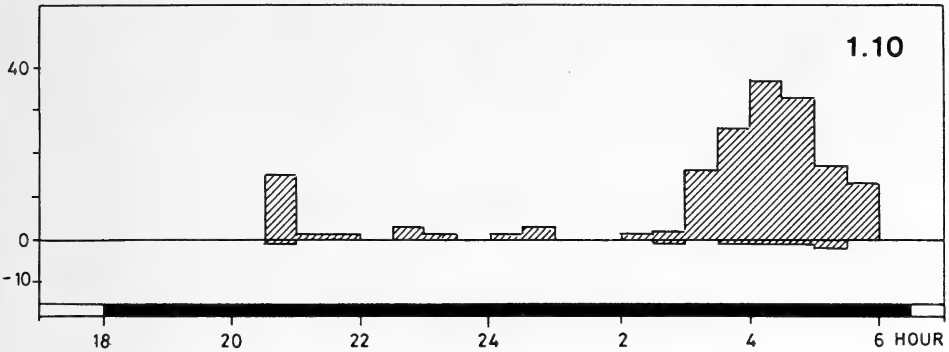

Fig. 5. Bat activity during a night in the last part of the arrival period (October 1.).

nate. In the last half of August the activity pattern is more unstable. The number of outflights sometimes exceeds the number of inflights. Still a considerable number of bats depart from the mine before midnight in most nights.

An example of the activity during a typical night of the last part of the arrival period is shown in figure 5. Nearly all the activity is directed into the mine and takes place 03–06 h. Activity ends shortly before sunrise.

Discussion

The method described above has disadvantages, mostly connected to technical problems. But it yields quantitative data and – at least in theory – it works automatically all year round and is less time consuming than other methods. Another major advantage is that bat workers do not interfere with the normal behaviour of the bats.

The species cannot be separated. But in the present study this was a minor problem because knowledge about the behaviour and gross numbers of the five species had been accumulated previously. By combining this information the characteristic periods of bat activity throughout the year can be defined and described.

Hibernation period (November–late March).

Many *Myotis*-species including *M. daubentoni* wake up spontaneously several times during hibernation (Daan 1973). This was also found in Mønsted Limestone Mine (Degn 1987). However, from the present study we conclude that only very few bats ventured out through the exit in winter. In a Dutch cave (Daan 1970) using photographic recording also found that only a very small part of the bats waking up actually flew out from the cave.

The outflights in early March represent very little outflux as most outflights were followed 1–2 minutes later by an inflight. We interpret this as the same individual flying out, finding the weather unfavourable, and entering again immediately.

Departure period (late March–mid May).

Baagøe et al. (1988) found that captures at the exit gave a more realistic picture of the departure than counts in the mine, which have earlier been used. The present data correspond well with the trap-captures. The conclusion of Baagøe et al. (1988) can therefore be extended to say that the most correct picture of the departure is obtained by measuring the activity at the exit either by capture or by automatic registration.

In the first half of May only few bats are observed in the mine. Nearly all of them are *M. brandtii* (pers. obs.), and we therefore suggest that the flight recordings at this time are mostly caused by this species. It is also known to depart very late from other Danish limestone mines: Daugbjerg (EGSBÆK and JENSEN 1963), Smidie and Tingbæk (B. JENSEN, pers. comm.).

Summer activity period (mid May–mid June).

Until the automatic recording system was set up, activity in the middle of the summer at the hibernaculum was not known. Later it was reported by DEGN (1989) that the bats were male *M. daubentoni* arriving after midnight, staying in the mine the next day, and leaving the mine again after sunset. More than thousand bats visited the mine only once during the summer. This shows that these males did not use the mine as a permanent day roost during summer, but as some sort of transitional roost.

Arrival period (late July–November).

We found arrival to start in late July and stop around the end of November. Most other studies on *M. daubentoni* report a shorter period of arrival (KRZANOWSKI 1959; EGSBÆK 1962; ROER and EGSBÆK 1966; DAAN and WICHERS 1968; DAAN 1973), but these authors counted bats hanging in the hibernacula.

KLAWITTER (1980) found two periods of immigration of *M. daubentoni* in the Spandauer Citadelle in Berlin. The first lasted from late July to the end of August. The bats gathered in groups and showed great activity also during daytime. The second period lasted from the beginning of September to the end of October, although it could continue into December. In this period the bats rested solitarily and were inactive.

For *M. lucifugus* FENTON (1969) and THOMAS et al. (1979) found two similar phases. In the first one ("swarming"), the animals only stayed in the cave for a few hours per night. They were active, but did not mate. During the second phase they were mostly hibernating, yet matings occurred.

Our results confirm that the arrival period can be divided into two parts with a gradual transition from one to the other. In the first part there is a balance between out- and inflights, indicating that the bats did not hibernate. FENTON (1969) suggested several theories for this behaviour involving dispersion, migration, or some kind of prenuptial activity. The second part of the arrival period is clearly the preparation for hibernation. From the start of September the number of outflights per night decreases rapidly, and most bats have arrived before the end of October.

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Zusammenfassung

Ganzjährige automatische Registrierung der Fledermausaktivität in der Mønsted-Kalkgrube, Dänemark.

Das ganze Jahr hindurch wurde die Fledermausaktivität mit Hilfe einer doppelten Lichtschranke am Eingang der Mine automatisch registriert. Diese Methode liefert quantitative Daten ohne das natürliche Verhalten der Fledermäuse zu stören.

Vier Perioden wurden definiert: 1. Eine Winterschlafperiode mit sehr geringer Aktivität von November bis Ende März. 2. Eine Abflugperiode von Ende März bis Mitte Mai mit einem markanten Maximum im April und einer zweiten kurzen Abflugperiode in der ersten Maihälfte, die den Abflug von *Myotis brandti* markiert. 3. Eine Sommeraktivitätsperiode von Mitte Mai bis Mitte Juni; in dieser Zeit benützt eine große Anzahl von Männchen der Art *Myotis daubentoni* die Mine als zeitweiligen Aufenthaltsort. 4. Eine Ankunftsperiode von Ende Juli bis November, in der sich Ein- und Ausflüge in der Zeit von Ende Juli bis August die Waage halten, und in der ab September die Einflüge mehr und mehr überwiegen und den Beginn des Winterschlafes anzeigen.

Die einzelnen Arten konnten nicht unterschieden werden; dies wird aber nur als ein geringer Nachteil angesehen, da die Anzahl und das Verhalten der verschiedenen Arten mit Hilfe anderer Methoden bekannt wurde. 80–90% der Tiere gehören zu der Art *Myotis daubentoni*.

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Age determination in the Red fox in a Mediterranean habitat

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Abstract

The age determination of red foxes *Vulpes vulpes* was studied in Pisa Province, Central Italy, from January to May 1992. The presence of incremental lines in the cementum of canine teeth after decalcification, sectioning and staining has been checked for the first time in a Mediterranean species. We compared the weight of the eye lens and the width of pulpar cavity of canine teeth as methods of discriminating yearlings from adults with the incremental line count (a more reliable, but more time-consuming technique). 330 foxes (125 F; 205 M) were collected, but sample size was variously reduced for different methods. Incremental lines (up to 8) were clearly visible. Neither the eye lens nor the pulpar cavity methods discriminated unequivocally the two age classes, but a discriminant function using the two variables achieved 100% success. Pulpar cavity of females closed during their first oestrus. Geographical variability in the development rates of different organs suggests that no method (except incremental lines) can be used without prior verification.

Introduction

A variety of methods has been used to determine the age of various Carnivora: external measurements (SARGEANT et al. 1981); weight or shape of baculum (HARRIS 1978; NELSON and CHAPMAN 1982; OGLE et al. 1990); weight of eye lens (HARRIS 1978; NELSON and CHAPMAN 1982); fusion of cranial or epiphyseal sutures (HARRIS 1978; NELSON and CHAPMAN 1982; YONEDA and MAEKAWA 1982; HANCOX 1988; OGLE et al. 1990; ROSAS et al. 1993); width of pulpar cavity of teeth, as measured by either sectioning (ROOT and PAYNE 1984; GOSZCZYNSKI 1989) or radiographing (TUMLISON and MCDANIEL 1984; OGLE et al. 1990) one of the teeth; distance of the enamel line from the edge of the alveolus (ALLEN 1974; ROOT and PAYNE 1984); tooth wear (VAN BREE et al. 1974; HARRIS 1978; ROOT and PAYNE 1984; HANCOX 1988); presence of the apical foramen of canine teeth (ROOT and PAYNE 1984); enumeration of incremental lines ot either teeth cementum (SAUER et al. 1966; JENSEN and NIELSEN 1968; GRUE and JENSEN 1973; MONSON et al. 1973; ALLEN 1974; VAN BREE et al. 1974; HARRIS 1978; ARTOIS and SALMON 1981; NELSON and CHAPMAN 1982; YONEDA and MAEKAWA 1982; GOSZCZYNSKI 1989; OGLE et al. 1990; ROSAS et al. 1993), or teeth dentine (HARRIS 1978; DRISCOLL and JONES 1985) or bones (HARRIS 1978). Whereas a variety of techniques appears suitable to separate young from adults, the most reliable method to estimate age is enumeration of cementum lines (e.g. HARRIS 1978). Lines are formed during winter in temperate areas, and during dry season(s) in the tropics. Dark annuli may therefore be related to nutritional stress (COY and GARSHELIS 1992). None of the above studies, however, was conducted in Mediterranean areas, where winters are mild and aridity during summers is not extreme. Under these conditions, food limitation is probably not highly seasonal, especially for an animal with a catholic diet such as the red fox (e. g. Cavallini and Lovari 1991; Cavallini 1994). Red foxes, having only one oestrus cycle per year (in spring: Lloyd and Englund 1973; Cavallini 1994), have a discrete age structure. Determination of age is therefore facilitated when date of sampling is known. Determination of age is most difficult in late winter and spring, when yearlings approach the size of adults (Harris 1978).

The aim of this study is to verify the suitability of three ageing techniques (eye lens weight, pulpar width and incremental lines) in a sample of red foxes *Vulpes vulpes* collected in late winter and spring from a Mediterranean area.

Material and methods

Foxes were collected by hunters in the Pisa province (43° N, 10–11° E), Central Italy, from January to May 1992, during the main fox hunting season. The area (52 km E-W by 75 km N-S; 2 448 km^2) is mostly flat and intensively cultivated (mainly cereals) in the north, becoming increasingly hilly (up to 800 m a. s. l.) and wooded towards the south. The climate is Mediterranean, with mild winters and dry, hot summers. In 1992, minimum temperatures (monthly average) ranged from 3.4 °C to 19 °C, and maximum temperatures from 12 °C to 31 °C. Monthly means were below 10 °C for 3 months, and above 20 °C for 4 months. Rainfall is heavier in autumn (35.9% ot total rainfall), in winter (28.9%) and in spring (23.7%), whereas only 11.5% of total rain occurs during summer. Interannual variation is large: in 1992, the least rainy months (less than 20 mm of rain per month) were January, February, March, August, and May (in increasing order; Cavallini 1994).

We collected foxes (N = 330; 125 females and 205 males) from hunters within 6 hours of death and stored them in plastic bags in a refrigerator cell (≤48 hours, −2 °C) until dissection (within 2 days from refrigeration). The protocol of Harris (1978) for measuring eye lens weight (±0.1 mg) was followed without modifications. The average between the two lenses was taken, and pairs of lenses that differed by more than 1% were discarded. We extracted both right (or, in their absence, left) canine teeth from the skull after maceration (6 months) in water. They were radiographed using standard techniques (courtesy of Hospital "Le Scotte", Siena). After tracing a perpendicular to the major axis of the tooth in the point of its maximum width, we measured external diameter of the tooth and diameter of the cavity (±0.1 mm) with a calliper. The ratio of the two measures was used for subsequent analyses. In the case of teeth damaged during the life of the animal, dentine deposition is inhibited, and this technique cannot give unequivocal results.

The same teeth were then decalcified in aqueous solution of HNO_3 (10%) for 36–48 h (according to tooth dimension). The tooth was then rinsed for 24 h under running tap water and cut sagittally (20 μm) with a freezing microtome (–20 °C). After air-drying (24 h), sections were stained with ematossilyne and mounted with standard histological techniques. This protocol is slightly modified from that of Grue and Jensen (1973). Incremental lines were counted by use of an optical microscope (40×).

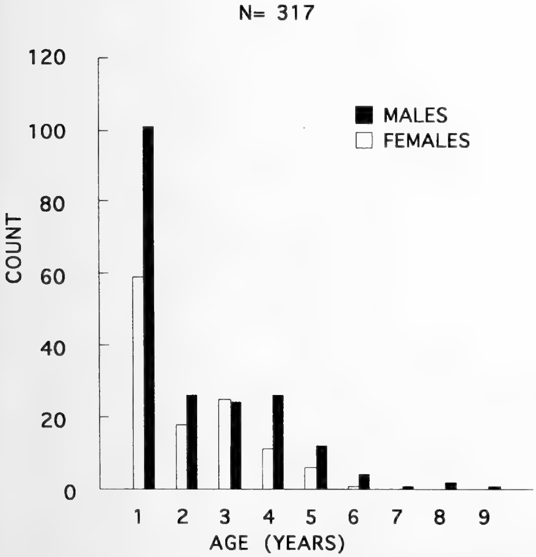


Fig. 1. Age composition (as determined by incremental annuli) of 317 foxes sampled in Pisa Province, Central Italy, January–May 1992.

Results

Microscopic analysis of decalcified sections showed that approximately one half of the samples did not show any incremental lines; these foxes were therefore considered to be in their first year. In the other foxes, lines (up to 8, corresponding to an age of 9 years) were clearly visible (Fig. 1).

Weights of eye lens showed two peaks, one around 200 mg (yearlings) and the other around 240 mg (adults). However, the overlap between the two distributions was very high (Fig. 2 a). Both the effect of age (pooling samples ≥4 years) and that of sex on eye lens weight were significant (age: $F = 167.3$, $p < 0.0001$; sex: $F = 19.6$, $p < 0.0001$, $N = 179$). Their interaction did not have an effect ($F = 1.2$, $p = 0.3$).

However, separation of male and female samples did not improve the discriminant power of this technique (Fig. 2 b, c). Weights of eye lens of juvenile foxes averaged 198.0 ± 13.4 mg ($N = 90$), whereas lenses of adults were heavier (244.4 ± 17.8; $N = 88$; Mann-Whitney $U = 181.5$, $P < 0.0001$). Eye lens weight continued to increase with age, although slowly (Fig. 3 a). Most foxes with eye lenses heavier than 210 mg were adults (82 of 95, or 86%), whereas those with lenses lighter than 210 mg were mostly yearlings (77 of 81, or 95%).

The effects of age (pooling samples ≥4 years) and sex on pulpar cavity ratio were significant (age: $F = 309.0$, $p < 0.0001$; sex: $F = 10.4$, $p = 0.001$, $N = 304$). Their interaction did not have an effect ($F = 0.3$, $p = 0.8$). When ages are pooled, pulpar cavity ratio was higher for males than for females, although they were not statistically different (upper: 0.332 ± 0.174; $N = 194$ vs. 0.301 ± 0.165; $N = 110$; Mann-Whitney $U = 11\,911.5$, $p = 0.092$; lower: 0.285 ± 0.155; $N = 192$ vs. 0.253 ± 0.139; $N = 117$; Mann-Whitney $U = 12\,703.5$, $p = 0.053$). The frequency distribution of pulpar cavity ratios showed two peaks (wide cavity, i. e. yearlings, and narrow cavity, i. e. adults). The discrimination based on the upper canine tooth was more reliable than that on the lower canine (Fig. 4). For females,

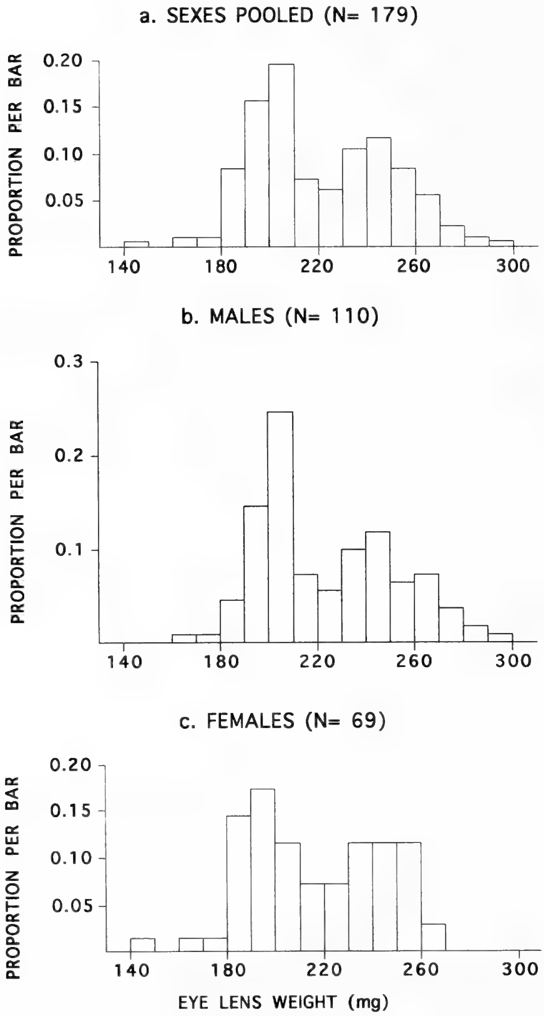


Fig. 2. Frequency distribution of lens weight of foxes from Pisa Province. The distributions for sexes pooled (a), for males (b) and for females (c) are shown. N is the number of individuals.

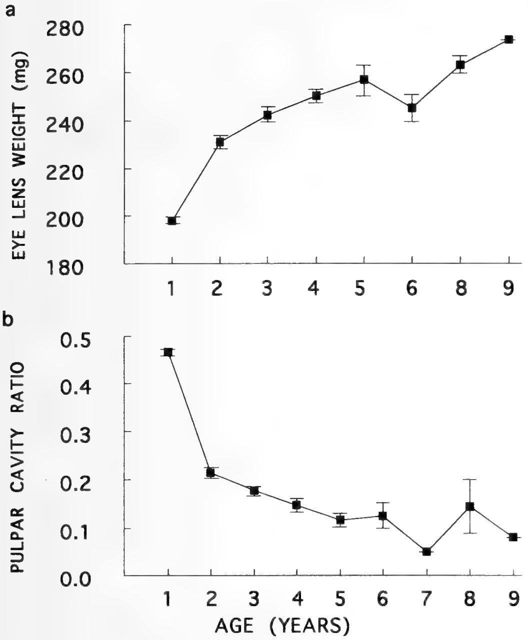
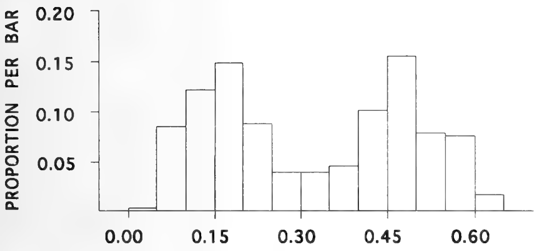


Fig. 3. Variation with age of: (a) lens weight; (b) ratio of pulpar cavity diameter to external diameter of the upper canine tooth. Averages and standard errors are shown. Sample sizes are the same as in Fig. 2 a and 4 a.

a. UPPER (N= 304)



b. LOWER (N= 309)

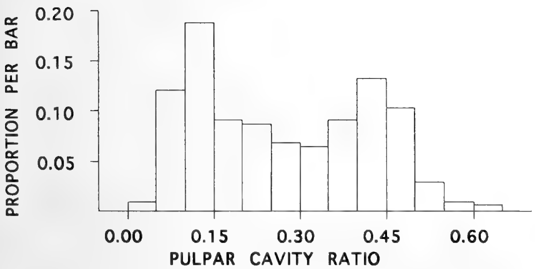


Fig. 4. Frequency distribution of the ratio of pulpar cavity diameter to external diameter ot the canine tooth of foxes from Pisa Province. The distributions for upper (a) and lower (b) canine teeth are shown. N is the number of individuals.

there was no overlap between the upper canine pulpar width of young and adults in the period before oestrus (until 23 February; Cavallini 1994). The females with a ratio of less than 0.3 were adults, whereas those with a ratio >0.4 were yearlings, i. e. before their first oestrus (Fig. 5 a). During the period of oestrus (9 to 31 March), the overlap increased (Fig. 5 b), until after oestrus (from 12 to 30 April), when the two peaks were not noticeable (Fig. 5 c). For males, no gap was evident in any period. The cavity ratio of yearlings was significantly higher than that of adults (0.466 ± 0.090; N = 155 vs. 0.170 ± 0.079; N = 149; Mann-Whitney U = 22 609, P < 0.0001). The ratio was 0.521 ± 0.074 (N = 43) at the beginning of the sampling period (until 20 February), and dropped to 0.403 ± 0.087 (N = 38) at the end (after 31 March; sexes pooled). Closure of the cavity is rapid in the first year, thereafter it is continuous, but very slow (Fig. 3 b).

Better results could be obtained by combining the results of the above analyses (Fig. 6): all points above the line indicated adults, whereas all the points below the line indicated yearlings. A Fisher Linear Discriminant Function (following Wilkinson 1990) was calculated. Complete discrimination of the two age classes was achieved without misclassifications (Wilks' L = 0.106, F = 702.45, P < 0.0001, N = 169). The classification functions were: $136.5x + 0.909y - 124.9$ for yearlings and $61.6x + 1.073y - 136.8$ for adults (where x = pulpar cavity ratio and y = eye lens weight). These functions can be applied to new data and each case may be assigned to the group with the largest function for that case.

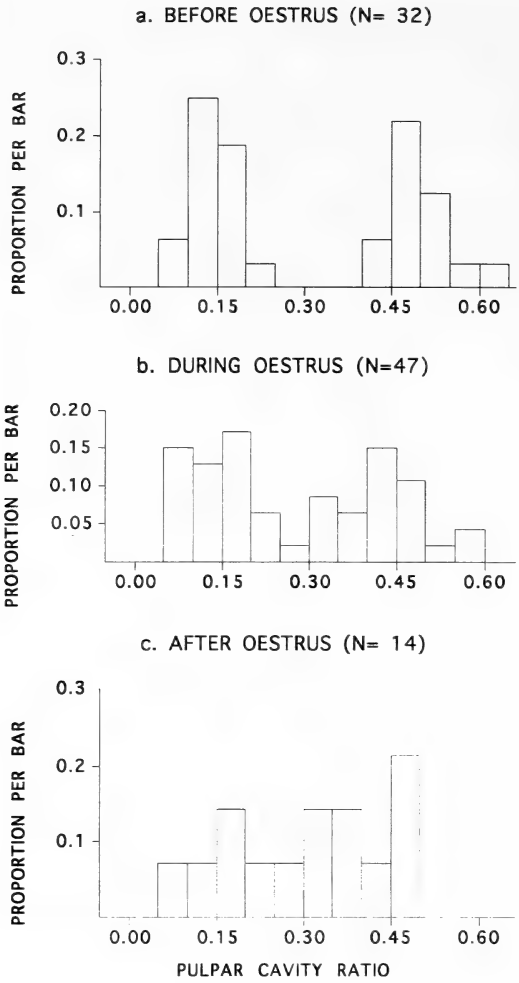


Fig. 5. Frequency distribution of pulpar cavity ratio of the upper canine tooth of female foxes from Pisa Province, divided in to three sampling periods (before oestrus (a): until 23 February; during oestrus (b): 9 to 31 March; after oestrus (c): from 12 to 30 April). N is the number of individuals.

Discussion

In our area, incremental lines were clearly shown even in the absence of snowy winters or dramatically dry summers. This technique appears therefore suitable (though time consuming) not only in cooler northern environments or dry-and-wet tropics, but also in warm Mediterranean areas. By contrast, eye lens weight was related to age, but it was not a reliable indicator of age in late winter and spring. The point (210 mg) that allows a partial separation between yearlings and adults among foxes from North America (Friend and Linhart 1964), from Switzerland (Wandeler 1976) and from surburban London (until March; Harris 1978) is also partially discriminating for our population. This coincidence is surprising, given the morphological differences among these fox populations (e.g. Cavallini 1994), and the different sampling periods (September and October in North America, October to March in London, January to May in Central Italy). In Australia, the 200 mg point seems a better separation point, but this method has limited applicability (until January or February, i.e. when juveniles are about 6 months old, judging from Fig. 4 of Ryan (1976), or until December, according to the author (Ryan 1976)). Reasons for this discrepancy are not clear.

The pulpar cavity method is not suitable for separating yearlings from adults in spring, especially for males. The cavity of females closes rather quickly during their first oestrus, thus yearling females can be identified only up until their first oestrus. This is in contrast to the findings for foxes in Poland, where clear results can be obtained at least until the end of March (Goszczynski 1989) and in London where foxes in their second autumn can be separated from older ones (Harris 1978). Other differences between our results and those from Poland (Goszczynski 1989) are evident: (1) within each age class, females have lower ratios than males in Italy, whereas no difference was found in Poland; (2) the ratio of upper canines was different from that of lower canines in Italy, but not in Poland. Absolute values of the ratio for yearlings (60% in autumn, 40% after the end of March), however, are similar in the two areas. Geographical variation in both indices of age classes is therefore important, and only incremental lines can be recommended. Other

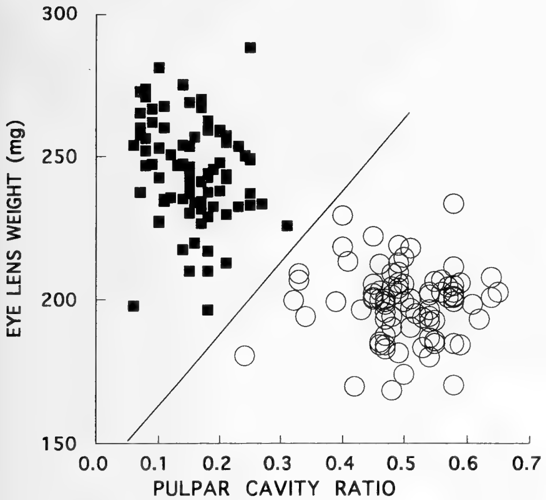


Fig. 6. Scatter plot diagram of pulpar cavity ratio vs. lens weight. Closed squares are adult foxes (> 1 year), open circles are yearlings (≤ 1 year).

methods should be validated for each population (as suggested by HARRIS 1978). The combination of the two less time-consuming techniques (eye lens and pulpar width; see Fig. 6) gave good results for the population studied, in spite of the late sampling period (until May), and may be useful for other areas. The numeric values of the discriminant functions should be verified on other populations.

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Zusammenfassung

Altersbestimmung beim Rotfuchs in einem mediterranen Habitat

Wir haben verschiedene Methoden zur Altersbestimmung des Rotfuchses (*Vulpes vulpes*) in Zentralitalien (Region um Pisa) von Januar bis Mai 1992 getestet. Erstmalig wurde in einem mediterranen Habitat die Anwesenheit von Wachstumslinien im Zement der Eckzähne nach deren Entkalkung, Sektion und Färbung untersucht. Messungen von Augenlinsengewichten und Pulpahöhlenweiten der Eckzähne als Methoden zur Unterscheidung einjähriger von erwachsenen Tieren wurden mit der Methode der Zählung von Wachstumslinien verglichen. Insgesamt 330 Füchse (125 W; 205 M) sind gesammelt worden, aber die Stichprobenzahl für die verschiedenen Methoden war unterschiedlich. Bis zu 8 Wachstumslinien waren deutlich erkennbar. Weder die Methode der Augenlinsengewichte noch die der Pulpahöhlenweite bestimmten die beiden Altersklassen eindeutig, aber eine Diskriminanzfunktion der zwei Variablen erreichte einen 100%igen Erfolg. Die Pulpahöhle weiblicher Tiere schließt sich während des ersten Oestrus. Die geographischen Unterschiede in der Wachstumsrate verschiedener Organe lassen vermuten, daß nur die Methode der Wachstumslinien zu gesicherten Altersangaben führt.

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Ontogeny of the rest-activity rhythm in the Wild boar

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Abstract

Continuous biotelemetry records of the wild boar (*Sus scrofa* L.) under natural conditions were used to study the ontogeny of its rest-activity rhythm. A nycthemeral component was found in the rhythms of all individuals investigated, both juveniles and adults at the various stages of the reproductive cycle. In contrast, ultradian rhythms were typical of immaturity; they were present in juveniles and in females accompanied by unweaned piglets and disappeared in adult females with weaned piglets or without piglets and in adult males. The detected ultradian rhythms had periods of approximately 3 hours or multiples of 3 hours according to age for juveniles and to the lapse of time since farrowing for females. Results are discussed with respect to uniform influences of internal processes and environmental factors on the individual behavior.

Introduction

According to Aschoff (1957), animals possess an endogenous sleep-wake rhythm which is solely influenced by the fluctuations of the internal environment. Biological events, such as oestrous (Cushing 1985), rut (Hansen 1984), parturition (Mauget 1980), weaning (Astic et al. 1979) and aging (Büttner 1980) are the principal factors modifying this internal rhythm. But this primitive rhythm is not often detectable since, in wild animals and especially in ungulates, many activities are modified in frequency, amplitude and time of occurrence by the effect of ambient physical and biological factors. The main physical factors modifying endogenous rhythms are temperature (Bigler 1974) and photoperiod (Campbell and Tobler 1984); the biological factors include food availability (Arnold 1964), the influence of predators (Meddis 1975) and of congeners (Harcourt 1977).

The aim of the present study was to investigate variations of the rest-activity rhythm in free-ranging wild boars, dividing the studied animals into three groups: (i) adult females between farrowing and weaning (2–3 months, Newberry and Wodd-Gush 1985), (ii) juveniles (from weaning to 9 months, Spitz 1992) and (iii) adult females after weaning of their piglets, adult females without piglets and adult males. This classification allowed us to identify some rules about the influence of age and of farrowing on adult females.

Material and methods

Study areas

The data were collected from two study sites in southern France (i) in the Camargue from 1985 to 1987, where the technique was developed and checked (Janeau and Hachet 1991) then (ii) in the Caroux and Montagne Noire massifs from 1989 to 1991. The Camargue is a flat area (around sea level), with a Mediterranean type climate; the area consists of a similar proportion of crop lands and marshes, with very small scattered woods and shrublands (Dardaillon 1984). The Caroux Espinouse and Montagne Noire massifs belong to the same extended mountain area; elevation ranges from 200 to 1 200 m a. s. l. The climate is also Mediterranean, with montane influence, according to altitude and orientation. The vegetation is diverse (holm oak, chestnut, conifer or beech stands, various types of heathlands, chapparal and grasslands; Auvray 1983; Anonymous 1979).

Data acquisition

The boars were captured and fitted with leather collars, using extendible type for young animals, onto which a radio emitter was fixed. The animals were classified according to their weight as juveniles or adults (Pepin et al. 1986; Spitz 1992). The exact dates of farrowing were deduced from the daily movements of the females (Janeau and Spitz 1984), since the emitter collar also provided radio locations.

To record activity, an inclination sensor, linked to the emitter, transmitted information to an automatic acquisition system working in real time (Janeau et al. 1987). The set-up was composed of omni-directional antennas, receivers and two interfaces; the first transformed the radio signal into a 5-volt signal and the second was for input management (up to 15 channels), dating the occurrence of the data and transmitting them to a microcomputer for storage. Each continuous record was analyzed with a time step of one minute and a predominant activity type attributed to each step. As recommended by Bubenik (1960), the only distinction made in the present report was between real rest and activity in a general sense (including locomotion, feeding and social activities).

Thirty-eight sessions of 24 hours, some consecutive, were recorded on 14 animals, 7 adult females at various stages of the reproductive cycle (in winter, spring and summer), 2 adult males (in winter), 3 juvenile males (between 6 and 8 months of age) and two slightly younger juvenile females (3 to 4 months) in spring and summer. Ten records of 48 hours were considered (Tab. 1). In the study of the 24-h sessions the individuals followed for 48 hours were only taken into account for one of the two consecutive 24-h periods. For a given individual, only records separated by at least 5 days were considered (Tab. 2).

Data analysis

Classical methods (Broom 1979) of detecting rhythms could not be used with these data. The 48-h data samples were processed with a time step of 15 minutes and those of 24 hours with a time step of 5 minutes to give a sufficient number of events in each series. Each interval was attributed a number corresponding to the total number of minutes of activity it included. A 48-h record was then reduced to a chronological series of 192 values and a 24-h record to a chronological series of 288 values. The chronological series were analysed on the principle of the auto-correlation method. For each shift of the series with itself, we calculated the proportion of cases (pobs) for which the two corresponding values were below or greater than the median of the studied series (pobs + qobs = 1, qobs was the proportion of the complementary event). For each series of n events, n/3 shifts were made.

The observed proportions were compared to the limits of the confidence interval of a theoretical proportion. This theoretical proportion was determined assuming the null hypothesis of an equiprobable distribution of the values with respect to the median ($p = q = 0.5$). In this way, each shift for which the observed proportion was outside the limits of the interval of confidence enabled the identification of a significant period with an error risk fixed at 0.05. For each series, we obtained several groups of values outside of the confidence interval, and calculated a mean period for each group (values below the confidence interval gave 1/2 periods). All mean periods obtained for each group corresponded to a fundamental period and its harmonics. Only fundamental periods were taken into account.

Figure 1 shows a graphic representation of a chronological series recorded on a juvenile female (97-days old) and of the observed proportions according to the number of shifts.

The χ^2, Mann-Whitney tests and Spearman's coefficient were used to compare the samples.

Results

Nycthemeral rhythms

From the 48-h records, rhythms were detected with a period of 24 h or less. Table 1 reports the mean periods obtained with respect to the biological characteristics of the animals. All the individuals studied showed a rhythm with a nycthemeral component. These

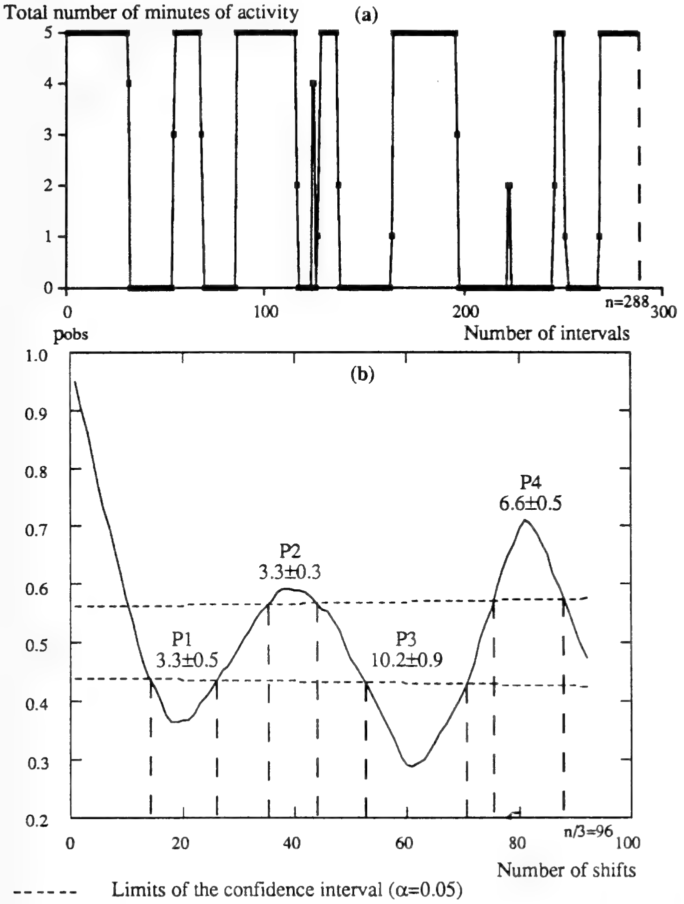

Fig. 1. Example of (a) the original chronological series (median = 5) and (b) the data analysis of the 24-h session on the 97-day-old juvenile. pobs = proportions of cases for which the values of the original and the shifted series were both below or greater than the median. All obtained ultradian periods P and standard deviations are in hours.

mean periods were between 21 and 24 hours (Tab. 1). The data obtained on a per class basis were insufficient (2 records on adult females with unweaned piglets, 6 on juveniles and 2 on adults outside the farrowing season) to test significant differences in the durations of the periods obtained.

Ultradian rhythms

From 24-h samples, only rhythms with a period of less than 12 hours could be detected. We assumed that the weaning of piglets had an influence on the rhythm of the mother. Thus the classification of animals that was used in table 2 differenciated adult females according to whether they had weaned or unweaned piglets. Ultradian rhythms (Regal and Connelly 1979) were more often observed ($n = 10$, $\chi^2 = 3.6$, $dl = 1$, $\alpha < 0.05$) in females with unweaned young and in juveniles than in other adults (including females with weaned piglets). According to our findings, the complete disappearance of the ultradian rhythm for the adult females seems to occur before the 4 h month after farrowing (Tab. 2), but an ultradian component still subsists in juveniles at the 7 h month of life.

Table 1. Mean circadian periods (in hour) and standard deviations using 48-h records.
Age or elapse of time since farrowing are noted in days (d) or in months (m).
AF: adult female; AM: adult male; J: juvenile.

Animals	Mean period
AF 35 d	21 ± 1
AF 80 d	24 ± 2.5
J 80 d	23.5 ± 4.5
J 80 d	23.2 ± 4.6
J 6 m	22 ± 2.5
J 6 m	21.1 ± 2.4
J 7 m	22.5 ± 1.5
J 7 m	22 ± 4.2
AF 130 d	22 ± 4.25
AM	24 ± 0.7

Influence of age on ultradian rhythms

Tests were made for the occurrence of significant differences in the mean ultradian periods obtained – at least when they did exist – in juveniles. The Mann-Whitney test showed that the mean periods of ultradian components of 6-month-old juveniles were significantly ($n1 = 3$, $n2 = 7$, $U = 18$, $\alpha < 0.02$) longer than those of 3-month-old juveniles. Mean period durations tended to be around 3 hours for the youngest animals, and around 6 hours for 6-month and 7-month old juveniles.

Table 2. Mean ultradian periods (in hour) and standard deviations using 24-h records. Records showing no ultradian period are also reported (/).
Age or elapse of time since farrowing are noted in days (d) or in months (m).
AF: adult female; AM: adult male; J: juvenile.

Adult females with unweaned		Juveniles		Others adults	
Animal	Mean period	Animal	Mean period	Animal	Mean period
AF 00 d	6.7 ± 1.2	J 81 d	3 ± 0.3	AF 100 d	11.6 ± 1.2
AF 00 d	0.7 ± 0.1	J 81 d	5.6 ± 0.3	AF 105 d	10.1 ± 1.5
AF 15 d	2.9 ± 0.1	J 97 d	3.3 ± 0.6	AF 120 d	–
AF 35 d	2.6 ± 0.9	J 6 d	5.7 ± 1.3	AF 130 d	–
AF 50 d	–	J 6 d	6.5 ± 0.2	AF 6 m	–
AF 51 d	6.2 ± 0.7	J 6 d	5.8 ± 1.3	AF	–
AF 65 d	2.7 ± 0.7	J 6 d	–	AM	–
AF 80 d	4.7 ± 0.5	J 7 d	6.7 ± 1.4	AM	–
AF 80 d	3.8 ± 0.8	J 7 d	6.6 ± 0.4		
AF 86 d	–	J 7 d	–		

Influence of distance from farrowing on ultradian rhythms

For the adult females, we examined the relation between the duration of the mean ultradian periods and the lapse of time since farrowing by way of Spearman's correlation (Tab. 2). Mean period duration tended to increase with the elapse of time since farrowing ($n = 10$, $Rho = 0.567$, $z = 1.709$, $\alpha < 0.05$); they were around 3 or 6 hours for females with unweaned piglets (one farrowing female excepted) and approximately 10–11 hours for females with weaned piglets.

Discussion

A nycthemeral component is typical of all studied wild boars, juveniles and adults at various stages of the reproductive cycle. The presence of such a component, regardless of the study area or the season, prompts us to envisage it as a circadian (Halberg 1959) rhythm.

The latter is commonly brought about by periodic factors in the environment, commonly called Zeitgeber (Aschoff 1957). In adult wild boars, as in many other ungulate species, sunset appears to be the principal factor involved (Mauget 1980; Niethammer and Krapp 1986; Janeau et al.1994).

In contrast to this circadian rhythm, the presence of ultradian rhythms is characteristic of the juvenile phase. The most frequently quoted hypothesis is that these ultradian rhythms are imposed by the metabolic and physiological requirements of the newborn. In contrast, Dallaire et al. (1974) and Hoppenbrouwers and Sterman (1975) estimated that the ontogenesis of the sleep rhythm in young mammals appears to be linked to the maturation of the central nervous system. In the child, de Roquefeuil et al. (1993) hypothesize that the period of the ultradian rhythm would be unstable and would tend to lengthen during individual development, sometimes progressively and sometimes by "fits and starts". Schmid et al. (1988) also state that the stabilization of distinct circadian rhythmicity is an indication that the ultradian rhythmicity, until then predominant, was superseded by nycthemeral rhythmicity.

In the same way, the rest-activity rhythm in the young wild boar could initially be represented by a primitive ultradian rhythm of the order of 3 hours and by a circadian one (this latter rhythm could be induced by maternal transfer of photoperiodic information, Horton and Stetson 1992). Progressively, through the ontogenetic processes, such as maturation of the nervous system and the disappearance of the various constraints linked to suckling, the ultradian rhythm would tend to disappear; this dissapearance would be due to an increase in the fundamental period towards its harmonics until it was superceded by the nychtemeral rhythm. Adult females which had just farrowed would recover this primitive rhythm by induction from the newborn (induction of suckling phases, Gill and Thomson 1955), or modification of their hormonal state.

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Zusammenfassung

Ontogenese des Aktivitäts-Rhythmus beim Wildschwein

Kontinuierliche biotelemetrische Aufzeichnungen am Wildschwein (*Sus scrofa* L.) unter natürlichen Bedingungen wurden zum Studium der Ontogenese des Aktivitätsrhythmus genutzt. Bei allen untersuchten Individuen, ob juvenil oder adult in verschiedenen Stadien des Reproduktionszyklus, wurde eine nychtemerale Komponente gefunden. Ultradiane Rhythmen traten bei Juvenilen sowie bei Weibchen mit Jungen auf. Sie fehlten bei adulten Bachen mit abgesetzten Jungen oder ohne Junge und bei adulten Keilern. Die gefundenen ultradianen Rhythmen hatten Perioden von circa 3 Stunden oder harmonische Schwingungen von 3 Stunden entsprechend der Distanz zum Wurftermin.

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Genetic variation of Woodland caribou (*Rangifer tarandus*) in North America

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Abstract

Polyacrylamide gel electrophoresis was used to examine genetic variation in nine wild populations of woodland caribou, *Rangifer tarandus*, in North America. Serum samples were typed for 19 presumptive loci, of which only one was variable. Eleven alleles were identified at the transferrin locus. Significant variation in allele frequencies and substructuring was found throughout the range, although relatively little genetic heterogeneity occurred within populations and most of the variation was contained between population. Geographic and genetic distance were significantly related. The endangered Selkirk population appears fixed for a single allele at the transferrin locus. To maintain the residual genetic variation in this population and to slow the rate of accumulation of inbreeding, we recommend the division of Anahim and Revelstoke populations into neighborhoods and a conservative strategy of transplants from these groups, without symmetrical exchange among populations in the western region.

Introduction

Previous attempts to conserve genetic diversity in wild mammals have generally relied on the species as the conservable unit. However it is becoming increasingly evident from the experience of ex situ propagation, that long term conservation of gene pools requires the preservation of populations from various geographic regions, whether or not these are formally or taxonomically recognized subspecies, evolutionary significant units, or populations (Ryder 1986). Spatial structuring of species has implications for both management practices and refuge design. Hence understanding the geographic distribution of genetic variation within and between populations is a fundamental prerequisite for conservation efforts.

The number of caribou (*Rangifer tarandus* L.) in North America declined in the 1800's and early 1900's because of increased hunting mortality and natural predation of some herds (Bergerud 1974). Today the woodland caribou is widely distributed below the tree line in Canada but has disappeared from the contiguous United States except for a small remnant population located in the southern Selkirk Mountains of northeastern Washington, northern Idaho, and an occasional occurrence in northwestern Montana. The Selkirk population has different habitat requirements and is distinct from other caribou in being larger, darker, and more heavily antlered. Although protected, the population does not appear to be increasing in size and has been stable at 25–30 animals since 1972 (Scott and Servheen 1985). In 1984 the Selkirk caribou herd, comprising 28 animals, was listed as an endangered species (Scott and Servheen 1984). A recovery plan was approved by the U. S. Fish and Wildlife Service, which has undertaken to augment the small, isolated

Selkirk population with animals from non-endangered herds of the same subspecies (U. S. Fish and Wildl. Serv. 1985).

Whereas several investigators have examined the genetics of European, semi-domestic and wild caribou herds (Brænd 1964; Røed 1985 b, c), with the exception of the Canadian Arctic islands (Røed et al. 1986), the genetic status of North American herds has not been explored. At present little is known about genetic variation in wild populations of woodland caribou that could guide in situ genetic management of endangered herds. We thus examined the genetic variation present in nine North American caribou populations separated by distances of 20 to 4 800 km in order to identify levels of genetic variation in caribou from the Selkirk area and compare this to the levels in other populations of woodland caribou, document potential inbreeding effects, and inspect the genetics of potential transplants.

Material and methods

Blood samples were obtained from 238 caribou belonging to eight populations in northwestern and east-central Canada, and a single population in the United States (Fig. 1). Samples were collected in the course of routine management practices from Brunette Island, 1980; George River, 1982; Labrador, 1980; Pic Island, 1980; Sasaginnigak Lake, 1980–81; Slate Island, 1979, 1980, 1982–1985; Selkirk 1985; Revelstoke, 1987, and Anahim, 1987. Blood samples were collected in heparinized tubes, transported as whole blood on dry ice, and stored at –80 °C until analyzed.

Vertical slab polyacrylamide gel electrophoresis (7% gel, tris-HCl pH 8.5) was used to type each animal at the following 19 presumptive loci: acid phosphatase (3.1.3.2), albumin, alcohol dehydrogenase (1.1.1.1), aldolase (4.1.2.13), catalase (1.11.1.6), esterase-1,2,3,4(4.2.1.11), α-globulin, β-globulin, glucose-6-phosphate isomerase (5.3.1.9), glutamate-oxaloacetic triaminase 1-2 (2.6.1.1), β-hemoglobin, isocitrate dehydrogenase (1.1.1.42), lactate dehydrogenase 1-2 (1.1.1.27), mannose-6-phosphate isomerase (5.3.1.8), nucleoside phosphorylase (2.4.2.1), phosphoglucomutase 1,2,3 (5.4.2.2), 6-phosphogluconic acid dehydrogenase (1.1.1.44), sorbitol dehydrogenase (1.1.1.14), and transferrin. Upper and lower tank electrode buffers were tris-HCl (pH 7.3) and tris-glycine (pH 8.8) respectively. Serum samples were diluted 1 : 1 with blucrose, electrophoresed at 5 °C, 38 mA for approximately 10 hours, and stained according to Harris and Hopkinson (1976). Transferrins were stained with Coomassie Brilliant Blue R250 general protein stain overnight, destained in 11% acetic acid, and the mobilities of transferrin bands scored relative to two known standards.

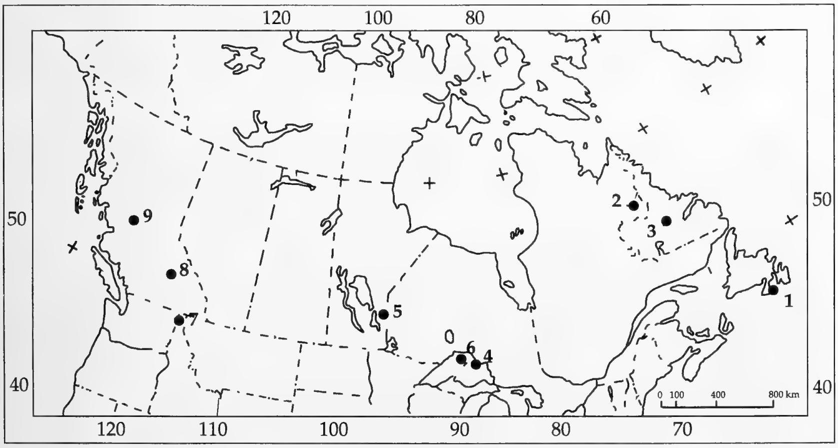

Fig. 1. Locations of nine North American *Rangifer tarandus* L. populations sampled in three regions. East: 1. Brunette Island; 2. George River; 3. Labrador, Central: 4. Pic Island; 5. Sasaginnigak Lake; 6. Slate Island, West: 7. Selkirk; 8. Revelstoke; 9. Anahim Lake.

Hierarchical analysis of population differentiation (F-statistics) was performed using the formulation of Wright (1965) as modified by Nei (1977). Chi-square contingency tables were used to determine whether populations were in Hardy-Weinberg equilibrium, and the genetic distance between each pair of populations was calculated from allelic frequency data (Rogers 1972). These data were summarized in a distance dendrogram constructed using the unweighted pair group method based on arithmetic averages (UPGMA; Sneath and Sokal 1973). The association of the matrices of genetic distance and linear, geographic distance between populations was tested using the general regression method of Mantel (1967). Changes in allele frequency of the Slate Island population over a 6-year period were analyzed by normalising the distribution (squared and arcsine transformed) and performing ANOVA using the different alleles as replicates within years.

Results

Eighteen of the loci examined were monomorphic, but the transferrin locus was highly variable with 11 alleles. Table 1 shows the allele frequencies, and heterozygosity for each population. The most common alleles were E and C for most populations. The number of alleles per population ranged from one in the Selkirk population, which appears fixed for the C allele (n = 3), to 10 in the Labrador population (n = 37; mean = 4.78). Only three of the 11 transferrin alleles were found in the British Columbia area. Woodland caribou from eastern portions of their range exhibit higher levels of polymorphism (11 alleles) and greater mean heterozygosity at the transferrin locus than do those in the west (0.50 and 0.27 respectively). All but one of the heterozygotes in the Anahim Lake and Revelstoke areas had the A_2 allele, and all of the calves (n = 5) examined from the Anahim Lake area were homozygous for the A_2 allele.

Chi square test for adherance to Hardy-Weinberg predicted frequencies (Tab. 1) indicated that the Anahim and Revelstoke populations are in Hardy-Weinberg proportions. Brunette Island, Sasaginnigak Lake, and Pic Island populations appear to conform to expectations but small sample size precludes adequate statistical testing. Slate Island ($X^2 = 36.36$, $p \leq 0.001$), Labrador ($X^2 = 12.69$, $p \leq 0.01$) and George River ($X^2 = 22.70$, $p \leq 0.001$) herds deviated significantly from Hardy-Weinberg.

Rogers' (1972) coefficients of genetic similarity (S), and distance (D), were calculated for all paired combinations of the nine populations (Tab. 2). The mean value of S was 0.5066 (range 0.125 to 0.862) and the mean D was 0.4934 (range 0.138 to 0.875). Genetic distance was greatest between the Brunette Island and Selkirk populations (0.875) and smallest between the George River and Labrador populations (0.138; Fig. 2). Predictably the Selkirk population is more similar to the Revelstoke herd (S = 0.644) than to the

Table 1. Transferrin allele frequencies (A_1–H) and heterozygosity (*H*) for nine north American *Rangifer tarandus* populations. Genotypes for three populations deviate significantly from Hardy–Weinberg, ** $0.05 < P \leq 0.01$; *** $0.01 < P \leq 0.001$. (Selkirk not tested due to small sample size). n = sample size.

Population	n	A_1	A_2	B	C	D_1	D	E_1	E	F	G	H	*H*
Brunette Island	8	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.87	0.00	0.00	0.00	0.25
George River***	46	0.04	0.15	0.24	0.03	0.00	0.20	0.02	0.28	0.04	0.00	0.00	0.74
Labrador**	37	0.03	0.08	0.15	0.03	0.05	0.30	0.00	0.19	0.08	0.05	0.04	0.51
Pic Island	4	0.00	0.13	0.25	0.25	0.00	0.00	0.00	0.37	0.00	0.00	0.00	0.75
Sasaginnigak Lake	5	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.30	0.00	0.20	1.00
Slate Island***	104	0.00	0.06	0.15	0.13	0.00	0.03	0.03	0.43	0.02	0.01	0.14	0.53
Selkirk	3	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Revelstoke	12	0.00	0.33	0.00	0.63	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.43
Anahim Lake	19	0.00	0.50	0.00	0.11	0.00	0.39	0.00	0.00	0.00	0.00	0.00	0.37

Table 2. Matrix of paired comparisons of ROGERS' (1972) genetic similarity (above diagonal) and genetic distance (below diagonal) between all pairs of nine north American populations of *Rangifer tarandus.*

Population	1	2	3	4	5	6	7	8	9
1 Brunette Island	****	0.506	0.447	0.585	0.280	0.648	0.125	0.249	0.234
2 George River	0.494	****	0.862	0.770	0.502	0.804	0.243	0.473	0.604
3 Labrador	0.553	0.138	****	0.686	0.524	0.722	0.256	0.473	0.637
4 Pic Island	0.415	0.230	0.314	****	0.547	0.834	0.375	0.559	0.490
5 Sasaginnigak Lake	0.720	0.498	0.476	0.453	****	0.535	0.564	0.641	0.412
6 Slate Island	0.352	0.196	0.278	0.166	0.465	****	0.294	0.475	0.474
7 Selkirk	0.875	0.757	0.744	0.625	0.436	0.706	****	0.644	0.223
8 Revelstoke	0.751	0.527	0.527	0.441	0.359	0.525	0.356	****	0.540
9 Anahim Lake	0.766	0.396	0.363	0.510	0.588	0.526	0.777	0.460	****

more geographically distant Anahim herd (S = 0.223) although there has been no recorded migration between these herds this century.

MANTEL matrix correlations (MANTEL 1967) indicated a significant correlation between the matrices of linear, geographic distance and ROGERS' genetic distance ($P = 0.004$; $r = 0.551$), suggesting that greater genetic divergence is associated with increased separation distance.

Hierarchical analysis of population differentiation indicates that considerable genetic heterogeneity exists among populations (Tab. 3). The total gene diversity at the transferrin locus was 36.9% with most of this attributable to between population variability. Within population variability is relatively low (9%). Regional subdivision of the total into western, central and eastern regions indictated that less than 10% of the variability is contained between regions ($F_{IT} = 0.2625$ and $F_{IS} = 0.1811$).

Microgeographic division of populations within the western region (viz. Anahim, Revelstoke, and Selkirk) indicated substantial differentiation of at least one of these populations ($F_{ST} = 0.3676$). Although most of the variation in this region is between populations, there is also substantial variation within populations (27%). In the central region, most of the variation is between populations (12%), but in comparison to east and particularly

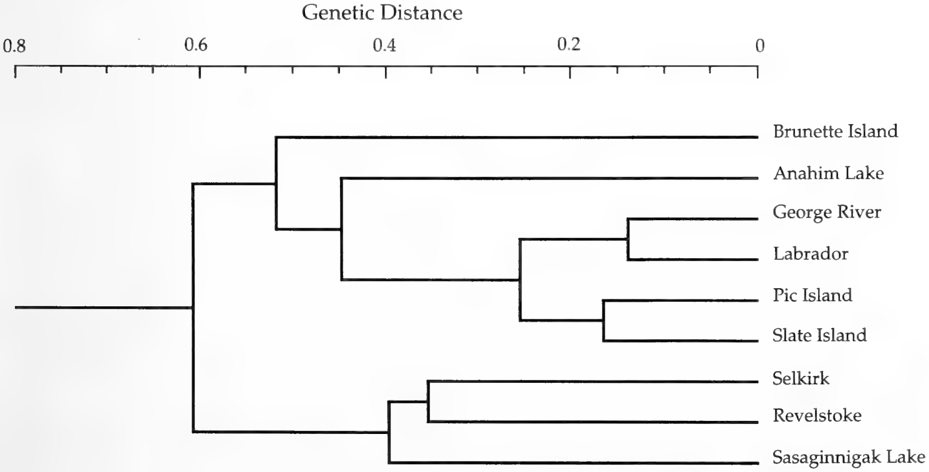

Fig. 2. Distance phenogram of nine populations of *Rangifer tarandus* clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient is 0.785.

Table 3. Hierarchical F-statistics (Wright 1978) for nine *Rangifer tarandus* populations within three regions of north America and when data for animals from all regions were combined. Significance of the F_{ST} values was determined by Chi-square and is indicated by asterisks, *** $P \leq 0.001$.

	F_{ST}	F_{IS}	F_{IT}	X^2	d.f.
Within regions					
West	.3676	.2728	.5401	249.94***	20
Central	.1245	–.0899	.0458	281.42***	20
East	.1690	.1892	.3254	307.54***	20
Between regions	.0995	.1811	.2625	473.41***	20
Total	.3070	.0906	.3698	1461.23***	80

western regions, such differentiation is relatively low. In the east almost 17% of the variation is between the populations, with 19% within populations, and the largest proportion within individuals with respect to the region.

Although there were differences in the alleles present each year, ANOVA indicated no significant changes in allele frequencies for Slate Island over a 6-year period.

Discussion

Caribou populations in North America are characterized by low levels of genetic polymorphism but relatively high heterozygosity. Polymorphism (0.053) is less than half that of previously reported values (0.24 to 0.28; Røed 1985b) and low even in comparison with isolated, island forms (0.11; Storset et al. 1978). However the average heterozygosity of 0.027 over 19 loci compares favorably with that for Swedish and Alaskan caribou (0.014 ($n = 20$) and 0.000 ($n = 4$) respectively; Baccus et al. 1983).

There is substantial variation at the transferrin locus in the nine populations of caribou investigated. These populations have between one and 10 transferrin alleles, with two of the island populations among the least variable. This is concordant with the findings for animal species in general (Selander 1976), as well as for other subspecies and populations of caribou. In the latter case estimates range from two to 18 (Storset et al. 1978; Røed and Whitten 1986). Maxima of 12, 13, and 18 alleles have been reported for populations in Norway, the Soviet Union, and Alaska, respectively (Shubin and Matyokov 1982; Røed 1985a; Røed and Whitten 1986), making transferrin a potential indicator locus for monitoring genetic changes in this species.

Hierarchical F-statistics indicate that considerable genetic divergence has occurred among caribou populations within restricted geographical areas, with relatively little differentiation between the three major geographic regions. The average differentiation among populations is approximately 31% ($F_{ST} = 0.3070$; Tab. 3) which is higher than that of moose from different Scandinavian countries (9%; Ryman et al. 1980), and an order of magnitude greater than that reported for semi-domestic reindeer herds ($F_{ST} = 0.029$; Røed 1985c). The particularly high level of differentiation noted within the western region is attributable to the fact that the Anahim population occurs on the plateau of a separate mountain range from that of the Selkirk and Revelstoke populations.

Stochastic processes such as genetic drift may play a substantial role in differentiating these populations. If migration between populations acts simply to counterbalance genetic drift then the number of caribou dispersing from different populations may be estimated by $N_em = (1/4) F_{ST} - 0.25$ (e.g., Ryman et al. 1980). For caribou in this study this implies that less than one individual (–0.17) need migrate per generation in order to maintain the current level of genetic differentiation among all populations. The discrepancy between levels of variability in transferrin and the other loci investigated suggests that there may be significant selection on the transferrin locus, and there is some evidence that balancing selection maintains transferrin variation in caribou (RØED 1987).

Significant deviation from Hardy-Weinberg proportions was noted for Slate Island, Labrador, and George River populations. A significant WAHLUND effect (WAHLUND 1928) may be implicated for the latter populations. The George River population is large and migratory, with extensive calving grounds in Labrador, which potentially overlap the region from which the Labrador sample was derived. Additionally, the insular Slate population may be subject to strong selection pressures from maritime weather that ices vegetation (SKOOG 1968), and from extremely high population density (BERGERUD 1980).

A significant association was found between linear, geographic distance, and ROGERS' genetic distance, indicating that those populations separated the farthest geographically were also the most genetically divergent. This isolation by distance effect was apparent despite the inclusion of three insular populations. The genetic distance values for these nine populations are high compared to those reported between subspecies of caribou (0.045; RØED 1985 a), but are consistent with expectations based on direct observation of dispersal and mating patterns. Woodland caribou have a polygynous breeding structure (BANFIELD 1974), which lowers the effective population size and enhances genetic differentiation between groups. The large distance between some populations is responsible for limited gene flow among them, but genetic exchange may result in similar variation at adjacent populations (cf. George River and Labrador). In some cases, gene flow between adjacent populations occurs only under specific climatic or social conditions. For example, Pic and Slate populations, although insular, have one of the lowest genetic distance values measured, presumably because they are close enough to allow exchange of animals across the ice in winter (BERGERUD 1985). Additional opportunities for exchange of individuals occur during three periods of annual concentration, and when the paths of grazing bands cross.

There is evidence to suggest that movement restrictions on herds has profound effects on the genetic variability of wild and semi-domestic caribou herds (BRÆND 1964; RØED 1985 b), and extinction rates of insular populations (BERGERUD 1985). Such restriction would accentuate pre-existing levels of genetic differentiation and be particularly significant if, as it appears, caribou populations exhibit microspatial genetic heterogeneity. The latter is indicated by a deficiency of heterozygotes in the Svalbard caribou, and by the occurrence of different populations in different regions of the Nordenskold Land area (RØED 1985 c).

Woodland caribou from the Selkirk herd appear to be homogeneous at the transferrin locus. Possible explanations include inbreeding, a founder effect, or small and biased sampling (n = 3 representing 11% of the population). There are striking genetic differences between populations within the western caribou region. About 37% of the total genetic variance is explained by differences between populations. This is consistent with behavioral studies in British Columbia that indicate relatively restricted movement and philopatry of females to their calving locations (HATLER 1982, 1985). No inbreeding is indicated within the Anahim Lake or Revelstoke herds although some genotypes are not in expected proportions. Genotypes of Anahim calves suggest that either the breeders are a non-random subset of the population or a biased sample was obtained. If the sample of calves from Anahim Lake is representative then the subsequent generation may have greatly reduced genetic variation.

Extreme caution is advisable in making management recommendations based on a single variable locus, particularly one which may be under some form of selection. However the precarious situation of the small Selkirk population justifies some generalisations regarding the probable short and long term outcomes of genetic management of the region. Much will depend on the strength of the caribou social system. According to Calef (1981), there is a high degree of plasticity in the behavior of caribou within subspecies, such that populations vary in behavior and appearance depending on their habitat and degree of isolation from other populations. If polygynous breeding is common in woodland caribou then genetic variation within herds will be lost more rapidly, whereas genetic divergence among herds will accrue more rapidly than predicted.

If indeed the low rate of population increase indicates that inbreeding has accumulated in the Selkirk population, then the first goal is to alleviate this as quickly as possible. The apparent polygynous breeding structure and relatively large harem size of the woodland caribou would enable such a reduction to occur rapidly. In the short term, transplants from Anahim and Revelstoke should reduce inbreeding and retain alleles of the Selkirk herd, thus preserving what little variation exists.

Exchange of individuals among a limited number of small populations such as in the western region may not be adequate to maintain genetic variation in the long term. While it may slow the accumulation of inbreeding, it does not alleviate the probable loss of fitness indefinitely. A higher coefficient of relationship would result among all individuals of all populations and inbreeding would increase along with a loss of alleles. The rate of accumulation of inbreeding may be slowed by avoiding symmetrical exchange amongst populations and by dividing the populations into neighborhoods with a rate of exchange between them (Chesser 1983). Similarly, if a species regularly undergoes cycles of inbreeding and outbreeding, a high degree of relatedness among individuals within breeding units will minimize loss of genetic variability overall, as units will be fixed for different alleles. Were genetic management paramount, this might be achieved by avoiding, or intermittently adopting, ungulate predator management to create population fluctuations and cycles of greater or lesser inbreeding in the western region.

The success of such in situ management of confined populations is difficult to predict in small, natural populations where stochastic processes predominate. Observation of natural movements (Ferguson 1982; Bergerud and Elliot 1986) and introductions to the Svalbard population (Røed 1985 c) have demonstrated that ecological and behavioral isolation may limit the potential contribution of transplanted animals. However given the increasing environmental pressures on the Selkirk population and the paucity of information regarding fitness determination in large mammals, conservation of the current level of genetic variation is prudent.

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Zusammenfassung

Genetische Variabilität beim Karibu (Rangifer tarandus) in Nordamerika

Die genetische Variabilität von neun nordamerikanischen Populationen des Waldkaribu (*Rangifer tarandus*) wurde mittels Polyacrylamidgel-Elektrophorese untersucht. Serumproben wurden auf genetische Variation an 19 auswertbaren hypothetischen Genloci geprüft, wobei sich am Transferrinlocus ein Polymorphismus für 11 Allele nachweisen ließ. Es zeigten sich signifikante Unterschiede in den Allelhäufigkeiten und ein hoher Anteil der genetischen Variabilität entfiel auf die genetische Differenzie-

rung zwischen den Populationen. Die genetischen Distanzen waren mit den geographischen Abständen signifikant korreliert. In der bedrohten Population von Selkirk scheint am Transferrinlocus ein Allel fixiert zu sein. Um die noch verbliebene genetische Variabilität in diesem Bestand zu erhalten und den Anstieg des Inzuchtgrades zu verringern, empfehlen wir die Aufteilung der Populationen von Anahim und Revelstoke in „Nachbarschaften". Eine kontrollierte Einbringung von Individuen dieser Gruppen nach Selkirk ohne symmetrischen Austausch zwischen den Populationen der westlichen Region erscheint angezeigt.

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The chromosomes of *Gazella bennetti* and *Gazella saudiya*

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Abstract

Seven individuals of captive *Gazella bennetti* were found to have chromosomal complements of 2n = 49–52, and seven captive *G. saudiya* had complements of 2n = 46–53. G-banded karyotypes revealed that variation in diploid number was the result of an autosome-to-X chromosome translocation and four independent Robertsonian translocations. There were no fixed chromosomal differences between *G. bennetti* and *G. saudiya*, but two pericentric inversions distinguished Pakistani *G. bennetti* from Iranian *G. bennetti* and *G. saudiya*. Several pairs of metacentric chromosomes of both species were monobrachially homologous with metacentrics of *G. dorcas* and *G. gazella*, indicating *G. bennetti* and *G. saudiya* are reproductively isolated from *G. dorcas* and *G. gazella*. As with other species of gazelles, chromosomal studies of natural populations are needed for these species.

Introduction

Gazelles (genus *Gazella*) occur in arid and semi-arid habitats from northern Africa to central Asia. Sixteen species make *Gazella* one of the most diverse genera of artiodactyls (Grubb 1993). Ability to exploit a variety of niches in a stressful environment with few competitors has enhanced the radiation of gazelles. As a result of their diversification, the taxonomy of gazelles is complicated and uncertain (Groves 1988), particularly with regard to the Indian gazelle, *G. bennetti*, and the Saudi gazelle, *G. saudiya*. Ellerman and Morrison-Scott (1951) considered *bennetti* a subspecies of the mountain gazelle, *G. gazella*, and *saudiya* was treated as a subspecies of the dorcas gazelle, *G. dorcas*. Based on skull measurements, both *bennetti* and *saudiya* were placed with *G. dorcas* by Groves (1969) and Lange (1972). More recently, *G. bennetti* and *G. saudiya* have been recognized as distinct species (Groves 1988).

Chromosomal data suggest that *bennetti* and *saudiya* are not conspecific with *G. gazella* or *G. dorcas*. The chromosomal complements of *G. dorcas* and *G. gazella*, respectively, are 2n = 30, 31 (♀, ♂) and 2n = 34, 35 (Hsu and Benirschke 1967/77; Wurster 1972, Wahrman et al. 1973; Effron et al. 1976; Kingswood and Kumamoto 1988; Vassart 1994). Previous investigations have found chromosomal complements of 2n = 50, 51 in *G. bennetti* (Furley et al. 1988) and 2n = 47, 50–51 in *G. saudiya* (Rebholz et al. 1991). These investigations presented nondifferentially-stained karyotypes and, in the case of *G. bennetti*, C-banded chromosomes. With G-banding however, it is possible to determine the extent of chromosomal homology between taxa. The present cytogenetic study documents nondifferentially-stained, C-banded, and G-banded karyotypes of captive *G. bennetti* and *G. saudiya*. These data are compared with G-banded karyptypes of *G. dorcas* and *G. gazella* in order to delineate chromosomal relationships among these four gazelles.

Material and methods

Seven specimens of *G. bennetti* (5♀♀, 2♂♂), seven *G. saudiya* (5♀♀, 2♂♂), two *G. dorcas* (2♂♂), and two *G. gazella* (1♀, 1♂) were examined, all of them belonging to captive populations at Al-Areen Wildlife Park (Bahrain), Al-Wabra (Qatar), and King Khalid Wildlife Research Center (Saudi Arabia). Origins of the *saudiya* individuals were uncertain, but they were likely from an introduced island population off the northern coast of Qatar that was established with animals from different locales on the mainland (F. Al-Timimi, pers. comm.; East 1992). The *bennetti* specimens apparently originated from Iran and Pakistan, but their exact geographic origins were unknown. The *dorcas* individuals were apparently from Sudan, but origin of the *gazella* specimens were unknown.

Specimens of the four gazelle taxa were phenotypically distinguishable on the basis of characteristics described by Groves (1988). Horns of the *bennetti* and *saudiya* were long, straight and well-formed in both sexes while horns of the *dorcas* and *gazella* were shorter by comparison. The male Indian gazelles differed from the Saudi gazelles by having horns that were distinctly ringed. Horns of the dorcas gazelles were S-shaped and curved inward at the tips; horns in the male mountain gazelle were stout but were delicate in the female. Pelage characteristics included differences in the development of body and facial stripes. Body markings were nearly absent in the specimens of *saudiya*, poorly developed in the *bennetti* (both body and facial stripes), a poorly marked flank stripe but well-marked facial stripes in the *dorcas*, and well-marked flank and facial stripes in the *gazella*.

Heparinized whole blood (5–10 ml) and/or skin biopsies (ca. 5 mm^2) were collected for cell culture and transported to the Conservation Genetics Laboratory of the Zoological Society of London. Short-term lymphocyte culture followed a modified technique of Moorhead et al. (1960) and Wiley and Meisner (1984) using pokeweed mitogen (0.3 ml) and co-mitogen phorbol 12-myristate 13-acetate-4-0-methyl ether (final concentration 6 mcg/ml). Blood cultures were harvested at 94 h and after a 1 h exposure to colcemid (final concentration 0.025 mcg/ml). Skin biopsies were processed for fibroblast cell culture using a collagenase-disaggregation technique. Cell harvest followed the general protocol for monolayer cultures (Barch 1991). At peak mitotic activity, monolayer cultures were exposed to colcemid (final concentration 0.025 mcg/ml) for 10–30 min, and cells were then exposed to 0.075 M KCl for 10 min prior to fixation of cells.

G-band, C-band, and nondifferentially-stained preparations were prepared from the mitotic cell harvests. G-banding followed Verma and Babu (1989), and C-banding followed Sumner (1972). Because of the difficulty in comparing G-band homologies between taxa without a standardized nomenclature, G-banded chromosomes were numbered according to the standard karyotype of cattle, *Bos taurus*, presented by Ford et al. (1980) and Iannuzzi (1990). Gallagher and Womack (1992) demonstrated extensive arm homologies among several species of bovids using the cattle standard. Because chromosome-arm homologies between the karyotypes of gazelles and cattle were extensive, we referenced gazelle chromosomes strictly by cattle homology to facilitate comparisons between our specimens. (Note: chromosome 3 of *B. taurus* differed from chromosome 3 of the gazelles by a paracentric inversion.) Thus, assignment of different numbering systems to the karyotypes of each species was avoided. Robertsonian fusions that were polymorphic are indicated in parentheses to distinguish them from fusions that were fixed.

Results

The chromosomal complement of *G. saudiya* was 2n = 46–53, and *G. bennetti* was 2n = 49–52 (Tab. 1). All specimens possessed an autosome-to-X translocation; thus, one element of pair 5 occurred as an additional acrocentric autosome in males (Figs. 1, 2). Four independent Robertsonian (Rb) translocations were polymorphic in *saudiya* with seven different karyotypic configurations. Three independent Robertsonian translocations were polymorphic in Iranian *bennetti* while Pakistani *bennetti* was polymorphic only for Rb(8;14). Pakistani specimens could also be distinguished from *saudiya* and Iranian *bennetti* by two pericentric inversions in the small autosomal pairs 22 and 25. The difference

Table 1. Summary of chromosomal data for *G. saudiya* and *G. bennetti*

Case no.	Sex	2n	NAA	(4;12)	(8;14)	(9;23)	(11;17)	22	25
G. saudiya									
8 349	♀	46	60	X	XX	X	XX	m	m
8 348	♀	48	60	–	XX	X	X	m	m
8 358	♀	49	60	–	XX	X	–	m	m
8 346	♂	49	61	–	X	X	XX	m	m
8 350	♀	50	60	X	–	X	–	m	m
8 347	♀	50	60	–	X	X	–	m	m
8 351	♂	53	61	–	–	–	–	m	m
G. bennetti (Iran)									
8 339	♂	49	61	–	XX	X	X	m	m
8 338	♀	52	60	–	–	–	–	m	m
G. bennetti (Pakistan)									
8 342	♀	50	56	–	XX	–	–	a	a
8 340	♀	51	56	–	X	–	–	a	a
8 344	♀	51	56	–	X	–	–	a	a
8 345	♀	51	56	–	X	–	–	a	a
8 341	♂	52	57	–	X	–	–	a	a

2n = diploid number, NAA = autosomal arm number, (4;12), (8;14), (9;23) and (1;17) = Robertsonian translocations, 22 and 25 = autosomal pairs rearranged by pericentric inversion, XX = translocation homozygous, X = translocation heterozygous, – = translocation not carried, m = metacentric, a = acrocentric

in autosomal arm number between the two groups was due to metacentric versus acrocentric forms of pairs 22 and 25 in Iranian and Pakistani specimens, respectively. The inversion polymorphisms were difficult to detect in G-banded karyotypes because of the small size of the chromosomes, but were obvious in nondifferentially-stained and C-banded karyotypes.

Taking the various rearrangements into account, comparison of G-bands among the 14 specimens of *bennetti* and *saudiya* revealed consistent band patterns (Figs. 1, 2), and 17 chromosomal pairs were homologous (Tab. 2). Autosomes were G-band negative around the centromere, corresponding to lightly-stained C-band positive regions. Acrocentric autosomes of both taxa had tiny p-arms (short arms) and size polymorphisms were evident in some of the pairs; particularly in pairs 1, 3, 7, and 18. Autosomes exhibited pericentromeric heterochromatin, but the degree to which they stained for heterochromatin was not consistent. The X chromosomes of *bennetti* and *saudiya* were large submetacentric elements with identical G-banding patterns and autosome 5 fused to the q-arm (long arm) of the X chromosome. The short arm of the X was polymorphic in size and was heterochromatic. The Y chromosomes of both taxa were submetacentric with identical G-banding patterns, and they appeared heterochromatic by C-banding. Taking into account chromosomal differences between males and females, the karyotypes of a male Iranian *bennetti* (2n = 49, case no. 8 339) and a female *saudiya* (2n = 48, case no. 8 348) were identical, as were the karyotypes of a female Iranian *bennetti* (2n = 52, case no. 8 338) and a male *saudiya* (2n = 53, case no. 8 351) (Figs. 1, 2).

Comparison of G-banded karyotypes of *bennetti* and *saudiya* with those of *dorcas* and *gazella* (Fig. 3), indicated autosome 5 was the only element unchanged among the four taxa (Tab. 2). Chromosome 5 was involved in the autosome-to-X translocations of all four species. Rb(8;14) was polymorphic in *bennetti* and *saudiya* but was fixed in *dorcas* and *ga-*

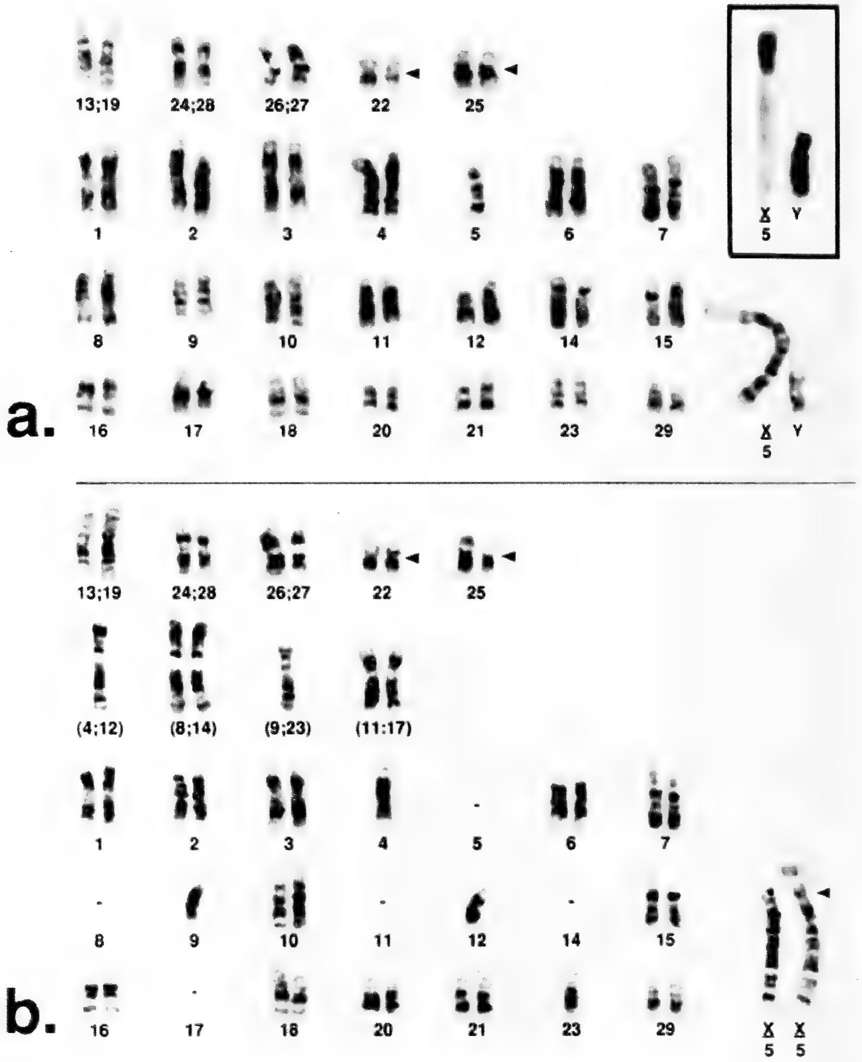

Fig. 1. G-banded karyotypes of *G. saudiya*: *a*–male 2n = 53 (case no. 8 351); *b*–female 2n = 46 (case no. 8 349). Boxed inset: C-banded sex chromosomes. Arrowhead indicates centromere position.

zella. Pairs 20, 21, and 29 were conserved among *bennetti*, *saudiya*, and *gazella* but were rearranged in *dorcas*. Between *bennetti*/*saudiya* and *dorcas*/*gazella*, all other chromosomes were rearranged. There were 9 monobrachially homologous metacentrics among *bennetti* and *gazella*, 10 among *bennetti* and *dorcas*, 11 among *saudiya* and *gazella*, and 12 among *saudiya* and *dorcas*. Ten metacentric pairs and one acrocentric pair were conserved between the karyotypes of *dorcas* and *gazella* (Tab. 2). These two species were distinguishable from each other by one Robertsonian translocation (Rb 20;29) and three monobrachially homologous metacentrics in *dorcas* (2;24, 21;23, and 25;28) and two in *gazella* (2;25 and 23;24). Acrocentric chromosome 28 in *gazella* was single-arm homologous to *dorcas* metacentric 25;28.

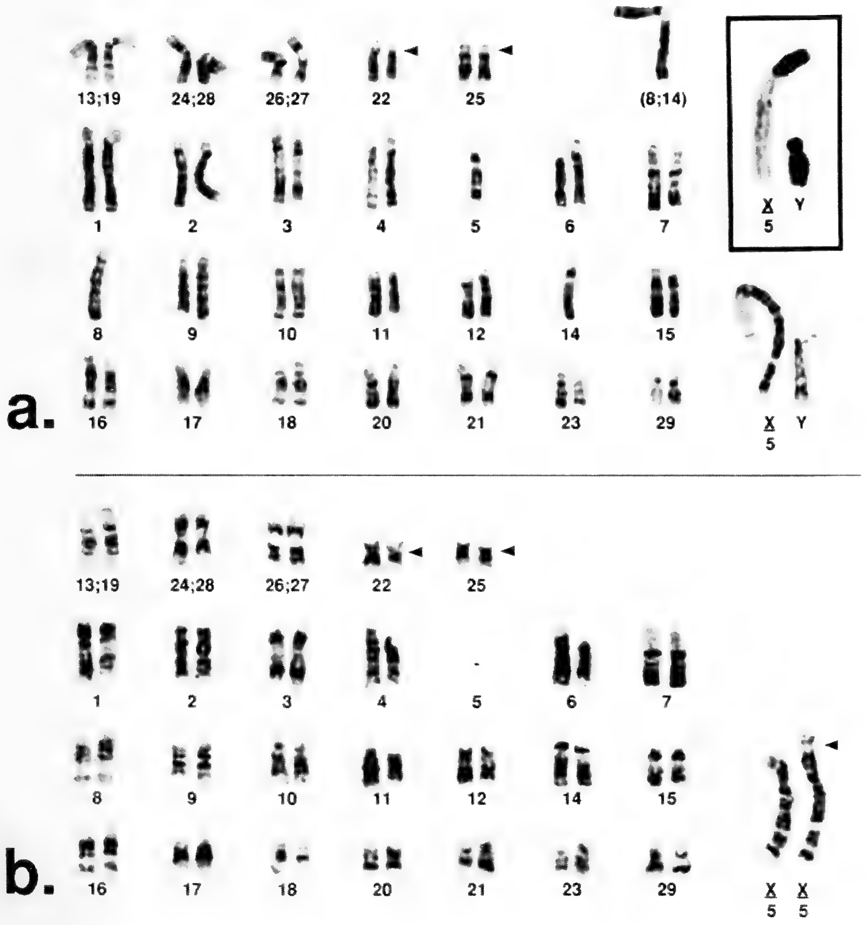

Fig. 2. G-banded karyotypes of *G. bennetti*: *a*–male 2n = 52 (case no. 8341); *b*–female 2n = 52 (case no. 8338). Boxed inset: C-banded sex chromosomes. Arrowhead indicates centromere position.

Table 2. Conserved and rearranged autosomes for *G. saudiya*, *G. bennetti*, *G. gazella*, and *G. dorcas*

	G. saudiya		*G. bennetti*		*G. gazella*		*G. dorcas*
CONSERVED AUTOSOMES	5	=	5	=	5	=	5
	(8;14)	=	(8;14)	=	8;14	=	8;14
	20	=	20	=	20		–
	21	=	21	=	21		–
	29	=	29	=	29		–
	1	=	1		–		–
	2	=	2		–		–
	3	=	3		–		–
	6	=	6		–		–
	7	=	7		–		–
	10	=	10		–		–
	15	=	15		–		–
	16	=	16		–		–
	18	=	18		–		–
	20	=	20		–		–
	(9;23)*	=	(9;23)*		–		–
	(11;17)*	=	(11;17)*		–		–
	13;19*	=	13;19*		–		–
	24;28*	=	24;28*		–		–
	26;27*	=	26;27*		–		–
	–		–		1;10	=	1;10
	–		–		3;27	=	3;27
	–		–		4;7	=	4;7
	–		–		6;19	=	6;19
	–		–		9;12	=	9;12
	–		–		11;18	=	11;18
	–		–		13;15	=	13;15
	–		–		16;22	=	16;22
	–		–		17;26	=	17;26
REARRANGED AUTOSOMES							
Pericentric inversions	22	inv	(22)		–		–
	25	inv	(25)		–		–
Robertsonian translocation	(4;12)*	Rb	4 and 12		–		–
	–		–		–	Rb	20;29
Monobrachial homologs	–		–		2;25		2;24
	–		–		23;24		21;23
	–		–		28		25;28

Autosomes in parentheses were polymorphic. Metacentric autosomes of *G. saudiya* and *G. bennetti* that were monobrachially homologous with metacentrics of *G. gazella* or *G. dorcas* are marked with an asterisk.

While the sex chromosomes of *bennetti* and *saudiya* were identical, differences were found between those of *dorcas* and *gazella*. The X chromosome of *gazella* was a large submetacentric with autosome 5 fused to the distal end, but a small pericentric inversion differentiated it from the X of *bennetti* and *saudiya*, such that in *gazella*, a G-band positive band appeared in the p-arm adjacent to the centromere (Fig. 3 b). Like *bennetti* and *saudiya*, the Xp of *gazella* was polymorphic in size and entirely heterochromatic, however, in *gazella* a single light interstitial C-band positive band was apparent on the Xq (Fig. 3 b). The X chromosome of *dorcas* was a large acrocentric element, homologous to Xq of *bennetti* and *saudiya*. The pericentromeric region of the *dorcas* X was C-band positive (Fig. 3 a). The Y chromosome of *dorcas* was a tiny metacentric element.

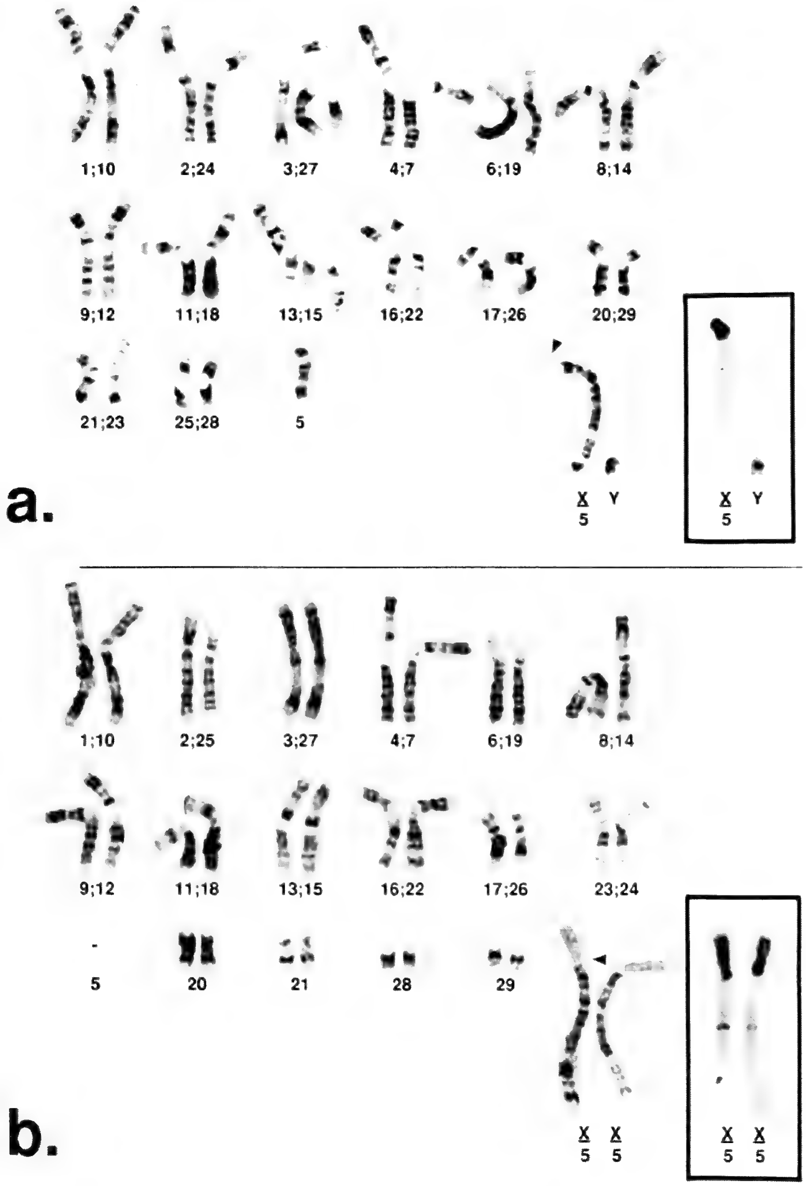

Fig. 3. *a*–G-banded karyotype of a male *G. dorcas* 2n = 31 (case no. 8 334); *b*–G-banded karyotype of a female *G. gazella* 2n = 34 (case no. 8 319). Boxed insets: C-banded sex chromosomes. Arrowhead indicates centromere position.

Discussion

Chromosomal complements of 2n = 49–52 in *G. bennetti* and 2n = 46–53 in *G. saudiya* found in this study are consistent with previous reports of 2n = 50, 51 and 2n = 47, 50–51, respectively, for the two species (Furley et al. 1988; Rebholz et al. 1991). It is worth noting that none of the gazelles karyotyped here were the same individuals as described in the previous reports. These data contrast remarkably with complements of 2n = 30, 31 in *G. dorcas* and 2n = 34, 35 in *G. gazella* (Hsu and Benirschke 1967/77; Wurster 1972; Wahrman et al. 1973; Effron et al. 1976; Kingswood and Kumamoto 1988; Vassart 1994). Despite the chromosomal differences, the autosome translocated to the X chromosome is the same element in all four taxa and in seven other species of gazelles, as well as in *Antilope cervicapra* (Vassart 1994), suggesting the autosome-to-X translocation occurred only once during the evolution of gazelles.

G-banded karyotypes demonstrate extensive monobrachial homology between metacentric chromosomes of *bennetti* and *saudiya* on the one hand, and *dorcas* and *gazella* on the other. Monobrachial centric fusions are believed to have been fundamental in the chromosomal evolution of gazelles and other bovid taxa (Effron et al. 1976; Gallagher and Womack 1992) and are thought to effect reproductive isolation (Baker and Bickham 1986). The extent to which multiple Robertsonian rearrangements potentially reduce fertility and effect reproductive isolation has been demonstrated in gazelles. Wahrman et al. (1973) reported that when captive *dorcas* and *gazella* hybridized, male offspring were sterile and female hybrids had reduced fertility. Five metacentric pairs were monobrachially homologous among the *dorcas* and *gazella* in our study. Although we have no direct information regarding the consequences of crossing either *bennetti* or *saudiya* with *dorcas* or *gazella*, the monobrachial rearrangements distinguishing their karyotypes indicate they are reproductively isolated. Thus, chromosomal data support the suggestion by Groves (1988) that *bennetti* and *saudiya* are not conspecific with either *dorcas* or *gazella*.

While cytogenetic data clearly indicate that neither *bennetti* nor *saudiya* are conspecific with *dorcas* or *gazella*, chromosomal differences between *bennetti* and *saudiya* are less obvious. The only chromosomal rearrangement that could be used to distinguish *bennetti* from *saudiya* was the 4;12 translocation carried by two specimens of *saudiya*. If specimens of *saudiya* did not carry the 4;12 translocation, however, karyotypic differences between individual specimens were not definitive for either taxon. Taking into account chromosomal differences between females and males, G-banded karyotypes of two specimens of *bennetti* could not be distinguished from those of two *saudiya*. There were no fixed chromosomal differences between *bennetti* and *saudiya* and, more importantly, there were no monobrachial homologues. Thus, our data indicate that *bennetti* and *saudiya* are not cytogenetically distinct. This finding is consistent with the review of Corbet (1978), insofar as both taxa have been regarded as subspecies of *dorcas*, and the suggestion by Furley et al. (1988) that *bennetti* and *saudiya* might form a taxonomic complex.

The uncertain geographical origin of our panel of specimens makes it difficult to draw conclusions about taxonomic relationships between *bennetti* and *saudiya*. Based on differences between the karyotypes of three specimens of *saudiya* (2n = 47, 50, and 51), Rebholz et al. (1991) suggested that their group might have represented hybrids. Our panel of *saudiya* did not include individuals studied by Rebholz et al. (1991), but it represented the same captive populations (Al-Areen Wildlife Park and King Khalid Wildlife Research Center). Just as in the earlier study, the karyotypes of all seven *saudiya* in our study were different from each other. If hybridization with *bennetti* occurred, as a result of mixing both taxa on an island or in captivity, it may be that historical populations of *saudiya* had chromosomal numbers closer to 2n = 46 and 47 than to the 2n = 49–52, and possibly 53, of *bennetti*. On the other hand, Benirschke et al. (1984) raised the possibility that the karyotypic variability (three independent Robertsonian polymorphisms) observed in captive

G. soemmerringi might not be the result of hybridization with related species but may, instead, be correlated with different subspecies. Thus, the possibility cannot be ruled out that chromosomal polymorphisms occurred naturally in different populations of *saudiya*.

Questions regarding hybridization in *saudiya* raises the possibility that our panel of *bennetti* also included hybrids. Chromosomal data for the five Pakistani animals are consistent with data for the three animals studied by FURLEY et al. (1988), also from Pakistan. Our Pakistani specimens were distinguishable from *saudiya*, and Iranian *bennetti*, by two pericentric inversions. If there were hybrids among our panel of Pakistani *bennetti*, inversion heterozygotes would have been expected. However, cytogenetic similarities between two Iranian *bennetti* and two *saudiya* leave open the possibility that the so-called Iranian specimens might be hybrids.

Another possibility suggested by the occurrence of the same translocation polymorphisms in *saudiya* and Iranian *bennetti* is that gene flow between their populations has prevented the fixation of different chromosomal rearrangements. The pericentric inversions that distinguish these two taxa from Pakistani *bennetti*, however, appear to be fixed. Populations of *bennetti* in the Seistan and Thar deserts are thought to be separated be either the Indus river or the edge of the Iranian plateau (GROVES 1969). Assuming that our Iranian *bennetti* represent the Seistan population (*G. b. fuscifrons*) and that Pakistani specimens are from the Thar population (*G. b. christii*), it is possible that the chromosomal differences observed in captive *bennetti* reflect these natural populations and are the result of their geographic isolation. However, uncontrolled transport of live gazelles throughout the Middle East for the pet trade adds to the difficulty of making inferences about the origin and taxonomic status of any captive specimens (FURLEY et al. 1988).

Cytogenetic studies of gazelles across their natural geographic range are urgently needed to define the occurrence of intraspecific chromosomal variation that has been documented in captive populations. Although *G. bennetti* has been greatly reduced in numbers or eliminated from many areas, it still occurs locally in good numbers from central Iran to central India (EAST 1993). Unfortunately, *G. saudiya* is believed to be extinct in the wild (GROOMBRIDGE 1993) so it is unlikely that karyotypes of natural populations will ever be known. Thus, chromosomal studies of captive and introduced populations of *saudiya* have added significance in terms of conservation and breeding efforts, particularly since intraspecific chromosomal variation represents a potential threat to reproduction (for reviews see BENIRSCHKE and KUMAMOTO 1991; ROBINSON and ELDER 1993). Therefore, cytogenetic studies should include evaluations of the effects that chromosomal polymorphisms have on the fertility of these threatened species.

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Zusammenfassung

Die Chromosomen von Gazella bennetti und Gazella saudiya

Sieben in Gefangenschaft gehaltene Gazellen der Art *Gazella bennetti* hatten eine Chromosomenzahl von 2n = 49–52, und sieben *G. saudiya* hatten 2n = 46–53. Die Giemsa Bandmuster der Chromosomen

zeigten, daß die Variation der diploiden Chromosomenzahl zum Teil auf die Autosom/X-Chromosomen Translokation, und zum Teil auf vier unabhängige Robertsonische Translokationen von Autosomen zurückzuführen ist. Keine beständigen Chromosomenunterschiede bestanden zwischen *G. bennetti* und *G. saudiya*, hingegen unterschied sich *G. bennetti* von Pakistan von *G. bennetti* aus Iran und *G. saudiya*, durch zwei perizentrische Inversionen. Mehrere der metazentrischen Autosomen beider Arten hatten monobrachiale Homologie mit metazentrischen Autosomen von *G. dorcas* und *G. gazella*. Dieser Befund beweist, daß *G. bennetti* und *G. saudiya* von *G. dorcas* und *gazella* reproduktiv isoliert sind. Wie es auch für andere Gazellenarten der Fall ist, sind cytogenetische Untersuchungen von wilden, natürlichen Populationen dieser zwei Gazellenarten unentbehrlich.

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Reproductive cycle of *Microtus pyrenaicus* De Sélys-Longchamps, 1847 (Mammalia, Rodentia) in the Western Pyrenees

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Abstract

Studied was the reproductive cycle of *Microtus pyrenaicus* in the Quinto Real Mountains (Western Pyrenees, Iberian Peninsula). 131 specimens (61 males, 70 females) were analyzed. Results indicate the presence of sexually active males throughout the year, ranging from 25% in winter to 100% in spring. Females have a similar cycle, although in December, January and March no sexually active female was found and in February only 20% showed signs of activity. The female breeding season is April–November, with a significant decline from December to March. From June to September all mature females are sexually active, and 67.9% of females were pregnant. The average litter size was 2.5 (se = 0.15; 1–3; n = 18) and the average of the placental scars was 2.4 (se = 0.15; 2–3; n = 11). In comparison with other voles closely related phylogenetically, *Microtus pyrenaicus* has a lower average litter size than cited by Krapp (1982) for *Microtus savii*. The winter break in reproductive activity suggests a relation to the annual cycle of food availability (prairie grasses) or perhaps to the harsh climate endured.

Introduction

The Pyrenean vole, *Microtus pyrenaicus* occupies areas in the Iberian Peninsula and France with the southern limits in the Pyrenees (Niethammer 1956, 1964; Castién and Mendiola 1984; Gosálbez 1987) and northern limits in Central France (Spitz 1984; Krapp 1982).

Information on its reproductive cycle is scarce. Only Saint-Girons (1973) provides data on litter sizes. The purpose of this study is to define the most relevant characteristics of the reproductive cycle of this species in the wild.

Materials and methods

The 131 specimens analysed (61 males, 70 females) were captured between September 1984 and August 1986 in the Quinto Real mountains (Western Pyrenees, northern Iberian Peninsula) at altitudes of between 660 and 850 m. Average annual rainfall in the study area was 2.138 l/m^2. Maximum rainfall occurred in April (243.5 l/m^2) and November (253.2 l/m^2) and the minimum in July (68.4 l/m^2). Temperatures were at minimum in January (= 2.9 °C) and maximum in August (= 16.6 °C). The average annual temperature was 8.8 °C. Most animals were captured in small clearings in the forest, except for three specimens from shrubland and river banks.

In each specimen the external features relevant to reproduction were noted: in males, the position of testicles (abdominal or scrotal), in females, vaginal perforation, presence of sperm plugs or symptoms of weaning, as shown by size and development of teats. In males the length of the seminal vesicle and the maximum orthogonal length of each testicle were measured. A smear of testicular material and epididymis was also carried out. The cell content of this smear was stained according to the criteria mentioned by Gosálbez et al. (1979). In females the reproductive apparatus was extirpated and characteristics of irrigation and dilatation of the uterus were noted as symptoms of reproductive activity. In pregnant females the number of embryos in each uterus was noted. The number of recent placental scars was taken, and these were differentiated from older ones.

The samples were classified according to the criteria of Ventura and Gosálbez (1987). In males three categories have been established depending on sexual maturity. Immature: specimens with no spermatid or spermatozoa in the testicles. Submature: animals with few spermatids or spermatozoa in the testicles. Mature: animals with a large amount of spermatozoa in the testicles. The observations of the epididymis supported this classification and, in some cases, provided complementary information.

In females the following categories were established: Immature: closed vulva, poorly developed uterus, lack of placental scars. Inactive mature: closed vulva, partly developed uterus but scantily vascularized. These may present placental scars but not embryos. Active mature: open vulva, fully developed and well vascularized uterus. They may present embryos or placental scars.

Results

Reproduction in males

Figure 1 shows the relation between the product of the major testicular diameters and the length of the seminal vesicle, differentiating the sexual stage of each specimen. Immature animals showed values of less then 7.6 mm in the length of the seminal vesicle and 29.8 mm^2 in the product of the major testicular diameters. Submature males had a wide range (seminal vesicle length from 1.5 mm to 11.5 mm and the product of the major testicular diameters ranges from 14.3 mm^2 to 35.7 mm^2). Mature animals had a seminal vesicle over 6 mm long and a product of the major testicular diameters over 12.0 mm^2. The highest value found in seminal vesicle length was 14.5 mm and for the product of the major testicular diameters 79.6 mm^2.

Data derived from the study of spermatozoid presence in the testicle and epididymis indicate that, in animals with seminal vesicle between 6.0 mm and 11.4 mm, there are spe-

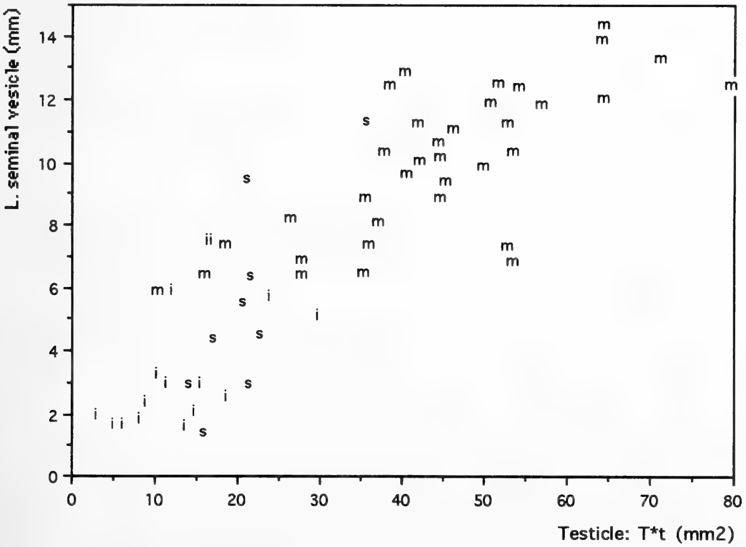

Fig. 1. Relationship between the length of the seminal vesicle and the product of the major testicular diameters, differentiating the sexual maturity. i: immature, s: submature and m: mature. n = 60.

cimens with no trace of spermatozoa and others that have initiated spermatogenic activity. Specimens with seminal vesicle length over 11.4 mm all show the presence of spermatozoa in the gonad. Several low weight specimens are active, while all animals over 21.3 g are sexually active (the lightest sexually active animal found was captured in January 1985; its body mass was 11.8 g).

The variation in the average testicle length throughout the year (Fig. 2) present a variation with a significant decrease during the winter months, especially in January and an increase from spring onwards, registering maximum values in May and August with another marked decline in activity during July. In interpreting this variation, it should be taken into consideration that in July immature and submature specimens from the first litters of the year are included, thus causing a decline in the dimensions of the parameters commented on. These variations indicate a tendency towards a seasonal biological cycle, although in the case of males this tendency is dominated by the constant presence of sexually active animals (Tab. 1). The presence of high vesicular lengths in December may by due to an artefact of the sample.

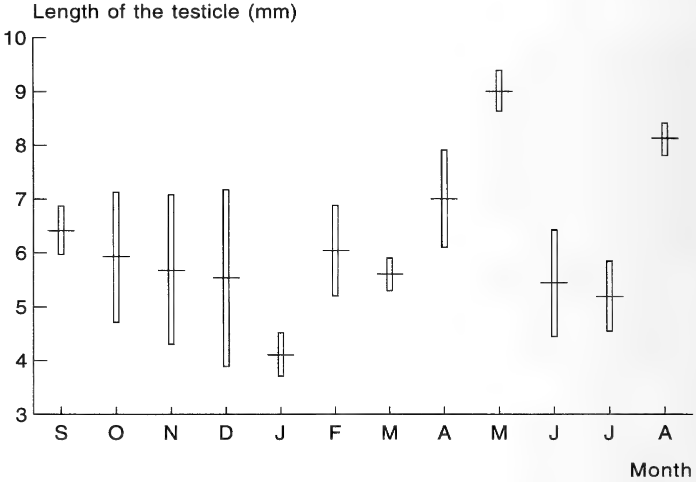

Fig. 2. Variation of the average testicular length (mm) with their standard error, throughout the study period. n = 61.

Table 1. Number and percentage of males of *M. pyrenaicus* distributed by months and reproductive categories.

	Sp		Oc		Nv		Dc		Jn		Fb	
	%	n	%	n	%	n	%	n	%	n	%	n
Immatures	16.6	1	25.0	1	75.0	3	33.3	1	75.0	3	40.0	2
Submatures	16.6	1	25.0	1	0.0	0	0.0	0	0.0	0	20.0	1
Matures	66.7	4	50.0	2	25.0	1	66.7	2	25.0	1	40.0	2

	Mz		Ap		Mi		Jn		Jl		Ag	
	%	n	%	n	%	n	%	n	%	n	%	n
Immatures	11.1	1	0.0	0	0.0	0	33.3	2	60.0	3	0.0	0
Submatures	44.4	4	0.0	0	0.0	0	16.7	1	20.0	1	0.0	0
Matures	44.4	4	100.0	4	100.0	5	50.0	3	20.0	1	100.0	6

Table 1 shows the proportion and number of reproductive classes for each month of the year. The presence of mature specimens throughout the year should be noted. After September there is an increase in the number of immature animals, which reaches maximum between November and January. From this month on there is a progressive increase in the number of mature animals, due to the acquisition of sexual maturity by specimens born at the end of the previous year. This is demonstrated by the capture of submature specimens in subsequent months, until April, when 100% of male captures were mature. After June immature specimens began to appear again, which, on the basis of their weight, correspond to the first litters of the year. These animals were soon incorporated into the group of reproducers, as can be seen from the simultaneous presence of submature animals.

Reproduction in females

All females weighing less than 14.5 g were immature. Mature, inactive and active specimens ranged from 14.5 g to 24.2 g. The heaviest female captured without sign of sexual activity weighed 19.6 g.

Table 2 represents the proportion and number of females in each reproductive category throughout the year. The results show that from September onwards the number of immature specimens increased progressively due to delayed sexual maturity in winter. During December and January no sexually active specimen was captured. From then on there was a progressive incorporation of active animals, so that between June and September all mature females were capable of reproduction. Pregnant females were found between April and November (Tab. 2).

The average litter size, calculated from embryo counts, is $\bar{x} = 2.5$ (se = 0.15; 1–3; n = 19). The resulting value of placental scar counts is $\bar{x} = 2.4$ (se = 0.15; 2–3; n = 11). It is worth noting that average litter sizes in summer ($\bar{x} = 2.14$, n = 7, se = 0.26) were slightly lower than those in spring ($\bar{x} = 2.67$, n = 6, se = 0.21) and autumn ($\bar{x} = 2.80$, n = 5, se = 0.20), although the comparison of averages (Student's t test) does not show any significant difference, (summer – spring: t = 1.525; p = 0.155, summer – autumn: t = 1.856; p = 0.093). The percentage of pregnant females compared with active mature specimens in the period June–September is 67.9%.

Table 2. Number and percentage of females distributed by months and reproductive categories. Number and percentage of sexually active *M. pyrenaicus* pregnant each month related to matured females.

	Sp		Oc		Nv		Dc		Jn		Fb		Mz		Ap		Mi		Jn		Jl		Ag	
	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n
Immatures	0.0	0	33.3	2	25.0	1	100.0	2	75.0	3	40.0	2	33.3	2	50.0	5	14.3	1	64.3	9	0.0	0	33.3	1
Inactive matures	0.0	0	50.0	3	25.0	1	0.0	0	25.0	1	40.0	2	66.7	4	0.0	0	14.3	1	0.0	0	0.0	0	0.0	0
Active matures	100.0	2	16.7	1	50.0	2	0.0	0	0.0	0	20.0	1	0.0	0	50.0	5	71.4	3	35.7	5	100.0	6	66.7	2
Pregnant matures	100.0	2	25.0	1	66.7	2	0.0	0	0.0	0	0.0	0	0.0	0	60.0	3	50.0	3	100.0	5	50.0	3	0.0	0

Sex ratio

Table 3 shows the sex ratio in each season through the chi-square test. In autumn and winter the proportions are similar, while in spring and summer there are more females. The value of chi-square indicates that there is no significant variation on the expected value 1:1. The same result is applicable to the total number of captures.

Table 3. Number and proportion of sexes obtained in each season of the year.

	Autumn		Winter		Spring		Summer		Total	
	n	%	n	%	n	%	n	%	n	%
Females	12	(46.2)	12	(50.0)	23	(56.1)	23	(57.5)	70	(53.4)
Males	14	(53.8)	12	(50.0)	18	(43.9)	17	(42.5)	61	(46.6)
Chi-Squ.	0.154		0.000		0.610		0.900		0.618	
Deg. fr.	1		1		1		1		1	
p	0.695		1.000		0.453		0.343		0.431	

Discussion

There are few reports in the literature on the biological cycle of *Microtus pyrenaicus*. In relation to litter size, Saint-Girons (1973) mentions the capture of 3 active females in the Pyrenees, one with four placental scars, another with two and a third pregnant with one embryo. Those figures concord with ours, though in the study population no animal was found with 4 embryos.

In comparison with other voles closely related phylogenetically, Krapp (1982) states that the average litter size in *Microtus savii* is 3.3 (2–4, n = 9) which is larger than the average obtained for *Microtus pyrenaicus* in this study ($t = 5.485$; $p < 0.01$).

The winter break in reproductive activity suggest a relation to the annual cycle of food availability (prairie grasses) or perhaps to the harsh climate endured by these nuclei of Pyrenean mountain voles.

The sex ratio shown is similar to that found in other European Microtinae (Winking 1976; Palomo et al. 1989; Kratochvíl 1969).

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Zusammenfassung

Fortpflanzungszyklus von Microtus pyrenaicus de Sélys-Longchamps, 1847 (Mammalia Rodentia) in den Westpyrenäen

Es wird über den jährlichen Fortpflanzungszyklus der Pyrenäen-Kleinwühlmaus (*Microtus pyrenaicus*) im Quinto Real Gebirge (Westpyrenäen, Iberische Halbinsel) berichtet. Es wurden insgesamt 131 gefangene Exemplare (61 Männchen, 70 Weibchen) ausgewertet. Im untersuchten Gebiet treten geschlechtsreife Männchen in allen Monaten auf. Jedoch schwankt ihr Prozentsatz in bezug auf die Gesamtanzahl der Männchen bemerkenswert im Jahreslauf. Der niedrigste Wert wird im Winter erreicht (25%), der höchste im Frühjahr (100%). Die Fortpflanzungsperiode der Weibchen beginnt offenbar im April und kann bis Ende November dauern. Jedoch prägt sich die Fortpflanzungsintensität von

Juni bis September am stärksten aus. In diesem Zeitraum sind alle geschlechtsreifen Weibchen fortpflanzungsaktiv, die meisten (67,9%) sogar trächtig. Von Dezember bis Ende März nimmt die Geschlechtstätigkeit der Weibchen ab. Der Gesamtmittelwert der Embryonen je Wurf und der Placentanarben je Weibchen beträgt jeweils 2,5 ± 0,15 (1–3, n = 18) und 2,4 ± 0,15 (2–3, n = 11).

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Craniometric variation and subspecific differentiation in *Thrichomys apereoides* in northeastern Brazil (Rodentia: Echimyidae)

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Abstract

Thrichomys apereoides is an echimyid rodent which ranges in distribution from northeastern and central Brazil into Paraguay. Five subspecies are recognized, although each form is not well characterized and diagnosis is based primarily in pelage color variation. In this study we employed procedures from multivariate statistics to assess the systematic status of subspecies described from northeastern Brazil. The results of the craniometric analysis cannot be reconciled with the subspecies currently recognized for northeastern Brazil. Populations assigned to *T. a. laurentius* and *T. a. inermis* form a continuum of variation in cranial size, although they differ in cranial shape from a population from the locality of Bodocó in the state of Pernambuco. The implications of these findings for the systematics of *T. apereoides* are discussed.

Introduction

Thrichomys apereoides (Lund, 1841) is an echimyid rodent commonly found in the savannas of eastern and central Brazil and Paraguay, often associated with rocky habitats (MARES et al. 1981; ALHO 1982). This species also inhabits the dry caatingas of northeastern Brazil (MARES et al. 1981; MARES and OJEDA 1982), although it reaches higher densities in mesic refuges. *Thrichomys apereoides* has been the subject of confusing nomenclatural and taxonomic assignements (PETTER 1973), and five subspecies are currently recognized (MOOJEN 1952). The ranges of the subspecies are not well defined and the data available refer primarily to locality records. These are summarized in MOOJEN (1952), as follows: *T. a. cunicularius* known from the region of Rio São Francisco in Minas Gerais; *T. a. pachyurus* recorded from Paraguay and Mato Grosso and northern São Paulo; *T. a. inermis* described from Jacobina in the state of Bahia; *T. a. apereoides* ranging from western Minas Gerais to Goiás; and *T. a. laurentius* occurring in the states of Ceará through Pernambuco.

The subspecies of *T. a. apereoides* have been described primarily on the basis of pelage color variation (see MOOJEN 1952), and little is known about patterns of within and among-population variation in other character systems. In this study we employ multivariate morphometric procedures to examine variation in cranial metric traits in population samples of *T. a. apereoides* from northeastern Brazil which were allocated to the two subspecies, viz. *T. a. laurentius* and *T. a. inermis*, recognized for this area. The objectives of this study were (1) to assess the nature, extent, and magnitude of cranial differentiation in *T. apereoides*, and (2) to determine whether the pattern of population differentiation based on multivariate analyses of cranial metric characters is consistent with the subspecific structure established on the basis of pelage variation.

Material and methods

A total of 243 specimens of *T. apereoides* available in the mammal collection of the Museu Nacional (Rio de Janeiro) was examined in this study. All specimens were classified to one of the seven age classes defined in Moojen et al. (1988) on the basis of tooth eruption and occlusal surface wear criteria. Only individuals belonging to age classes 5–7 were selected for the analysis of geographic variation because they were considered adults by the criteria of Moojen et al. (1988). Statistically significant sexual size dimorphism has been detected for a few cranial traits in *T. apereoides* (Moojen et al. 1988), although in this study sexes were pooled to increase samples sizes.

The specimens analyzed in this study represent samples collected at the following localities in northeastern Brazil (Fig. 1): state of Ceará. Itapagé (3°41′ S, 39°35′ W: n = 13), Campos Sales (7°4′ S, 40°22′ W: n = 7); state of Pernambuco. Bodocó (7°42′ S, 39°53′ W: n = 11), Triunfo (7°51′ S, 38°8′ W:

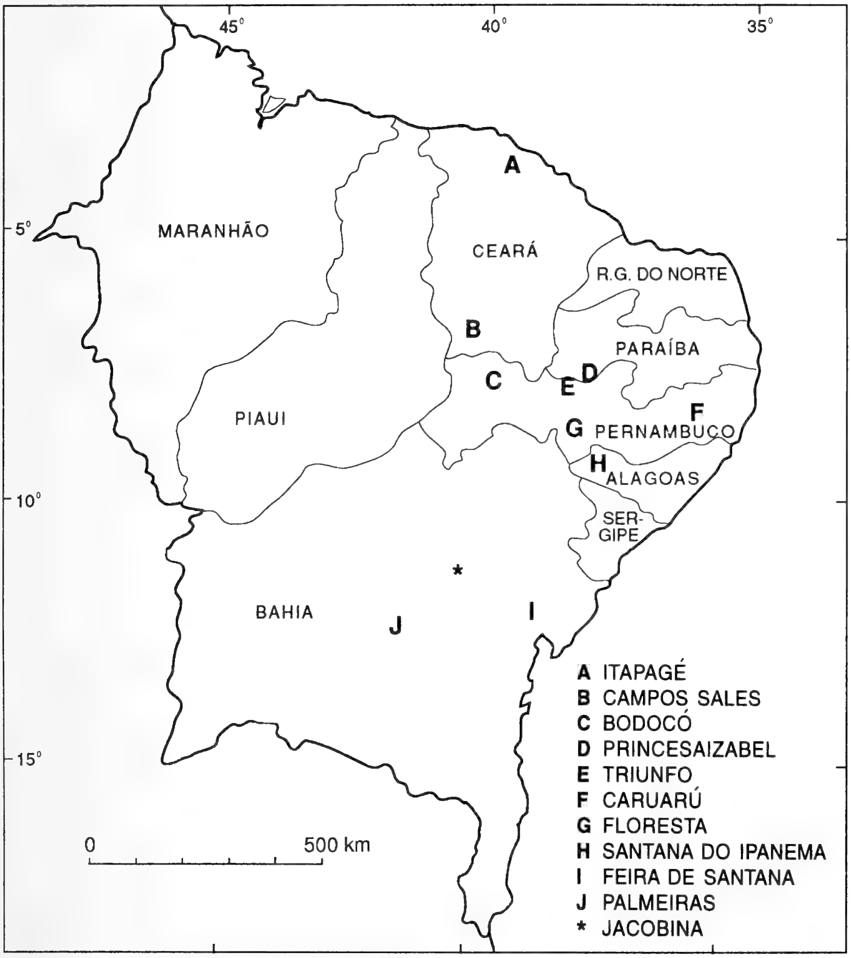

Fig. 1. Population samples of *Thrichomys apereoides* used in this study. Localities as indicated. The star denotes the type locality of *Thrichomys apereoides inermis*

n = 15), Caruaru (8°14′ S, 35°55′ W: n = 9), Floresta (8°36′ S, 38°44′ W: n = 8); state of Paraíba. Princesa Izabel (7°44′ S, 37°59′ W: n = 8); state of Alagoas. Santana do Ipanema (9°20′ S, 37°16′ W: n = 16); state of Bahia. Feira de Santana (12°15′ S, 38°57′ W: n = 9), Palmeiras (12°30′ S, 41°34′ W: n = 7). The population samples from the states of Ceará, Paraíba, and Pernambuco were assigned to *T. a. laurentius*, and the two populations from Bahia were allocated to *T. a. inermis* (Moojen 1952). The population from Santana do Ipanema in the state of Alagoas does not fall into the ranges of either *T. a. laurentius* or *T. a. inermis* and thus was not formally assigned to either of the subspecies.

Thirteen quantitative cranial measurements defined in Smith and Patton (1988) in addition to two mandibular measurements were taken with electronic digital calipers, as follows: occipito-nasal length (ONL), basilar length (BAL), zygomatic breadth (ZB), mastoid breadth (MB), rostral length (RL), nasal length (NL), rostral width (RW), diastema (D), maxillary tooth row length (MTRL), palatal width (PW), bullar length (BUL), rostral depth (RD), cranial depth (CD), mandible length (ML), and mandible height (MH).

Character variation in *T. apereoides* was analyzed by univariate and multivariate statistical procedures (Morrison 1976; Sokal and Rohlf 1981). Cranial size and shape variation among population samples of *T. apereoides* was evaluated using principal components analysis (Morrison 1976), a multivariate statistical procedure designed to summarize major patterns of covariation among metric traits. The values for all characters were transformed to logarithms to equalize variances and produce scale-invariant covariances that linearize allometric relationships (Bookstein et al. 1985). Principal components were extracted from the covariance matrix of log-transformed data. The principal component scores for the first three axes were plotted to assess patterns of cranial size and shape variation within and among populations of *T. apereoides*.

All principal-component variate loadings are expressed as vector correlations (directional cosines; Morrison 1976), estimated for each character by its correlation with projection scores across individuals. Vector plots graphically portray the principal directions of variation of each character within the corresponding principal component space. All statistical analysis were performed with SAS-PC (SAS Institute 1988).

Results

The statistics of variation in cranial dimensions in *T. apereoides* are given in Table 1. Cranial dimensions do not show a clear pattern of variation in population samples from the

Table 1. Mean (±*SE*) and analysis of variance for 15 cranial characters in populations of *Thrichomys apereoides* from ten localities in northeastern Brazil.

Character	Localities		
	Itapagé	Campos Sales	Bodocó
	X ± *SD*	*X* ± *SD*	*X* ± *SD*
Occipito-nasal length	51.48 ± 2.50	49.19 ± 1.61	49.78 ± 1.83
Basilar length	43.90 ± 2.28	42.66 ± 1.20	43.16 ± 1.76
Zygomatic breadth	25.71 ± 1.12	24.66 ± 0.42	25.00 ± 0.86
Mastoid breadth	19.84 ± 0.82	19.11 ± 0.37	19.46 ± 0.50
Rostral length	19.64 ± 1.22	18.90 ± 0.95	19.35 ± 1.11
Nasal length	17.92 ± 1.00	17.05 ± 0.87	16.89 ± 0.91
Rostral width	9.58 ± 0.74	8.92 ± 0.41	10.53 ± 0.58
Diastema	9.98 ± 0.65	9.33 ± 0.44	9.57 ± 0.48
Maxillary tooth row length	9.15 ± 0.25	8.52 ± 0.19	8.61 ± 0.42
Palatal width	2.98 ± 0.52	3.12 ± 0.24	3.43 ± 0.30
Bullar length	11.29 ± 0.47	11.48 ± 0.33	11.62 ± 0.54
Rostral depth	10.61 ± 0.64	9.94 ± 0.51	11.68 ± 0.68
Cranial depth	13.21 ± 0.49	13.13 ± 0.42	14.60 ± 0.62
Mandible length	27.57 ± 1.43	26.06 ± 0.71	26.41 ± 0.86
Mandible height	11.85 ± 0.85	11.33 ± 0.39	11.56 ± 0.54

first four localities, whereas in the remaining populations there is an overall trend of decreasing cranial dimensions from northern to southern localities. The decrease in mean values is more pronounced in the two southernmost populations from Feira de Santana and Palmeiras in the state of Bahia (Tab. 1). Univariate analysis of variation indicates significant heterogeneity among populations in all characters except nasal length (Tab. 1).

Variation in craniometric measurements among populations of *T. apereoides* was assessed by principal components analysis. The first principal component (PC) accounts for

Table 1. Continued

Character	Localities		
	Princesa Izabel	Triunfo	Caruaru
	X ± *SD*	*X* ± *SD*	*X* ± *SD*
Occipito-nasal length	49.49 ± 3.26	52.35 ± 2.09	51.39 ± 1.28
Basilar length	42.30 ± 3.45	45.10 ± 2.14	44.25 ± 1.21
Zygomatic breadth	24.93 ± 1.55	25.91 ± 0.90	26.09 ± 1.15
Mastoid breadth	19.54 ± 0.88	20.22 ± 0.82	20.13 ± 0.43
Rostral length	19.14 ± 1.66	20.37 ± 1.07	19.75 ± 0.60
Nasal length	17.09 ± 1.91	18.29 ± 1.26	17.50 ± 1.03
Rostral width	9.24 ± 0.66	9.82 ± 0.79	9.57 ± 0.69
Diastema	9.40 ± 0.85	10.33 ± 0.45	10.16 ± 0.39
Maxillary tooth row length	8.28 ± 0.75	8.80 ± 0.21	8.79 ± 0.31
Palatal width	2.98 ± 0.43	3.37 ± 0.40	3.48 ± 0.38
Bullar length	11.27 ± 0.47	11.63 ± 0.64	11.75 ± 0.37
Rostral depth	9.99 ± 0.78	11.56 ± 0.59	10.92 ± 0.65
Cranial depth	13.27 ± 0.78	13.99 ± 0.63	13.53 ± 0.52
Mandible length	26.36 ± 1.71	27.76 ± 1.27	27.68 ± 1.24
Mandible height	11.06 ± 0.80	12.30 ± 0.66	11.90 ± 0.64

Table 1. Continued

Character	Localities		
	Floresta	Santana do Ipanema	Feira de Santana
	X ± *SD*	*X* ± *SD*	*X* ± *SD*
Occipito-nasal length	50.77 ± 2.02	51.38 ± 2.53	49.47 ± 2.09
Basilar length	43.85 ± 1.66	44.28 ± 2.40	42.24 ± 1.77
Zygomatic breadth	25.41 ± 0.65	25.26 ± 0.98	24.51 ± 0.97
Mastoid breadth	20.04 ± 0.48	19.79 ± 0.77	18.83 ± 0.66
Rostral length	19.59 ± 0.83	20.11 ± 1.25	19.38 ± 1.26
Nasal length	17.64 ± 0.74	17.77 ± 1.22	17.49 ± 1.28
Rostral width	9.89 ± 0.89	9.13 ± 0.61	9.60 ± 0.47
Diastema	10.01 ± 0.45	10.15 ± 0.92	9.20 ± 0.55
Maxillary tooth row length	8.41 ± 0.41	8.80 ± 0.30	8.14 ± 0.30
Palatal width	3.54 ± 0.33	3.24 ± 0.58	3.24 ± 0.39
Bullar length	11.39 ± 0.56	11.87 ± 0.57	11.08 ± 0.53
Rostral depth	10.29 ± 0.29	10.84 ± 0.67	10.03 ± 0.62
Cranial depth	13.38 ± 0.46	13.32 ± 0.58	12.88 ± 0.60
Mandible length	27.70 ± 1.27	27.20 ± 1.36	25.54 ± 1.12
Mandible height	11.38 ± 0.67	11.55 ± 0.95	11.39 ± 0.63

Table 1. Continued

Character	Localities		
	Palmeiras		
	$X \pm SD$	F	P
Occipito-nasal length	47.35 ± 1.65	4.33	0.0001
Basilar length	41.50 ± 1.62	2.93	0.0042
Zygomatic breadth	23.66 ± 0.74	4.85	0.0001
Mastoid breadth	18.26 ± 0.69	7.17	0.0001
Rostral length	18.63 ± 0.79	2.26	0.0243
Nasal length	16.75 ± 0.53	1.99	0.0496
Rostral width	8.67 ± 0.56	6.09	0.0001
Diastema	9.22 ± 0.26	5.08	0.0001
Maxillary tooth row length	8.16 ± 0.36	8.45	0.0001
Palatal width	3.24 ± 0.32	2.08	0.0388
Bullar length	10.66 ± 0.41	4.40	0.0001
Rostral depth	9.60 ± 0.48	12.96	0.0001
Cranial depth	13.65 ± 0.51	7.89	0.0001
Mandible length	25.03 ± 0.85	5.72	0.0001
Mandible height	10.03 ± 0.51	6.40	0.0001

82.7% of the total variation, whereas PC-2 and PC-3 explain 4.3% and 3.0% of the variation, respectively. Because all cranial characters were positively and significantly ($P < 0.0001$) correlated with the first pooled among-group principal component extracted from the covariance matrix of log-transformed character values, the first axis can be used as a general variable expressing overall cranial size. All populations overlap extensively in the space defined by the first two principal components (Fig. 2 A, B). On the other hand, the plot of PC-2 against PC-3 indicates the existence of two cranial shape morphologies; one represented by the population of Bodocó (state of Pernambuco) and the other by a major cluster including all other populations (Fig. 3 A). The vector plot (Fig. 3 B) indicates that individuals in the population from Bodocó differ by having higher skulls and shorter rostra relative to individuals in the other populations.

To further clarify the ordination of *T. apereoides* we performed canonical discriminant function analysis (Morrison 1976). The pattern of ordination is similar to that uncovered with principal components analysis (Fig. 4 A), in that the population from Bodocó is fully discriminated. Ordination of the remaining populations is more informative in the canonical discriminant analysis. The populations from Itapagé, Campos Sales, Triunfo, Caruaru, Floresta, Princesa Izabel, Santana do Ipanema, Feira de Santana, and Palmeiras are distributed along an axis (CV-2) of increasing cranial size starting with the population from Itapagé and ending with the population from Palmeiras (Fig. 4 A). Canonical variate 2 is clearly an axis of size since all cranial characters have positive correlations with this vector (Fig. 4 B).

Discussion

The statistical analysis of cranial metric traits in *T. apereoides* in northeastern Brazil revealed the existence of two groups of populations which lie in discrete regions in multivariate character space and differ in cranial shape. One major group is widespread in distribution and includes population samples assigned to *T. a. laurentius* and *T. a. inermis* from the localities of Itapagé, Campos Sales, Triunfo, Caruaru, Floresta, Princesa Iza-

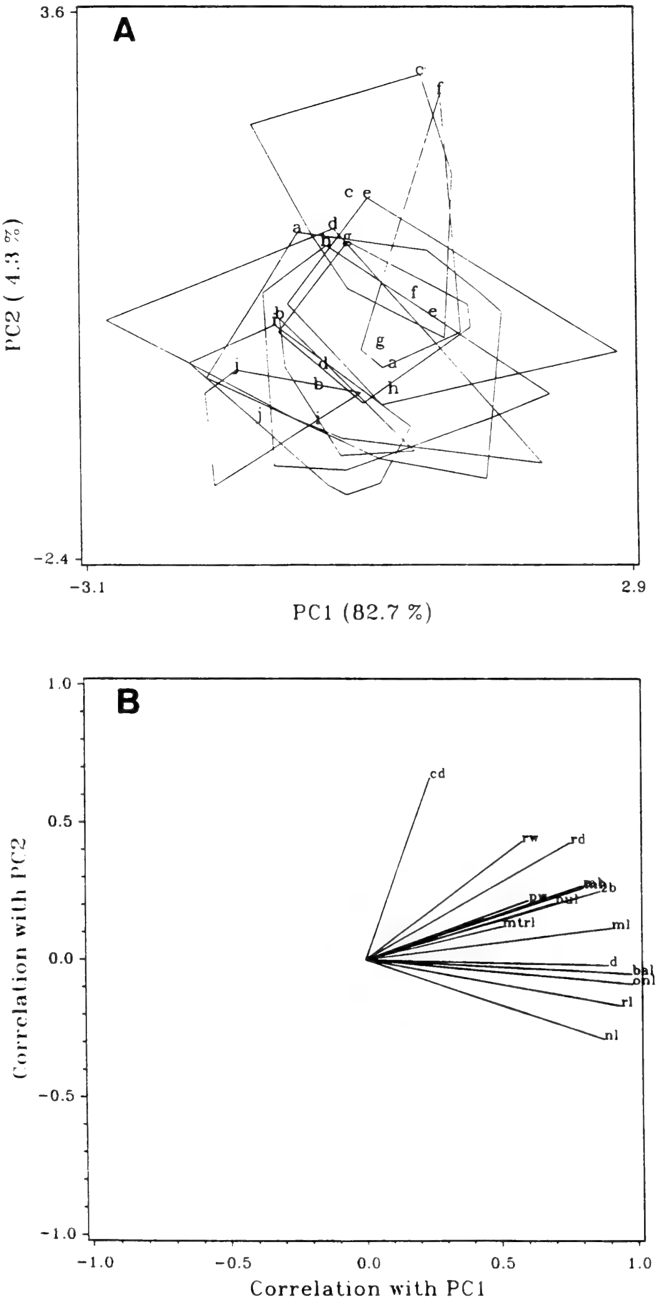

Fig. 2. Principal components analysis for ten populations of *Thrichomys apereoides.* (A) Bivariate plots of projection scores on principal components 1 and 2. Letters at the tip of polygons indicate sample locality and letters at the middle of polygons indicate sample centroids. (B) Vectors portraying the principal directions of character variation in the plane of the first two principal components

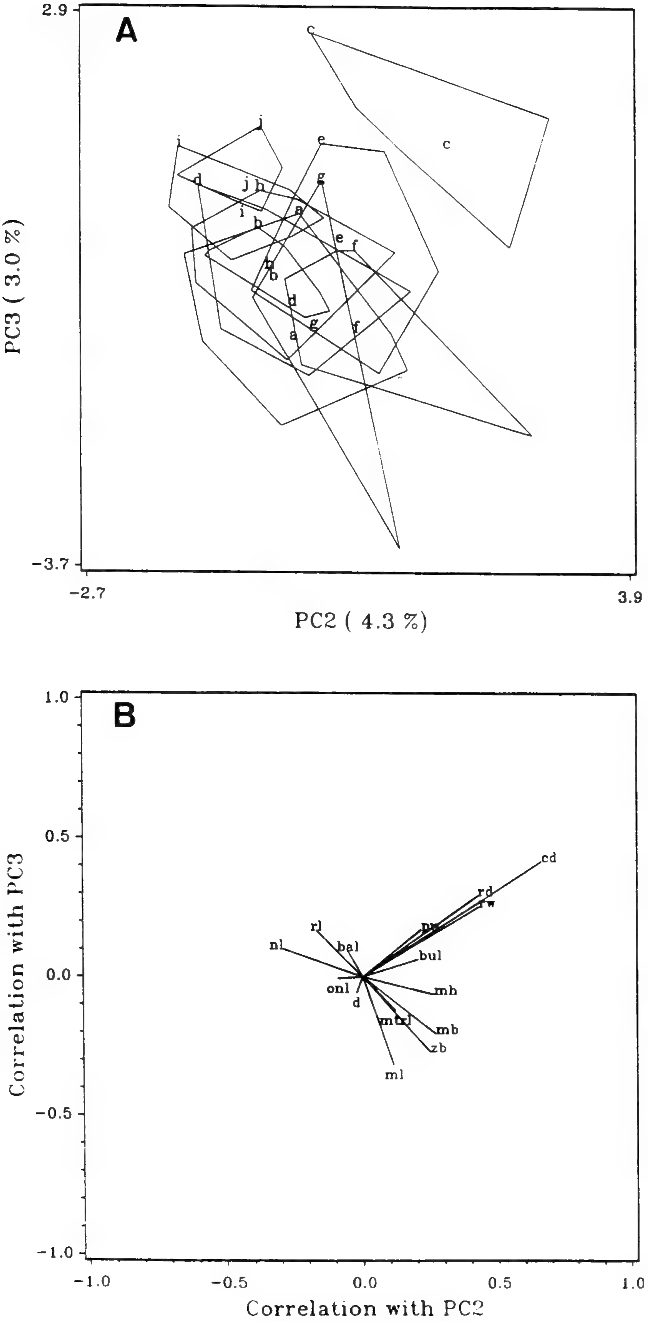

Fig. 3. Principal components analysis for ten populations of *Thrichomys apereoides.* (A) Bivariate plots of projection scores on principal components 2 and 3. Letters at the tip of polygons indicate sample locality and letters in the middle of polygons indicate sample centroids. (B) Vectors portraying the principal directions of character variation in the plane of the principal components 2 and 3

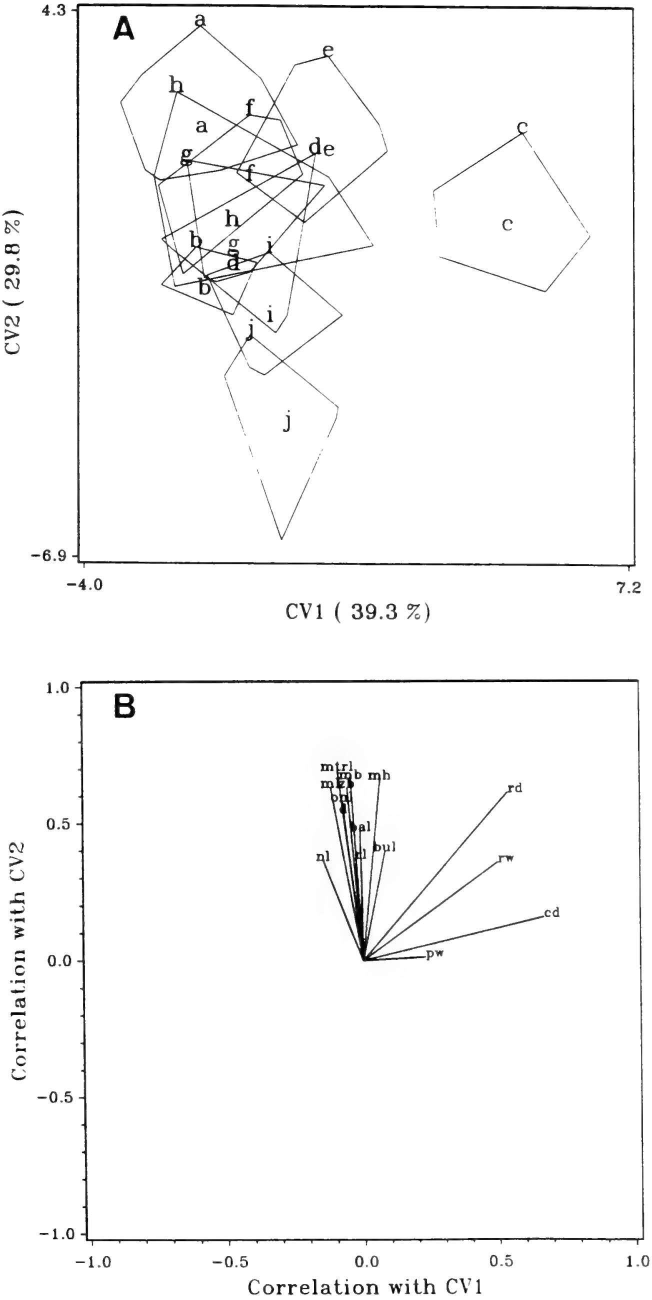

Fig. 4. Canonical discriminant analysis for ten populations of *Thrichomys apereoides*. (A) Bivariate plots of projection scores on canonical variates 1 and 2. Letters at the tip of polygons indicate sample locality and letters at the middle of polygons indicate sample centroids. (B) Vectors portraying the principal directions of character variation in the plane of the first two canonical variates

bel, Santana do Ipanema, Feira de Santana, and Palmeiras. Variation in this group is structured in a cline of decreasing cranial dimensions from northern to southern localities. The second group is represented by a single population from Bodocó, which was allocated to *T. a. laurentius*, and does not fall on the cline of decreasing cranial dimensions.

The morphologic evidence presented here for the patterns of variation in *T. apereoides* can be interpreted according to current views on the structure of subspecific variation. Barrowclough (1982) and Thorpe (1987) have stressed that evidence for the recognition of subspecies should not be based on continuous clinal variation, but that populations should occupy discrete regions in character space. The nature of cranial differences among populations of *T. apereoides* is also relevant to the definition of infraspecific differentiation. The two components of form, i. e., size and shape have been attached different weights in taxonomy and systematics, with the latter component (shape) being held as a better predictor of genetic variation and relatedness and phylogeny (Gould and Johnston 1972; Thorpe 1983; Rohlf and Bookstein 1987). Recently, Patton and Brylsky (1987) demonstrated that size is phenotypically plastic in populations of the pocket gopher *Thomomys bottae*, and shifts in cranial size are a response to environmental (nutritional) quality. On the other hand, cranial shape variation was found to be correlated with genic differences in recognized subspecies of *T. bottae*. Smith and Patton (1988) elaborated further on the relation between cranial size and shape and ecologic and historical (phylogenetic) components of differentiation, and suggested that independent evolutionary units (= subspecies, sensu Smith and Patton, 1988) should be recognized for geographic units showing concordant patterns of cranial shape and genetic variation.

Based on current view of the structure of subspecific variation (cf. Barrowclough 1982; Patton and Brylski 1987; Thorpe 1987; Patton and Smith, 1989, 1990), the craniometric data suggest the existence of two geographic units based on cranial shape: one represented by the population from Bodocó and the other including populations from Itapagé, Campos Sales, Triunfo, Caruaru, Floresta, Princesa Izabel, Santana do Ipanema, Feira de Santana, and Palmeiras. This result is not consistent with Moojen's (1952) subspecific arrangement of *T. apereoides* in northeastern Brazil and raises two points. First, *T. a. laurentius*, which according to Moojen (1952) ranges in distribution from the state of Ceará to the state of Pernambuco, may not be monophyletic but rather be composed of two geographic units. Second, the populations from Feira de Santana and Palmeiras in the state of Bahia which were allocated to *T. a. inermis*, were shown in fact to be continuously connected with other populations assigned to *T. a. laurentius*. Our samples from the state of Bahia are not from Jacobina, the type locality of *T. a. inermis*, and thus definition of the status of this subspecies can only be established when material from this locality becomes available. Additional sampling will also be necessary to determine the geographic extent of the cranial morphology represented by the population from Bodocó. A finer geographic sampling of the cranial morphology coupled with surveys of genic and chromosomal variation will be needed to better understand the structure of variation and evolution in *T. apereoides*.

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Zusammenfassung

Kraniometrische Variation und Unterartgliederung bei Thrichomys apereoides in Nordost-Brasilien (Rodentia: Echimyidae)

Das Verbreitungsgebiet der Stachelratte *Thrichomys apereoides* reicht von Nordost- über Zentral-Brasilien bis nach Paraguay. Fünf Unterarten werden gegenwärtig anerkannt, auch wenn diese Formen nicht deutlich charakterisiert sind und ihre Diagnosen meist auf Färbungsmerkmalen basieren. Für die vorliegende Studie wurden Schädel von 243 Exemplaren vermessen und die Werte einer multivariaten statistischen Analyse unterzogen. Die Resultate stimmen nicht mit der gegenwärtigen Unterartgliederung überein. Populationen, die traditionell als *T. a. laurentius* und *T. a. inermis* bestimmt wurden, bilden in bezug auf ihre Schädelmaße ein Kontinuum, unterscheiden sich andererseits aber in der Schädelform von einer Population aus Bodocó im Bundesstaat Pernambuco. Innerhalb *T. apereoides* gibt es offenbar zwei gut unterscheidbare Populationen, deren systematischer Status diskutiert wird.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Extra-pair copulations in monogamous wild white-handed gibbons (*Hylobates lar*)

By U. Reichard

Institut für Anthropologie, Universität Göttingen, Göttingen, BRD

Receipt of Ms. 16. 05. 1994
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Ever since the earliest field study of gibbons (Carpenter 1940) it has been suggested that these Asian apes form monogamous pairs, live in small groups of 2–6 members and are territorial. Pairs are commonly believed to remain together for many reproductive cycles or even for a lifetime (Gittins and Raemaekers 1980), and mating is assumed to occur exclusively between pairmates (Brockelman and Srikosamatara 1984). However, relatively few actual data are available concerning sexual behaviour in wild populations (e. g. Ellefson 1974; Reichard 1991). Hence, most aspects of gibbons' reproductive biology lack firm quantitative information. Most importantly, during many field studies, researchers habituated only one group, which made it difficult or even impossible to document intergroup behaviour and to test the prediction of mate fidelity.

Elaborations of Darwin's sexual selection theory have produced several links concerning genital morphology and mating behaviour of primates living in one-male mating systems (Short 1981) including the lack of female anogenital swellings and colour changes during menstrual cycles (Harcourt 1981), as well as small testes of males (Harcourt et al. 1981). Gibbons are commonly believed to conform to most of these predictions. Gibbon females, however, develop relatively complex genital structures which sometimes change in turgidity and/or colouration during the menstrual cycle (Nadler et al. 1993). Testes of males are medium-sized compared to chimpanzees and gorillas (Harcourt et al. 1981) and might therefore be classified as "moderate". Moreover, extra-pair copulations have recently been reported for the siamang (*Hylobates syndactylus*) (Palombit 1994).

The present study was conducted in the primary rain forest of the Khao Yai National Park, Thailand (2.168 km^2; 101°22′ E, 14°26′ N). Data were collected from October 89 through January 90 and from January 92 through May 93. J. Neudenberger and B. Klausen contributed data during the latter period. The composition of the study groups A, B and C were: (A) 1 adult female, 1 adult male, 1 juvenile male, 1 infant male; (B) 1 adult female, 1 adult male, 1 subadult female (which left the group in August 93), 1 juvenile female, 1 infant female; (C) 1 adult female, 1 adult male, 2 subadult males, 1 juvenile male, 1 infant male. Observations of extra-pair copulations (EPC) were made by the author while following group A. In this group, regular observations were conducted for 3–12 days during each month of the study period, usually from 06:00–16:00 hrs. No observations were undertaken during August 92.

In group A, an infant was born around September 90. Resumption of sexual activity of the pair was first noticed in May 92. Frequent matings were recorded from December 92–April 93. Over a 10 month period, 59 in-pair copulations (IPC) were observed on 31 days. In addition, the female was seen to engage in 7 EPCs with the adult male of group C (27 January and 11 March 93) and in one EPC with the adult male of group B (25 April 93). Hence, 12% of observed copulations of this female were EPCs and they occurred on 9% of the days on which sexual behaviour was recorded. During the last EPC, however, the female was presumably already pregnant, because she gave birth in mid October 93.

EPCs might be an adaptation of gibbon females' to increase the chance of fertilisation by a male of superior genetic qualities (Fisher 1930). They might also increase offspring survival by, e. g., enhancing access to food sources. The study groups' home ranges overlapped substantially. Group encounters in these areas were frequent but not always agonistic (pers. obs.). This tolerance was potentially linked to the occurrence of EPCs. Furthermore, EPCs might lower the risk of infanticide after mate changes (van Schaik and Dunbar 1990). Although, infanticide has not yet been observed in gibbons, evidence is mounting that male replacements and group composition changes are more frequent than has previously been reported (e. g. Treesucon and Raemaekers 1984; Palombit 1992).

Gibbon males could benefit from EPCs by leaving more offspring as compared to strictly monogamous males. Even though copulating with several females does not always result in a reproductive pay-off when compared with monogamous mating (Dunn and Robertson 1993). Additionally, a paired male which searches for a chance to copulate with a second female must leave his mate and thus risks her infidelity. Therefore, a male will have to balance the search for EPC opportunities with the need to insure paternity of the offspring of the mate.

The behaviour of gibbon males as observed in the present study support these predictions. Groups were cohesive and individuals spent most of the day in close proximity. Therefore, a female was rarely found without the company of her pair-male. During group encounters, males usually positioned themselves between their mate and the neighbouring male(s) presumably to prevent close proximity through their physical presence. Thus, the circumstantial and behavioural observations illustrate the males' conflicting interests of guarding their mate and searching for additional reproduction opportunities.

In summary, the sexual behaviour of wild white-handed gibbons as described here suggests more reproductive flexibility for these Asian apes than expected from the earlier descriptions of a strictly monogamous mating system.

Acknowledgements

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Z. Säugetierkunde **60** (1995) 189–190

Effect of weather and snow factors on the mobility of the Red Squirrel (*Sciurus vulgaris* Linnaeus, 1758) in the forest zone of Finnish Lapland

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Our previous research in the forest zone of Finnish Lappland (Pulliainen 1973) showed that the European red squirrel (*Sciurus vulgaris* Linnaeus, 1758) tends to reduce its mobility to a very low level in midwinter, when the days are shortest and temperatures generally the lowest. We have continued these gross activity surveys, and have also carried out a tracking study on the effects of weather and snow conditions on the mobility of these mammals for one winter. The present note reports our new findings.

The tracking was carried out in November-March 1991/92 in the Värriö Nature Reserve, eastern forest area of Finnish Lapland (67°44′ N, 29°37′ E). This is an area populated by conifers, birch and mixed forests of the taiga type, and can be characterized as being in a virgin state and uninhabited. The forests are old and mature, and the density of trees is generally very low. In some areas there are young spruce and pine saplings among the very old trees. When possible, squirrels were followed during their movement from one drey to the next, the tracking being carried out on skiis. Sometimes the observer was able to keep the animal in view the entire time, but sometimes it was only seen occasionally or not at all. If the squirrel appeared to be disturbed by the observer, it was left alone. The tracking was not continuous, and the animals were not marked. Only the trackings from one drey to another (13 in November, 12 in December and 7 in January) were included for statistical testing, covering the period 9 Nov–23 Jan, when daylight lasts for 0–6 hours (see Pulliainen 1973). The mean monthly temperatures were –3.5 °C in November, –7.5 °C in December and –8.2 °C in January, and the minimum temperature on the days concerned was –15.2 °C.

Line transects in the area showed that the local squirrel population reached its peak in 1989/90 (7.0 crossings/10 km in December–March). Although the population was decreasing, the number of squirrels in winter 1991/92 was still relatively high (5.2 crossings/10 km). The squirrels were tracked for 51 km, consisting of 75 trackings. The mean distance travelled from drey to drey was 670 m (max. 3 030 m, min. 150 m, n = 32). The animals sank into the snow from 1 cm to 10 cm, and the more the squirrel sank the shorter was the day's journey (Spearman $r_s = -0.470$, $n = 32$, $p < 0.01$). Temperature, wind and cloudiness did not affect the activity of the squirrels.

The squirrels left the drey (83.3%, n = 49) and went into it (89.8%, n = 30) mainly by jumping from tree to tree. In 78.8% of the cases (n = 33), the squirrel returned to the same drey as it had left. Jumping from tree to tree was observed 0.8 times/100 m, the maximum continuous movement in the canopy being 80 m. The distance travelled in the canopy averaged 9.1% of the total day's journey. The more the squirrel sank into the snow

(Spearman $r_s = 0.531$, $n = 18$, $p < 0.05$) or the colder the weather ($r_s = -0.472$, $n = 32$, $p < 0.01$), the more the animals travelled in the canopy. Furthermore, the shorter the day's journey, the greater the part of it was performed in the canopy ($r_s = -0.766$, $n = 30$, $p < 0.001$).

The squirrel tracks were most often found in pine forest (71% of the tracking). According to direct observations, 70.6% of the feeding events were on Scots Pine, *Pinus sylvestris*, and 28.0% on Norwegian Spruce, *Picea abies.* Pine had a very good cone yield in the year concerned, but not the spruce, which produced only a few cones. The rest of the food consisted of mushrooms from caches at the bases of branches (0.8%) and berries (0.5%).

Two individuals in different colour phases were observed to live in the same 0.24 km^2 area of pine forest and to feed together at least in the interval 1 Dec 1991–6 March 1992, and were observed on nine occasions to share one of the four nests found in the area.

In summary, temperature, wind and cloudiness did not affect the activity of the squirrels, whereas sinking into the snow reduced the length of the daily journey and the squirrels moved from the surface of the snow into the canopy of the trees. This latter change was also prompted by low ambient temperatures.

Tonkin (1983), reviewing earlier research of effects of weather on squirrel activity, showed that contradictory conclusions can be drawn from the effect of a particular weather factor. Thus, it is easy to find support for the present results. This emphasizes the complexity of the background of the response, which comprises at least the condition of the individual in question, the availability of food and the structure of the microhabitat, together with the various weather factors.

Our earlier studies (Pulliainen 1973) showed that winter dreys are very important for thermoregulation in the European red squirrel, as it is able to keep its drey temperature 20–30 °C degrees above the ambient air temperature. When food is scarce, it may be more reasonable to stay in the drey at very low temperatures instead of attempting to find something to eat (Pulliainen 1973). During the present survey, when pine seeds were plentiful and the temperature was not very low, energy was conserved by avoiding moving about on the surface of the very soft snow. Probably greater speed was also attained when jumping from tree to tree than when trying to move in the soft snow.

One detail also worth noting here is the case in which two individuals shared the same nest. Wauters and Dhondt (1990) reported that nest sharing is rare and usually occurs only between partners in the mating season, most nests being used by only one squirrel. The present case was recorded outside the mating season, in a situation in which empty dreys were available in the vicinity.

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Buchbesprechungen

Priede, I. G.; Swift, S. M. (eds.) **Wildlife Telemetry:** remote monitoring and tracking of animals. Ellis Horwood Series in Environmental Management, Science and Technology. Chichester: Ellis Horwood Ltd 1992. 708 pp. ISBN 0-13-957994-X

For more than a decade telemetry and radiotracking have been integral components of the standard methods employed in behaviour-biological and physiological field research. At the beginning of the 1980s, publications dealt primarily with the technique of transmitters and receiving sets. Over the past few years the number of publications concerned with observational results has increased exponentially: The present volume deals with both, technique and research results. It contains contributions from the Fourth European Meeting on Wildlife Telemetry, University of Aberdeen. History and possibilities of telemetry are well presented in an overview article. 19 chapters deal with technical problems, 9 with radiotracking in general and with satellite assistance in particular, 5 with evaluation methods, 18 with telemetry used on fish and crustaceae, 9 with telemetric work on small terrestrial animals, 9 with telemetric studies on birds, and 7 chapters bring results obtained on larger animals. Examples taken from mammalian research are presented in 16 reports (field mice, rodents, predators, seals, wild boar, wallaby). This enumeration shows the richness of this volume; it is surely the most comprehensive survey published to date. The individual articles contain a variety of different information, some of which are very short. Altogether, the more than 70 articles provide an abundance references from the literature. As software plays an important role when evaluating telemetric data, an appendix refers to 7 software packages and their possible usage.

This book can be highly recommended to those using telemetry in order to check critically their own work; there are numerous suggestions and possibilites for further planning in this field.

R. Schröpfer, Osnabrück

Klös, H.-G.; Frädrich, H.; Klös, U.: **Die Arche Noah an der Spree.** 150 Jahre Zoologischer Garten Berlin. Eine tiergärtnerische Kulturgeschichte von 1844–1994. Berlin: FAB-Verlag 1994. 504 S.; über 600 Abb. DM 48,–. ISBN 3-9227551-29-5

Zoologische Gärten finden heute in mannigfacher Sicht das Interesse breiter Öffentlichkeit. Begegnungen mit einer Vielfalt von Tieren auf engerem Raum in fast greifbarer Nähe führen zu persönlichen Erlebnissen, die weder bildliche Darstellungen noch moderne Filme zu ersetzen vermögen. Dies belegt die sehr hohe Besucherzahl moderner Zoologischer Gärten. Doch es werden auch Stimmen laut, welche sich zu Tierhaltungen in Zoologischen Gärten sehr kritisch äußern. Sehr oft beruhen solche Stellungnahmen auf unzureichender Kenntnis moderner Betreuungsweisen. In modernen Zoologischen Gärten ist die Tierhaltung meist artgerechter als jene vieler Heim- oder Haustiere. Gewiß lassen sich in biologischer Sicht gegen Tierhaltungen in früheren Menagerien viele Einwände erheben, obgleich auch diese die Menschen in damaliger Zeit faszinierten. Seither hat sich in der Haltung von Zootieren eine bemerkenswerte Änderung vollzogen; Zoologische Gärten sind zu Stätten geworden, welche dem Fortbestand bedrohter Tierarten dienen.

Die Entwicklung eines Zoologischen Gartens macht das lebendig geschriebene Buch des Ehepaars Klös und Hans Frädrich deutlich. Sie berichten über Aufbau und Ausbau des vor 150 Jahren gegründeten Zoologischen Garten Berlins, der weltweite Anerkennung genießt. Dies verdankt er tatkräftigen, kenntnisreichen Direktoren, denen es gelang auch schwierige Zeiten und die weitgehenden Zerstörungen nach dem 2. Weltkrieg zu meistern. Es gelang nicht nur ein Wiederaufbau, der den Tieren artgemäßere Bauten schuf, auch in der Ernährung und Betreuung vollzogen sich artgerechte Fortschritte. Darüber geben Berichte verschiedener Reviertierpfleger interessante Sachverhalte zumal über gehaltene Tiere und deren biologische Besonderheiten Hinweise gegeben werden.

Das Werk ist gewinnbringend für kulturgeschichtlich Interessierte, für Zoofreunde und für Zoologen. Meine eigene Verbundenheit mit Zoologischen Gärten begann als Schüler in Halle. Als Student erlebte ich 1927 eine eindrucksvolle Führung durch Geheimrat Dr. Ludwig Heck und Dr. Oskar Heinroth im Berliner Zoo. Seither verfolge ich die Geschicke des Berliner Zoologischen Gartens mit Anteilnahme. Die jetzt vorgelegte Zusammenschau habe ich als Erinnerungserlebnis genossen.

W. Herre, Kiel

Buchbesprechung

Born, E. W.; Dietz, R.; Reeves, R. R. (eds.): **Studies of White Whales (*Delphinapterus leucas*) and Narwhals (*Monodon monoceros*) in Greenland and adjacent waters.** Meddelelser om Grönland, Bioscience **39**, 1994; Commission for Scientific Research in Greenland. 259 pages, many illustrations and tables, four colour plates. 380,– Danish Kroners, 55,– US Dollars. ISBN 87-601-4129-8, ISSN 0106-1054. Distributed by Danish Polar Center, Strandgade 100 H, DK-1401 Copenhagen K, Denmark.

In this Danish series of publications contributing to the fauna and flora of Greenland, a special issue deals with two Arctic whale species, the white whale or beluga (*Delphinapterus leucas*) and the narwhal (*Monodon monoceros*). Both cetacean species are not only found in Greenland waters, but are circum-Arctic marine mammals. Most of the twenty studies in this book are multi-authored and researchers from Denmark, Greenland and Canada represent the main contributors. However, authors from Norway, the United Kingdom, Germany and Hong Kong have also contributed to this book. Nine contributions deal exclusively with the white whale, seven exclusively with the narwhal and four articles present data on both species.

After an introductory overview written by the three editors, six studies deal with the "Distribution and abundance", especially of the narwhal and, in less detail, of the beluga. Four articles present balanced information on "Exploitation and status" of both Arctic whale species and the following section consists of one contribution on "Habitat and behaviour" of the narwhal and another on the white whale. The book concludes with seven studies dealing with different subjects which are compiled under the heading "Life history, stock identity and toxicology".

The narwhal is an ice-associated cetacean and the studies dealing with its distribution and abundance are mainly based on aerial surveys or on observations from high vantage points on cliffs. On the other hand, studies dealing with the beluga or white whale are based mainly on opportunistic observations by hunters and local residents, or from mariners. In East Greenland, at least, the difficulty to observe white whales might not only be related to the rarity of this species in this area, but also to the general lack of suitable shallow-water habitats (Dietz et al., pages 69–86). On the other hand, narwhals "were concentrated in waters 350 m or more in depth ..." in waters of the Canadian High Arctic (Richard et al., pages 41–50).

Savelle (pages 101–117) contributes a study on the prehistoric exploitation of white whales and narwhals in the eastern Canadian Arctic. The Palaeo-Eskimo population living in this area before 1000 A. D., probably lacked a sophisticated whale-hunting technology. The two cetacean species are extremely rare in these archaeological sites. In Inuit sites subsequent to 1000 A. D. white whale and narwhal remains are more common, but make up relatively insignificant portions of the total faunal assemblages. The author speculates that the two whale species might not have contributed to the diet of the Inuit during prehistoric and early historic times.

The last study published in this book (Stern et al., pages 245–259) immerses the reader into the problems of the 20th century: Blubber, skin and kidney samples of the white whale from northwest Greenland were analysed for polychlorinated biphenyl compounds (PCB's) and other organochlorines. The highest contaminant levels were observed in animals of about three months of age, very probably because lower chlorinated PCB's and more water-soluble organochlorines are preferentially transferred during lactation.

The original material published in this volume, of which just a very small selection was mentioned above, contributes to the understanding of and gives valuable information on two fascinating species of marine mammals that live in a forbidding environment. The present reviewer missed two additional sections in this book: An index that would make the wealth of information more readily acessible, as well as a list of the authors and their addresses.

P. Langer, Giessen

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A laboratory study of agonistic behaviour in the Red musk shrew, *Crocidura flavescens* (I. Geoffroy, 1827)

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Abstract

Investigated the agonistic behaviour in male and female *Crocidura flavescens* under conditions of increasing confinement in the laboratory. Nine sexually mature shrews (four male and five female) were used and six paired encounters were run for each sex. Initially each pair was confined to 1 800 cm^2 but this was reduced to 900 cm^2 and finally 450 cm^2 before the encounter was ended. No encounter lasted more than 12 minutes and all audible and visible behaviour was recorded. Two encounters were filmed for analysis.

Seven postures and 16 other non-fighting behaviours can be distinguished and the frequency of eight of these differs significantly between the sexes. These components of agonistic behaviour may have preparatory, sensory, communicative and regenerative value and a hierarchy, which would preclude fighting under natural conditions, may exist.

Males are significantly more aggressive than females both in the frequency and latency of fighting. Increasing spatial confinement significantly increases the frequency of fighting in both males and females.

C. flavescens is considered to be asocial with males indicating a greater tendency for territorial behaviour through being more aggressive and scent marking more frequently than females.

Introduction

In general, studies on the agonistic behaviour and social organization of shrews have been restricted to European and North American species in captivity; inter alia *Sorex araneus* (Crowcroft 1957), *Blarina brevicauda* (Olsen 1969), *Crocidura russula* (Vogel 1969), *Neomys fodiens* (Michalak 1983) while Goulden and Meester (1978) and Baxter and Meester (1980, 1982) have provided some qualitative data on some southern African species. Field studies on social organization and territoriality in inter alia *B. brevicauda* (Platt 1976) and *C. russula* (Cantoni and Vogel 1989) as well as inter- and intraspecific competition in *S. araneus* and *S. minutus* (Croin Michielsen 1966) provide valuable data.

As yet, no detailed quantitative research on agonistic behaviour has been conducted on an African soricid. Consequently, this study was undertaken to describe, analyse and determine the possible functions of the components of agonistic behaviour in *Crocidura flavescens* as well as determine whether differences exist between males and females in this regard.

C. flavescens is a large shrew with a mean total length of 149.1 mm (Meester 1963) and usually a mass of between 20 and 30 g. There is significant sexual dimorphism (Meester 1963) with a mean mass difference of 4.5 g in favour of males (Rautenbach 1978).

Material and methods

The shrews were trapped during winter in Scottsville, Pietermaritzburg using PVC livetraps (Willan 1979) baited with minced oxheart. Prior to experimentation all shrews had attained sexual maturity. Exact ages were not determined but all would have been born during the preceding summer because older adults do not appear to survive the onset of a second winter (Baxter 1977).

Captive shrews were kept singly in glass aquaria (60 × 30 × 30 cm) under semi-controlled conditions at 20–25 °C with a 14 h : 10 h light : dark regime. The minimum period in captivity prior to experimentation was four weeks. During this period the animals were sexed and marked in order to allow easy individual recognition.

All trials were carried out in a neutral, territorially unproclaimed glass aquarium (floor area = 1 800 cm^2) which had 5 cm of soil in the bottom. After each trial, the area was swept thoroughly to disperse odour left by scent marking, all faeces were removed and the inner surface of the glass was cleaned with a wet cloth. The trial area could be partitioned into two separate areas of variable size by inserting a sheet of hardboard. All trials were run indoors between 10.00 h and 18.00 h when the activity profile of captive *C. flavescens* approximates to its mean daytime value in captivity of 13% (Baxter et al. 1979). Light was provided by fluorescent tubes and daylight, and temperature ranged from 18–25 °C. Noise and disturbances were kept to a minimum. No two shrews encountered one another more than once and then always one of the same sex.

The male sample (n = 4) allowed six paired combinations without repetition and although there were five females, only six trials were run so that the resultant data were more readily comparable. All trials involving a specific individual were run at least 24 hours apart in order to prevent fatigue. Trials were run by partitioning the trial area, releasing a shrew into each half and allowing them to settle down for about a minute. The pairs were subjected to three conditions of increasing spatial confinement; 1 800 cm^2, 900 cm^2 and 450 cm^2. This meant that one of the shrews was progressively forced into the area occupied by the other. This method would have biased the results if winners/losers were being determined but as this was not the case, potential bias was nullified.

Initially the partition was removed for 5–6 minutes, resulting in the two shrews being jointly enclosed in a total area = 1 800 cm^2. Thereafter they were again separated for 30 s. The shrews were then confined in one half of the trial area (900 cm^2) for 2.5–3 minutes, briefly separated again, before being confined in one quarter of the area (450 cm^2) for 2.5–3 minutes. The shrews were then returned to their "home" aquaria.

The full duration of each trial was timed and all visible and audible behaviour was recorded by dictation into a cassette tape recorder. This provided data regarding the nature, frequency and duration of observed behaviours. Two encounters, one between males and another between females, were filmed using a cine camera (Paillard-Bolex H16 Reflex) with lighting provided by a 500 watt incandescent bulb supported 120 cm above the trial area.

Results

Statistical analysis

The total time spent under all conditions by males was 62 min 30 s and by females, 76 min 20 s. The total number of fights (directed aggressive physical contact) was recorded under each condition and fighting frequency (fights/min) for both sexes was calculated for these conditions (see Tab. 1), and then subjected to a Friedman two-way analysis of variance (Siegel 1956).

The effect of confinement in increasing fighting frequency was found to be highly significant in both sexes (M, $p = 0.0046$; F, $p = 0.0007$). Neither males ($p = 0.446$) nor females ($p = 0.5$) differed significantly among themselves. Mean fighting frequency was calculated for each shrew across all three conditions (Tab. 1) and males showed an overall mean significantly higher than that of females ($p = 0.016$).

The mean latency of fighting under condition 1 (1 800 cm^2), being the time from removal of the partition to the first fight or in the case of some females the period in which no fighting occurred, was 60 seconds in males and 4 min 28 s in females (three females did not fight). Males came into conflict significantly sooner than females ($p = 0.013$) indicating a higher level of agonistic activity.

Table 1. Mean frequencies of fighting for each individual shrew under each experimental condition. The means were obtained from three trials for each male and three or less for each female.

Male *C. flavescens*					Female *C. flavescens*				
Area/ shrew	1 800 cm^2	900 cm^2	450 cm^2	$\bar{x}$(M)	Area/ shrew	1 800 cm^2	900 cm^2	450 cm^2	$\bar{x}$(F)
M1	1.66	4.58	7.79	**3.13**	**F1**	0.17	1.29	6.80	**0.92**
M2	2.22	2.30	13.00	**3.37**	**F2**	0.22	1.78	6.97	**0.98**
M3	1.12	3.22	5.65	**2.06**	**F3**	0.00	1.24	5.65	**1.52**
M4	1.57	4.77	12.00	**3.50**	**F4**	1.04	3.16	6.40	**2.50**
					F5	0.80	1.60	5.23	**1.73**
$\bar{x}$/area	**1.64**	**3.71**	**9.61**		**$\bar{x}$/area**	**0.45**	**1.81**	**6.21**	
	Overall mean (M)			**3.01**		**Overall mean (M)**			**1.52**
	S.D.			**0.654**		**S.D.**			**0.635**

Postures

Seven postures were distinguished in *C. flavescens* and the differences between the sexes in their frequency of occurrence, as well as those of a variety of other behaviours associated with agonism, are summarized in table 2.

Hunched: This is a squat posture with the head lowered and back slightly arched. Unlike freezing it often involves walking or, when seen in resting shrews, is associated with grooming, scratching and orientation reactions (Fig. 1 A).

Raised I: This is a quadrupedal stance similar to Hunched but with the head raised in orientation to sensory stimuli (Fig. 1 B).

Raised II: This is an extension of Raised I with the forequarters raised 1–2 cm above the substrate by extending the forelimbs (Fig. 1 C). This posture was noted in *Crocidura flavescens herero* (= *C. occidentalis* MEESTER et al. 1986) by MARLOW (1955). Raised I and II are referred to collectively as "stance" by OLSEN (1969) and PLATT (1976), and are often accompanied by vocalization and bared teeth. They may precede either avoidance or attack.

Hunched and Raised I and II are more common in females.

Tripedal: This is an important preparatory posture characterized by raising the forefoot nearest the opponent shrew (Fig. 1 D). Tripedal posture is known in several soricids (OLSEN 1969; PLATT 1976). It may precede or follow a number of other behaviours. It is regarded as aggressive by PLATT (1976) and is more common in *C. flavescens* males.

Sideways: This is a side-on orientation of the body to the opponent (tripedal or quadrupedal) and is usually defensive. This posture may lead to the shrew rolling over with the fore- and hind limb on one side raised, exposing the belly, and ultimately to "Tantrum". In *C. flavescens* the sideways posture was always very brief and was significantly more common in males ($p = 0.032$). PLATT (1976) considers this to be a submissive posture.

Rearing: This is equivalent to the 'upright' posture described by OLSEN (1969), involving raising the body to a vertical position on the hind limbs, exposing the ventrum. This posture is well known in intraspecific conflicts in shrews (CROWCROFT 1957; EISENBERG 1964; OLSEN 1969; BAXTER and MEESTER 1982). It is usually accompanied by vocalization

Table 2. Summary of observed agonistic behaviours in *Crocidura flavescens* showing the observed frequency of occurrence of the behaviours as well as the frequencies per unit time. The probabilities reported were obtained by testing for differences between the frequencies per unit time for males and females. An asterisk indicates significance at the 95% level and the final column indicates in which sex the behaviour is most common.

Behaviour		Duration of M encounters 62 min 30 s		Duration of F encounters 76 min 20 s			Most common in … M/F
		Frequency of Occurrence	Frequency per Unit Time	Frequency of Occurrence	Frequency per Unit Time	Probability	
Postures	Hunched	5	8.0	12	15.7	0.119	F
	Raised I	2	3.2	3	3.9	0.206	F
	Raised II	13	20.8	17	22.2	0.278	F
	Tripedal	21	33.6	6	7.8	0.278	M
	Sideways	7	11.2	2	2.6	0.032*	**M**
	Rearing	6	9.6	3	3.9	0.206	M
	Tantrum	17	27.2	5	6.5	0.095	M
	Baring teeth	9	14.4	10	13.0	0.548	
Passive avoidance	Freezing	7	11.2	29	37.9	0.016*	**F**
Active avoidance	Running	11	17.6	8	10.4	0.321	M
	Jumping	19	30.4	6	7.8	0.024*	**M**
	Escape	15	24.0	22	28.8	0.206	F
Approach		25	40.0	24	31.4	0.365	M
Attack	Chasing and biting	43	68.8	13	17.0	0.016*	**M**
	Jumping	9	14.4	3	3.9	0.056	M
	Hopping	16	25.6	3	3.9	0.024*	**M**
Fighting		187	299.0	103	134.8	0.016*	**M**
Other activities	Grooming	26	41.6	31	40.5	0.365	F
	Scratching	3	4.8	4	5.2	0.365	F
	Digging	20	32.0	9	11.7	0.056	M
	Redirected attack	4	6.4	0	0	0.001*	**M**
Scent marking	Flank	2	3.2	0	0	0.001*	**M**
	Chin	24	38.4	6	7.8	0.032*	**M**
	Anal	4	6.4	3	3.9	0.452	M

and 'boxing' with the forepaws (Fig. 2 A). However, when observed under neutral conditions in *C. flavescens* Rearing was transient, usually leading immediately to either avoidance or "Tantrum" postures. It was observed twice in an inoffensive situation when a shrew reared up to scent the air with the tail providing extra support. Rearing is more common in males and is probably submissive.

"Tantrum": This was called 'back' by Olsen (1969) and may be described as a period (1–8 s) of vocalization and kicking while the shrew lies on its back, with the head slightly

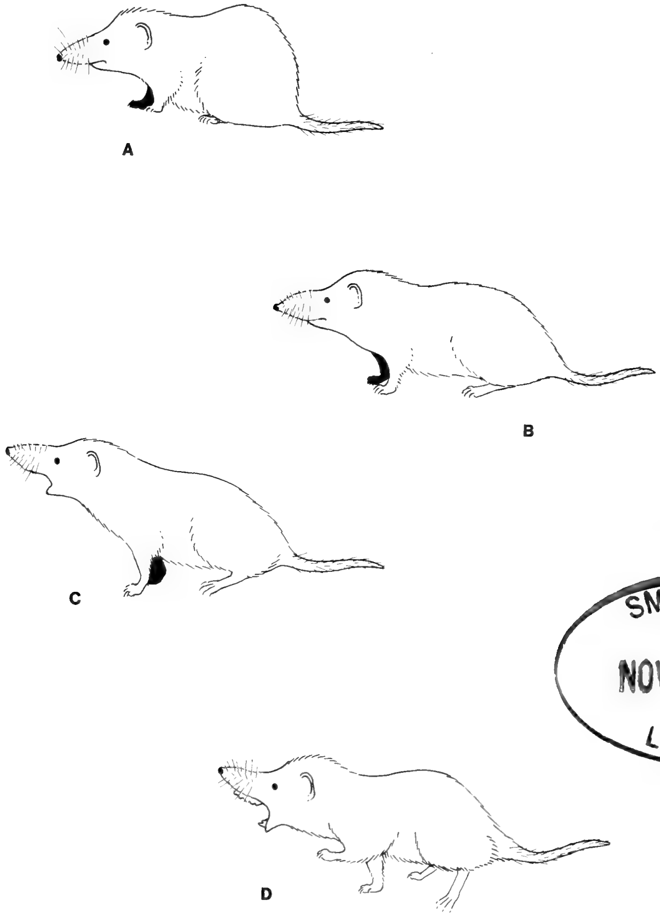

Fig. 1. Some postures seen during agonistic encounters; A. Hunched; B. Raised I; C. Raised II; D. Tripedal with teeth bared.

raised. It is considered submissive here, as in PLATT (1976), but BUNN (1966) considers it dominant.

"Tantrum" did not always result in cessation of attack. Frequently both shrews performed this behaviour simultaneously after a fight. "Tantrum" always followed either Sideways or Rearing postures. It was more common in males ($p = 0.095$) (Fig. 2 B).

No characteristic tail postures were noted in *C. flavescens.* EISENBERG (1964) and OLSEN (1969) have noted such postures in *Sorex* and *Blarina* sp. and HANSELL and AITKEN (1977) refer to tail-lashing in *Sorex*. Stamping of the forefeet (PLATT 1976) was not seen in *C. flavescens.*

Baring of the teeth with the lips drawn back to reveal the upper premolars was noted in all postures except Hunched. Exposure of the teeth while vocalizing was not regarded as 'baring teeth', hence the low recorded frequency of this activity in table 2.

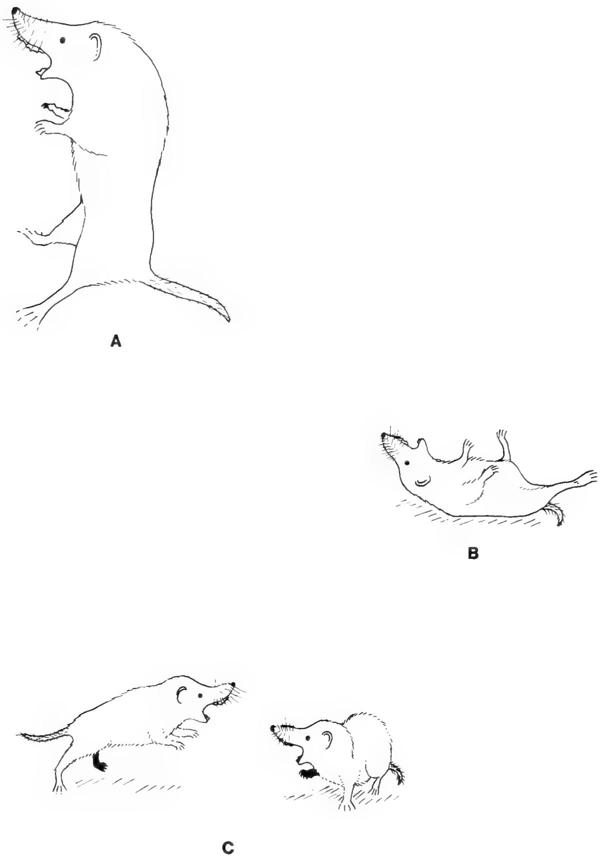

Fig. 2. Additional postures seen during agonistic encounters; A. Rearing; B. "Tantrum"; C. A hopping attack against a tripedal, sideways *C. flavescens.*

Vocalization

This occurred in all individuals and had communicative value. The short high-pitched squeak which is characteristic of agonistic behaviour, is known in many soricids (see inter alia Gould 1969; Baxter and Meester 1982; Churchfield 1990). In *C. flavescens* it showed frequencies of 10–50 kHz, and was emitted singly or in sporadic bursts and associated with all activities except the Hunched posture, freezing, grooming, scratching and scent marking.

Platt (1976) reported vocalization in nine out of ten tripedal and all quadrupedal 'stances'.

Avoidance

Passive avoidance (freezing) resulted in the entire shrew, except the vibrissae and snout, being immobile. Freezing was seen to occur in Hunched, Raised I and II and Tripedal postures; it was significantly more common in females ($p = 0.016$). Active avoidance involved running and jumping. Mutual avoidance, however, was overall the most common behaviour pattern noted, but decreased in frequency under more confined conditions. It occurred most often on accidental physical contact, whereupon both shrews would leap apart and possibly vocalize, as has been reported by CROWCROFT (1957), EISENBERG (1964), BAXTER and MEESTER (1980, 1982).

Running was generally thigmotaxic and often led to the shrews encountering one another yet again whereupon fighting occurred. It was more common in males, as was avoidance by jumping over or away from the opponent shrew ($p = 0.024$). OLSEN (1969) reported jumping as a means of avoidance in *B. brevicauda*. Avoidance was sometimes preceded by Raised, Tripedal, Sideways or Rearing postures in *C. flavescens*.

It appears then that males, being more active under the experimental conditions, attempted to avoid one another by actively running or jumping. More activity resulted in frequent contact, reflected in the high frequency and low latency of fighting. In contrast, females moved about less than males, avoiding one another passively by freezing and hunching at opposite ends of the trial area. The result was fewer physical contacts, shown by their low frequency and high latency of fighting.

All individuals unsuccessfully attempted to escape from the trial aquarium by jumping or by digging under the partition when it was in place. This behaviour was more common in females.

Approach

This was defined as locomotion directed towards the opponent shrew regardless of the orientation of the shrews relative to one another. It occurred with similar frequency in males and females and included running and walking but not hopping or jumping.

Attack

This involved directed antagonistic behaviour such as biting and chasing and was sometimes mutually undertaken. OLSEN (1969) considered chasing rare on neutral ground while EISENBERG (1964) found that almost all chasing, fighting and flight occurred during interaction between strange shrews. In *C. flavescens* attack was significantly more frequent in males ($p = 0.016$).

In hopping attacks (Fig. 2 C) the forefeet were lifted clear of the ground as the shrew moved towards its opponent in jerky hops of 0.5–1.5 cm. Hopping attacks were significantly more common in males ($p = 0.024$).

In jumping attacks the aggressor jumped onto its opponent from a distance of 5–15 cm. Again, this was significantly more common in males ($p = 0.056$).

Other activities

These were evident during the agonistic behaviour of *C. flavescens*. Grooming consisted of rubbing the muzzle, and nibbling and licking the forepaws. Scratching of the body was done with either hind foot. They were performed in the Hunched posture only, consequently occurring more frequently in females.

Digging was more common in males ($p = 0.056$) and usually occurred after fighting. It could be distinguished from escape attempts as it was performed aimlessly, was never prolonged, and was frequently accompanied by vocalization. The hind feet were often employed to some extent, unlike directed digging where only the forefeet were used.

Redirected attack on the sides of the trial aquarium, or on what appeared to be an invisible opponent, occurred only in males and was rare, usually beginning as a jump and leading to digging, running, or further jumping. It most probably indicates a higher level of agonistic arousal.

Scent marking

This can be performed in three different ways (Baxter and Meester 1982). Flank marking using the lateral glands was seen only in males. Neck marking, the most commonly used method in *C. flavescens* which involves ploughing the chin and neck along the substrate with slight side to side movements, was significantly more frequent in males ($p = 0.032$). Dryden and Conaway (1967) regard the neck glands as the most important area for scent production. Anal marking is described as 'ventral rub' by Platt (1976) who found it more common in males of *B. brevicauda*. It involved dragging the ventral surface (especially the anogenital region) along the substrate, often with a concave shaping of the back. It was performed with approximately equal frequency by both sexes although Baxter and Meester (1982) noted it only after fighting in males.

As scent is used for territorial demarcation in shrews (Platt 1976) the frequency of scent marking may be regarded as an index of territoriality. Neutral ground may be rapidly proclaimed as territory. This was suggested by the frequent return of each shrew to the end of the trial area into which it was first released, before commencement of regenerative behaviour or scent marking. The higher frequency of scent marking in males suggests that they are territorial, which would coincide with their aggressiveness and low tolerance of conspecifics.

Perception

There are no quantitative data on the acuity of the various senses in soricids. Vision appears to be poorly developed, as no evidence of visual communication has been found (Gould 1969; Churchfield 1990). A mirror placed in the trial aquarium with a single male *C. flavescens* elicited no agonistic behavioural response.

Olfaction appears to play an important role in agonistic behaviour, as suggested by the frequency of scent marking and by smelling of the air and surroundings by shrews in Hunched, Raised I & II and Rearing postures.

Tactile cues were used extensively. The mystacial vibrissae were extremely sensitive to stimulation; accidental contacts were frequently avoided by tactile sense when the two shrews appeared to be unaware of one another's positions in the trial area.

Hearing is acute in shrews (Gould 1969; Grünwald 1969; Baxter and Meester 1982), but unlike some other soricids (Gould et al. 1964; Buchler 1976; Tomasi 1979), *C. flavescens* does not echolocate (Irwin and Baxter 1980).

Directed vocalization by an opponent in a Raised II or Tripedal posture often resulted in an instantaneous orientation reaction (Raised I, II or Tripedal postures) or fear reaction (passive or active avoidance) in the perceiving shrew. Similar reactions occurred in response to digging, movement of the partition, and voices.

The relationship between the observed behaviours are summarized in figure 3.

Discussion

The functional value of the postures and associated agonistic behaviours may be assessed from the point of view of the animals performing them, to which the outcome is of primary importance. Four functions are proposed; preparatory, sensory, communicative and regenerative.

Preparatory: All these behaviours begin either tri- or quadrupedally and the include Raised I and II, Tripedal, Sideways and Rearing postures, and baring the teeth. Each of these prepares the animal for either fighting or avoidance.

Sensory; Freezing, Hunched, Raised I and II, Tripedal and to a lesser extent Sideways and Rearing postures are involved in sensory orientation. Hunching is a lower-order sensory posture, which through stimulation gives rise to higher-order postures such as Raised II and Tripedal. Sideways has limited sensory function while freezing is a higher-order sensory (and passive protective) behaviour, always accompanied by olfaction.

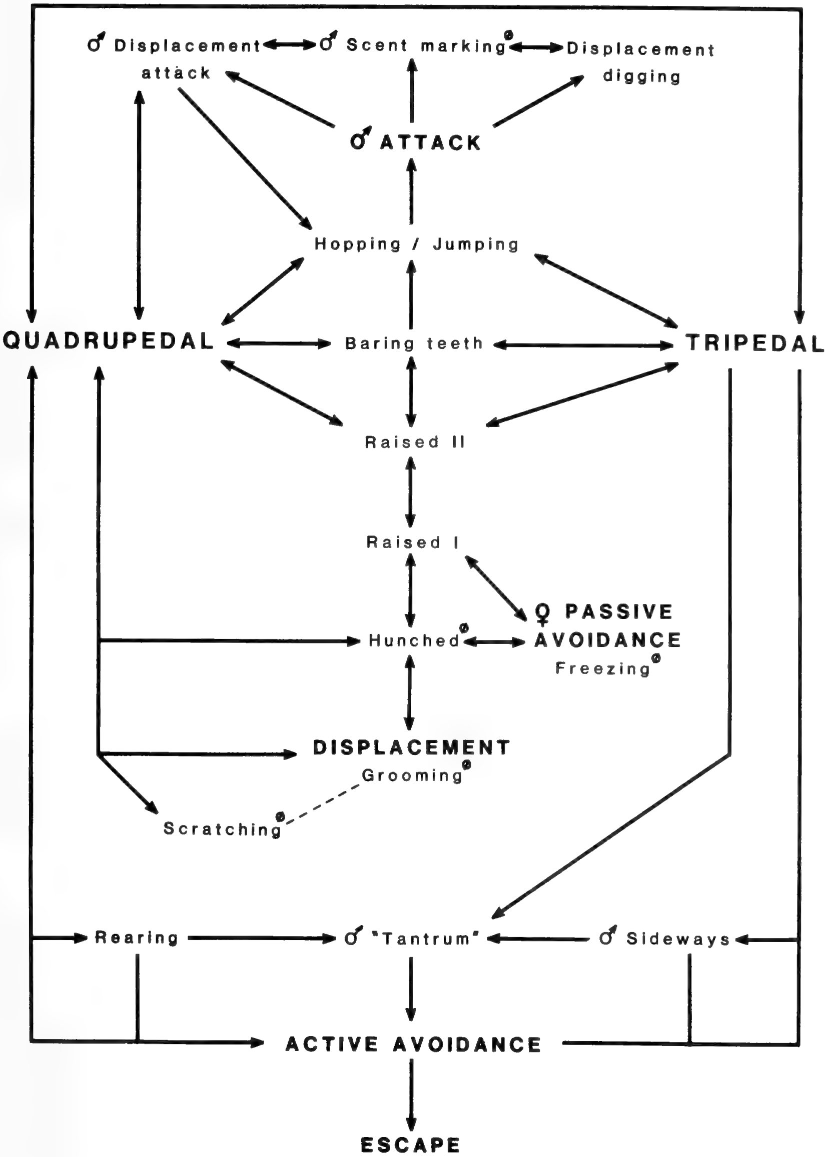

Fig. 3. The progression of and relationship between the observed agonistic behaviours. The presence of ♂ or ♀ signs at a particular behaviour indicates that it is significantly more common in that particular sex. (∅ indicates absence of vocalization.)

Communicative: Probably the most important function of posturing is communication. It is doubtful whether postures have any visual communicative value (Gould 1969), considering the poor vision of soricids.

Olsen (1969) considered the five postures of *B. brevicauda* to have 'threat' and possibly species-recognition function, as they served to intimidate conspecific opponents.

The signal value of Raised I and II, Tripedal, Sideways, Rearing and "Tantrum" postures is mainly the accompanying vocalization, which has high communicative value. All of the above also expose scent-producing areas on the body. The most important area, the neck (Dryden and Conaway 1967), is exposed Raised I and II, Tripedal and Rearing while lateral glands are exposed in Sideways and Rearing and anogenital glands in Rearing and "Tantrum" postures. Baxter and Meester (1982) suggest that exposing the neck in the raised posture acts aggressively by transmitting individual odour to the opponent.

Olsen (1969) suggests that scent may also be related to the species-recognition function in reducing conspecific predation. Cannibalism is, however, known in captive shrews (Baxter and Meester 1982) and attack on the ventral surface is not always inhibited by submissive and scent-emitting postures.

Regenerative; Sporadic interludes in fighting occurred by 'mutual consent' in all trials, and were characterized by hunching postures to groom and lick wounds. It is doubtful whether such a stage would be reached in agonistic behaviour under natural conditions where avoidance may be more permanent.

A hierarchy of behaviours may be suggested for agonistic interactions in *C. flavescens*.

1. On neutral ground, vocalization (in Raised I, Raised II or Tripedal posture) and mutual avoidance would occur.
2. Should one shrew persist in aggressive behaviour, as in territorial conflicts, chasing and avoidance would ensue.
3. If long-term avoidance (escape) is not possible in 1 or 2 above, posturing would become more intense.
4. If these mechanisms failed to achieve separation of the two shrews, fighting would ensue.

C. flavescens (and probably most other soricids) would therefore only fight if other separating mechanisms lower in the hierarchy failed. The four levels described in this hierarchy correspond with the four levels of aggression described by Baxter and Meester (1982).

Under natural conditions fighting between shrews is a rare occurrence (Crowcroft 1957; Eisenberg 1964; Olsen 1969), with mutual avoidance being the predominant response to contact on neutral ground and chasing and active avoidance the main responses to territorial conflict (Crowcroft 1957). Churchfield (1990), however, has observed fighting under natural conditions.

The results of this study indicates that *C. flavescens* males are more aggressive and perform more scent marking than females. The fact that they are both highly aggressive, suggests they both maintain territories but that the females' territories are less rigorously maintained. It is likely that they are asocial as Baxter (1977) has indicated that when paired in captivity, the individuals show continuing aggression for up to a week, before nesting together. After mating, the female becomes highly aggressive and drives the male from the shared nest. Under natural conditions, Baxter (1977) suggests that this manifest aggression would preclude any form of social organization other than asocial. The levels of aggression shown in this study tend to support this suggestion. Vogel (in litt.) has found the level of aggression shown by *C. flavescens* in contradiction with the high population densities he found in Mali, but Rowe-Rowe (pers. comm.) has found distinct territorial boundary between two wild males, thus supporting the suggestions of this study.

Vogel (1978) states that the Crocidurinae tend to show low territoriality and Cantoni and Vogel (1989) have shown that *C. russula* have communal nests in winter. They state further that the offspring are tolerated for several weeks after weaning, a situation very different from that of *C. flavescens*. BAXTER (1977) found that the young of this species have to be removed from their natal cage by Day 28 in order to prevent parent-offspring aggression which can lead to death. This, together with the fact that both male and female *Myosorex varius*, a species sympatric with *C. flavescens*, are relatively social in captivity (eight adults as opposed to two *C. flavescens*, cohabit peacefully in captivity (BAXTER unpubl. data), but maintain territories throughout the year (BAXTER and LLOYD unpubl. data), implies that the present suggestion of asocial territoriality in *C. flavescens* is valid.

Solitary habit and territoriality serve several functions in small predators, the most important of which is the reduction of intraspecific competition for the available food by spacing the population out evenly over the available habitat (CROWCROFT 1957; EISENBERG 1964; CROIN MICHIELSEN 1966; OLSEN 1969; PLATT 1976). Rigorous territoriality regardless of sex is found in *S. araneus* and *S. minutus* populations and is considered to have the primary function of conserving a food supply that will last through the winter when prey density is low. This is described as 'single unit' territoriality (one animal of the species per territory, without overlap); such territories alter their size and position in response to factors such as prey density and the energy requirements of the shrew populations (CROIN MICHIELSEN 1966).

M. varius does not show single unit territoriality (BAXTER and LLOYD unpubl. data) and one might expect the same in *C. flavescens* as the sub-tropical African climate is not as severe as that of the Northern temperate regions. It is doubtful whether the food supply is affected adversely enough in winter to demand 'single unit' territoriality in southern African soricids.

The territories of males and females may overlap (as has been found in *Myosorex varius* (BAXTER and LLOYD unpubl. data)) if competition for food is not intense. This overlap may increase during summer (when food is more readily available) allowing breeding to occur without the massive breakdown of territorial boundaries noted in *Sorex* (CROIN MICHELSEN 1966).

Obviously further research is needed to investigate the pugnacious *C. flavescens* and the nature of its aggression, preferably using marked animals in a field situation.

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Zusammenfassung

Eine Laboruntersuchung über das agonistische Verhalten der afrikanischen Roten Riesenspitzmaus, Crocidura flavescens (I. Geoffroy, 1827).

Diese Laboruntersuchung befaßt sich mit dem agonistischen Verhalten von männlichen und weiblichen *Crocidura flavescens* unter eingeschränkten Raumverhältnissen. Neun fortpflanzungsfähige Spitzmäuse (vier männliche und fünf weibliche) wurden untersucht indem Auseinandersetzungen in jedem Geschlecht durchgeführt wurden. Anfänglich standen jedem Paar 1 800 cm^2 Fläche zur Verfügung. Der vorhandene Raum wurde noch vor Beendigung der Auseinandersetzung auf 900 cm^2 und schließlich auf 450 cm^2 verringert. Keine Auseinandersetzung dauerte länger als 12 Minuten und alle akustischen und sichtbaren Verhaltensweisen wurden aufgenommen. Zwei Auseinandersetzungen wurden gefilmt, um anschließend im Detail untersucht werden zu können.

Sieben körperliche Stellungen und 16 andere nicht kämpferische Verhaltensweisen können unterschieden werden. Von den 16 nicht kämpferischen Verhaltensweisen unterschieden sich acht im Vor-

kommen ihrer Häufigkeit wesentlich zwischen den Geschlechtern. Diese Bestandteile des agonistischen Verhaltens könnten einen vorbereitenden, sensorischen kommunikativen und regenerativen Wert haben, und somit könnten Verhaltensweisen in bestimmter Hierarchie vorliegen, die unter natürlichen Lebensbedingungen kämpferische Auseinandersetzungen nicht aufkommen lassen.

Männchen sind wesentlich angriffslustiger als Weibchen sowohl in der Häufigkeit wie auch der Länge der Auseinandersetzung. Zunehmende räumliche Einengung steigert wesentlich die Häufigkeit der kämpferischen Auseinandersetzung sowohl bei den Männchen als auch bei den Weibchen.

Crocidura flavescens wird als unsozial betrachtet. Männchen zeigen eine größere Tendenz für territoriales Verhalten durch stärkere Aggressivität und häufigeres Duftmarkieren im Vergleich zu Weibchen.

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Seasonally dependent testicular apoptosis in the tropical Long-fingered bat (*Miniopterus inflatus*)

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Abstract

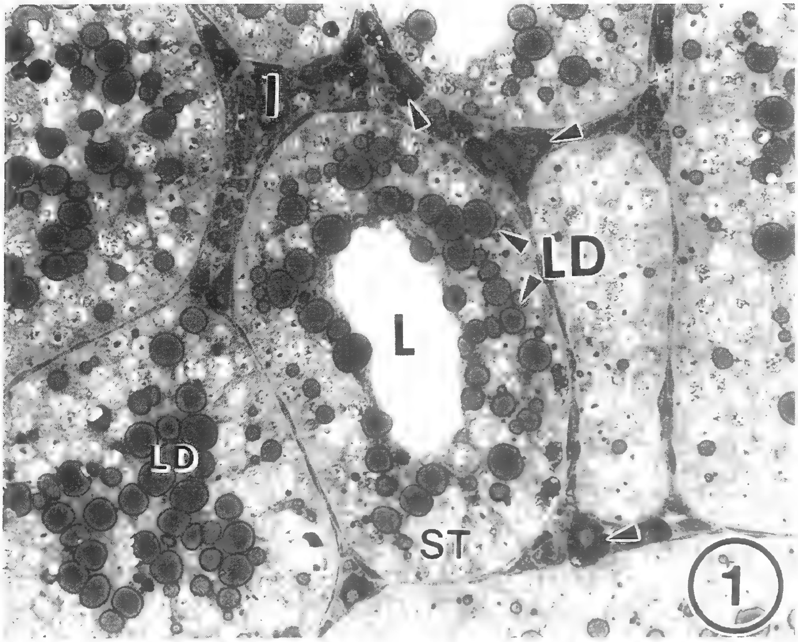
Testicular morphology of long-fingered bats trapped in March and early April (a period of sexual dormancy) was studied using both light and electron microscopy. The interstitial tissue, generally smaller in proportion to the seminiferous tubules, was largely made up of compactly arranged interstitial (Leydig) cells. Physiological cell death (apoptosis) was characterized by the occurrence of dense cytoplasm obscuring most of the subcellular organelles, myelin-like whorls of residual bodies and lipid inclusions in the cytoplasm, and roughly spheroidal nuclei. Normal mitochondria were round in outline. Some of these apoptotic cells were phagocytosed by the interstitial tissue macrophages. In the seminiferous tubules this degenerative process was marked by spermatogonial karyolysis, apoptosis of spermatocytes and extensive accumulation of large lipid droplets in the Sertoli cell cytoplasm. The tubular walls and lumen were completely devoid of spermatids and spermatozoa.

These observations suggest that the sexual dormancy in these bats is characterized by a marked apoptosis of testicular micro-structural components hitherto unreported.

Introduction

Long-fingered bats are members of the Miniopterinae subfamily occupying varying ecological niches ranging through most of the tropical old world; Africa, Madagascar, southern Europe, South-East Asia to Philippines, New Caledonia, Loyalty Islands and the northern areas of Australia (Kingdon 1974; Walker 1975; Hill and Smith 1984). Within the subfamily, there are eleven species (Hill and Smith 1984) of which three are well-known and widely distributed in Africa. These are; *M. minor* whose distribution is restricted to the tropical coast of Africa, Congo river and islands off Africa; *M. schreibersi* found in Australia, South-East Asia and southern Europe stretching down to Africa and the cape; and *M. inflatus* which is largely distributed in tropical Africa and sometimes found in areas adjacent to the more widely distributed *M. schreibersi* (Kingdon 1974; Smithers 1983). The distinction among the three species is often less clear-cut and measurements particularly those of the skull have been used to differentiate the individual members. The bats live in groups or clusters and primarily inhabit caves where they roost in dark crevices. They feed mainly on flying insects.

Reproduction in the temperate long-fingered bats is a unique phenomenon whereby mating occurs prior to winter hibernation and the reproductive activity remains dormant throughout the hibernation period (Courrier 1927; Gustafson 1979). Thus in females, the ovum is fertilized before hibernation and further development of the embryo is minimal during the same period (Kingdon 1974). In males, however, the reproductive system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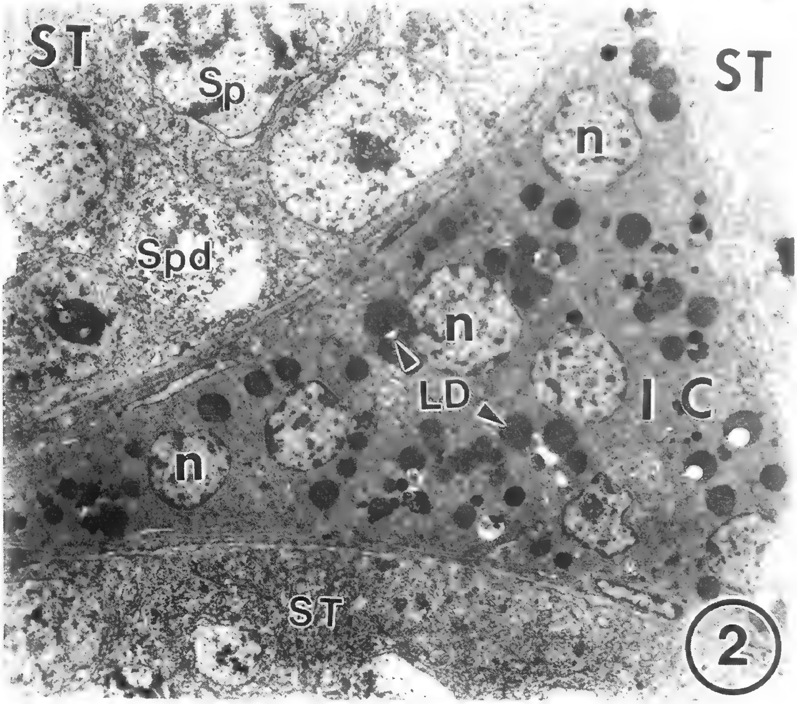
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regresses after mating but prior to hibernation (Courrier 1927). Available reports on the tropical species, *M. minor*, of the coastal region of Kenya similarly suggest a period of testicular degeneration followed by recrudescence (McWilliam 1988). These reports appear to have been based on behavioural as well as macro-anatomical observations. Consistently missing, however, are the micro-structural accounts of these degenerative changes. This study therefore aims at investigating the testicular micro-anatomical changes associated with the degenerative process in these bats during dormancy.

Material and methods

Thirteen bats trapped between March and early April at Mt. Suswa a few kilometers from Naivasha, Kenya were immediately transported to the laboratory and kept in temporary roosts overnight before commencement of the study. At the time of study, the bats were anaesthetized using chloroform, perfused with phosphate buffered 2.5% glutaraldehyde through cardiac puncture and the perfusate drained via the caudal vena cava. The testes were dissected out of the scrotum and further immersed in the same fixative for 24 hours. The fixed testes were then removed from the fixative, trimmed of excess fatty tissue, diced into approximately 1 mm cubes and processed for light and electron microscopy. In brief, the cubes were washed in phosphate buffer, post-fixed in osmium tetroxide, dehydrated in ascending concentrations of ethyl alcohol and embedded in epoxy resin mixture. Approximately 1 mm thick sections were obtained from the embedded tissues, stained with toluidine blue and observed under the light microscope. From the same blocks, 60 nm thick sections were obtained, mounted on 300 mesh copper grids, stained with uranyl acetate and counter-stained with lead citrate. The stained sections were then viewed under the Zeiss 10 electron microscope.

Results

Histological observations on the testes showed that the seminiferous tubules comprised a large volume of the parenchyma compared to the interstitial tissue which were generally restricted to the narrow intertubular spaces (Fig. 1). The interstitial tissue consisted of a continuous sheet of compactly arranged interstitial cells of Leydig held together by connective tissue fibres. The nuclei of the interstitial cells were roughly spheroidal and predominantly euchromatic. The cytoplasm was dense, abundant and contained accumulations of lipid droplets and roughly spheroidal mitochondria while the rest of the subcellular organelles were poorly discerned (Figs. 2, 3). In some cells, myelin-like whorls of residual bodies were encountered (Fig. 3). Interstitial tissue macrophages appeared to be phagocytizing the degenerating interstitial cells (Fig. 4). The walls and lumen of the seminiferous tubules were devoid of spermatids and spermatozoa respectively (see Fig. 1). The tubular epithelium appeared to be undergoing various degrees of degenerative changes. Spermatogenic cell changes appeared as either occasional spermatogonial karyolysis (Fig. 5) or apoptosis of the primary spermatocytes (Figs. 2, 6) among apparently normal cell popula-

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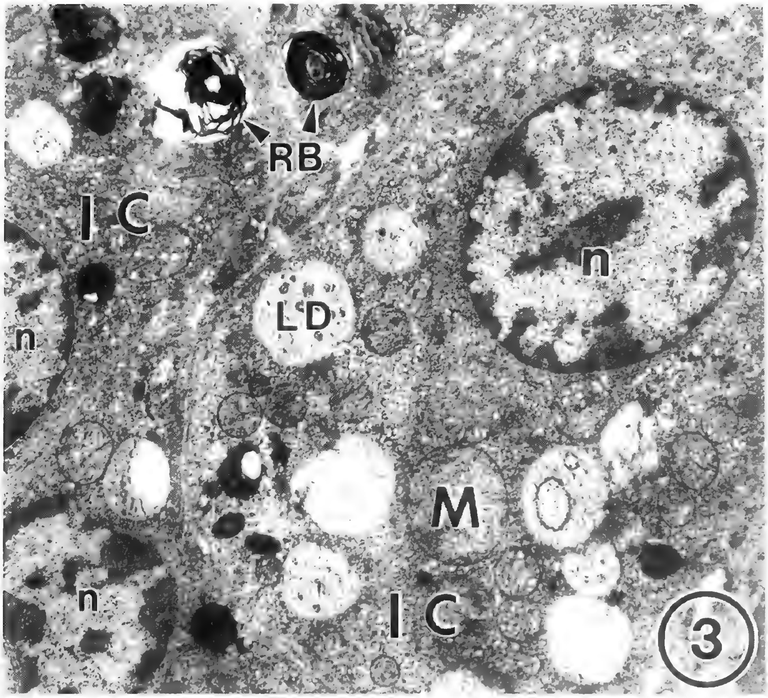
Fig. 1. A photomicrograph of a semithin (1 mm thick) section of plastic embedded testis of the long-fingered bat (*Miniopterus inflatus*). The interstitial tissue (I), mainly comprising compactly arranged interstitial (Leydig) cells, occupy narrow intertubular spaces. The cytoplasm of these interstitial cells have aggregations of lipid droplets (arrow heads). Seminiferous tubules (ST) show conspicuous accumulation of numerous and unusually large lipid droplets (LD) mainly distributed in the apical cytoplasm. The tubular wall and lumen (L) are devoid of spermatids and spermatozoa respectively. Mag. ×400.

Fig. 2. Electron micrograph of the interstitial tissue and parts of seminiferous tubules (ST). The interstitial cells (IC) show spheroidal nuclei (n) and dense cytoplasm with lipid droplets (LD). Note that most of the subcellular organelles are obscured by the dense cytoplasm. Degenerating spermatogenic cells (Spd) occur in the tubules among the normal spermatocytes (Sp). Mag. ×2,500.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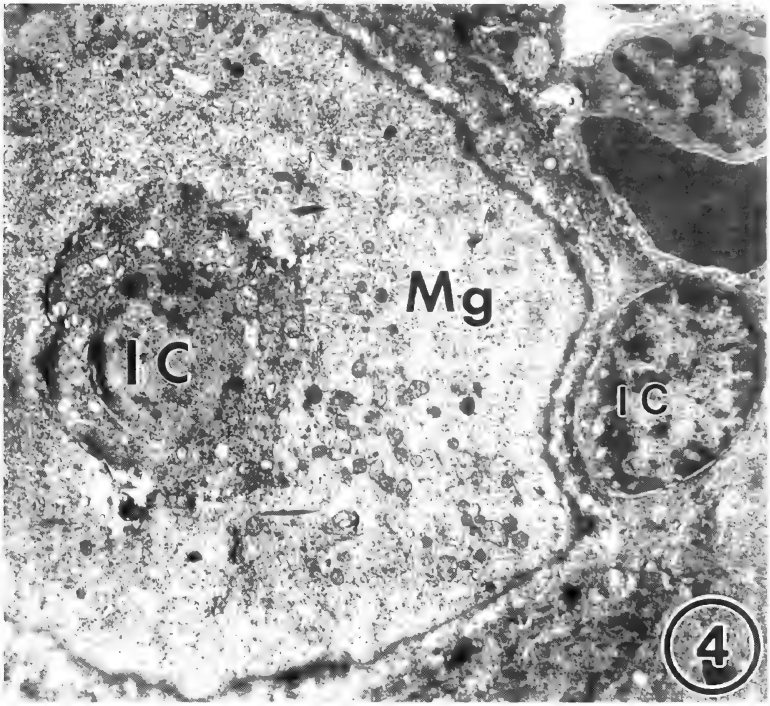
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tions. As a result of the disintegration of spermatogenic cell membrane during apoptosis, the cellular organelles (especially the smooth endoplasmic reticulum) were scattered within the Sertoli cell cytoplasm (Fig. 7). Numerous and unusually large lipid droplets were distributed in the apical cytoplasm of the Sertoli cells (Figs. 1, 8).

Discussion

Bats exhibit varied breeding patterns with some, mainly the hibernating Rhinolopidae and Vespertilionidae showing an asynchronous seasonal reactivation of the primary and secondary sexual organs (COURRIER 1927; KINGDON 1974; GUSTAFSON 1979; RACEY 1982; MERWE and RAUTENBACH 1989; HAPPOLD and HAPPOLD 1990; KRUTZSCH and CRICHTON 1990). Non-hibernating bats, on the other hand, breed all the year round (KINGDON 1974; KRUTZSCH 1979). The long-fingered bat (a Vespertilionid), however, shows an extreme kind of seasonal breeding. Behavioural and macro-anatomical studies have shown that the females experience delayed implantation corresponding to the time when males undergo sexual dormancy (GUSTAFSON 1979; RACEY 1982) characterized by degenerative changes in the reproductive organs (COURRIER 1927; MCWILLIAM 1988). The present microscopical observations in the dormant males confirm the previously reported behavioural and macro-structural changes.

The volume of seminiferous tubules compared to that of the interstitial tissue can be used to group various animal species (FAWCETT et al. 1973). In this study the long-fingered bats resemble rats, mice and guinea pigs in having a large volume of seminiferous tubules among which are small quantities of interstitial tissue. The occurrence of poorly defined cytoplasmic organelles, myelin-like whorls of residual bodies and accumulation of lipid droplets in the apparently dense and abundant cytoplasm of the interstitial (Leydig) cells are suggestive of a period of dormancy accompanied by physiological cell death otherwise referred to as apoptosis (DAVIES 1984). In normal circumstances, active interstitial cells secreting testosterone are characterized by the presence of smooth endoplasmic reticulum, mitochondria, Golgi apparatus and lipid inclusions in the cytoplasm (CHRISTENSEN and GILLIM 1969; CHRISTENSEN 1975). As expected therefore, a depression in interstitial cell activity inevitably leads to a reduction in the volume of these organelles (SINHA HIKIM et al. 1993). Although these investigators reported no effect on testosterone levels during early regression, previous studies in the cape horse-shoe bat (BERNARD 1986) and Schreiber's long-fingered bat (BERNARD et al. 1991) during the period of dormancy showed a marked reduction in testosterone production related to the status of subcellular organelles. Hence, the occurrence of dense cytoplasm with poorly defined organelles may suggest a phase of reduced steroidogenic activity and testosterone production. Accumulation of lipid inclusions in the cytoplasm of inactive cells is not an uncommon finding. In the ovary of the leaf-nosed bat (*Macrotus californicus*), for example, the accumulation of lipid droplets and reduction of smooth endoplasmic reticulum content was associated with a depression in steroid secretion (CRICHTON et al. 1990). Similarly such accumulation has been associated with cell inactivity in the testes of a non-breeding fossorial tropical rodent, the naked mole-rat (ONYANGO et al. 1993). The myelin-like whorls of residual bodies

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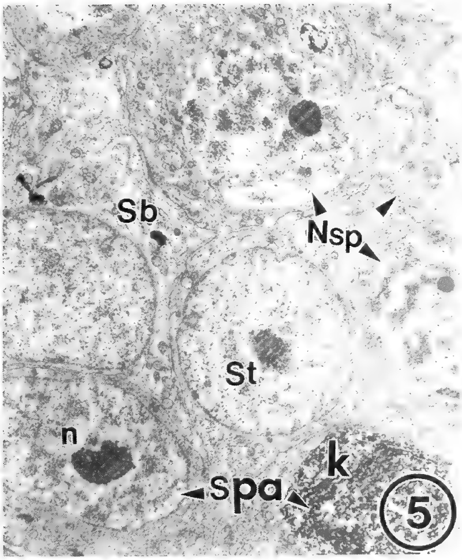
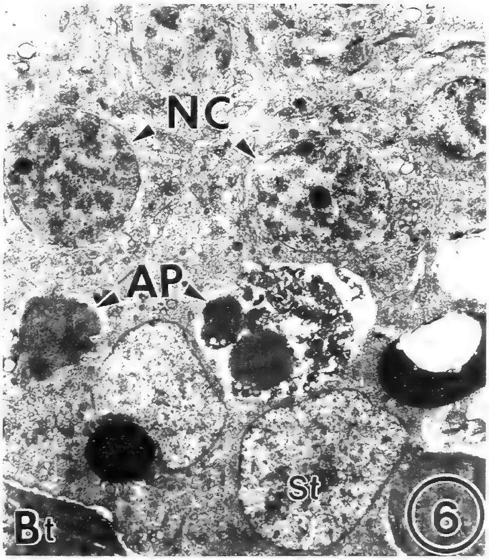
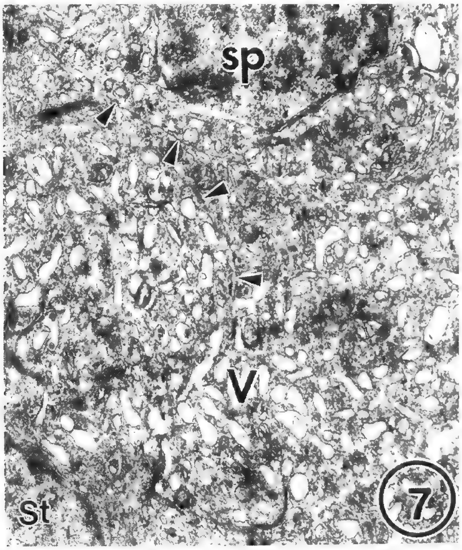
Fig. 3. An electron micrograph of the interstitial cells (IC) showing features of degeneration namely; dense cytoplasm containing poorly outlined subcellular organelles, accumulation of lipid droplets (LD) and myelin-like whorls of residual bodies (RB), and presence of spheroidal and euchromatic nuclei (n). Normal spheroidal mitochondria (M) also occur. Mag. ×8,000.

Fig. 4. An electron micrograph showing a testicular macrophage (Mg) phagocytizing degenerative interstitial cells (IC). Mag. ×5,000.







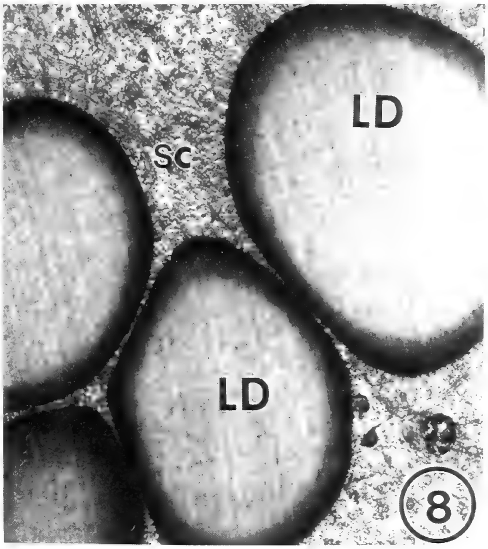


Fig. 5. A photomicrograph of a part of the seminiferous tubule showing two spermatogonia (Spa); one undergoing karyolysis (k) and a normal one (n). Normal spermatocytes (Nsp) are surrounded by Sertoli cell branches (Sb). St = Sertoli cell. Mag. ×3,200.

Fig. 6. A photomicrograph of a part of the seminiferous tubule showing some apoptotic primary spermatocytes (AP) and neighbouring normal spermatocytes (NC). St = Sertoli cell; Bt = Boundary tissue. Mag. ×2,520.

Fig. 7. An electron micrograph showing presence of spermatogenic cell vesicles (V) in the Sertoli cell cytoplasm (St)-an indication of phagocytosis. A poorly defined spermatogenic cell nucleus (Sp) and remnants of the disintegrating cell membrane (arrow heads) are apparent. Mag. ×6,480.

Fig. 8. An electron micrograph of the apical cytoplasm of a Sertoli cell (Sc) with accumulation of very large lipid droplets (LD). Mag. ×4,000.

are thought to originate from the mitochondria (Sandborn 1970; Davies 1984). There are speculations that they may represent the degenerative form of mitochondria (Davies 1984). If this is true then their existence in these cells at the time of study serves to emphasize the thesis that these cells were indeed degenerating. Furthermore, there is evidence here suggesting that these degenerating cells were being phagocytosed by the testicular macrophages.

The degenerative process in the seminiferous tubule is marked by the occurrence of karyolytic spermatogonia and apoptotic spermatocytes in the tubule, sequestered cytoplasmic materials of spermatogenic cells and accumulation of unusually large amounts of lipid droplets in the Sertoli cell cytoplasm. It is probably due to the observed karyolysis and apoptosis of the immature spermatogenic cells that the spermatids and spermatozoa were absent altogether from the tubular wall and lumen. One of the primary functions of the Sertoli cells is to phagocytose the degenerating spermatogenic cells (Soderstrom and Nikkanen 1979; Fawcett 1986). In connection with this, the observation of the spermatogenic cell organelles in Sertoli cell cytoplasm in this case may imply phagocytosis. The large accumulation of apically disposed lipid droplets in the Sertoli cell cytoplasm is rather unusual though similar findings have previously been reported. In hypospermatogenic men large quantities of lipid droplets were also encountered in the Sertoli cell cytoplasm (Soderstrom and Nikkanen 1979). In *Myotis lucifugus lucifugus* (Gustafson 1987), seasonal changes in lipid inclusions were reported in the seminiferous tubules though no specific reference was made to Sertoli cells. Ordinarily, Sertoli cells participate to some degree in androgen biosynthesis (Christensen 1965; Pudney 1986). Therefore the accumulation of these inclusions in the Sertoli cells of these bats may indicate an impaired utilization of cholesterol reservoirs, hence, a reduction in androgen biosynthesis. The present study has not addressed the issue of regeneration time of various testicular cell populations during recrudescence. We hope to follow this up in our next study.

In conclusion, the micro-structural apoptosis of testicular tissue observed in this study generally confirms the previously described behavioural and macro-structural changes in the long-fingered bats during dormancy (see Courrier 1927; McWilliam 1988). However, of particular interest are the causes of these degenerative changes. Although this is beyond the scope of this work, it is speculated that the intricate paracrine inter-relationship among the various testicular cells may play a part. It is now widely believed that there is a complex inter-relationship between the testicular interstitial cells of Leydig and Sertoli cells, Sertoli and spermatogenic cells, and among the spermatogenic cells themselves (Krester et al. 1991; Sharpe et al. 1990, 1993). This bat species therefore provides an excellent model for studying these influences.

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Zusammenfassung

Saisonabhängige Apoptose im Hoden der tropischen Langflügelfledermaus (Miniopterus inflatus)

Hoden von Langflügelfledermäusen der Art *Miniopterus inflatus* wurden während einer sexuellen Ruhephase in den Monaten März und April licht- und elektronenmikroskopisch untersucht. Das interstitielle Gewebe, im allgemeinen relativ klein proportional zu den Tubuli contorti seminiferi bestand überwiegend aus kompakt arrangierten interstitiellen (Leydig) Zellen. Physiologischer Zelltod (Apoptose) wurde gekennzeichnet durch das Vorkommen von dichtem Cytoplasma bei verborgenen Zellorganellen, myelinähnlich gewundenen Residualkörpern und Lipideinschlüssen im Cytoplasma und annähernd kugelförmigen Zellkernen. Die normalen Mitochondrien erschienen im Umriß abgerundet. Einige dieser apoptotischen Zellen wurden von im interstitiellen Gewebe auftretenden Makrophagen phagozytiert. In den Tubuli contorti seminiferi waren diese degenerativen Prozesse markiert durch Spermatogonienkaryolyse, Apoptose von Spermatocyten und starke Ansammlung von großen Lipidtropfen im Cytoplasma der Sertoli-Zellen. In den tubulären Wandungen und den Hohlräumen befanden sich weder Spermatiden noch Spermien. Diese Beobachtungen lassen annehmen, daß der sexuelle Ruhezustand der männlichen Fledermäuse durch ausgeprägte Apoptose mikrostruktureller Komponenten bedingt ist.

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Cytogenetics of the genus *Arvicanthis* (Rodentia, Muridae).
1. *Arvicanthis niloticus* from Republic of Benin (West Africa)

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Abstract

Arvicanthis niloticus is characterized, according to previous karyological studies, by a wide chromosome variability. In distinct populations of its wide area of distribution, the diploid number ranges from between 2n = 44 and 2n = 62. The present study analysed the karyotype of 13 *Arvicanthis niloticus* from South Benin, Guinea Gulf (West Africa). The constitutive heterochromatin pattern was evidenced by C-banding and the location of Nucleolar Organiser Regions was assessed by $AgNO_3$ plus G-banding reactions. The G-banding pattern was also performed both on cultured fibroblasts and bone marrow preparations. The 2n = 62 and the aFN = 74 characterize the South Benin cytotype which was found to be identical to that described for Southern Senegal specimens. A few chromosomal rearrangements (3 pericentric inversions) are enough to transform the Benin cytotype into the ANI-3 cytotype described in animals from Mali and Burkina Faso. A polymorphism of the X chromosome is described; three different forms (i. e. metacentric, submetacentric, and subtelocentric) were observed both in homomorphic and heteromorphic conditions. The problem of intraspecies chromosomal variability in *Arvicanthis niloticus* is discussed.

Introduction

The genus *Arvicanthis* Lesson, 1842 includes numerous species of African grass rats. The systematic relationships within this genus have been a matter of debate since the first revisions by Dollman (1911) and Allen (1939). More recent taxonomical revisions (Rosevear 1969; Dorst 1972; Yalden et al. 1976; Corbet and Hill 1980; Rousseau 1983) disagreed with the opinion of Allen (1939) and proposed a reduction of the number of valid species. Musser and Carleton (1993) consider only five species as valid for the genus *Arvicanthis*, i. e. *A. abyssinicus* (Rüppel, 1842), *A. blicki* Frick, 1914, *A. nairobae* J. A. Allen, 1909, *A. niloticus* (Desmarest, 1822), *A. somalicus* Thomas, 1903. All systematic revisions recognized *Arvicanthis niloticus* as a valid species. Systematic debate has recently been reopened (Volobouev et al. 1988; Granjon et al. 1992) concerning precisely *Arvicanthis niloticus* on the basis of genetic and cytogenetic evidence diversifying the genetic structure of different African populations ascribed to *Arvicanthis niloticus* on the basis of their morphological characters. The diploid number (2n) and the autosomal fundamental number (aFN) actually vary widely within the species: i. e. 2n from 62 to 44 and a FN from 62 to 76 (Tab. 1).

The dramatic karyological differences characterizing the Somalian population (2n = 44; FN = 72) and that of the Central African Republic (2n = 56; aFN = 60) clearly differentiate them from the others and could justify assigning them to different species. The voucher specimen from Somalia we studied (Capanna and Civitelli 1988) is deposited in the collection of the Muséum National d'Histoire Naturelle in Paris (no. 1983–840) and can be re-examined. Furthermore, also some of the populations with 2 n = 62 display a different fundamental number after substantial structural modifications of the genome, which also in this case could be an indication of genetic differentiation. This opinion is supported by Volobouev et al. (1988) who identify the three West African populations they analysed as separate species and have named them with the provisional acronyms ANI-1 (2 n = 62; aFN = 62), ANI-2 (2 n = 58; aFN = 70), and ANI-3 (2 n = 62; aFN = 76). Granjon et al. (1992) are correctly more cautious in this regard. They do not exclude the possibility that in some cases the difference in the aFN may identify a new species, but consider that more biological evidence in support needs to be collected. The evolutionary status of *Arvicanthis niloticus* seems to be that of a complex of cryptic species.

In such an uncertain context, we deemed it opportune to analyse the chromosome assessment of populations of *Arvicanthis niloticus* from a region facing the Gulf of Guinea, in order to add further evidence to the complex problem of chromosomal variability in *A. niloticus* and to verify the spreading of different cytotypes of the species towards the southernmost part of West Africa.

Material and methods

The 13 animals (4 males and 9 females) studied came from three localities of South Benin: Attogon (cultivated fields, 2° 10′ 03″ E; 6° 43′ 01″ N), Lokossa (open savanna, 1° 37′ 10″ E; 6° 43′ 42″ N), and Toffo (forest, 2° 05′ 58″ E; 6° 49′ 30″ N).

The specimens are held in the collections of the Museum of Comparative Anatomy of the University of Rome "La Sapienza" under the numbers B.0014.92; B.0021.92; B.0024.92; B.0034.92; B.0036.92; B.0037.92; B.0038.92; B.0039.92; B.0042.92; B.0044.92; B.0045.92; B.0047.92; B.0048.92.

Somatic metaphases were obtained both from bone marrow, by means of the method of Hsu and Patton (1969), and from in vitro cultured fibroblasts derived from ear pinna biopsies according to Stanyon and Galleni (1991). Male meiotic patterns were studied in testis preparations according to Evans et al. (1964). Standard staining of the metaphases was performed using Giemsa 4% in phosphate buffer pH7. Differential staining was also carried out. G-bands were obtained according to Seabright's (1971) method, and C-bands according to Bickman (1979). Nucleolus Organizer Regions (NORs) were enhanced by means of the silver reaction according to Howell and Black (1980). In order to identify the chromosomes carrying NORs, the silver-stained metaphases were treated also with trypsin to highlight the G-banding.

Table 1. Karyological data on *Arvicanthis niloticus*

Locality	2 n	aFN	References
Egypt	62	62	Viegas-Péquignot et al. (1983)
Centro African Rep.	56	60	Matthey (1965)
Centro African Rep.	58	70	Volobouev et al. (1987)
Burkina Faso	62	76	Volobouev et al. (1988)
Mali	62	76	Volobouev et al. (1988)
Senegal	62	62	Volobouev et al. (1988)
Senegal (West)	62	64	Granjon et al. (1992)
Senegal (South West)	62	74	Granjon et al. (1992)
Senegal (South East)	62	66	Granjon et al. (1992)
Niger	62	64	Granjon et al. (1992)
Somalia	44	72*	Capanna and Civitelli (1988)

* The FN is reported in this case because females only were studied and heterochromosomes were not identified

Results

The autosomal set

The diploid number of *Arvicanthis niloticus* from Benin is 2 n = 62 in all animals studied, and the structure of the karyotype is identical as far as the autosomal set is concerned. Chromosomal polymorphism was found concerning the X chromosome.

The two largest autosomal pairs are composed of large subtelocentric chromosomes, and the third pair by submetacentric chromosomes. The subsequent 23 pairs (from no. 4

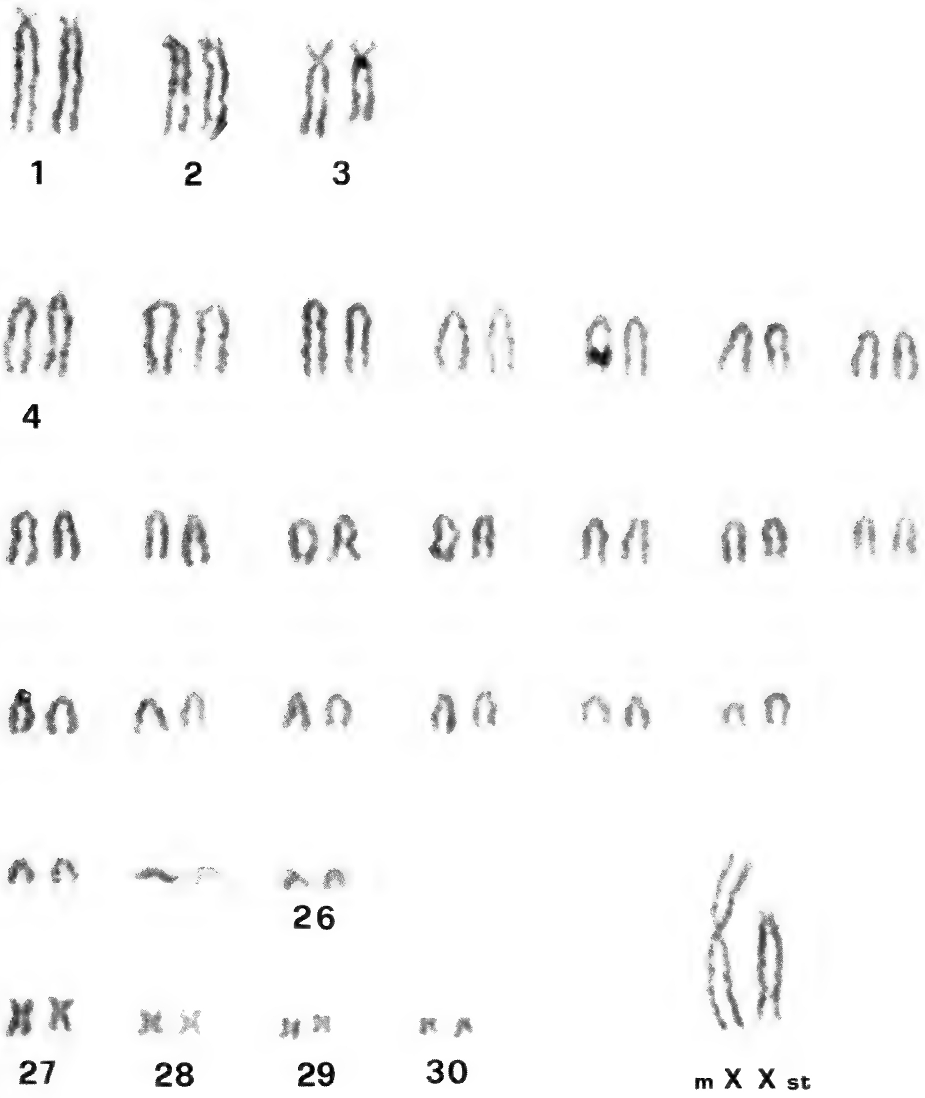

Fig. 1. Giemsa stained karyotype from a female of *A. niloticus*. X chromosomes are in a heteromorphic state [metacentric (m), subtelocentric (st)].

to 26) are acrocentrics, the size of which gradually decreases from medium sized to very small. The last four pairs (from no. 27 to 30) are composed of small metacentrics (Fig. 1). The resulting aFN is 74.

The G-band pattern (Fig. 2) allows accurate pairing of the acrocentric autosomes and assures correct comparison with different R-band patterns suggested by Volobouev et al. (1988) for the cytotypes they proposed for the West African *Arvicanthis niloticus*.

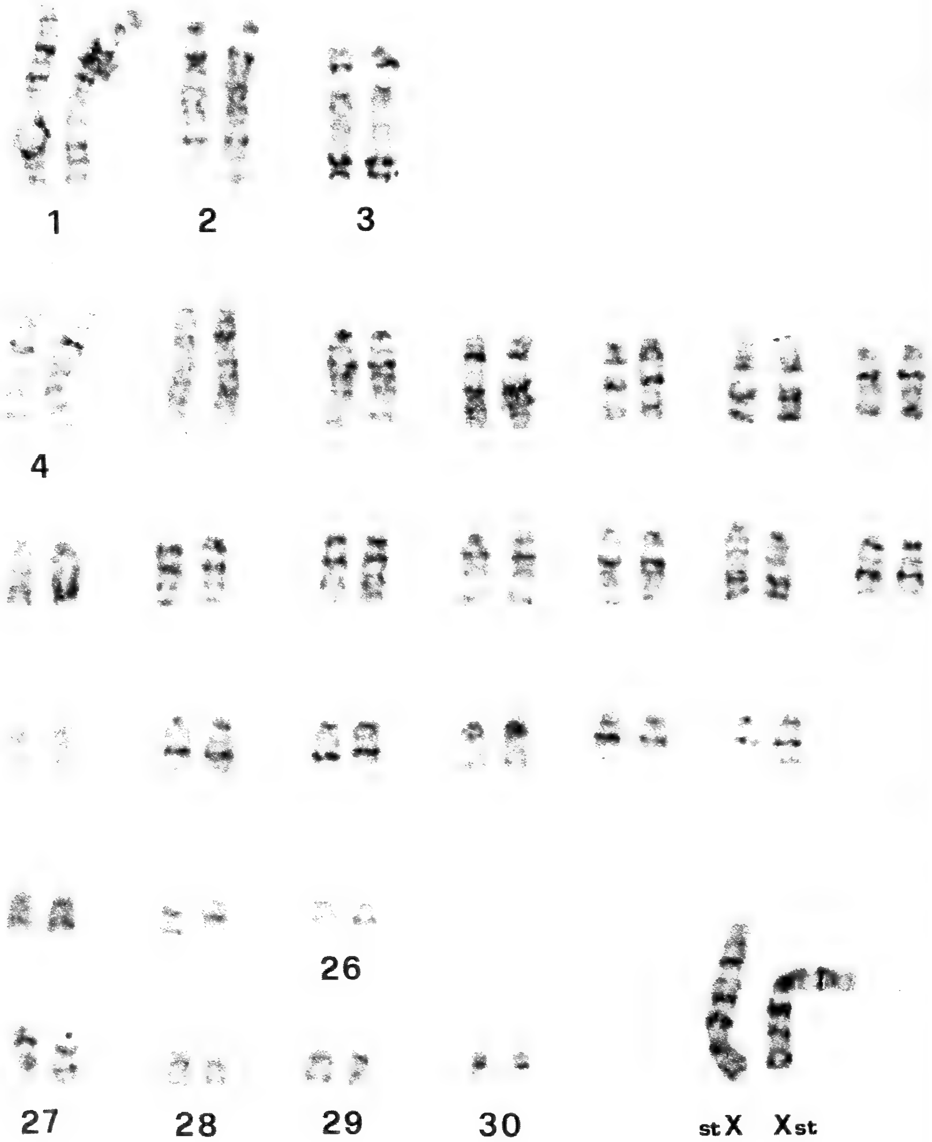

Fig. 2. G-banded karyotype from a female of *A. niloticus*. Both X chromosomes are subtelocentric (st).

Heterochromosomes and X chromosome polymorphism.

The X chromosome appears in three different forms (Fig. 3): metacentric, submetacentric, and subtelocentric. The analysis of the G-bands and the allocation of the constitutive heterochromatin (C-bands) is particularly important in ascertaining the homology of the three forms of the X chromosome. The long arms of the metacentric and submetacentric forms show an identical G-band pattern. Likewise, the pattern of the short arm of the submetacentric X chromosome G-bands corresponds to the closest to centromere part of the short arm of the metacentric form. The short arms of these types of X chromosomes are entirely heterochromatic. Most of the long arm of the subtelocentric form shows the

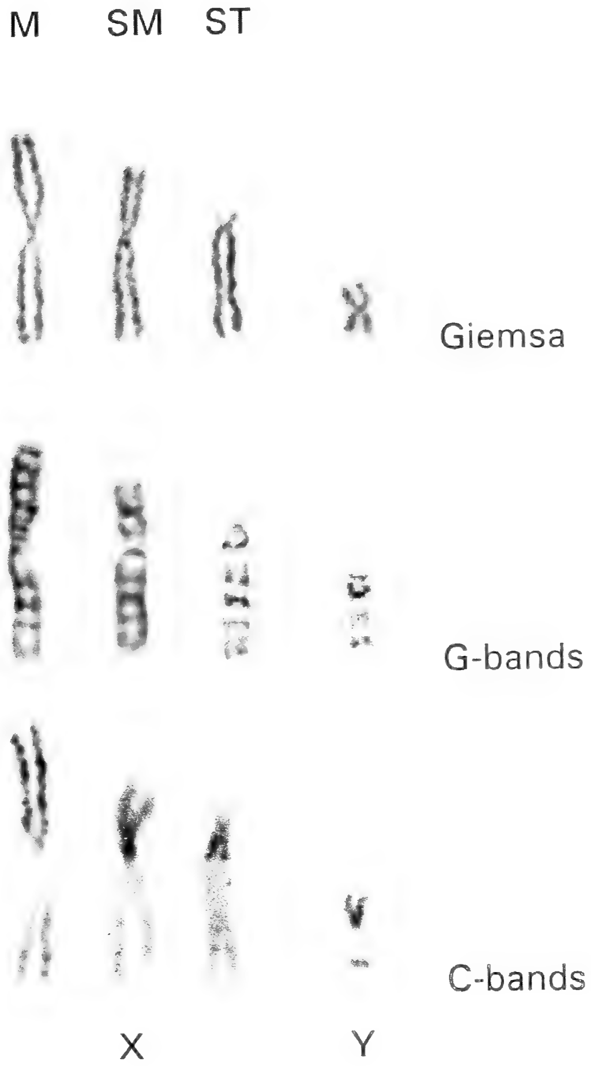

Fig. 3. *A. niloticus* sex chromosomes stained using different methods. M, SM, and ST indicate the different types of X-chromosomes, respectively metacentric, submetacentric, and subtelocentric.

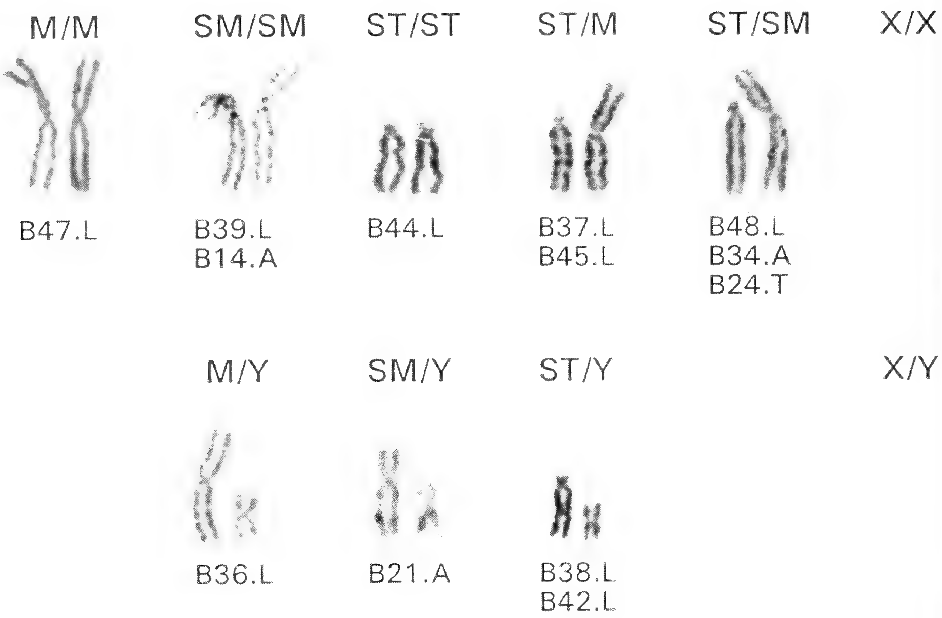

Fig. 4. Sex complements of the specimens studied. For each specimen the acronym and the collecting site is indicated: A – Attogon, L –Lokossa, and T. – Toffo.

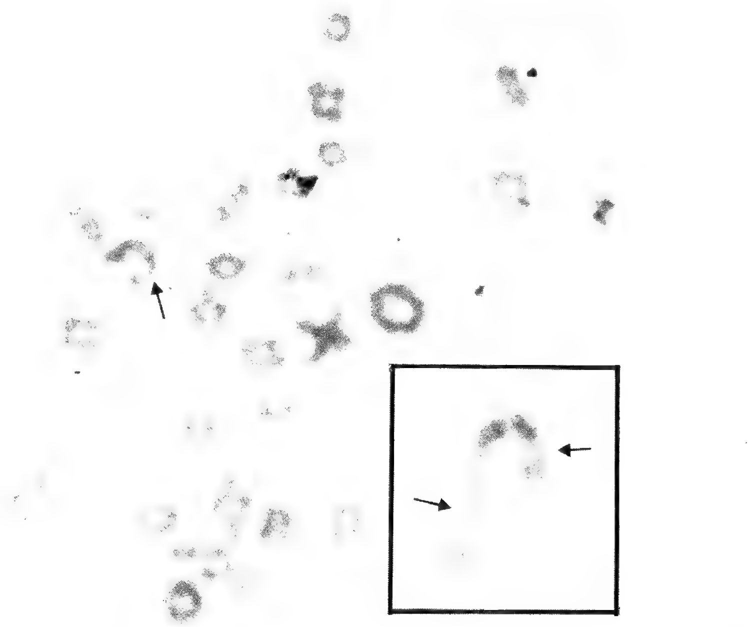

Fig. 5. Meiotic late diakinesis of B21, a Xsm/Y male. The sex bivalent shows one uncoiled tail (arrow). At the diplotene stage (inside the box) the sex bivalent shows two tails (arrows).

same G-band pattern as the long arm of the metacentric and submetacentric form. The rest of the long arm and the short arm are completely heterochromatic.

The small number – i. e. only 13 – of animals analysed does not allow any within-population statistical evaluation of the frequencies of each form. Nonetheless, no form seems to be more extensively represented than any other. In females no greater frequency of the homomorphic state was observed than the heteromorphic one. In males all three forms of X chro-

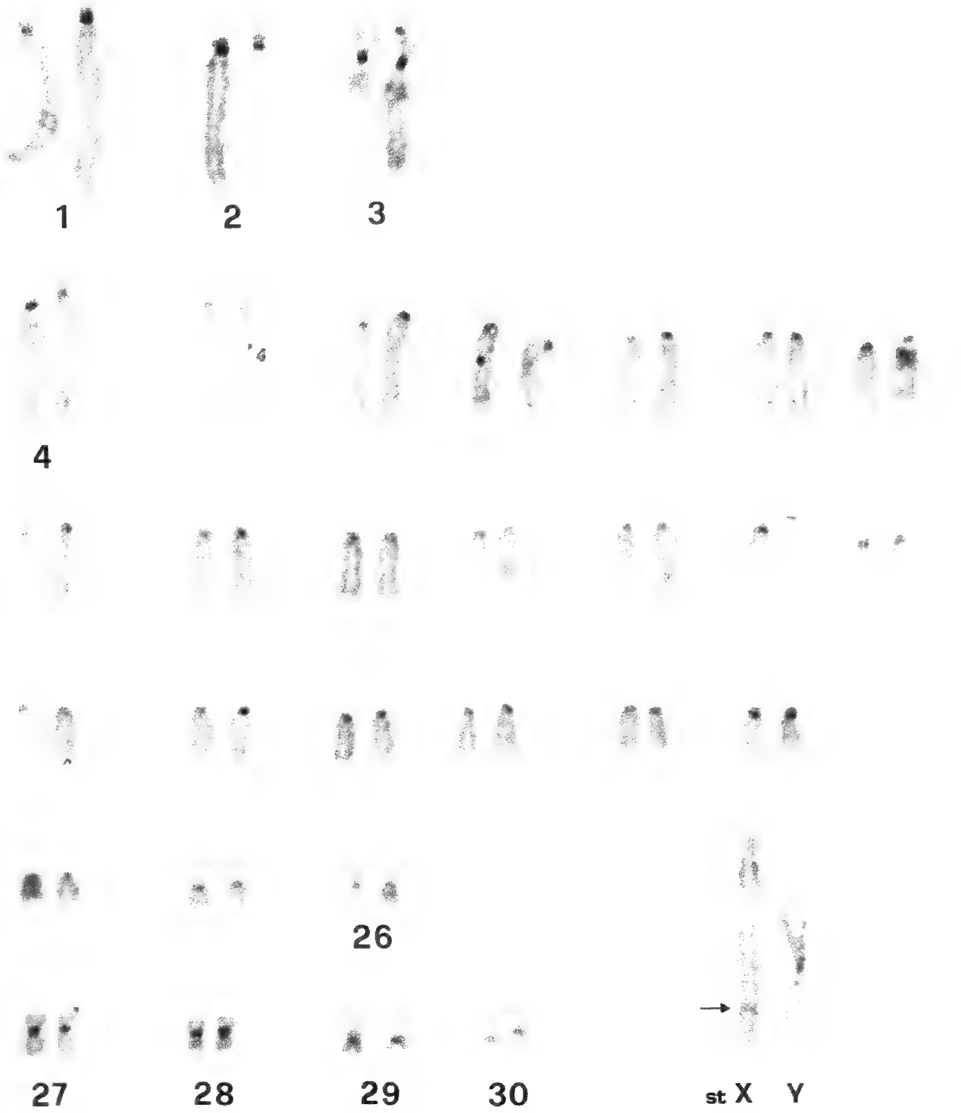

Fig. 6. C-banded karyotype of a Xst/Y male of *A. niloticus.* Arrow indicate a thin C-band on the distal part of the long arm of the X-chromosome.

mosomes were observed to be paired with a medium size metacentric Y chromosome (Fig. 4). The distal part of the Y chromosome long arm shows a G-band corresponding to the distal part of the long arm of the X-chromosomes. The short arm of the Y chromosome is entirely heterochromatic. An evident C-positive band is located on the distal part of the long arm of the Y chromosome (Fig. 3). At the different stages of the male meiotic process the sex bivalent shows one (at diakinesis) or two (at pachytene-diplotene) unpaired uncoiled tails probably due to the heterochromatic region of the heterochromosomes (Fig. 5).

Heterochromatin pattern and Nucleolar Organizers.

C-banding (Fig. 6) reveals heterochromatic centromeric spots in all autosomes; larger heterochromatic blocks are pericentromerically located on the chromosomes of the three first pairs of biarmed chromosomes, and on two pairs of small metacentrics (pairs 27 and 28).

Fig. 7. Ag-NOR location on autosomes of *A. niloticus*. First row: NOR-bearing chromosomes are identified by combined $AgNO_3$/G-band staining. Numbers indicate the autosomal pairs.

Ag-NORs (Fig. 7) are located on four different pairs of autosomes, i. e. the two largest subtelocentrics (pairs no. 1 and 2), the larger of the acrocentric pair (pair no. 4) and the smaller one of the acrocentric pair (pair no. 20). Pairs no. 1 and no. 20 bear NORs on the short arm, near the centromere, whilst pairs no. 2 and no. 4 show terminal NORs on the long arm.

Discussion

As far as the 2n and aFN are concerned, the karyotype we describe for South Benin animals corresponds exactly to that described by Granjon et al. (1992) for *Arvicanthis niloticus* from a Senegal population located south of the River Gambia. The karyotype coded ANI-3 by Volobouev et al. (1988) found in animals from Mali and Burkina Faso (2 n = 62; aFN = 76) shows remarkable morphological similarity, above all as far as the larger elements, i. e. chromosome pairs no. 1, 2, and 3, are concerned. Nevertheless, these three large chromosomes of the Burkina Faso karyotype display no centromeric heterochromatin, which is instead observed in the corresponding elements of the Benin karyotype. G-band comparison allows the pericentric inversions responsible for the reciprocal changes of the two karyotypes involving chromosomes no. 8, no. 14 and one among the smallest metacentric chromosomes to be identified. Granjon et al. (1992) consider ANI-3 as an intraspecies variant of the karyotype described by them for Southern Senegal animals. This hypothesis is supported by biochemical data provided by Kaminski et al. (1987) concerning genetic affinities between South Senegal and Burkina Faso populations of *Arvicanthis niloticus.* Conversely, the Senegal population, located north of the Gambia River (2 n = 62; aFN = 64–66) could be included in the polymorphous complex ANI-1 (2 n = 62; aFN = 62) of Volobouev et al. (1988). The small numbers of animals analysed by the above authors – only one or two in each locality – do not allow the current existence of these supposed polymorphisms to be ascertained, or to establish whether the chromosomal variants coexist in a Hardy-Weinberg equilibrium. The same limitation on the number of animals studied also ruled out identification of the X chromosome polymorphism. Consequently, the differences in the X chromosome morphology were misinterpreted as a stable element of the karyotype diversity between cytotypes. Both karyotypes described by Granjon et al. (1992) for Senegal *Arvicanthis niloticus* display a submetacentric X chromosome, while all forms of X chromosomes are found in the karyotypes described by Volobouev et al. (1988); i. e. metacentric in ANI-1, submetacentric in ANI-2; and subtelocentric in ANI-3. Our observations, based on the analysis of a relatively large number of animals, demonstrate that the morphological variants of the X chromosomes are maintained in a balanced state in the South Benin population.

No hypothesis can be put forward at present concerning either the direction of the evolutionary process or which form is to be considered primitive. Nonetheless, the chromosomal rearrangement responsible for the change in the three X chromosomes forms appears to be a pericentric inversion of the apical heterochromatic segment of the subtelocentric form that originally produces the submetacentric form. Further addition of heterochromatin can change the submetacentric into metacentrics.

In accordance with the premises set out in the introduction, we have clarified the karyological situation of the *A. niloticus* population of Benin, on the one hand, and, on the other, we have shown how a cytotype of *A. niloticus*, identical to the one described in Southern Senegal, extends as far as the Gulf of Guinea. As far as the premises are concerned, the finding of a self-maintained polymorphism of the X chromosome was an unexpected result.

Nevertheless, the problem of karyotype variability in *Arvicanthis niloticus* in West Africa still appears unresolved. New problems are posed by the extended distribution from Gambia River to the Guinea Gulf: is this wide distribution continuous? Does a retained chromosomal polymorphism actually exist in this area? Is the ANI-3 cytotype also present in this area? It is not possible to answer these questions without a detailed cytogenetic analysis of the *Arvicanthis niloticus* populations from Burkina Faso to South Benin.

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Zusammenfassung

Zytogenetik der Gattung Arvicanthis (Rodentia, Muridae).
1. Arvicanthis nilotlcus aus der Republik Benin (Westafrika)

Karyotypen von 13 *Arvicanthis niloticus* (4♂, 9♀) aus dem Süden Benins (Westafrika, Golf von Guinea) wurden studiert. Das konstitutive Heterochromatin wurde durch C-Banden und die Lage der NORs durch Silbernitratreaktion und G-Banden sichtbar gemacht. G-Bandenmuster wurden an Fibroblastenkulturen und Knochenmarkspräparaten studiert. Der Karyotyp der untersuchten Population aus dem südlichen Benin ist mit $2n = 62$ und $aFN = 74$ identisch mit dem von Granjon et al. (1992) beschriebenen Karyotyp aus Süd-Senegal. Mit wenigen Schritten (3 perizentrische Inversionen) läßt sich der Benin-Karyotyp überführen in den von Volobouev et al. (1988) als "ANI-3" bezeichneten Karyotyp von Grasratten aus Mali und Burkina Faso. Das X-Chromosom ist polymorph. Es wurden meta-, submeta- und subtelozentrische Formen in homo- und heteromorpher Verbindung vorgefunden. Das Problem intraspezifischer Chromosomenvariabilität bei *Arvicanthis niloticus* wird diskutiert.

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The diet of the Crested porcupine *Hystrix cristata* L., 1758 in a Mediterranean rural area

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Abstract

Studied was the diet of crested porcupines by faecal analysis in a rural hilly area in central Italy. Food categories were identified by comparison with either isolated sections of fresh plant material or digested fragments obtained from captive porcupines fed experimentally. Roots predominated in the diet and were consumed at a similar frequency all year round. Herbs were the most eaten epygeal category especially in winter and spring. Possibly the winter consumption of herbs was related to a decrease in the availability of other food categories, such as grass inflorescences and fruits. Consumption of these two food categories was positively correlated and inversely associated with herbs. Grass inflorescences (mainly *Hordeum murinum*) were an important diet component in summer. Porcupines fed on fruits mainly in summer and autumn. The consumption of storage organs increased in winter and in spring. The values of trophic niche breadth and overlap suggested that porcupines are generalist foragers. These feeding habits, combined with the abandonment by man of the countryside in the last few decades, may partly explain the recent range expansion of the crested porcupine in Italy.

Introduction

The crested porcupine *Hystrix cristata* is a large rodent widely distributed in Africa, while in Europe it is present only in Central and Southern Italy, recently expanding its range northward and eastward (Pellegrini et al. 1991; Amori and Angelici 1992; Lovari 1993). Since 1974 it has been protected by the Italian law, but poaching for meat is still widespread. Crested porcupines are active all year round, mainly at night and spend most daylight hours in natural caves or burrows (Pigozzi and Patterson 1990; Corsini et al. 1995). Detailed information on diet of porcupine is scanty, often anecdotal and mainly based on non-systematic observations of feeding activity. Santini (1980) reported that porcupines use especially hypogeal parts (taproots, bulbs, tubers and rhizomes) of wild and cultivated plants. They also eat seeds, fruits, sprouts and green vegetation on the ground. In the Maremma Natural Park, Western Tuscany, Italy, porcupines fed on grain and sunflower seeds, as well as underground organs and grasses (Pigozzi and Patterson 1990: samples for July only). Porcupines have been reported to debark young trees, e. g. *Fraxinus ornus*, *Ficus carica* and conifers in winter (Santini 1980; Tinelli and Tinelli 1988, in the Maremma Natural Park; Zavalloni and Castellucci 1991, in the North-eastern Italian Apennines).

The aims of our research were to set up a technique for analysis of crested porcupines' faeces and to study the monthly/seasonal variation of the diet (in terms of plant parts) in a Mediterranean rural area.

Material and methods

Study area

The study was carried out in a 750 ha rural hilly area in Siena county, Tuscany, Italy (200–388 m a.s.l.), from July 1990 to June 1991. Temperature and precipitation are shown in Figure 1. The soils are mainly Miocene and Pliocene clays, sandstones and lacustrine conglomerates (Lazzarotto and Mazzanti 1976). Oakwoods cover 48.9% of the area, with *Quercus cerris* and *Q. pubescens* being the main species, with some *Acer campestre*, *Fraxinus ornus*, *Carpinus betulus* and *Juniperus communis*. Various trees and shrubs, mostly belonging to the Rosaceae, make up hedges (4.9%): *Prunus spinosa* often forms very thick bushes, while *Rosa canina*, *Pyrus pyraster*, *Malus sylvestris*, as well as *Spartium junceum*, *Cornus mas* and *Robinia pseudoacacia* are also present. Interspersed fields cover 38.8% of the study area; they are set aside (according to EEC programs), but a few of them are used as sheep and cattle pasture. Grasses (*Avena fatua*, *Bromus* spp. and *Hordeum murinum*) predominate in the fields, and, among forbs, *Rumex crispus* and *Rumex conglomeratus* are very frequent species. Names of plant species according to Pignatti (1982).

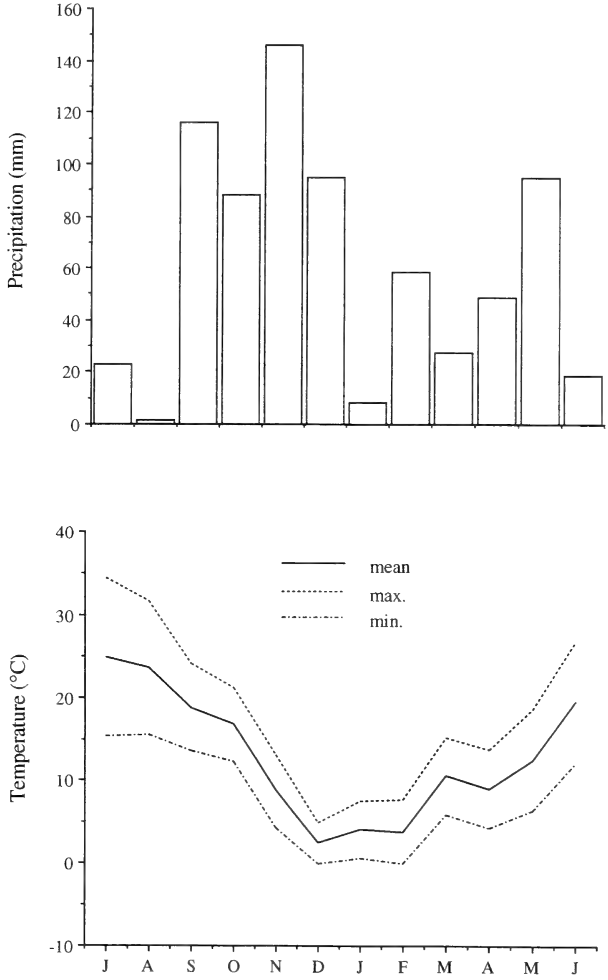


Fig. 1. Monthly precipitation and mean temperature during the study period.

Diet analysis

Droppings were collected weekly on fixed routes from July 1990 to June 1991. The samples were stored in plastic bags and frozen. A monthly mean of 9.3 (range: 5–11) droppings (a total of 111 samples) was analysed.

Each sample was dipped in a 0.06 M NaOH solution (e.g. ZYZNAR and URNESS 1969; ORMEROD 1985) for about 24 hours, to dissolve the mucous coat covering the faeces; then it was washed through a 1 mm square mesh sieve (Endecotts Ltd.) (HOLECHECK 1982; GARCIA-GONZALEZ 1984; CHAPUIS and DIDILLON 1987). The washed sample was placed in water and the fragments were segregated by hand, according to the food categories they belonged to. They were identified either by eye or by using a stereomicroscope at 25× to 125× magnification, by comparison with either digested fragments obtained from experimental meals or isolated sections of bulbs and tubers of Liliaceae, Araceae and Iridaceae occurring in the study area. Leaves and stems of herbs could be identified as either Monocotyledons or Dicotyledons by eye. When not large enough, leaf fragments were distinguished under a dissecting microscope at 100× magnification on the basis of epidermal diagnostic features such as venations and stomata, typically arranged in parallel lines only in Monocotyledons. Grass inflorescences were identified to species by comparison with herbarium specimens. In the fruits category, seeds, peel, pulp fragments and petioles were found. Volume was measured by water displacement (e. g. JACKSON 1980; STAINES et al. 1982; MARTINEZ et al. 1985). Volumes less than 0.1 ml were recorded as "traces". This procedure actually measures the volume of indigestible food remains, so the resulting data must be interpreted with caution.

Feeding experiments with captive porcupines

Adult porcupines, held in outdoor enclosures, were fed experimental meals to obtain reference faecal samples of food categories, such as: a) taproots of herbs, b) fruits of shrubs and trees and c) bark of shrubs and trees. Experimental meals were composed of plant species sampled in the study area. On the three days preceding each test, porcupines were maintained on ad libitum water and not fed, so only indigested remnants of the food given them should have been included in faecal samples. On the day of test, all accumulated faeces were removed from the enclosure and the animals were fed the experimental meals. Faeces were collected each following day, until 2–3 days after the last experimental meal had been eaten.

Porcupines were offered taproots of herbs (*Rumex* spp., *Linaria vulgaris*, *Amaranthus retroflexus*, *Tussilago farfara* and *Inula viscosa*) in experiment a (eight days) and fruits of *Pyrus pyraster*, *Malus sylvestris*, *Sorbus domestica*, *Prunus* spp., *Rosa canina* in experiment b (twelve days). Experiment c needed to be carried out twice, because porcupines did not eat stripped tree bark (*Quercus cerris*, *Acer campestre*, *Ulmus minor*, *Prunus spinosa*). Therefore, in the second trial, porcupines were offered a bunch of branches of the same tree species fastened to the enclosure. Parts of the branches were then eaten. This experiment lasted three days.

Statistics

Data for each month were analysed as:

1. Percent frequency of occurrence for each food category:

$$OF_{ij}\% = n_{ij}/N_j \times 100$$

where OF_{ij} % is the percentage of faeces in which the i_{th} category occurs in the j_{th} month; n_{ij} is the number of times in which the i_{th} category occurs in the j_{th} month out of the total of frequencies of all the food categories in the j_{th} month (N_j).

2. Percent volume of each food category:

$$V_{ij}\% = \Sigma v_{ij}/\Sigma V_j \times 100$$

where V_{ij} % is the percent volume of the i_{th} category in the j_{th} month; Σv_{ij} is the sum of volumes (ml) of the i_{th} category in the j_{th} month and ΣV_j is the total volume analysed in the j_{th} month.

The χ^2 test for one sample was used to evaluate differences in the annual occurrence frequency of food categories. To estimate the association level between monthly frequency of occurrence and both monthly mean temperature and precipitation we applied the Spearman rank correlation coefficient (SIEGEL and CASTELLAN 1988). This test was used also to evaluate monthly statistical associations between food categories. No inter-category statistical comparisons were made on volume data because of the possible different rates of digestibility of different plant parts. To compare seasonal compositions of diet (in terms of occurrence frequency), monthly data were combined in groups of three (e. g., winter was made up of data from January, February and March) and the χ^2 test for two independent samples was applied. We cannot exclude some dependence of our samples because faeces might belong to the same individual/s. Nevertheless, we would regard our tests as significant even in case of some level of sample dependence, because of the very high levels of significance obtained (see Tabs. 2–3).

Monthly trophic niche breadth was estimated by the standardized Levins index (B_{sta}) (COLWELL and FUTUYMA 1971):

$$B_{sta} = B - 1 / B_{max} - 1$$

where B is the Levins index and B_{max} is the total number of food categories composing the diet. The value of B_{sta} varies from 0 (the smallest niche breadth) to 1 (the largest niche breadth). The Levins index formula (LEVINS 1968) is:

$$B = 1/\sum_{i=1}^{n} p_i^2$$

where n is the number of food categories and p is the proportion (as frequency of occurrence) of the i-$_{th}$ category. B varies from 1 to n.

Monthly trophic niche overlap was estimated by the Pianka index O (PIANKA 1973):

$$O_{jk} = \Sigma p_{ij}\, p_{ik} / \sqrt{\Sigma p_{ij}^2 \Sigma p_{ik}^2}$$

where p_{ij} is the proportion (as frequency of occurrence) of the i_{th} category in the j_{th} month and p_{ik} is the proportion of the same category in the following k_{th} month. O varies from 0 (the smallest niche overlap) to 1 (the largest niche overlap).

Results

Fragments found in faeces were segregated in the following food categories: grass inflorescences; herbs; fruits; roots; storage organs; unidentified material. Since bark could not be distinguished from roots under the stereomicroscope in material obtained from experi-

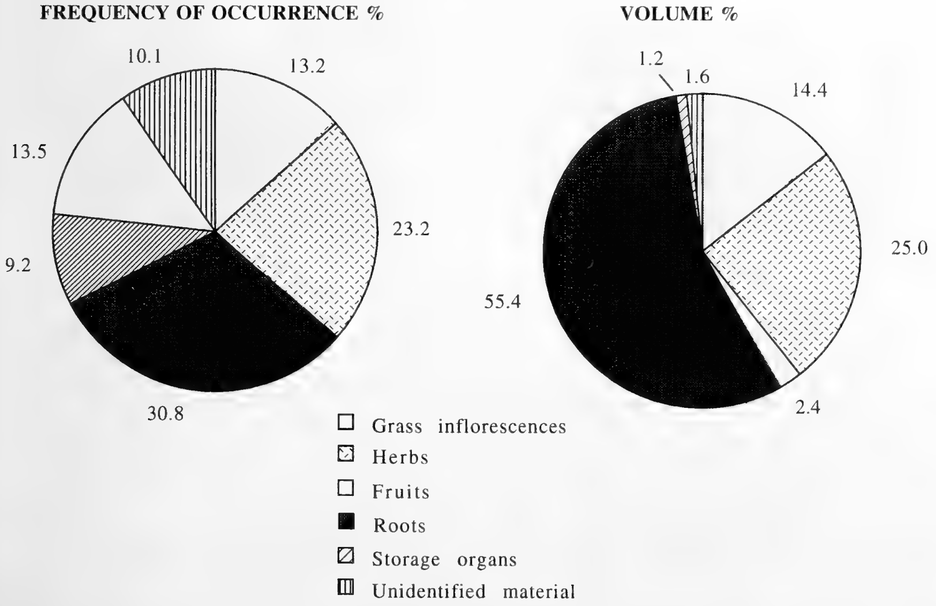


Fig. 2. Annual composition of diet in food categories.

mental meals, we cannot exclude the possibility that the roots category contained some bark fragments.

Annual diet

Roots constituted the main category in annual diet, both in frequency of occurrence and especially in volume (Fig. 2). Herbs ranked as the second food category, with similar values of occurrence and volume. Fruits and grass inflorescences were present with about the same frequency. Unidentified material made up a small portion of the analysed matter as both frequency and volume. Storage organs showed the smallest values of frequency and volume. Differences among food categories proved significant ($\chi^2 = 77.2$, d. f. = 5, $p = 0.0001$).

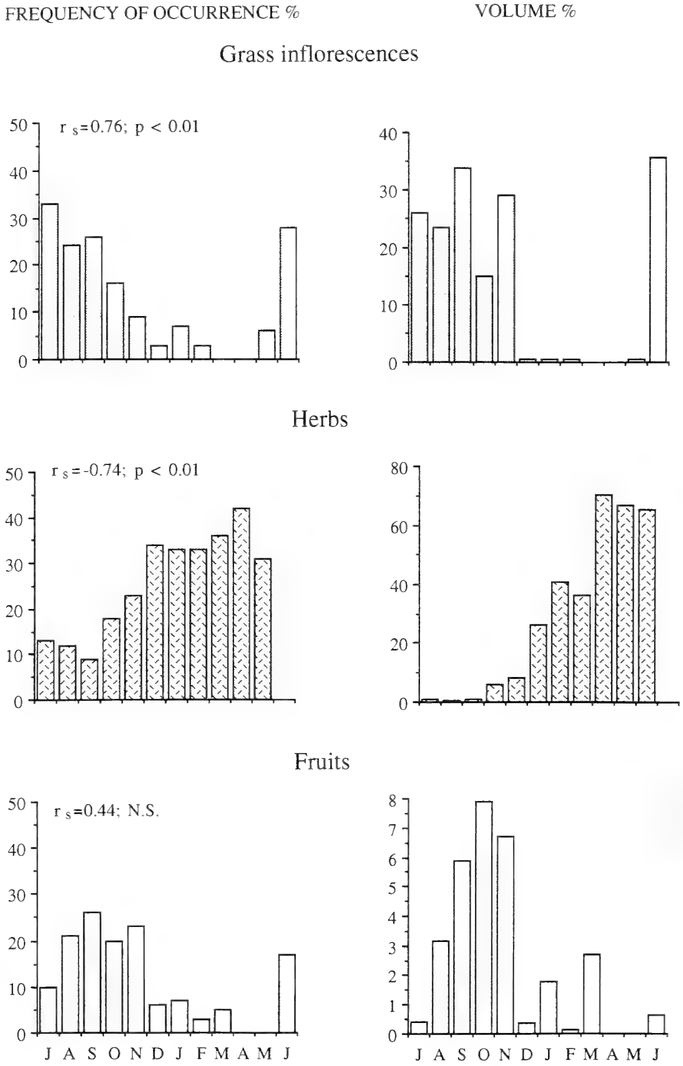


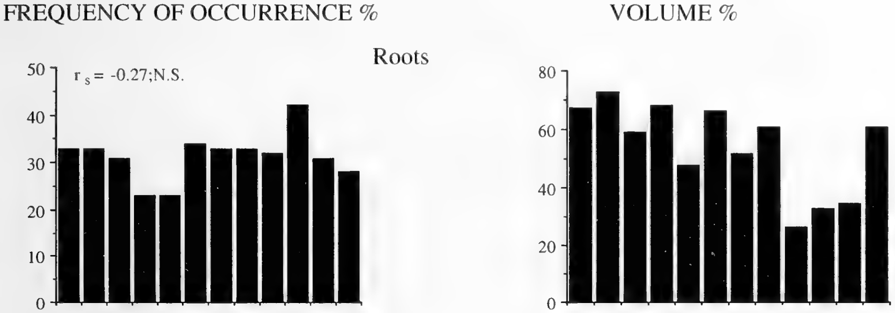
Fig. 3. Monthly percent frequency of occurrence and volume of epygeal food categories (r_s = Spearman 2-tailed rank correlation coefficient between occurrence frequency and monthly temperature; N = 12).

Monthly diet

As regards food categories made up by epygeal plant parts (Fig. 3), grass inflorescences showed the highest values of occurrence in summer months, while they tended to decrease from October to March and April, when this category disappeared, although it was present again in May. In terms of volume, grass inflorescences followed a similar trend, but their contribution to the diet from September to November was relatively higher. A positive correlation was found between the mean monthly temperature of the study area and the frequency of occurrence of this food category (Fig. 3). *Avena fatua*, *Bromus* spp. panicles and mainly *Hordeum murinum* spikes made up this category. On the contrary, herbs, negatively correlated to grass inflorescences (Tab. 1), showed the lowest values of

Table 1. Monthly correlations between food categories (r_s = Spearman 2-tailed rank correlation coefficient; N = 12; p = significance level)

Food categories	r_s	p
Herbs vs Grass inflorescences	–0.92	<0.01
Fruits vs Herbs	–0.76	<0.01
Fruits vs Grass inflorescences	0.72	<0.02
Roots vs Grass inflorescences	–0.39	N. S.
Roots vs Herbs	0.56	N. S.
Roots vs Fruits	–0.50	N. S.
Roots vs Storage organs	–0,12	N. S.
Storage organs vs Herbs	0.03	N. S.
Storage organs vs Fruits	–0.36	N. S.
Storage organs vs Grass inflorescences	-0.05	N. S.



Storage organs

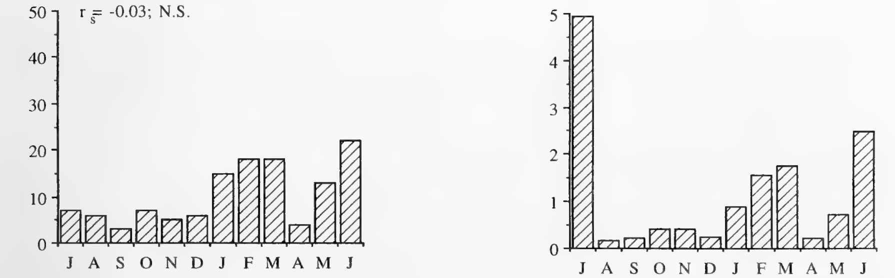


Fig. 4. Monthly percent frequency of occurrence and volume of hypogeal food categories (r_s = Spearman 2-tailed rank correlation coefficient between occurrence frequency and monthly temperature; N = 12).

frequency, as well as of volume, in the summer months and the highest ones from October to May. In June herbs surprisingly disappeared. The consumption of herbs was negatively correlated with temperature (Fig. 3). Dicotyledons disappeared from the diet of September and October, but occurred again in November, with increasing values to March, when they constituted more than 50% of the total herbs. Fruits, negatively correlated to herbs and positively to grass inflorescences (Tab. 1), were eaten mainly (both in terms of frequency and volume) at the end of summer to October and November. They were also consumed in winter months, but at lower values, and in April and May they did not occur at all but were again in the diet in June (Fig. 3). We could identify fruits of *Malus sylvestris* and *Pyrus pyraster*, very frequently in September and October, but only once (in September) we found one seed of *Cornus mas.*

As to food categories composed of hypogeal plant parts (Fig. 4), roots were consumed at a steady frequency all year round, but with varying quantity, showing the lowest relative volume from the end of winter to spring. Among root fragments we found taproot of *Rumex* spp. to be very frequent within this category (24% to 48% of total roots in summer and winter diet, respectively). Storage organs were made up of bulbs (particularly frequent in winter months); tubers of *Arum italicum*, occurring in July and in the winter months; corms of *Gladiolus italicus*, in August and May. On the whole, storage organs showed varying values in both frequency of occurrence and in volume, increasing in winter and again in spring months.

No food category showed significant correlations with monthly mean precipitation.

Seasonal diet

Seasonal compositions of diet proved significantly different at χ^2 test (Tab. 2). To explain which food category/ies caused these significant differences, we applied the χ^2 test to seasonal values of frequency of occurrence and volume of each category (Tab. 3). Roots and storage organs were the only food categories whose frequency of occurrence and volume, respectively, did not vary significantly from season to season.

Table 2. Comparisons of seasonal composition of diet (χ^2 = chi square test values, d. f. = 5; p = significance level)

Seasons	χ^2	p
Summer vs Autumn	47.9	0.0001
Autumn vs Winter	68.6	0.0001
Winter vs Spring	11.0	0.005
Spring vs Summer	85.4	0.0001

Table 3. Seasonal comparisons of each food category (χ^2_{OF}, χ^2_{V} = chi square test values applied to occurrence frequency and volume, respectively; d. f. = 3; p = significance level)

Food category	χ^2_{OF}	p	χ^2_{V}	p
Grasses inflorescences	24.43	0.0001	63.70	0.0001
Herbs	11.80	0.01	71.40	0.0001
Fruits	15.50	0.001	8.04	0.04
Roots	1.41	N. S.	44.06	0.0001
Storage organs	9.56	0.03	2.84	N. S.
Unidentified material	9.06	0.02	8.70	0.03

Trophic niche breadth and overlap

Monthly breadth of porcupine trophic niche was variable, with the largest values in the autumn and the smallest ones from late autumn to late winter. Monthly trophic niche overlap proved steady and large all year round. Diet overlap level decreased to smaller values only between May and June (Fig. 5).

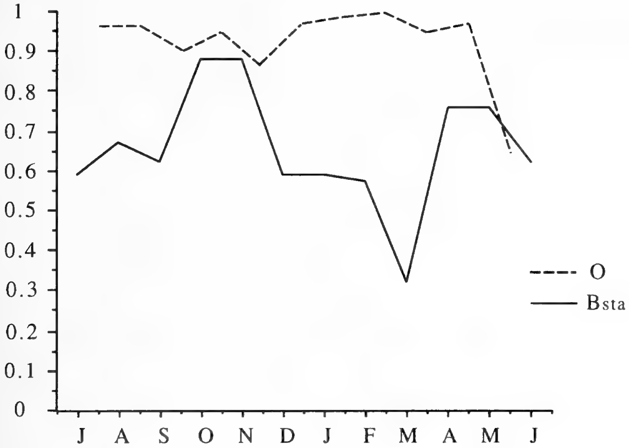


Fig. 5. Monthly trophic niche breadth and overlap values (B_{sta} = standardized Levins index; O = Pianka index).

Discussion

Our study showed that the crested porcupine is not only a consumer of hypogeal, but also of epygeal plant parts e. g. grass inflorescences, fruits and especially herbs. *Hystrix indica* has been observed eating green grass in the coastal plain of Israel (SEVER 1985). In the desert *H. indica* mostly forages on below-ground plant organs (GUTTERMAN 1982; ALKON and OLSVIG-WHITTAKER 1989), reflecting the abundance of geophytes relative to other plants in such an environment. In our research above-ground vegetation was a more important part of the porcupine diet, reflecting higher availability of fresh nutrient herbs in our study area. Roots were used with the highest frequency all year round, even if sometimes in relatively small quantities, e. g. in some spring months. They constituted, together with storage organs, an important component of the diet, showing no significant seasonal differences in their consumption. In fact, hypogeal parts of perennial plants are a continually-available food resource. They were mostly *Rumex* spp. taproots, which were apparently very abundant in our study area. We observed several diggings of porcupine with fragments of *Rumex* spp. plant, as well as with *Allium* spp. The consumption of *Arum italicum* tuber was surprising, since this genus is known to be toxic, at least to domestic animals (VERONA 1984). Debarking activity has been recorded for *Erethizon dorsatum* (TENNESON and ORING 1985) and *Hystrix indica* (SHARMA and PRASAD 1992). In Italy, it has been noticed in areas where *H. cristata* occurs, but debarked trees or shrubs were never observed in our study area. Considering also the difficulty we found in making captive porcupines feed on bark, we suggest that, in our study area, bark is not an important food resource.

As regards its feeding behaviour, the porcupine is reported as a generalist (SANTINI 1980). Its diet would therefore be expected to vary in relation to availability of numerous vegetable food resources, which in turn depend on environmental variables (e. g. CAVALLIni and Lovari 1991; Lucherini et al. 1991; Lovari et al. 1994 for Mediterranean habitat). Our analysis showed seasonal variations in the consumption of epygeal plant parts. The direct correlation between the frequency of grass inflorescences in the porcupine diet and the temperature suggested a consumption of this food category proportional to its availability: the peak of consumption was in summer months, when flowering occurred, but this category was not found in the early spring diet, when environmental availability of grass inflorescences is expected to be very low. The consumption of herbs was complementary to that of grass inflorescences, being very high in early spring (possibly reflecting a use proportional to the seasonal availability) and in winter, when their consumption could suggest an active search for them by the porcupines. On the other hand, the probable winter decrease in the availability of nutritious epygeal food categories, could have constrained porcupines to choose herbs. The autumnal peak of fruits in diet probably reflected their abundance on trees and, consequently, on the ground, where porcupines had access to them. Moreover, the changing seasonal availability of this diet component, together with that of grass inflorescences, was likely compensated by feeding on herbs.

The variable levels of trophic niche breadth supported further the hypothesis that the crested porcupine adopts a generalist feeding behaviour: it consumes hypogeal plant parts, fruits and grass inflorescences with a frequency reflecting their availability in the study area and uses herbs with a pattern apparently compensating the seasonal variations of food resources. The small niche breadth observed from winter to early spring could be caused by a decreased availability of food resources. Alternatively, it might be accounted for by an active selection of a few highly-preferred food categories. We think that this second hypothesis is less probable, because of the winter dormancy of vegetation. The high level of trophic niche overlap all year round, accounted for by the high monthly proportion of roots, indicated quite a homogeneous composition of the diet.

Its ability to feed on the most abundant food resources in its habitat makes this rodent a potential cause of crop damage, especially where it occurs at high density. On the other hand, olives and grapes, cultivated in the study area, were never found in porcupine faeces, although fragments of other fruit tree seeds were identified. Furthermore, no cases of feeding by porcupines in house-gardens have been reported.

Thus, the recent spread of the range of *H. cristata* in Italy can be accounted for by the wide ecological tolerance common to the *Hystrix* genus (e. g., Sever and Mendelssohn 1988 for *H. indica*; Haim et al. 1990 for *H. africaeaustralis*) and, particularly, by the generalist feeding behaviour found in this study combined with the abandonment by man of the countryside in the last few decades.

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Zusammenfassung

Die Zusammensetzung der Nahrung des Nordafrikanischen Stachelschweines (Hystrix cristata L., 1758), in einem mediterranen, ländlichen Habitat

Die Zusammensetzung der Nahrung des Nordafrikanischen Stachelschweines wurde in einem ländlichen, hügeligen Gebiet Mittelitaliens durch Kotanalysen untersucht. Nahrungsgruppen wurden sowohl durch den Vergleich von Proben aus frischem Pflanzenmaterial als auch von verdautem Material von in menschlicher Obhut gehaltenen, experimentell gefütterten Stachelschweinen identifiziert. Wurzeln waren vorherrschend und wurden das ganze Jahr hindurch in ähnlichem Ausmaß aufgenommen. Kräuter, negativ korreliert mit der Lufttemperatur, stellen die von den oberirdisch wachsenden Pflanzenteilen am häufigsten aufgenommene Pflanzengruppe dar, vor allem im Winter und im Frühling. Die winterliche Aufnahme von Kräutern war möglicherweise durch die Abnahme des Angebots an anderen Pflanzengruppen bedingt, z. B. an Blütenständen der Gräser und an Früchten. Die Aufnahme von diesen beiden letztgenannten Futtergruppen war positiv korreliert und umgekehrt korreliert mit der Aufnahme von Kräutern. Blütenstände der Gräser waren wichtige Futterbestandteile im Sommer, und deren Aufnahme war positiv mit der Temperatur korreliert. Stachelschweine nahmen Früchte besonders im Sommer und im Herbst auf. Die Aufnahme von unterirdischen Pflanzenteilen stieg im Winter und im Frühjahr an. Die Breite der Nahrungsnische und deren Überlappung weist darauf hin, daß es sich bei den Stachelschweinen um Futtergeneralisten handelt.

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Proechimys albispinus minor, a new subspecies from the state of Bahia, northeastern Brazil (Rodentia: Echimyidae)

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Abstract

Described a new subspecies, *Proechimys albispinus minor*, based on specimens from the highlands locality of Morro do Chapéu in the state of Bahia, in northeastern Brazil. The new subspecies can be distinguished by a smaller body and cranial size, finer pelage, absence of an ochraceous subapical zone in the aristiform hairs in the middorsal region, and ochraceous-orange subapical region in the setiform hairs in the middorsal region and outer thighs.

Introduction

Proechimys albispinus was originally described by I. GEOFFROY (1838) as *Echimys albispinus* from the Island Madre de Deus, in Todos os Santos Bay in the state of Bahia in northeastern Brazil. In his study of spiny rats from southeastern Brazil, THOMAS (1921) established the identity of *E. albispinus* as belonging to the genus *Proechimys*, and also examined specimens from the inland locality of Lamarão which he assigned to a new subspecies, *P. a. sertonius*. Both subspecies occur in the state of Bahia in northeastern Brazil, although they differ in their habitats. *Proechimys a. albispinus* occurs in the islands of the Todos os Santos Bay and the valley of the Paraguassú River in the adjacent mailand, whereas *P. a. sertonius* ranges further inland inhabiting drier habitats (MOOJEN 1948).

In his review of the taxonomy of the Brazilian forms of *Proechimys*, MOOJEN (1948) recognized the two subspecies of *P. albispinus* and provided detailed diagnoses of the two forms, which differ in characteristics of the pelage and the skull. As part of a study of the sources of non-geographic variation in cranial metric traits and pelage color variation in *P. albispinus* (PESSÔA and REIS 1991; PESSÔA and REIS 1995), we examined specimens of *P. a. albispinus* and *P. a. sertonius* and specimens from the highland locality of Morro do Chapéu in the state of Bahia. The specimens from Morro do Chapéu differ in cranial and pelage traits from the two recognized subspecies of *P. albispinus*, and are thought to represent a new form which is described herein.

Material and methods

The specimens examined in this study are housed in the Museu Nacional (MN), Universidade Federal da Paraíba (UFPB), Museu de Zoologia da Universidade de São Paulo (MZUSP), Field Museum of Natural History (FMNH), Museum of Comparative Zoology (MCZ), and the National Museum of Natural History (USNM). The specimens of *P. a. albispinus* and *P. a. sertonius* used for comparison with the new subspecies were identified with the aid of diagnoses based on standard features of the skull and pelage provided in Moojen (1948). Bacular morphology was also used to ascertain the identity of individuals assigned to the new subspecies. The baculum in the new subspecies is similar in morphology to that of *P. a. albispinus* described in Pessôa and Reis (1992). The following specimens, all from the state of Bahia, were examined: *Proechimys a. albispinus*: Jequié, MN 13 906, 13 907, 13 913, 13 917, 13 938, 13 942, 13 943, 13 948, 13 949, 13 952, 13 954; Macaco Seco, FMNH 18 196, 20 391-20 394, 20 396, 20 397, 20 399, 20 403, 20 404, 20 406-20 410, MCZ 38 311. *Proechimys a. sertonius*: Vila Nova, MN 6 454; Senhor do Bonfim, MZUSP 2 632, 2 633, 2 635-2 637; Lamarão, MZUSP 2 003, MCZ 17 847, USNM 172 952.

Descriptions of hair characteristics are based on Moojen (1948), and hair measurements were taken (in mm) with an eyepiece micrometer. Color definitions follow Ridgway (1912). Cranial measurements were obtained with digital calipers accurate to 0.01 mm.

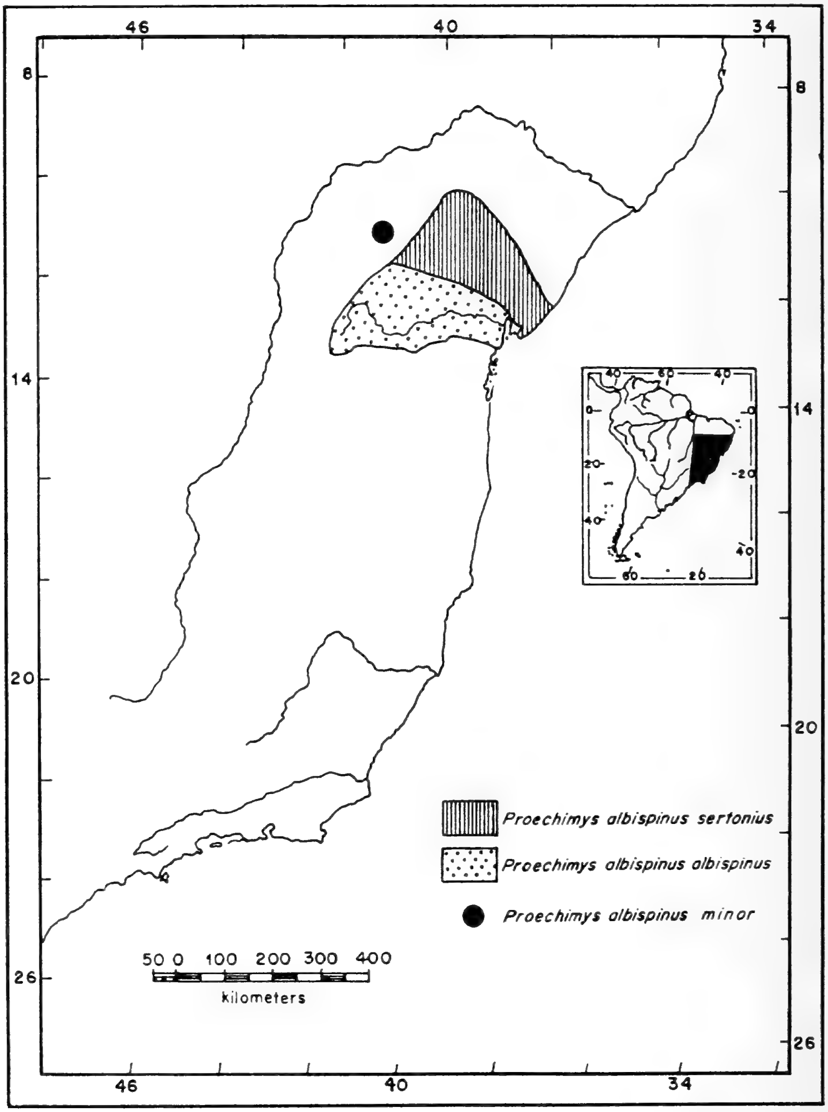

Fig. 1. Ranges for the subspecies of *Proechimys albispinus* according to Moojen (1948). The dot indicates the type locality of *Proechimys albispinus minor*

Results

Proechimys albispinus minor, new subspecies

Holotype: An adult female (MN 34491), dry skin and skull. Collected by O. S. Farias and M. T. Rodrigues on 28 August 1985 at Morro do Chapéu, state of Bahia, Brazil.

Type locality: Morro do Chapéu (11°33′S, 41°09′W), 800 meters above sea level, state of Bahia, Brazil.

Paratypes: Five specimens, all from Morro do Chapéu (UFPB 772; MZUSP 28885-28888).

Distribution: Known only from the type locality (Fig. 1).

Diagnosis: *Proechimys albispinus minor* can be distinguished from *P. a. albispinus* and *P. a. sertonius* by a smaller body and cranial size (Tab. 1), skull with the maxillary portion of the foraminal septum weakly developed, finer pelage, aristiform hairs on the middorsal region always whitish basally and gradually blackening toward tip, and setiform hairs with ochraceous-orange subapical zone.

Description

Pelage: Aristiform hairs on middorsal region: whitish basally, gradually blackening toward tip; total length (mean = 24 mm); maximum width (mean = 1.0). Aristiform hairs on outer thighs: two types of aristiforms. One type whitish basally and gradually blackening toward tip, and the other type whitish basally, grayish in the middle and ochraceous-buff toward the tip; total length (mean = 18.7); maximum width (mean = 0.7). Setiform hairs on mid-

Table 1. Sample size (N), means ($\overline{X}$), standard deviations (± SD), and minimal (Min.) and maximal (Max.) values for selected body and cranial measurements (in mm) in the three subspecies of *Proechimys albispinus*

	Proechimys albispinus albispinus				*Proechimys albispinus sertonius*			
Characters	N	$\overline{X}$ ± SD	Min.	Max.	N	$\overline{X}$ ± SD	Min.	Max
Head and body	6	189.6 ± 6.84	179	198	4	185 ± 7.07	175	190
Tail	6	170.4 ± 9.30	159	179	4	165 ± 10.80	150	175
Greatest skull length	6	46.1 ± 1.17	44.1	47.6	4	45.4 ± 1.47	43.8	46.7
Condylo-incisive length	6	40.1 ± 1.02	38.3	41.4	4	39.3 ± 1.55	37.6	40.6
Zygomatic breadth	6	23.9 ± 0.64	22.8	24.5	4	23.4 ± 0.59	22.8	24.2
Length of nasals	6	15.7 ± 0.46	15.1	15.7	4	15.7 ± 1.11	14.7	16.9
Interorbital constriction	6	10.7 ± 0.33	10.3	10.2	4	10.2 ± 0.55	9.6	10.7
Palatal length	6	15.9 ± 0.40	15.2	16.4	4	15.6 ± 0.92	14.5	16.1
Tooth row length	6	7.7 ± 0.44	7.3	8.3	4	7.3 ± 0.20	7.1	7.5

	Proechimys albispinus minor			
Characters	N	$\overline{X}$ ± SD	Min.	Max.
Head and body	2	160 ± 7.07	155	165
Tail	2	107 ± 26.87	88	126
Greatest skull length	4	40.8 ± 1.44	39.0	42.5
Condylo-incisive length	4	34.7 ± 2.08	32.2	36.9
Zygomatic breadth	4	22.6 ± 0.74	21.5	23.2
Length of nasals	4	13.9 ± 0.62	13.4	14.8
Interorbital constriction	4	9.5 ± 0.30	9.1	9.8
Palatal length	4	14.1 ± 0.49	13.5	14.7
Tooth row length	4	7.0 ± 0.05	6.9	7.1

dorsal region: whitish basally succeeded by grayish, then by subapical zone ochraceous-orange, and blackish tip; total length (mean = 23.0); maximum width (mean = 0.2). Setiform hairs on outer thighs: whitish basally succeeded by grayish, then ochraceous-orange subapical zone, and blackish at the tip; total length (mean = 18.8); maximum width (mean = 0.1).

Skull: Small; bullae small and smooth, jugals dorso-ventrally wide, with conspicuous transverse ridge; postorbital process of zygoma conspicuous and formed by both jugal and

Fig. 2. Ventral, dorsal, and lateral views of the skull of the holotype of *Proechimys albispinus minor* (MN 34 491). Scale at upper left represents 1 cm

squamosal; incisive foramen narrow and short, maxillary portion of the foraminal septum weakly developed; vomerine sheath complete, with the premaxillary part at a lower level than that of the maxillary part; mesopterygoid fossa extending forward as far as anterior plane of second molars (Fig. 2).

Teeth: Molariform teeth with only one counterfold.

Measurements: Measurements (in mm) of the holotype as follows: total length 291; tail 126; hindfoot 34; ear 25; greatest skull length 41.3; basilar length 31.2; palatal length 14.1; toothrow length 7.0; diastema 9.7; rostral length 16.1; nasal length 13.8; interorbital constriction 9.5; rostral breadth 6.4; skull depth 11.9; rostral depth 7.8; maxillary breadth 7.8; zygomatic breadth 22.9; bulla length 8.9; post-palatal length 19.7; incisive foramen length 3.9; mandibular length 21.7.

Habitat: Morro do Chapéu in the state of Bahia is located at the northern edge of the Espinhaço range. This range runs approximately in a south-southwest to north-northeast direction in the states of Minas Gerais and Bahia. Rock formations are the result of a geossinclinal of pre-Cambrian age, and altitudes vary from 800 to 2 000 meters above sea level. The occurrence of plant formations is associated with altitude and soil type. From 800 to 1 000 m the vegetation is characteristically savanna which grades into grasslands between 1 000 and 1 100. Meadows predominate in the highlands due to accumulation of organic matter.

Etymology: The name *minor* refers to the smaller size of *P. a. minor* relative to *P. a. albispinus* and *P. a. sertonius.*

Discussion

The new subspecies, *P. a. minor*, differs from *P. a. albispinus* and *P. a. sertonius* in body and cranial size. *Proechimys a. minor* is approximately 15% smaller in body size relative to *P. a. albispinus* and *P. a. sertonius.* While comparisons of body size are straightforward, differences in cranial size among forms in the genus *Proechimys* must be evaluated considering the problem of indeterminate growth in adults. PATTON and ROGERS (1983) demonstrated that, for *P. brevicauda*, an average 25% of the variation in cranial size within populations is due to post-ontogenetic growth. A similar result was obtained for *P. a. albispinus*, where variation in cranial size due to age amounts to 17% (PESSÔA and REIS 1991). This considerable effect of intrapopulation variation in cranial size may confound the analysis of size differences among populations (PATTON and ROGERS 1983) and, consequently, size comparisons must be made with individuals of equivalent age classes. Comparisons among *P. a. minor*, *P. a. albispinus* and *P. a. sertonius* were therefore performed with individuals of age classes 6 and 7, defined on the basis of tooth wear criteria and eruption (PESSÔA and REIS 1991). The cranial traits measured show that *P. a. minor* is smaller than the other two subspecies. The difference in size is particularly evident from greatest length of skull, which shows that *P. a. minor* is approximately 11% smaller than *P. a. albispinus* and *P. a. sertonius.*

Proechimys albispinus shows unique features of the pelage amongst the genus *Proechimys*, including the shape and color pattern of aristiforms hairs (MOOJEN 1948), and a case of partial albinism and white spottings (PESSÔA and REIS 1995). The new subspecies described here adds to the pattern of pelage variation in *P. albispinus* in that *P. a. minor* lacks an ochraceous subapical zone in the aristiform hairs in the middorsal region, and by the presence of an ochraceous-orange subapical zone in the setiform hairs in the middorsal region and outer thighs. The aristiform hairs in the middorsal region in *P. a. minor* are also thinner than in *P. a. albispinus* and *P. a. sertonius* (MOOJEN 1948), giving a less spiny appearance to the pelage of *P. a. minor.*

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Zusammenfassung

Proechimys albispinus minor, eine neue Unterart von Stachelratten aus dem Bundesstaat Bahia, Nordost-Brasilien (Rodentia; Echimyidae)

Es wird eine neue Unterart der Stachelratte *Proechimys albispinus* beschrieben, die bei Morro do Chapéu im Hochland von Bahia in Nordost-Brasilien gesammelt wurde. Das neue Taxon ist durch kleine Körper- und Schädelmaße, feinere Fellstruktur und abweichende Bindenmuster der Grannen- und Wollhaare gekennzeichnet.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Summer diets of Tibetan Red foxes in Khunjerab National Park, Pakistan

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Food habits of terrestrial predators in the mountains of northern Pakistan have received relatively little quantitative attention (Schaller 1972, 1976, 1977). Khunjerab National Park is Pakistan's second largest national park (2,269 km^2) and is located in the extreme northeastern corner of Pakistan. Tibetan red foxes (*Vulpes vulpes montana*) are the region's most common mammalian predator (Hess 1995). The purpose of this investigation was to study the diet of red foxes to aid in the effective conservation, management, and human coexistence with foxes and other wildlife in the Khunjerab region.

Our research had three broad goals. First to collect information on fox diets in a little studied location that would be useful in intraspecific studies (Iriarte et al. 1990). Second, to determine the frequency with which domestic animals were found in the scats of Khunjerab foxes. Third, to study the consistency of food items between seasons and years.

The 250 ha study area (36°81′ N, 74°95′ E) included an uninhabited high alpine meadow (Dhee Sar) and its surrounding ridges and valleys (elevation 3 500 m–4 500 m) in Khunjerab National Park, Pakistan. The study site was a fairly representative high pasture in Khunjerab; uninhabited yet seasonally grazed between mid-May and late June by several hundred domestic cattle, yaks, goats, and sheep (Blumstein 1995).

Red fox scats were collected opportunistically from 15 May to 15 September 1990, and again from 4 May to 18 August 1991 in and around Dhee Sar. After collection, scats were air dried and placed in plastic bags labeled with date and location. Fox scats were unambiguously identified by size and shape. An unknown number of foxes were present in 1990, while ≥ 10 different foxes were seen at Dhee Sar during 1991.

In the laboratory, scats were broken apart and contents sorted. Hairs were washed in 100% ethyl alcohol, air dried, mounted on glass slides using Permount, and all were identified by a single observer (M. R.). Sample hairs were compared with known reference hairs, mostly from Dhee Sar, but some from museum collections. Hairs were identified according to characteristics commonly described in guides to hair analysis (e. g., Ryder 1973).

Domestic goats and sheep, as well as wild ibex, marmots, and pikas could be unambiguously identified by their hair. Hares, voles, and mice had less distinctive hair characteristics, but could generally be distinguished by their cortex width, and distinctive medullary characteristics. Hair from domestic cattle and yak were generally distinguishable. Bones or feathers were identified when possible. M. R.'s intraobserver reliability in identifying hair samples was high; 86% of identified scat contents were consistently reidentified on a second appraisal.

Relative frequencies of occurrence (occurrences in different scats as a function of total number of scats) of prey items are reported. Domestic cattle and yak were combined for analysis and their joint frequency is reported. Early season versus late season frequencies were calculated by summing those items identified in scats collected in May and June and comparing frequencies with those scats collected in July and August.

Hair from nine mammalian species was identified in 177 fox scats (Tab. 1). Many scats contained multiple types of foods, so frequencies sum to >1.0.

Marmot hair was 2.5 times more common in fox scats collected at Dhee Sar (overall frequency = 0.32, n = 177 scats) than has been previously reported in areas with sympatric marmots (frequency = 0.13, n = 92 scats; SCHALLER et al. 1987). In addition, livestock hair occurred 4.5 times more frequently in fox scats collected at Dhee Sar (combined overall relative frequency = 0.50, n = 177 scats) than has been previously reported in the diets of Central Asian red foxes (weighted mean frequency = 0.11, n = 205 scats; SCHALLER 1977; SCHALLER et al. 1987). Plant material was about as common in the diets of Dhee Sar foxes (overall relative frequency = 0.36, n = 177 scats) as in other Central Asian red foxes (weighted mean frequency = 0.32, n = 274 scats; SCHALLER 1977; SCHALLER et al. 1987).

In the two years of our study, fox diets varied considerably both between seasons and between years. Pikas, marmots, voles, eggshells, and plant material were identified in relatively constant frequencies in early season and late season scats. Voles and eggshells were identified in relatively constant frequencies between years. All other food items appeared to vary seasonally and annually.

Foxes are reported to have opportunistic and catholic food habits (e. g., LLOYD 1980). In other places, mid-sized mammals such as lagomorphs and marmots are eaten by sympatric foxes (e. g., SCHALLER 1977, VON SCHANTZ 1980; HEWSON 1983; SCHALLER et al.

Table 1. Relative frequency of occurrence of food items in Tibetan red fox scats collected in 1990 and 1991 at Dhee Sar, Khunjerab National Park, Pakistan

Food Items	1990	1991	1990 and 1991[1]	M/J[2]	J/A[3]
Sample Size (no. of scats)	35	142	177	90	82
Wild Mammals					
Lepus capensis tibetanus	0.17	0.09	0.11	0.13	0.07
Ochotona roylei	0.11	0.01	0.03	0.02	0.05
Marmota caudata aurea	0.26	0.34	0.32	0.33	0.30
Apodemus sylvaticus	0.14	0.26	0.24	0.33	0.15
Alticola roylei	0.29	0.27	0.27	0.27	0.28
Capra ibex sibirica	0.09	0.01	0.03	0.06	0.00
Domestic Mammals					
Bos spp.	0.23	0.30	0.29	0.26	0.33
Ovis sp.	0.06	0.15	0.14	0.21	0.06
Capra sp.	0.00	0.08	0.07	0.08	0.06
Miscellaneous					
Feathers[4]	0.09	0.17	0.15	0.21	0.07
Eggshell	0.06	0.04	0.04	0.06	0.02
Plant material[5]	0.23	0.39	0.36	0.34	0.38

[1] Overall relative frequency of occurrence of food items in both years.

[2] May and June relative frequency of occurrence of food items in both years.

[3] July and August relative frequency of occurrence of food items in both years.

[4] Identified feathers included: 1 Redstart (*Phoenicurus* sp.), 2 Brown Accentors (*Prunella fulvescens*), 2 Rosy Finches (*Leucosticte* spp.), 2 Choughs (*Pyrrhocorax* spp.), and 4 Himalayan Snowcocks (*Tetraogallus himalayensis*).

[5] Included both vegetative remains of grasses and other herbaceous plants as well as remains of the fruit of *Ephedra gerardiana* and *Rosa webbiana*.

1987). Marmots were more common at Dhee Sar than hares and this was reflected in the diets of Khunjerab foxes. Observations suggest that both juvenile and adult marmots fell prey to foxes at Dhee Sar. In 1990 and 1991, D. T. B. observed foxes eating 2 recently killed adult marmots. Foxes were more frequently seen after marmot pups emerged (late June, early July), and at least 19% of marmot pups were probably killed by predators.

Plant material was commonly found in fox scats. Roberts (1977) reported that the red fox can subsist on fruit and insects, and plant remains have been reported to be a major component of fox diets elsewhere (Green and Osborne 1981; Calisti et al. 1990). Outside the study site, but within the national park, fox scats seen in the fall were often filled with *Ephedra* berries, suggesting that foxes were eating plants and plant parts rather than incidentally ingesting them.

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Burrowing behaviour and burrow architecture in *Apodemus sylvaticus* (Rodentia)

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The commonest kind of home constructed by mammals is a burrow. The order Rodentia comprises the largest concentration of burrowing species. The burrow is therefore an important part of the biology of rodents which needs to be understood in terms of both its construction and function.

Little is known about burrows and burrowing behaviour in *Apodemus sylvaticus*. A few studies have reported that this species has a burrow system consisting of a dwelling with distinct architectural features constructed by a single individual (Dufour 1971, 1978). The architecture of this system as dug in the natural habitat; was described from a small sample by Jennings (1975). It was found to consist of separate nest and food chambers usually well protected under the base of a tree, joined by a tunnel in the form of a loop giving access to between three and six radiating exit tunnels. Similar observations were previously reported by Cleminson (1966) from the wild. The burrows, apart from providing some benefits, are areas where interactions between individuals may be concentrated and intensified (Montgomery and Gurnell 1985).

The purpose of this study was to examine the burrowing behaviour of *A. sylvaticus*, a species with an extensive western Palaearctic range (Corbet 1978), in a laboratory environment to examine the details of burrow architecture, how burrows are created and how long they take to complete.

Twenty four sexually inactive adult wood mice *A. sylvaticus* (13 males and 11 females) were used in this study. The animals were caught using baited Longworth live traps in Garscube and Loch Lomond areas near Glasgow, Scotland. The respective mean body weights for the males and the females were 22.3 ± 2.6 g (range: 17.8–28.2) and 19.2 ± 2.6 g (range: 15.6–23.8). The mice were housed individually in plastic cages (15 × 27 × 13 cm). Lights were set on a 12:12 light-dark cycle and temperature varied between 21 °C and 23 °C. Mice were submitted to a period of acclimation of at least 6 weeks to these conditions before the onset of any test.

A terrarium (1.5 × 2.0 × 1.0 m high) made of 1.0 cm thick plywood panels and divided into two equal parts (1.0 × 1.5 m) was used. The top was covered with a wire lid. A perspex window (0.5 × 2.0 m) was fitted on one side to allow incidental observations. Dry food and water were provided in small containers placed in a corner. The terrarium was filled with a flattened 10-cm layer of fine yellowish wet sand to allow the mice to burrow. In order to simulate a natural tree or rock, a wooden box (0.4 × 0.4 × 0.2 m high), with two opposite sides parallel and sloping at an angle of 45° was placed on the surface of the sand in the centre of each of the two compartments.

The mice were tested in two test sets: one of 24-hour and the other of 72-hour duration. Subjects were placed individually in the terrarium approximately 30 min before light offset.

The whole burrow system was revealed by excavation. All traces of mouse activity on the surface and complete portions with all details of the burrows were accuretely mapped at a 1:5 scale on graph paper using a grid divided into 5×5 cm multiple squares drawn on a 0.5×1.0 m plastic sheet, and placed on the surface of the sand. Depths were recorded every time the slope changed.

After each set of records and before another mouse was tested, all of the sand was mixed and when necessary moistened, and the walls washed in order to remove any scent marks. The sand was replaced periodically throughout the test.

Mice burrowed very readily under the controlled conditions. Except for one mouse, all the others had dug at least one burrow of greater or lesser complexity. There were always mounds of excavated sand at the initiation entrances, well more frequently one mound per burrow system. Thirty-two burrows were constructed. Two types were recognised: simple tunnels and main burrows.

Eight simple tunnels were recorded. They consisted either merely of a dead-ending tunnel with an entrance aperture or of two apertures connected by a single tunnel. Their mean total length was 17.4 ± 9.8 cm (range 7.0–37.5; n = 8) and maximum depth 6.4 ± 1.7 cm (range 3.8–8.5; n = 7). Four mice dug such burrows. This type of excavation did not have any obvious function, except that one simple tunnel constituted an underground food cache. It was always found associated with main burrows.

Twenty-four main burrows (75%) were constructed (Tab. 1). Six of them (19%) consisted of one entrance hole followed by a tunnel joining a chamber, and an escape tunnel connecting the chamber to the surface. One junction of tunnels was recorded (Fig. 1 a). The others (56%) were more sophisticated. They contained one or several entrance and exit holes associated with several tunnels, among them "chimney" tunnels which serve as escape passages, one or two chambers, usually several junctions of tunnels, loops and store chambers and tunnels (Fig. 1 b and c). One female constructed two burrows of this type, one of the basic architecture and the other of the latter kind. Few of the burrows (29%) reached the bottom of the terrarium, and only an overall distance of 50.5 cm (2%) was dug against it. Resting chambers were generally the deepest part of the burrow. Nineteen burrows had only a single chamber, and five contained two chambers. Several exit holes (33%) were not yet popped; small cracked bulges appearing on the surface revealed their presence. Many other accesses (21%) and an overall distance of 73.5 cm (2.7% of the total length) of tunnels were plugged with sand. In four burrows the whole initiation entrances were blocked and left unused; they were very likely plugged while the animals were progressing in tunnelling. Most (63%) of the dead-ending tunnels were like the escape tunnels directed upwards, almost vertically at their end, to the surface. They stopped, however, at a distance of 3.2 ± 1.8 cm (range: 0.5–6.9) from the ground level. They very probably serve as latent escape passages.

Table 1. Mean ± SD and range of parameters of the 24 main burrows constructed after 24 hours. The measurements are computed from each single burrow. The 0 score of the failed male was not included in the analysis.
Tunnel lengths were calculated from the burrow representations on the graph paper. Any dead-ending tunnel of less than 5 cm length, which is assumed as being the minimum space large enough to admit a mouse, was omitted from the computations

Length (cm)	Depth (cm)	Surface (cm2)	Holes (n)	Tunnels (n)	Chambers (n)	Junctions (n)
108.1 ± 50.7 37.5–220.0	8.3 ± 1.5 5.0–10.0	559.3 ± 195.0 25.0–600.0	2.5 ± 2.1 1—12	5.7 ± 4.9 2–25	1.2 ± 0.4 1–2	2.6 ± 2.2 1–11

There was a significant positive linear correlation (Spearman test, r (32 burrows) $= 0.73$, $\mathrm{df} = 30$, $p < 0.001$) between the length of the burrows and their complexity, burrow complexity being obtained by combining all the architectural features numbers.

The burrows were not randomly located in the terrarium although the space available was quite limited. Nineteen burrows (59%) were wholly or partly located beneath the wooden box. The volume of sand excavated and the space used for burrowing are significantly larger (total length dug 1 242 cm vs. 1 492 cm, $\text{Chi2} = 3\,467.05$, $\mathrm{df} = 1$, $p < 0.001$; total surface 6 969 cm2 vs. 7 081 cm2, $\text{Chi2} = 22\,351.75$, $\mathrm{df} = 1$, $p < 0.001$), and significantly more chambers (17 vs. 12, $\text{Chi2} = 69.78$, $\mathrm{df} = 1$, $p < 0.001$) were dug beneath this box than in the area away from it. A signifcantly larger number of initiations of burrows (21 vs. 15, $\text{Chi2} = 10.67$, $\mathrm{df} = 1$, $p < 0.01$) and of entrance/exit holes (30 vs. 41, $\text{Chi2} = 2.96$, $\mathrm{df} = 1$, $p < 0.05$) was located along the box periphery. Moreover, 11 of the burrows (52%) were initiated and 15 of the entrance and exit holes (50%) were located against the overhanging side (respectively, $\text{Chi2} = 9.28$, $\mathrm{df} = 3$, $p < 0.025$; $\text{Chi2} = 10.0$, $\mathrm{df} = 3$, $p < 0.001$).

Males (the failed male is included) and females excavated statistically similar amounts of sand for burrowing. Yet, the female burrow systems each taken as a whole, i.e. simple tunnels when present lumped together with main burrows, showed significantly a higher number of features than those of the males (mean total number of features respectively 17.3 ± 12.2 vs. 9.3 ± 4.5; Mann-Whitney U test, $U = 37$, $p = 0.05$), differences still appear and approach statistical significance (Mann-Whitney U test, $U = 39$, $p < 0.10$) if only the main burrows are considered. As an example, one female constructed one burrow which consisted of 12 entrances, 25 short tunnels with 11 junctions, and 2 chambers; the burrow complexity for this individual, with a score of 50, is the highest.

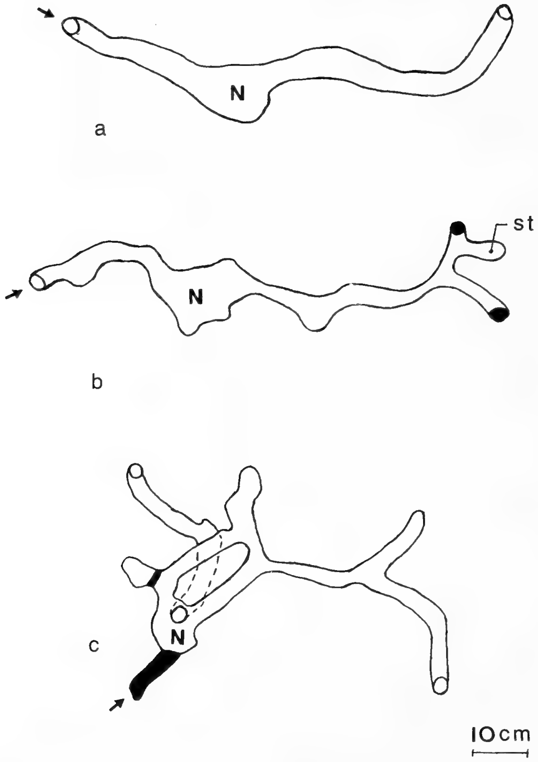

Fig. 1. Topviews of typical main burrows. a: a typical burrow system of the basic architecture; b and c: burrow systems of a more complex architecture. The only complete loop recorded is seen in c. The arrow indicates the initiation entrance. N: nest. st: store tunnel. Open circles: open entrances. Filled circles: plugged entrances. Filled areas: plugged tunnels.

Data were recorded from 23 mice. Mice had significantly dug more by 72 hours (mean total length per mouse 142.3 ± 83.7 cm vs. 113.9 ± 52.7 cm; Wilcoxon T test, $T = 69$, $p < 0.01$) and the 72-h burrows were significantly more sophisticated (total number of features 379 vs. 302; $\text{Chi2} = 8.7$, $\mathrm{df} = 1$, $p < 0.005$) than the 24-h ones. Yet, 80% of the total length were dug within the first 24 hours, and, considered separately, only the number of holes had significantly increased (68 vs. 96, $\text{Chi2} = 4.78$, $\mathrm{df} = 1$, $p < 0.05$). Larger parts of burrows were plugged after 72-hours (73.5 cm vs. 175.5 cm, $\text{Chi2} = 41.78$, $\mathrm{df} = 1$, $p < 0.001$).

The burrow systems constructed by *A. sylvaticus* under controlled conditions contained a nest chamber, a tunnel system with up to eleven junctions, a mean of more than two exits and in some, a store chamber as well. They are comparable with those described by CLEMINSON (1966) and JENNINGS (1975) for the natural environment. The burrow dug by an individual in some cases also included simple short tunnels which could represent a system abandoned before completion. One individual in addition to a complex burrow also dug a simple burrow with nest chamber. This possibly represented an incompletely abandoned system or else an additional home. These observations closely approximate those described by WOLTON (1985) on nest occupancy by *A. sylvaticus* in the wild. This author found that mice changed nest site frequently.

The differences between the burrows built after 72 hours compared with those examined after 24 hours were in certain respects not great. DUFOUR (1971, 1978) reported that wood mouse burrows remained unchanged during the first week with respect to the length and the complexity. During the second or the third week these burrows grew more sophisticated, and their length never exceeded after one month threefold that of the 24-hour burrows. This suggests that a largely completed burrow could be constructed in the natural environment in as little as 24 hours. This, however, assumes that the substrate will be as easy to burrow in as moist sand.

Sex differences in the burrow system were detected, with females creating a somewhat more complex architecture. The mice tested were not breeding but the differences do suggest that when breeding, the burrow system of females may have additional complexity. Albeit, DUFOUR (1978) found from a test on a small sample that the only difference between the burrows of breeding females and those of non-breeding ones lay in the padding of the nest chamber. This deserves further study.

The wooden box placed on the sand surface was highly attractive to the animals. Its position seemed to influence the architecture of the burrow system below ground with more of the burrow system being located under the shape than would be predicted by the area it occupied. This supports the field observations that burrow systems are located at the bases of trees (CLEMINSON 1966; JENNINGS 1975). According to CLEMINSON (1966) chambers in this protected position may be less subject to collapse, or to percolation of water from above. It was also clearly shown that the mice preferred to initiate the burrow along the side which sloped over them. However, from the spoil heaps of excavated sand and the subterranean architecture it was seen that burrow exits/entrances could be created and later closed during burrow construction so that the site of burrow initiation was not necessarily retained as an entrance. In the same way RODE (1929) reported from experiments on *A. sylvaticus* in outdoor terrariums that, except for few holes initiated against walls, all the burrows accesses changed over time. This behaviour and the presence, in our study, of burrows with just their entrance holes stopped suggests that in the natural environment the entrances and exits in current use may change over time possibly to confuse predators. The plugging/unplugging of accesses may also represent a regular behaviour which serves to protect burrows from flooding as observed by HAYNE (1936) in *Peromyscus polionotus.*

In conclusion therefore, this study shows that burrows of *A. sylvaticus* under controlled conditions varied in complexity but were typically similar to those described for mice in the wild. It also suggests that environmental and internal factors modulate altogether this behaviour. The natural architecture could thus change to adapt to local environmental circumstances.

Acknowledgements

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Z. Säugetierkunde **60** (1995) 251–254

Resting metabolism and thermal conductance in southern Africa's smallest rodent, the Pygmy mouse (*Mus minutoides*)

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Two parameters frequently determined in ecophysiological studies of mammalian thermoregulation and energetics are basal metabolic rate (BMR; the minimum metabolic rate in an euthermic mammal) and minimum thermal conductance (minimum C; the minimum rate at which heat is exchanged between an euthermic mammal and the environment). Both parameters scale allometrically with body mass across mammal species (e.g. Bradley and Deavers 1980; Hayssen and Lacy 1985) and deviations from values expected on the basis of body mass are often taken as representing adaptive mechanisms to ecological variables or environmental extremes (e.g. Scholander et al. 1950; Casey et al. 1979; Haim and Izhaki 1993). The pygmy mouse (*Mus minutoides*) is southern Africa's smallest rodent, is omnivorous, terrestrial, nocturnal, lives singly or in pairs in burrows, under logs and under stones, in both summer and winter rainfall regions and occupies a diversity of habitats of disparate aridity (Skinner and Smithers 1990). Because of its small size, *M. minutoides* is of particular interest in terms of its energetics and thermoregulatory biology.

Eight pygmy mice were trapped at 29 °S 30 °E in Natal, South Africa in July 1993. Mice were transported to Pretoria (28°15′E25° 45′S) where they were maintained under natural photoperiod at room temperature (20–23 °C) in individual cages for 6 weeks prior to experimentation. During experimentation oxygen consumption of solitary mice of known body mass was determined at 13 air temperatures of between 14 and 38 °C using an open-flow respirometry system. At each ambient temperature oxygen consumption was measured at one minute intervals over a two hour period in each of four randomly selected mice. Mice were observed frequently during measurement to ensure that they were inactive. Minimum oxygen consumption by a given mouse at a given ambient temperature was taken as the mean of the five lowest consecutive measures within the two hour measurement period. All measures of oxygen consumption were corrected to standard temperature and pressure of dry air. Although body temperatures were not taken, no mouse was found to show signs of hyperthermia (sluggishness, cold body surfaces) on removal from the respirometry system. In contrast at an ambient temperature of 8 °C, mice ($n = 2$) were unable to maintain euthermy for a two hour period and were thus removed from the respirometry system and rewarmed. No attempt was made to observe spontaneous arousal from hypothermy.

Thermoneutrality was defined as the range of temperatures within which oxygen consumption was independent of ambient temperature. Mean oxygen consumption at thermoneutrality was taken to represent basal metabolic rate (BMR). The slope of the linear regression of oxygen consumption on decreasing temperature below thermoneutrality was taken to represent minimum C (McNab 1980). The lower limit to thermoneutrality (lower critical), was estimated as the intersect between the regression of oxygen consumption on decreasing ambient temperature below thermoneutrality, and BMR.

Mean oxygen consumption was independent of air temperature between 32 and 38 °C (Fig. 1) and increased linearly with decreasing air temperature at and below 30 °C. There was no evidence for an elevation of metabolism at high air temperatures (up to 38 °C; Fig. 1). Estimates of BMR, minimum C and lower critical temperature are shown in table 1. Mean BMR was slightly higher while minimum C was substantially higher than predicted on the basis of body mass from other rodents and mammals respectively (Tab. 1). The slope of the regression of metabolism on air temperature usually underestimates minimum C as determined by simultaneous measures of metabolism and body temperature (McNab 1980). This implies that actual minimum C in *M. minutoides* will be even higher than our estimate.

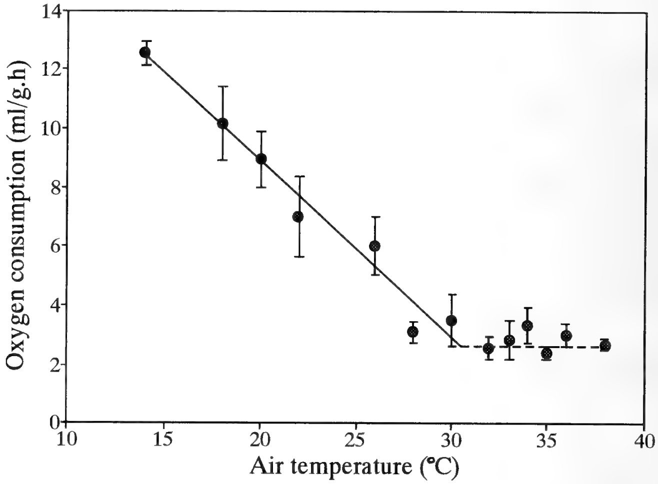

Fig. 1. The influence of air temperature on oxygen consumption in resting *Mus minutoides* of mean body mass 8.27 g. Each point represents the mean of 4 individuals randomly selected from a pool of eight. Errors are 1 se. The solid line represents the least squares regression of oxygen consumption on air temperature at and below 30 °C: $y = 20.8–0.597x$, $r^2 = 0.97$, $F_{1,5} = 148.9$, $P < 0.001$. The dashed line represents basal metabolic rate.

Table 1. Thermal parameters of *Mus minutoides*; n = 8 individuals. a – % of basal metabolic rate predicted for an 8.27 g rodent after Hayssen and Lacy (1985). b – % of thermal conductance predicted for an 8.27 g mammal after Bradley and Deavers (1980). c – Body temperature predicted by extrapolation of the regression of metabolism on air temperature to a metabolism of zero (McNab 1980).

	Mean ± sd	% of predicted
Body mass (g)	8.27 ± 1.82	–
Basal metabolic rate (ml O_2/g · h)	2.621 ± 0.636	106[a]
Minimum thermal conductance (ml O_2/g · h · °C)	0.597 ± 0.049	197[b]
Lower critical temperature (° C)	30.5 ± 1.1	–
Predicted body temperature (° C)[c]	34.8	–

Small mammals have high mass specific metabolic rates (Hayssen and Lacy 1985), and high mass specific minimum C (Bradley and Deavers 1980) reflecting their high surface area to volume ratio and low capacity for body insulation. Mammal species from cold climates often show lower minimum C than those from warm climates (Scholander et al. 1950) while minimum C is often higher in mammals in summer than in winter (Casey et al. 1979). In at least some winter acclimated mammals minimum C can be increased by exposure to summer conditions. These observations suggest an adaptive basis for residual variation in minimum C once the effect of body mass has been removed (Bradley and Deavers 1980) although some phylogenetic dependency is apparent (Bradley and Deavers 1980). The comparatively high minimum C demonstrated by *M. minutoides* in the present study (Tab. 1) implies that when exposed to cold, either energy expenditure in this species will be extremely high or individuals will resort to facultative or obligatory hypothermy (as evidenced by the demonstration of hypothermy in the two individuals exposed to 8 °C in the present study). The interspecific equation relating minimum C to body mass in the Muridae does not deviate significantly from that for mammals in general (Bradley and Deavers 1980) and although minimum C is comparatively high in *Mus booduga* (Gosh et al. 1979; 110% of that predicted for a mammal of the same body mass, Bradley and Deavers 1980) and *Mus musculus* from the Isle of May in Scotland (Jakobsen 1978; 118%) it is comparatively low in a population of *M. musculus* from Marion Island in the sub-Antarctic (P. I. Webb unpubl. data). There is thus no strong evidence to support a phylogenetic tendency for high minimum C within the genera *Mus*. We therefore suggest either that high minimum C in *M. minutoides* represents an adaptive trait (i. e. *M. minutoides* from the sampled population are either not frequently exposed to low temperatures, and/or are frequently exposed to high temperatures where dry heat loss is advantageous); that there is no adaptive pressure on minimum C in this population (e. g. because individuals are seldom exposed to temperatures at either extreme for prolonged periods); or that minimum C is restrained by some other ecophysio-morphological parameter.

Although in the area in which the *M. minutoides* were trapped mean monthly minimum daily air temperature falls to a yearly minimum of approximately 3–4 °C in July, while mean monthly maximum daily air temperature seldom falls below 18 °C or rises above 31 °C, these are not necessarily the temperatures to which the *M. minutoides* population is exposed. Day time use of burrows or other refugia as well as the timing and location of activity may all contribute towards a moderation of the extremes of temperature experienced. Further study on the behaviour of *M. minutoides* and the microclimate in which it lives is therefore required before the adaptive significance, if any, of high minimum C can be established.

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MITTEILUNGEN DER GESELLSCHAFT

III International Conference on Dormice (Rodentia, Gliridae)

The Third International Conference on Dormice (Rodentia, Gliridae) will be held at Mošćenička Draga, Croatia, from 10 October to 13 October 1996. The Conference will consist of oral presentations, poster papers and video presentations (all in English). Further information: Secretariat of 3rd International Conference on Dormice, Croatian Natural History Museum, Demetrova 1, 41000 Zagreb, Croatia, tel: ++38 51 42 86 28, fax: ++38 51 42 49 98.

Buchbesprechungen

Birney, E. C.; Choate, J. R. (Eds.): **Seventy-five Years of Mammalogy (1919–1994).** The American Society of Mammalogists: Special Publication No. 11, 1994. 433 pp., 140 ill., 15 tabls. ISBN 0-935868-73-9

This book was published on occasion of the seventy-fifth anniversary of the American Society of Mammalogists. In 21 chapters, each of them written – on average – by two authors, a detailed account is given of both the history of the American Society of Mammalogists, its functionaries and publications, and the development of various disciplines in the field of mammalogy. In particular, chapters 1–8 report on the origin of the society, provide biographies of its presidents, awardees, and some prominent members, and trace the major schools and research traditions within the community of mammalogists in the United States. They further analyze past and present topics and trends in publications of the society, report on committees and meetings, and give an outline on developments as to membership and finance. Chapters 9–21 are devoted to brief reviews of past achievments and present trends in taxonomy, paleomammalogy, biogeography, anatomy, physiology, reproduction, molecular systematics, cytogenetics, population ecology, community and ecosystem ecology, natural history and evolutionary biology, behavior, and conservation and management, with special emphasis, respectively, on the contribution of North American researchers.

For those interested in the development, the organization and the research interests of mammalogy in the United States, this Special Publication will provide a rich source of details. Especially the sections on the origin and the ramification of the various schools of mammalogists in the United States, on the history and scope of the various publications of the Society as well as the review chapters on mammalian disciplines may be of interest also to European mammalogists.

However, it is apparently beyond the scope of the book to give an outline of the history and development of mammalogy in general, as the title may suggest. Except for some honorary members (from Germany: Max Weber, Erna Mohr, and Klaus Zimmermann), there is also almost no reference to European mammalogists, neither in the section on prominent members nor in the chapters reporting on scientific development in disciplines of mammalogy.

G. B. Hartl, Kiel

Benecke, N.: **Der Mensch und seine Haustiere.** Die Geschichte einer jahrtausendealten Beziehung. Stuttgart: Konrad Theiss Verlag 1994. 470 S., 263 Abb., 32 Tab. DM 128,–. ISBN 3-8062-1105-1

Nachdem vor nunmehr 30 Jahren Frederick Zeuner seine „History of domesticated animals“ vorgelegt hat, der 1967 eine deutsche Übersetzung folgte, ist im Theiss Verlag ein Buch erschienen, das dieses Thema erneut aufgreift. Es geht um die wechselvollen und vielseitigen Beziehungen, die das vieltausendjährige Zusammenleben des Menschen mit seinen Haustieren geprägt haben. Das Buch stützt sich bei Berücksichtigung auch antiker historischer Quellen auf neuere und neueste, auch auf zahlreiche eigene Forschungsergebnisse, die in den zurückliegenden 3 Jahrzehnten im Zusammenwirken von Archäologie, Zoologie und Haustierkunde gewonnen wurden. Die Gliederung des Buches läßt die ganze Breite der Thematik erkennen: auf eine quellenkritische Betrachtung zur Haustiergeschichte folgen „Haustiere in zoologischer Sicht“, es schließen sich an der Abschnitt über Ort und Zeit der Entstehung von Haustieren („vom Wildtier zum Haustier“), über „Entwicklung der Haustiere in Europa“ und schließlich die „Haustiere in Einzeldarstellungen“, die mit den sogenannten traditionellen Haustieren wie Hund, Schaf, Ziege, Schwein, Rind, Pferd usw. einsetzen und mit den Fischen, Insekten, Heim-, Labor-, Versuchs- und Farmtieren enden. Erwähnt werden am Schluß die sogenannten Neudomestikationen wie Elch, Damhirsch, Elenantilope und Moschusochse und die wirtschaftlich genutzten Wildtiere, zu denen Elefant, Gepard und Mungo gerechnet werden. Beschlossen wird das Buch durch ein Literaturverzeichnis, eine Zeittafel und ein Sachregister. Der Text ist flüssig geschrieben, dem besseren Verständnis kulturgeschichtlicher wie auch naturgeschichtlicher Zusammenhänge dienen zahlreiche Abbildungen, graphische Darstellungen und Verbreitungskarten. Die Ergebnisse variationsstatistischer Auswertungen metrischer Daten unterstreichen, daß solchen methodischen Ansätzen bei Untersuchungen an prähistorischen Knochen große Bedeutung beizumessen ist. Die Fülle der auf rund 460 Seiten zusammengestellten Daten, Fakten und Informationen ist bemerkenswert. An mancher vorgetragenen Auffassung etwa über Ort und Zeitpunkt der Domestikation wird sich Kritik entzünden, was um so weniger verwundern sollte, als wir noch immer weit davon entfernt sind, vom „Wann“, „Wo“ und „Wie“ der Haustierwerdung ein lückenloses Bild entwerfen zu können. Dennoch hat seit den Zeunerschen Tagen ein enormer Wissens- und Erkenntniszuwachs stattgefunden, der zu einer neuerlichen Gesamtdarstellung herausforderte. Wer sich einem solchen Unterfangen stellt, wußte um die Mühen, die mit einer Sichtung der inzwischen unendlich angewachsenen und weit verstreuten Spezialliteratur zwangsläufig verbunden sind. Der Autor durfte aber auch sicher sein, daß das Erscheinen des Buches zu kritischer Stellungnahme Anlaß geben würde. Mein Einwand bezieht sich auf einen Mangel, der die gesamte Darstellung durchzieht und der dem Autor auch von anderer Seite Kritik eintragen wird: die Rede ist vom bewußten, ungewöhnlichen Verzicht auf Quellenangaben. Zwar werden in Tabellen und Abbildungen Herkunftsnachweise angeführt, man vermißt sie jedoch bei der Vielzahl von Einzelinformationen, ohne die das Buch nicht hätte geschrieben werden können. Dem Fachkollegen mag die Herkunft der einen oder anderen Information bekannt sein, dem mit der Materie nicht Vertrauten wird das Vordringen zu den eigentlichen Quellen erschwert. Trotz dieses Mangels sollte das Buch einen breiten Leserkreis finden, da nicht nur Archäozoologen, sondern auch Biologen, Tierzüchter, Archäologen, Historiker, Kulturgeschichtler, Landwirte, Volkskundler und alle sonstigen an Haustieren Interessierten angesprochen werden.

H. Reichstein, Kiel

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Geographical variation of body size in Western Mediterranean striped Dolphins (*Stenella coeruleoalba*)

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Abstract

The variation in maximum body size of striped dolphins, *Stenella coeruleoalba*, was studied in various areas of the Mediterranean Sea. Animals inhabiting the southern part of the Mediterranean are larger than those inhabiting the northern fringe. Although a number of ecological factors affecting maximum body size in mammals has been identified, their role in causing the variation observed is difficult to determine because of the lack of appropriate data. However, the southern fringe is characterized by stronger seasonality and lower density of dolphins, both factors likely to favour larger maximum individual body sizes in a population. The variation observed may reflect population stratification leading to a degree of genetic isolation within the western Mediterranean Sea.

Introduction

Intraspecific variation in body size occurs in many mammals, including a number of cetaceans. Brodie (1977) reported that southern baleen whales are larger than their northern hemisphere conspecifics and that body size was inversely correlated with the length of the feeding season but positively correlated with length of the migratory season. In blue and minke whales, the existence of "pygmy" forms with a sympatric distribution in relation to the larger forms has led to the recognition of nominal subspecies (Ichihara 1966; Best 1985). These smaller forms inhabit waters characterized by milder environmental conditions and carry out less extensive migrations. In small odontocetes with a wide geographical distribution, variations in body size within small distances have also been reported. This variation usually occurs among allopatric populations, between offshore and inshore forms (sometimes overlapping in distribution) or between animals inhabiting enclosed or open seas (Perrin 1984). Difference in water temperatures has also been suggested to affect body size in cetaceans (Kasuya and Tai 1993).

In the present study, variation in body size of the striped dolphin, *Stenella coeruleoalba*, has been studied throughout the western Mediterranean. Understanding of such patterns of variation is a prerequisite to establish the biological characteristics of a population and to determine length parameters associated with reproductive or growth events. Because a number of studies of this type on the striped dolphins inhabiting the western Mediterranean are currently underway, we considered the present research to be relevant.

Material and methods

Data from stranded or captured striped dolphins from the western Mediterranean and the eastern North Atlantic were compiled from the literature and from a database at the University of Barcelona.

A substantial part of the data originated from the stranding reports regularly published in Spain, France, Italy, Morocco and Algeria during the period 1971–1993 (CAGNOLARO et al. 1986; CASINOS and FILELLA 1975; CARLINI 1888; CENTRO DEI STUDIE CETACEI 1987, 1988, 1989, 1990, 1991; DUGUY 1972, 1973, 1974, 1975, 1976, 1977, 1978, 1979, 1980, 1981, 1982, 1983 a, 1983 b, 1984, 1985, 1986, 1987, 1988 a, 1988 b, 1989, 1990, 1992; DUGUY and BUDKER 1972; EL BUALI 1987; GARCIA-CASTILLO et al. 1988; GRAU et al. 1980, 1986; GUIRADO-ROMERO 1991; PELEGRÍ 1980; PEREZ and NORES 1986; PEREZ et al.. 1990; RADUAN and RAGA 1982; RAGA et al. 1991; REY and REY 1979; REY and CENDRERO 1979; SEQUEIRA et al. 1992; TXEIXEIRA 1979).

In order to restrict the analysis to adult individuals, and taking into account that previous studies on reproduction of this population suggested that sexual maturity is attained at a length of about 190 cm in both sexes (CALZADA unpubl. data), only those individuals longer than 195 cm were included in the data subset used in the analyses. This data subset contained information from 291 dolphins (157 males and 134 females) from the Mediterranean Sea and 96 dolphins (41 females and 55 males) from the Atlantic Ocean.

Initially, the western Mediterranean basin was divided into 8 subsectors (Fig. 1). An exploratory screening of the frequency distributions of lengths of individuals originating from each of these subsectors was carried out separately, but absence of variation in maximum body lengths between some of these subsectors was observed. Data were then pooled into larger areas because splitting of dolphin body-size data into small, oceanographically homogeneous subareas (corresponding with oceanographic divisions), would produce an extremely small sample size for each subarea and make the statistical analysis unreliable. Because data distributions had been truncated in their lower tails and were therefore expected to depart from normality, statistical comparisons between sectors were performed using nonparametric Kruskal-Wallis and Mann-Whitney tests.

Results

Preliminary analysis of the data suggested an increase in body lengths from north to south but an absence of variation from east to west. Therefore, we pooled body lengths from dolphins originating from subsectors located at the same latitude but different longitude. However, because efficient networks to collect strandings had not been developed in the central or southern fringes of the basin, the sample sizes of these areas were too small to allow robust comparisons. Therefore, the final analysis was performed combining the southern and central fringes and comparing the resulting subset with the northern one. Body length of dolphins below parallel 41°N (Fig. 1) was found to be significantly

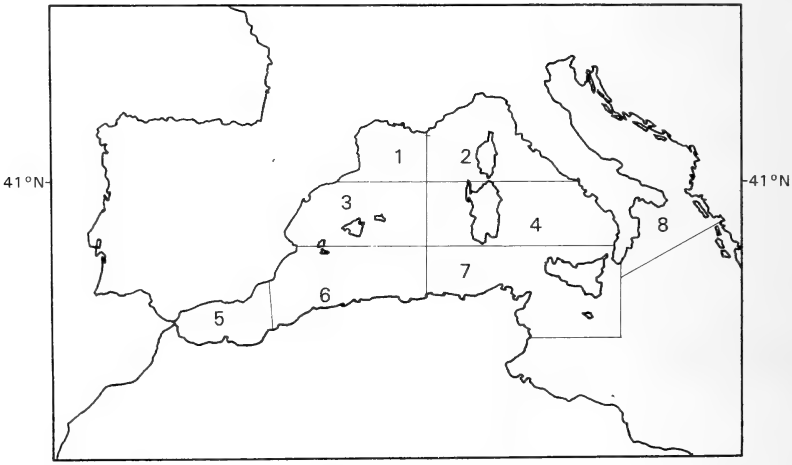

Fig. 1. Study area showing the divisions into 8 subsectors.

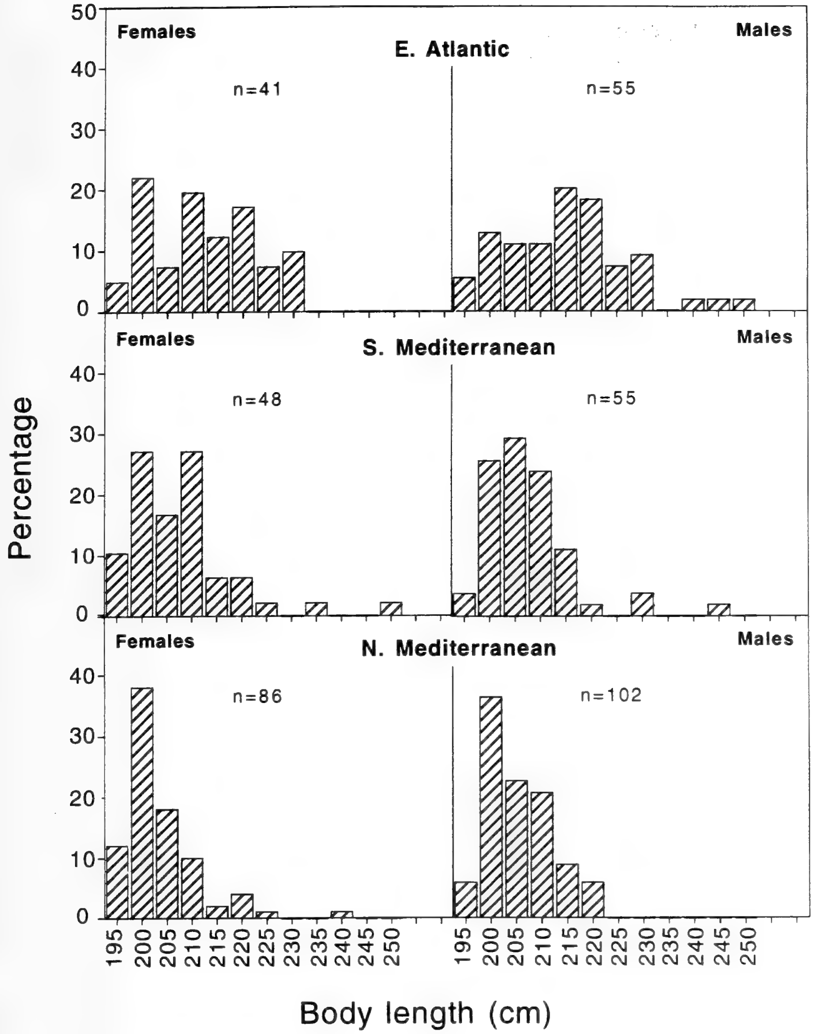

Fig. 2. Frequency distributions comparing the difference between maximum body size in males and females of the northern and southern fringes of the Mediterranean and the eastern Atlantic.

larger ($p < 0.05$) than that of dolphins originating north of this line, the difference being about 3 cm (Fig. 2).

This latitudinal cutpoint is, however, an artificial segregation of the data to facilitate statistical analysis, and body lengths actually increased progressively from north to south. Thus, maximum body lengths were attained in the southern fringe of the distribution range of the species. It should be pointed out that length distributions of southwestern Mediterranean striped dolphins were also significantly different ($p < 0.001$) from those of dolphins inhabiting the eastern North Atlantic, the latter being 5 to 8 cm longer than the former (Fig. 2). Since no variation in body size was found between the eastern and western sectors, the latitudinal cline observed in body lengths cannot be considered to be caused by an influx of dolphins from the Atlantic, passing to the Mediterranean through the Straits of Gribraltar, but rather to intrinsic variation in individuals inhabiting the western Mediterranean basin.

Males were found to be on average 2 cm longer than females, the difference being significant ($p < 0.02$) both in the northern and in the southern fringes. Such sexual dimorphism in body size positive to males is common to most odontocetes (e. g. Evans 1987) and probably reflects polygynic behaviour in species inhabiting environments with patched distribution of food resources (Jarman 1983; Vaughan 1986).

Discussion

Body size among homeotherms is greater in seasonal environments because they have greater lipid reserves which favours survival during periods of food shortage (e. g. McNab 1974; Brodie 1977; Lindstedt and Boyce 1985) and also, high mortality during seasonal food shortage reduces competition for resources, favouring larger sizes in survivors (Ashmole 1963; Boyce 1979). Because instability is greater in the southern basin of the western Mediterranean than in the northern basin, a greater selective pressure for large body sizes is to be expected in the southern fringe. This variability may be caused by the influx of Atlantic water, which enters through the straits of Gibraltar into the Alboran Sea creating an anticyclonic gyre. This gyre is characterized by high temporal variability in extent, shape, strength and location (Le Vourch et al. 1992). The Algerian basin acts as a buffer zone interfering with the Atlantic water that reaches the northern fringe (Estrada et al. 1985; Le Vourch et al. 1992). Because of this barrier, the level of instability induced by the Atlantic influence is lower in the northern fringe than in the southern and could favour larger sizes in the latter.

Furthermore, low population densities are known to affect individual body size by reducing competition for resources and, therefore, favour the achievement of larger size (Rosenzweig 1968; Lawton 1989). In this sense, recent surveys of striped dolphins in the western Mediterranean have estimated the density of this species in the northern fringe as 0.209 individuals per square km (Forcada et al. 1994), almost doubling the 0.115 dolphins per square km estimated for the southern fringe (Forcada 1995). Therefore, variation in dolphin density may also be adduced to explain the differences in striped dolphin body size observed between the northern and the southern fringe of the Mediterranean.

Moreover, Bergmann's rules states that warm-blooded vertebrates tend to be larger in colder climates than the ones living in warmer climates (Mayr 1963), the explanation being that larger individuals have a smaller surface-to-volume ratio which lowers their rate of heat loss. Several investigators have criticized and found exceptions to this rule (e. g. Scholander 1955; McNab 1971). In the western Mediterranean, data on surface water temperature are fragmentary, but, contrary to what might be expected from the size of the animals, the southern fringe, both in summer and winter, appears to be between 2 and 3°C warmer than that of the northern fringe (Anonymous 1990). Although this variable does not appear to play a role in the variation observed in striped dolphin body size, instead of attempting to explain size variation by considering only adaptation to cold, selective pressure for larger body size may rather be due to a combination of different climatological variables. Besides, Scholander (1955) argued that adaptation to cold depends mainly on improved insulation rather than on heat conservation and that small increases in body size will have little effect.

Finally, in mammals, size of available prey has also been positively correlated with predator size (McNab 1971; Searcy 1980) and this has also been observed in odontocetes (Ross 1984; Clarke 1980). Unfortunately, no information is available to test this hypothesis in the western Mediterranean striped dolphins. Studies carried out in the Liguro-Provezal basin indicate that striped dolphins are generalist eaters; cephalopods and bony fishes represent the regular source of food, although crustaceans are occasional prey (PULCINI et al. 1992; WURTZ and MARRALE 1991, 1993). The fauna of the southern fringe of the western Mediterranean include a number of species of Atlantic origin on which striped dolphins may feed. Taking into account the generalistic feeding of the species, it is likely that the diet of the dolphins inhabiting this area will be quite different from that of dolphins living in the northern fringe. However, no food studies are available for the southern waters, so it is not possible to ascertain the effect, if any, of prey size on dolphin body size.

Establishing relationships between ecological variables and body size of animals is complex, with many apparent exceptions occurring (PETERS 1991). However, the increase observed in body size from north to south may be examined taking into account some general, although gross, latitudinal trends in the factors mentioned above. Further research on the role played by these, and other as yet unidentified, variables may clarify their actual involvement in the variation observed in body size. However, although the mechanisms eliciting such variation have not been totally clarified, caution should be applied to the estimation of population parameters linked to body length or growth parameters. Data from striped dolphins originating in a given area of the western Mediterranean should not be combined with those coming from another.

Moreover, the existence of geographical variation could be indicative of a certain degree of genetic isolation among different areas of the western Mediterranean. Recognition of this fact is relevant for the management of the population or populations of the species. Particularly, the significance of mortality associated with fishing operations or epizootic diseases, two main problems currently affecting Mediterranean striped dolphins (NOTARBARTOLO DI SCIARA 1990; AGUILAR and RAGA 1993), should not be evaluated on a global scale for the whole western Mediterranean but, rather, the impact should be measured on a small-scale, local perspective.

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Zusammenfassung

Geographische Variationen der Körpergrösse von Streifendelphinen (Stenella coeruleoalba) im westlichen Mittelmeerraum

Diese Studie untersucht die Variationen der maximalen Körpergröße von Streifendelphinen, *Stenella coeruleoalba*, im Bereich des Mittelmeeres. Die im südlichen Teil des Mittelmeeres lebenden Tiere sind länger als die des nördlichen Bereiches. Obwohl eine gewisse Anzahl von ökologischen Faktoren festgestellt wurde, die diemaximale Körpergröße von Säugetieren beeinflussen, kann deren Rolle in der beobachteten Variation nur schwer beurteilt werden, da die notwendigen Daten fehlen. Jedenfalls besteht im südlichen Raum eine stärkere Saisonabhängigkeit und niedrigere Dichte der Delphinpopulation, beides Faktoren, die ein größeres Körpermaß der Individuen beeinflussen. Die beobachtete Variation könnte auf die Existenz einer Bevölkerungsschicht deuten, die zu einer genetischen Isolation innerhalb des westlichen Mittelmeeres führt.

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Habitatnutzung in Subpopulationen des Eichhörnchens (*Sciurus vulgaris* L., 1758)

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Abstract

Habitat utilization in subpopulations of the Red squirrel (Sciurus vulgaris L., 1758)

Three squirrel subpopulations were studied during a period of 35 months. The study areas were located in a commercial forest area of the western Wiehengebirge close to Osnabrück. The investigation was divided into a free range and a laboratory part. The squirrels were marked with a radio transmitter which was fixed around the neck. Thus the animals could be observed individually through periods between 3 and 12 months. The aim was to compare the ranges used by the squirrels in a large continuous forest area and in 2 isolated forest areas each of approximately 20 ha in size. The basis for this examination was the size of the home range and the core area by looking at the interindividual differences and those between groups. The mean home range size in the continuous forest was 11.1 ha (Concave Polygon Method), the average size of the core areas was 1.8 ha (Harmonic Mean Transformation). The mean home range size in the forest islands was 2.4 and 2.6 ha, the average size of the core areas 0.4 and 0.8 ha. The overlapping of home ranges was significantly higher in the forest islands than in the continuous forest. With the exception of 2 squirrels, female and male squirrels utilized their core habitats exclusively. Overlapping between home ranges could be seen for males and females. The number and location of the dreys was noted in the continuous forest. The average number of dreys per animal was 11. In winter the squirrels mostly used dreys in spruce trees. They were built close to the trunk. In summer, in contrast, they used dreys in pine trees. Here, they were mostly located in the branches. The whole day observations of these animals showed that there were differences in the tree species they used: the squirrels which preferred pine trees spent more time feeding and had shorter resting periods than those which preferred spruce seeds. The "spruce squirrels" had larger home ranges which they used more selectively for feeding while the "pine squirrels" had smaller home ranges which they used more continuously. The animals in the forest islands showed a more intense utilization of the home range, the core areas were larger compared to those of the squirrels in the continuous forest.

Einleitung

Das Eichhörnchen findet sich als stenotope Tierart in erster Linie in Waldbeständen mit hohem Koniferenanteil (Don 1983; Mollar 1983; Tonkin 1983; Wauters und Dhondt 1990, 1992). Als tagaktives Nagetier bietet es Möglichkeiten zur Direktbeobachtung; eine gezielte und kontinuierliche Beobachtung einzelner Individuen kann durch eine Sendermarkierung (Radio-Tracking) erfolgen (Tonkin 1983; Wauters und Dhondt 1990). Hierdurch ist es möglich, individuelle Verhaltensunterschiede, Habitatnutzung und Aktionsraumgrößen zu erfassen (Laidler 1980; Tonkin 1983; Gurnell 1987; Wauters und Dhondt 1987).

In der vorliegenden Studie soll die Lebensraumnutzung mehrerer Eichhörnchen innerhalb eines größeren zusammenhängenden Waldgebietes und vergleichend dazu in Waldinseln untersucht werden.

Folgende Zusammenhänge werden analysiert:

1. Aktionsraumgröße und Habitatqualität, 2. Aktionsraumgröße unter Berücksichtigung individueller und geschlechtsspezifischer Unterschiede, 3. Fortpflanzungsverhalten und Aktionsraumgröße.

Bei der Untersuchung der individuellen Habitatnutzung sollte die Erfassung von Nutzungsschwerpunkten (Kernbereichen) unter Berücksichtigung definierter Verhaltensweisen (Nahrungsaufnahme, Ruhen, Interaktion) in Abhängigkeit von Baumarten und ihrer Verteilung erfolgen.

In Norddeutschland findet sich eine ausgeprägte Waldflächenfragmentierung, bedingt durch partielle Abholzung und Nutzungswandlung (z. B. Landwirtschaft, Straßenbau) (Mader 1980). Im Rahmen der durchgeführten Untersuchung stand hierzu u. a. die Frage im Vordergrund, ob sich Unterschiede in den Aktionsraumgrößen und im Überlappungsgrad der in Waldinseln lebenden Eichhörnchen gegenüber Tieren aus einer Großwaldfläche feststellen lassen.

Material und Methode

Untersuchungsgebiete

Bei der ausgewählten Großwaldfläche (Untersuchungsgebiet 1 = UG1) handelt es sich um einen ca. 150 ha großen Sektor innerhalb eines Wirtschaftswaldes im westniedersächsischen Mittelgebirge (Wiehengebirge) 10 km nördlich von Osnabrück. Koniferenbestand dominiert gegenüber Laubwald (Tab. 1). Die Baumhöhen betragen 3–30 m. Die im Untersuchungsgebiet liegenden waldfreien Flächen sind Viehweiden, Äcker und Waldlichtungen.

Die anderen beiden Untersuchungsgebiete sind durch Äcker und Weiden, stark befahrene Straßen und durch einen Kanal isolierte Kleinwaldflächen. Diese Waldinseln sind abgegrenzte Flächen (z. B. durch Wiesen, Felder und Straßen) von weniger als 30 ha, die eine Distanz von mindestens 100 m zur nächstgelegenen Waldfläche besitzen.

Die eine der beiden Waldinseln (= UG2) ist ein ca. 17 ha großer Wirtschaftswald mit überwiegend älterem Baumbestand, in dem der Koniferenanteil überwiegt (Tab. 1). Die Waldfläche ist von Feldern umgeben. Sie wird zusätzlich durch eine Autobahn von einem abgrenzenden Waldgebiet getrennt. Die andere Waldinsel (= UG3) ist ein ca. 20 ha großer Wirtschaftswald. Dieses Untersuchungsgebiet wird durch einen ca. 10 m breiten Kanal, landwirtschaftliche Nutzflächen und eine Mülldeponie begrenzt. Innerhalb dieses Untersuchungsgebietes liegt zusätzlich eine kleine Wohnsiedlung. Auch in diesem Gebiet finden sich ältere, hohe Baumbestände, in denen der Nadelwaldanteil überwiegt (Tab. 1).

Fang und Sendermarkierung der Tiere

Der Zeitraum der Freilandarbeit erstreckte sich von Dezember 1987 bis Oktober 1990. Insgesamt wurden 15 Tiere, 4 Weibchen und 11 Männchen, mit Halsbandsendern (BIOTRACK, GB) markiert. Die Tiere trugen die Sender zwischen 3 und 12 Monate.

Tabelle 1. Relativer Baumartenanteil in den drei Untersuchungsgebieten (UG1, UG2, UG3) in %.

Baumart	UG1	UG2	UG3
Fichte (*Picea abies*)	55	15	38
Kiefer (*Pinus sylvestris*)	25	37	18
Lärche (*Larix decidua*)	3	8	3
Rotbuche (*Fagus sylvatica*)	15	25	26
Eiche (*Quercus spec.*)	5	10	13
Sonstige (z. B. *Betula pendula, Fraxinus excelsior*)	2	5	2

Eichhörnchen wurden in Drahtgitter-Trittbrett-Fallen (100×20×25 cm, Firma Ammenhäuser, Waldeck) nach Anködern mit Haselnüssen gefangen und nach einer 2- bis 3stündigen Erholungsphase an der Fangstelle wieder freigelassen.

Erfassung der Freilanddaten

Sieben sendermarkierte Eichhörnchen (A 1–A 7) wurden im UG1 abwechselnd ganztägig beobachtet. Alle Tiere, die sich in einem Radius von ca. 500 m befanden, konnten lokalisiert werden. Festgehalten wurden im Untersuchungsgebiet auch die Besonderheiten der Kobel (Baumart, Kobelhöhe, Entfernung vom Stamm), Aufenthaltshäufigkeit und Position auf der jeweiligen Baumart. Bei den Ganztagsbeobachtungen wurden das Verhalten und die Position (Standort, Baumart, Sitzposition) kontinuierlich protokolliert. Zusätzlich erfolgten Standortbestimmungen der in der Nähe befindlichen Tiere (in 1- bis 2stündigen Abständen je nach Entfernung). Bei den sendermarkierten Tieren aus den Untersuchungsgebieten UG2 und UG3 wurden nur die Aufenthaltspositionen lokalisiert. Zusätzlich erfolgten 1- bis 2stündige Kurzbeobachtungen.

Auswertung der Daten

Die erfaßten Freilanddaten wurden benutzt für:

1. Aktionsraumbestimmung: Hierzu gingen je Tier und Tag 1 bis 3 Lokalisationen ein. Drei Lokalisationspunkte pro Tag wurden verwendet, wenn eine zeitliche Unterteilung in morgens (ca. 1 Stunde nach Dämmerungsbeginn), mittags und abends (ca. 1 Stunde vor Dämmerungsbeginn) möglich war. Die Darstellung und Berechnung derAktionsräume (AR) erfolgte nach der Concave-Polygon-Methode (McPaal 1.2) und nicht, wie vielfach in der Literatur beschrieben, mit der Minimum-Convex-Polygon-Methode (Tonkin 1983; Wauters und Dhondt 1987, 1990), da das Eichhörnchen als waldlebende Nagetierart keine größeren Freiflächen beläuft. Mit der Minimum-Convex-Polygon-Methode würden waldfreie Partien ebenfalls in die Bestimmung des AR eingehen, da bei dieser Darstellungsart nur äußere Konturpunkte verbunden werden (Adam und Davis 1967; Samuel et al. 1985; Harris et al. 1990). Somit käme es zwangsläufig zu einer Überschätzung der AR-Größe (Schröpfer et al. 1989).

   Die Verwendung des Harmonic Mean Algorithmus (70% und 50%, McPaal 1.2) wurde zur Darstellung der Bereiche intensiverer Nutzung (Kernbereiche) eingesetzt (Don und Reynolds 1983; Samuel et al. 1985; Morris 1988; Harris et al. 1990).
2. Berechnung der Aktionsraumvolumina: Hierzu wurde das Untersuchungsgebiet in Sektoren mit möglichst übereinstimmender Baumhöhe eingeteilt und die durchschnittliche Baumhöhe pro Sektor bestimmt. Die Aktionsraumvolumina wurden unter Verwendung der Sektorenanteile berechnet.
3. Anhand der direkt zu beobachtenden Verhaltenskategorien Nahrungsaufnahme, Ruhen und Interaktion wurden individuelle Verhaltensmuster erstellt.

Ergebnisse

Aktionsräume und Kernbereiche

Untersuchungsgebiet 1 (UG1)

Wie die Concave-Polygon-Darstellung (CP) zeigt, sind die Lage und die Form der Aktionsräume (Jahres-Gesamt-AR) – für die Tiergruppe A1–A7 unterschiedlich (Abb. 1 a).

Kontur und Überlappungsgrad weisen bei A1, A3, A6 und A7 größere Gemeinsamkeiten auf als bei A4 und A5. A2 hat mit beiden Gruppen Verbindungspunkte, aber den insgesamt geringsten Überlappungsanteil.

Die AR-Flächen differieren zwischen 1,8 und 22,7 ha (Median = 11,1 ha), wobei das Weibchen A7 und das Männchen A6 relativ kleine AR aufweisen. A2 besitzt den mit Abstand größten AR (22,7 ha) (Tab. 2). Die Tiere weiten ihre AR vom Winter zum Sommer in unterschiedlichem Maße aus (Ausnahme: A4 und A7; es lagen wohl bei beiden Tieren zu wenig Sommerwerte vor). Die geringste relative Ausweitung zeigt A1, die größte A2 mit einer vierfach vergrößerten Fläche.

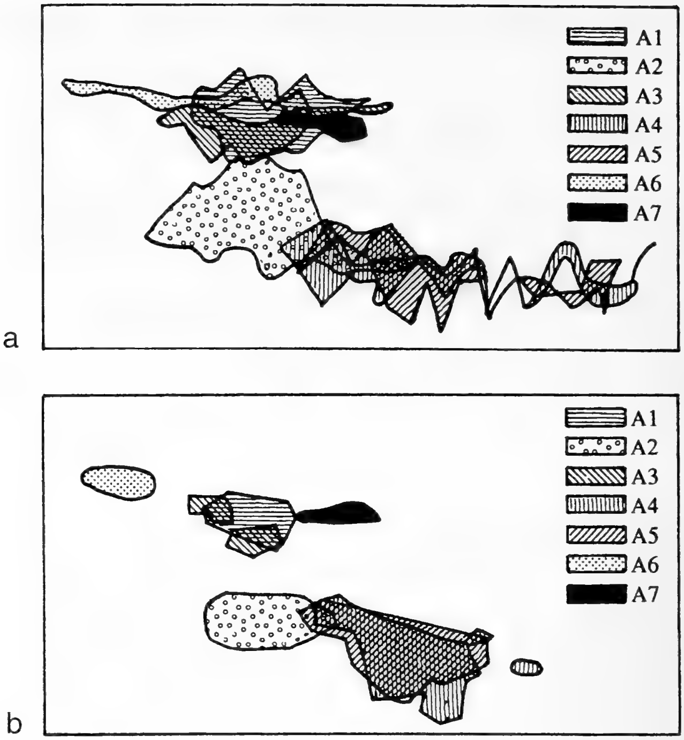

Abb. 1. Form und Lage der Aktionsräume der sendermarkierten A-Tiere der Gruppe UG1. a) Methode: CP – Concave Polygon. b) Methode: Harmonic Mean 70% (Erläuterungen im Text). (M) = Männchen, (W) = Weibchen; n = Anzahl der Lokalisationen. A1(M) n = 151, A2 (M) n = 191, A3 (W) n = 199, A4 (M) n = 78, A5 (M) n = 67, A6 (M) n = 131, A7 (W) n = 96

Unter Anwendung der Harmonic-Mean-Methode lassen sich je nach relativer Anzahl der einbezogenen Lokalisationspunkte (70% bzw. 50%) die Kernbereiche unterschiedlich konzentrieren und trennen. Auffällige Ausnahme bilden hierbei A4 und A5, deren AR noch erhebliche Überlappungen aufweisen. Beide Tiere zeigen gegenüber der CP-Auswertung eine Steigerung der AR-Flächen gegenüber der 70% HM-Darstellung, woraus eine eher gleichförmige Nutzung der Fläche hervorgeht. Die Fläche ist deutlich größer als bei den anderen Tieren. Diese beiden Tiere nutzen die Fläche homogener und dürften sich somit seltener begegnen.

Die Betrachtung der Kernbereiche in der 70%-Darstellung veranschaulicht ein gegenüber der CP-Darstellung reduziertes Überlappungsbild der AR. In Abb. 1b wird die kleinste Fläche gezeigt, die 70% aller Lokalisationspunkte repräsentiert. Finden sich bei A1 und A3 und vor allem bei A4 und A5 noch erhebliche Überlappungsbereiche, so sind A6 und A7 nun abgetrennt und A2 hat keinen gemeinsamen Bereich mehr mit A1 und A3.

In der 50% HM-Darstellung werden die AR noch weiter getrennt, so daß A1 und A3 nur noch einen geringen Überlappungsbereich besitzen und lediglich A4 und A5 einen gemeinsamen AR von >50% haben.

Die AR-Flächengrößen verringern sich individuell unterschiedlich stark vom CP über 70% HM zu 50% HM (Tab. 2). Nur bei A5 findet sich eine etwa 15%ige Vergrößerung des AR vom CP zu 70% HM, dann aber eine Reduktion auf etwa 10% (70% HM zu 50% HM).

Tabelle 2. Aktionsraumgrößen CP (= Concave-Polygon-Methode), Kernbereichsgrößen HM (= Harmonic-Mean-Transformation) in Hektar (ha) und Volumina der Aktionsräume (V) der Gruppen UG1, UG2 und UG3.

UG1 Tiere	Winter	CP (ha) Sommer	gesamt	HM (ha) 70%	50%	V(×1 000 m^3)
A1	6,3	7,3	11,5	5,1	1,9	285,4
A2	5,3	21,6	22,7	9,1	3,5	555,3
A3	3,1	7,4	9,0	2,7	1,8	184,4
A4	8,6	5,6	11,1	14,9	4,1	323,1
A5		12,1	12,1	13,9	1,5	309,0
A6	2,0	4,1	5,0	1,9	0,9	105,3
A7	1,5	0,9	1,8	1,9	1,1	42,4
Median	3,1	7,3	11,1	5,1	1,8	285,4

UG2 Tiere	CP (ha)	HM (ha) 70%	50%	V(×1 000 m^3)
B1	1,0	0,5	0,3	19,6
B2	2,9	1,9	0,8	89,4
B3	2,4	2,2	1,2	38,0
Median	2,4	1,9	0,8	38,0

UG3 Tiere	CP (ha)	HM (ha) 70%	50%	V(×1 000 m^3)
C1	2,6	1,0	0,4	84,5
C2	0,7	0,1	0,1	15,2
C3	1,4	0,6	0,3	33,9
C4	4,5	1,2	0,7	114,5
C5	5,0	0,8	0,5	149,5
Median	2,6	0,8	0,4	84,5

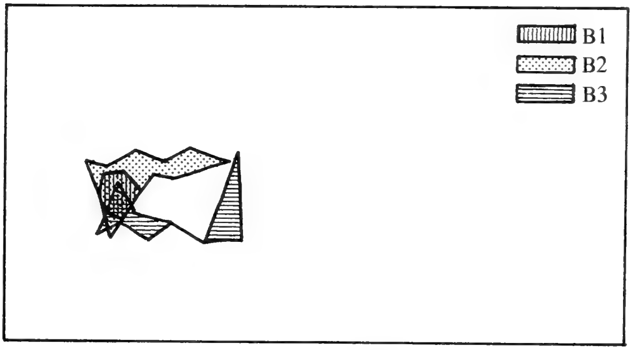

Abb. 2. Form und Lage der Aktionsräume der sendermarkierten B-Tiere der Gruppe UG2. Methode: CP – Concave Polygon, (M) = Männchen, (W) = Weibchen; n = Anzahl der Lokalisationen. B1 (W) n = 32; B2 (W) n = 48, B3 (M) n = 42

Die auf der Grundlage der CP-Darstellungen berechneten AR-Volumina bestätigen weitgehend die Unterschiede der AR-Flächen von Tier zu Tier: So haben z. B. A3 und A4 nur eine Differenz von ca. 20% in der Gesamt-AR-Fläche, A4 nutzt hingegen ein ca. 80% größeres Volumen.

Untersuchungsgebiet 2 (UG2)
In dieser Waldinsel wurden von den sieben untersuchten Hörnchen drei sendermarkiert. Auch hier finden sich Überschneidungen der drei AR bei der CP-Analyse, wobei der AR des Weibchens B1 nicht nur mit dem Männchen B3, sondern auch mit dem Weibchen B2 eine nahezu vollständige Überlappung aufweist (Abb. 2).

B2 und B3 besitzen beide etwa 3mal so große AR wie B1 (Tab. 2). Auf dem 50% HM-Niveau haben sich die AR-Größen etwa auf die Hälfte (B3) bzw. ein Drittel (B1 und B2) der CP-Fläche reduziert.

Die Volumina zeigen im Vergleich der drei Tiere größere Abweichungen zu den Relationen der CP-Fläche. So nutzen B2 und B3 deutlich größere Volumina als B1.

Untersuchungsgebiet 3 (UG3)
Hier wurden von den elf untersuchten Eichhörnchen fünf sendermarkiert. Die CP-Darstellung zeigt weitgehende Überlappung für die fünf männlichen Tiere.
Die AR-Größen variieren zwischen 0,7 und 5,0 ha (Tab. 2). Die Größen der Kernbereiche sind sowohl auf dem 70%-Niveau als auch auf dem 50%-Niveau teilweise bis auf 10% der CP-Fläche reduziert (C5).

Die Relationen der Volumennutzung zwischen den Tieren entsprechen größtenteils denen der CP-Flächen; deutlichere Unterschiede ergeben sich lediglich zwischen CP : V-Relation für C3 und C1 (ca. 1 : 2 bzw. 1 : 3) und C3 und C5 (ca. 1 : 3 bzw. 1 : 5) (Tab. 2).

Vergleich der Gruppen

Aktionsräume
Die CP-Auswertung ergibt für alle drei Gruppen deutliche Überschneidungen der AR. Die Kernbereichsanalyse (50% HM) führt allerdings zu erheblich kleineren Flächen mit z. T. nur 10–20% der CP-Fläche für die Gruppen UG1 und UG3, weniger verkleinert für die UG2-Gruppe (Tab. 2). Die durchschnittliche AR-Größe (CP-Methode) ist für die beiden Gruppen UG2 und UG3 etwa gleich (ca. 2,5 ha). Für die UG1-Gruppe beträgt diese etwa das Vierfache (11,1 ha).

Ähnliches zeigt sich beim Vergleich der Kernbereichsanalysen (50% HM), wobei die Relation UG1–UG3 5 : 1 beträgt, UG1–UG2 hingegen nur 2,5 : 1. Die entsprechenden Volumina weisen im Median für die UG2-Gruppe nur die Hälfte der UG3-Gruppe auf, während die UG1-Gruppe ein ca. 7 mal so großes Volumen nutzt.

Die Habitatqualität der Waldinseln war im Hinblick auf die Baumartenzusammensetzung und das Nahrungsangebot weitgehend ähnlich der Qualität der Großwaldfläche (UG1). In den Waldinseln lebten aber kleinere Gruppen und ihre AR waren deutlich kleiner, wobei aber die Kernbereiche im Verhältnis zum Gesamt-AR größer waren als bei den Tieren, die im zusammenhängenden Waldgebiet siedelten.

Verhaltensmuster A1–A7
Die Hauptanteile der Aktivität verteilen sich auf die beiden Kategorien Nahrungsaufnahme (N), Interaktion (I) und Ruhen (R) (Abb. 3). Die Kategorie „Interaktion“ spielt bei allen Tieren eine untergordnete Rolle (<5%). Die sieben Tiere unterscheiden sich aber deutlich in der Relation des Zeitanteils „Nahrungsaufnahme“ zu „Ruhen“. Hierbei sind insbesondere baumartenspezifische Präferenzen festzustellen. Während A7, A6 und A5 zwischen 30–65% ihrer Aktivität mit der Nahrungsaufnahme auf Kiefern verbringen,

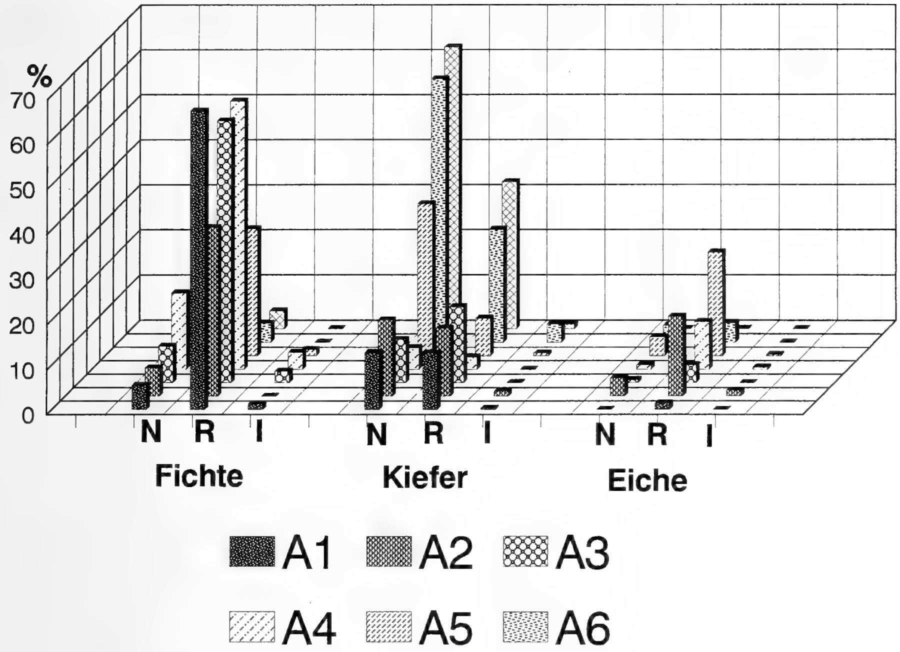

Abb. 3. Hörnchengruppe A des UG1: Individuelle Zeitdauer unterschiedlicher Verhaltensweisen differenziert nach Verhaltenskategorien (N = Nahrungsaufnahme, R = Ruhen, I = Interaktion) und Baumarten.

dominiert bei A1–A4 das Ruhen auf Fichten (36–63%). Der Zeitanteil „Nahrungsaufnahme“ ist bei A1 bis A4 stärker gestreut auf Kiefer, Fichte (A1, A3, A4) und Eiche (A2), anders bei den übrigen drei Tieren, die in erster Linie Kiefern nutzten.

Der Verweildauer auf Fichte, Kiefer und Eiche kam während des Untersuchungszeitraums eine vorrangige Bedeutung zu, während der Aufenthalt auf Lärche und Buche zusammen bei keinem Tier mehr als 6% des Aktivitätsanteils ausmachten.

Hervorzuheben ist, daß die Tiere, die Kiefernsamen bevorzugten, kleinere AR hatten als diejenigen, die Fichtensamen präferierten. Die „Kiefernhörnchen“ besuchten ihre AR aber flächendeckend, entsprechend der Verteilung des Kiefernbestandes in ihren Aktionsräumen. Die „Fichtenhörnchen“ konzentrierten ihre Nahrungsaufnahme hingegen auf begrenzte Fichtenbestände.

Baumhöhennutzung

Im Winter hielten sich die Tiere in erster Linie in Baumhöhen unter 20 m auf, mit einem Schwerpunkt im 10 m-Bereich, während im Sommer die Hauptverweildauer in Höhen bei 20 m und höher lag, aber auch der Bereich über 20 m war mit etwa 22% vertreten. Dem 5 m-Bereich kommt mit ca. 5% nur eine untergeordnete Bedeutung zu (Abb. 4).

Kobel

Die Anzahl der Kobel variiert zwischen 7 und 18 (Tab. 3). Die Kobel waren zu 70% auf Fichten und zu 30% auf Kiefern zu finden, mit folgenden Ausnahmen: A2 besaß zusätzlich einen Erlen-Kobel, A1 einen Buchen-Kobel, A5 einen Eichen-Kobel und A6 einen Lärchen-Kobel. Die mittlere Kobelhöhe auf Fichten lag mit 8,2 m deutlich niedriger als auf Kiefern mit 14,4 m (Tab. 3; t-Test: $t = 20{,}3$; $df = 73$; $p > 0{,}05$). Eine ähnliche Differenz

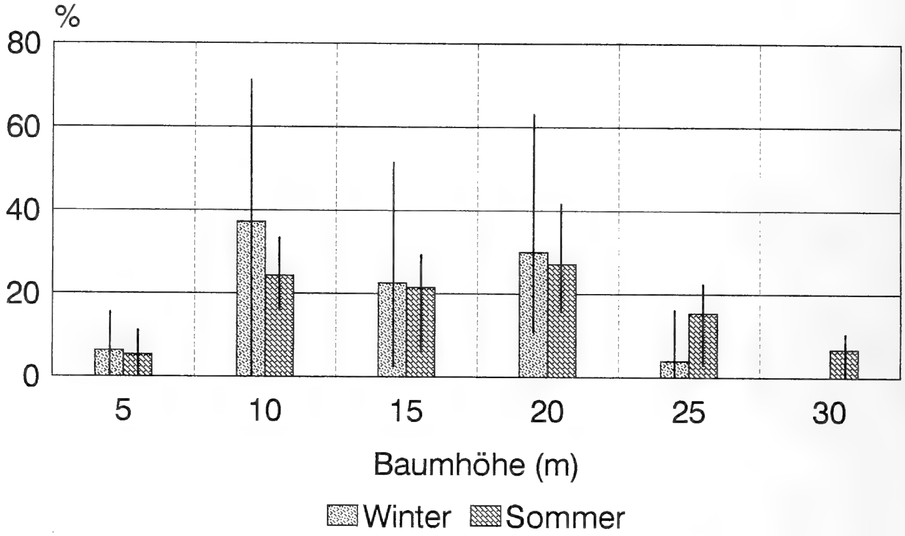

Abb. 4. Vergleich der saisonalen Baumhöhennutzung für die Hörnchengruppe A des UG1. Säulenhöhe: Mittelwert für A1–A7. Balken: min, max

Tabelle 3. Hörnchengruppe des UG1: Individuelle Kobelanzahl und Kobelhöhe in Kiefern und Fichten. Werte in Klammern geben die Gesamtkobelanzahl unter Einbeziehung weiterer Baumarten an, die nur bei den dort kenntlich gemachten Tieren gefunden wurden. MW: Mittelwert.

Tier	Kobelanzahl		
	Kiefer	Fichte	gesamt
A1	3	15	18
A2	4	6	10(12)
A3	2	7	9
A4	2	6	8
A5	2	7	9(10)
A6	7	7	14
A7	3	4	7
MW	3,3	7,4	10,7(11,2)
MW Kobelhöhe	14,4 m	8,2 m	
MW der Baumhöhe	18,8 m	11,4 m	

Tabelle 4. Individuelle Nutzung (in %) der Kobel, differenziert nach Baumarten. Die Beobachtungszeiträume je Tier variierten zwischen 3–12 Monaten.

Tier	Baumart		
	Kiefer	Fichte	Lärche
A1	21,6	78,4	
A2	54,5	45,5	
A3	7,0	93,0	
A4	16,0	84,0	
A5	11,8	88,2	
A6	29,4	54,4	16,2
A7	24,1	75,9	

bestand in der mittleren Baumhöhe bei der Fichte mit 11,4 m und der Kiefer mit 18,8 m (t-Test: t =12,09; df = 73; p > 0,05).

Für die Höhe der Fichtenkobel ergab sich eine erheblich breitere Streuung (5,6 m–12,1 m) als für die Kiefern-Kobelhöhe (13,4 m–17,0 m). Die Kobelpositionen waren typisch bei den Fichten mit über 90% im Stammbereich, dicht am Stamm an einem dort abzweigenden Seitenast. Bei den Kiefern hingegen lagen sie hauptsächlich im Seitenastbereich (78,3%).

Fichtenkobel wurden signifikant häufiger aufgesucht als Kiefernkobel (Tab. 4; t-Test: $t = 3{,}18$; $df = 6$; $p > 0{,}05$).

Diskussion

Lebensraumnutzung

Eichhörnchen ernähren sich bei jahreszeitlich schwankendem Angebot im wesentlichen von Baumsamen, die in Clustern verfügbar sind, z. B. auf Einzelbäumen oder auf Baumgruppen (Rohmeder 1972; Gurnell 1987).

Unter Berücksichtigung des Nahrungsangebots ist die Habitatqualität beim Eichhörnchen in erster Linie an das Vorkommen und den Ertrag der beiden Koniferenarten Kiefer (*Pinus*) und Fichte (*Picea*) gebunden (Zwahlen 1975; Tonkin 1983; Wauters und Dhondt 1985, 1987). Der Kiefer kommt gegenüber der Fichte die größere Bedeutung zu, da sie etwa 10 Monate pro Jahr samentragende Zapfen hat, die Fichte aber nur während eines Zeitraumes von etwa 8 Monaten Zapfen anbietet. Zudem zeigt sich bei der Fichte stärker das Vorkommen von sogenannten „Mastjahren", wobei dann die dazwischenliegenden Vegetationsperioden eine geringere Zapfenproduktion aufweisen (Rohmeder 1972). Wesentlich ausgeprägter ist diese zyklische Produktivität bei Eichen (*Quercus*) und Buchen (*Fagus*), die ebenfalls einen saisonal bedeutenden Anteil im Nahrungsspektrum stellen (Tonkin 1983; Wauters und Dhondt 1987). Samen dieser beiden Laubbaumarten stehen den Tieren nur etwa 2 Monate pro Jahr (Oktober und November) zur Verfügung. Ihre Nutzbarkeit kann jedoch durch Vergraben der Früchte im Erdboden um Monate verlängert werden (Eibl-Eibesfeld 1951).

Die Habitatqualität dürfte der wichtigste Grund dafür sein, daß A6 (hoher Kiefernanteil) einen nur halb so großen Gesamt-AR aufweist wie A3, dem ein geringerer Kiefernanteil zur Verfügung steht.

Die 50%-Kernbereiche dokumentieren die durch die Nahrungsaufnahme charakterisierten Nutzungsschwerpunkte. Die ausgeprägten „Kiefernnutzer" (A1, A5, A6, A7) besitzen daher kleinere Kernbereiche als die ausgeprägten „Fichtennutzer" (A2, A3, A4).

Aktionsraumgrößen von Tieren können artspezifisch saisonale Schwankungen aufweisen (Harestadt und Bunnell 1979; Schröpfer et al. 1989; Harris et al. 1990; Wiegand und Schröpfer 1990). Bei den beobachteten Eichhörnchen wurde im Frühjahr eine auffällige Ausweitung der AR gefunden. Nach Harestadt und Bunnell (1979) ist bei herbivoren Tierarten, insbesondere Kleinsäugetieren, die Verkleinerung der AR im Winter unter dem Gesichtspunkt der Nahrungssicherung zu sehen, während die Vergrößerung der AR zum Frühjahr u. a. mit der Veränderung des Nahrungsspektrums (Wauters und Dhondt 1992) und des Reproduktionsverhaltens (Schröpfer et al. 1989) interpretiert werden kann. So zeigen die Männchen eine stärkere AR-Ausdehnung, bedingt durch das Aufsuchen mehrerer Weibchen.

Der bei A4 (Männchen) und A7 (Weibchen) kleinere Sommer-AR läßt sich mit einer zu geringen Anzahl von Lokalisationspunkten für die Berechnung des Sommer-AR erklären, ist also methodenbedingt (vgl. auch Morris 1988 und Harris et al. 1990).

Die zum Teil erheblichen Unterschiede in den Gesamt-AR-Größen der sieben Eichhörnchen im UG1 können auf zweierlei Weise interpretiert werden. Größere AR lassen sich auf eine gleichförmigere Verteilung der Nahrung zurückführen, was z. B. auf A2 zutrifft, als bei kleinflächigeren AR, wie z. B. bei A6 zu beobachten war. Zudem ist an ein unterschiedliches Reproduktionsverhalten der Männchen zu denken, wenn z. B. A2 seinen AR vom Winter zum Sommer hin um etwa das Vierfache ausweitet, während A6 ihn nur verdoppelt.

In der Literatur finden sich Hinweise, daß *S. vulgaris* keine Territorien beansprucht (Mollar 1983; Tonkin 1983; Gurnell 1987). Betrachtet man allerdings ein Territorium als ein exklusiv genutztes Gebiet (Ostfeld 1990), dann muß man die 50%-Kernbereiche von A1, A2, A3, A6 und A7 als solche bezeichnen. Dieses ist bei A4 und A5 aufgrund der noch vorhandenen Überlappung nicht so offensichtlich. Auch Wauters und Dhondt (1992) beobachteten territoriales Verhalten, insbesondere bei weiblichen Eichhörnchen. Wauters und Dhondt (1986, 1987, 1990) verwendeten in ihren Untersuchungen zur Bestimmung der AR-Größen die Minimum-Convex-Polygon-Methode. Die dort untersuchte Waldfläche beinhaltete offensichtlich keine baumfreien Bereiche. Bei der vorliegenden Untersuchung wären unter Anwendung der Minimum-Convex-Polygon-Methode auch von Eichhörnchen nicht belaufene Freiflächen einbezogen worden, so daß nur die Concav-Polygon-Methode in Frage kam.

Ein Vergleich mit den Ergebnissen von Wauters und Dhondt (1986, 1987, 1990), die durchschnittliche AR-Größen von ca. 2 ha pro Tier ermittelten, zeigt deutliche Unterschiede in der AR-Größe, zumal in der vorliegenden Untersuchung der Median bei 11,1 ha liegt. Die von Wauters und Dhondt (1987) ermittelten AR-Größen stimmen eher mit denen der Tiere in den Habitatinseln überein (UG2, UG3). Dieser Unterschied in den AR-Größen könnte seine Ursache darin haben, daß die Individuendichte in der UG1-Population geringer war als in dem belgischen Untersuchungsgebiet. Denn die Populationsdichte der Eichhörnchen ist Schwankungen unterworfen (Wiltafski 1978), die sowohl kurzfristig im jährlichen Rhythmus auftreten können (Wauters und Dhondt 1990), als auch langjährig bis zu 10 Jahren dauernde Zyklen sein können (Mikheeva 1974; Lyubetskaja 1976).

Kobelnutzung

Die deutlichen individuellen Unterschiede in der Anzahl genutzter Kobel sind auch unter Berücksichtigung der abweichenden Beobachtungszeiträume und der damit verbundenen Verlagerung und Größenveränderung der AR zu sehen (Wiegand und Schröpfer 1990).

Da Kobel häufiger in Fichten als in Kiefern zu finden waren und auch die Nutzungshäufigkeit die gleiche Relation zeigt, liegt ein Zusammenhang mit der unterschiedlichen Struktur dieser beiden Baumarten nahe. In Fichten lagen die Kobel wahrscheinlich witterungsgeschützter als in der stärker aufgelockerten Kronenstruktur der Kiefern. Besonders im Winter suchten fast alle Tiere Fichtenkobel auf, die in der Regel in dichten, ca. 5–10 m hohen Beständen anzutreffen waren.

Im Hinblick auf die Kobelnutzung lassen sich häufiger genutzte „Hauptkobel“ (20–30% aller Kobel) von gelegentlich genutzten „Nebenkobeln“ unterscheiden wie es auch Wauters und Dhondt (1988) fanden. Die Kiefernkobel wurden in erster Linie im Frühjahr und Herbst gewählt, vor allem bei weniger extremen Witterungsverhältnissen. Im Vergleich zu der Untersuchung von Wauters und Dhondt (1988), die eine mittlere Kobelhäufigkeit von 4,5 pro Tier ermittelten, war in dieser Untersuchung eine etwa 3 bis 4 mal höhere Kobelanzahl je Tier festzustellen. Wenngleich sich bei den UG1 Eichhörnchen kein Zusammenhang zwischen AR-Größe und Kobelanzahl fand, muß beim Vergleich mit der belgischen Untersuchung berücksichtigt werden, daß dort die Beobachtungszeiträume deutlich kürzer (1–3 Monate pro Tier) und die AR im Durchschnitt etwa nur 20% der Größe von denen der UG1-Eichhörnchen besaßen. Auch wurde von Wauters und Dhondt (1988) die Nutzung bestimmter Kobel durch mehrere Tiere beobachtet, was bei den UG1-Eichhörnchen insgesamt lediglich nur zweimal festzustellen war.

Baumhöhe und Verhalten

Mit beginnender Verfügbarkeit der neuen Fruchtreife im Sommer und Herbst nutzten die Eichhörnchen hauptsächlich die Sämereien der höheren Bäume, um im Winter der Nahrungsaufnahme in den niedrigeren Beständen nachgehen zu können. Im Winter war die

Aktivität bis zu 80% durch die Nahrungsaufnahme bei kobelnahem Aufenthalt in relativ geringer Höhe gekennzeichnet (vgl. Tonkin 1983; Wauters und Dhondt 1987) und ihre lokomotorische Aktivität war gering. Zum Frühjahr hin nahm diese wieder deutlich zu, wobei sich aber das Nahrungsspektrum bei dieser Untersuchung nicht so deutlich wie bei denen von Mollar (1983), Tonkin (1983) und Wauters und Dhondt (1987) auf Blüten, Asttriebe und Insekten verschob.

Zusammenfassung

Untersucht wurden drei Eichhörnchen-Subpopulationen über einen Zeitraum von 35 Monaten. Die Untersuchungsgebiete lagen in Wirtschaftswäldern des westlichen Wiehengebirges. Die Eichhörnchen wurden mit Halsbandsendern markiert und konnten so individuell zwischen 3 bis 12 Monate beobachtet werden. Die Zielsetzung bestand darin, die Raumnutzung der Eichhörnchen in einem großflächigen, zusammenhängenden Waldgebiet und in zwei ca. 20 ha großen Waldinseln zu vergleichen. Die Grundlage hierfür bildete die Betrachtung der Aktionsaumagrößen und jener Flächen, die intensiv als Kernbereiche besucht wurden. Beachtet wurden dabei die interindividuellen und die zwischen den Gruppen auftretenden Unterschiede. Die mittlere Aktionsraumgröße in dem zusammenhängenden Waldgebiet lag bei 11,1 ha, die durchschnittliche Größe der Kernbereiche betrug 1,8 ha. Die mittlere Aktionsgröße in den Waldinseln war 2,4 bzw. 2,6 ha, die der Kernbereiche 0,4 bzw. 0,8 ha. Die Überlappung der Aktionsräume der Hörnchen in den Waldinseln war signifikant größer als die in der zusammenhängenden Waldfläche. Auch war auffällig, daß bis auf zwei Hörnchen sowohl Katzen als auch Kater eine exklusive Nutzung ihrer Kernbereiche zeigten, sich also territorial verhielten. Überlappungen der Aktionsräume waren aber stets zu beobachten zwischen männlichen und weiblichen Tieren. In dem zusammenhängenden Waldgebiet wurden zusätzlich die Zahl und die Lage der Kobel sowie die Baumartennutzung festgestellt.

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Influence of the subterranean rodent *Ctenomys australis* (Tuco-tuco) in a sand-dune grassland

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Abstract

Plant communities on sand dunes with and without burrows of the subterranean rodent *Ctenomys australis* (tuco-tuco) were studied to quantify this species participation on the landscape formation. Below- and above-ground plant biomass was estimated. Vegetation biomass, richness and diversity of patches with and without burrows (macrospatial scale) and vegetation associated to mound and intermound areas (microspatial scale) were compared. Total plant biomass was not different in areas with and without *C. australis*. Areas without tuco-tucos presented twofold numbers of different species and significantly higher species diversity than areas where animals were present. On the other hand, although plant biomass was higher in intermound areas neither species richness nor diversity values showed statistically significant differences. Results indicate that *C. australis* alters plant community composition and keeps succession on pioneer stages without altering total biomass. As an overall effect dune development is arrested and its stabilization is restrained.

Introduction

Effects of mound-building and feeding activities on plant community dynamics and soil nutrient status were evaluated for many species of subterranean rodents (Spencer et al. 1985; Grant and McBrayer 1981; Inouye et al. 1987; Swihart 1991). Disturbance related to burrowing can alter patterns of species richness and spatial and temporal aspects of plant succession (Tilman 1983). Moreover, Reichman et al. (1993) presented evidence that fossorial herbivores generate distinct edge patterns in overlying plant communities, and suggested that these patterns may initiate competition-induced waves of plant biomass. Despite the worldwide ecological importance of tuco-tucos and their widespread occurrence in South America (Reig et al. 1990), only Contreras (1973) emphasized the participation of *Ctenomys* sp. as an active agent modifying soil ecosystems. More recently, Contreras and Gutierrez (1991) analysed the impact of *Spalacopus cyanus* within Neotropical ecosystems.

Ctenomys australis inhabits sand dune grasslands. As these coastal sandy environments are very vulnerable to eolic and hydric erosion, vegetation plays an important role in the process of building the dunes and stabilizing the sand. In the present study, plant community on sand dunes with and without burrows of *C. australis* is characterized with the aim of quantifying tuco-tucos participation on the landscape formation.

Table 1. Comparisons of dry biomass of vegetation in absolute values (g/m^2), species richness and diversity (H) in areas with and without burrows of *C. australis.* Data are shown as X ± SE with percentage of total biomass in parenthesis (%). Percentage values lower than 1% are not given. $^*P < 0.05$

SPECIES	Areas with *C.a*	Areas without *C.a*	
Grasses			
Catapodium rigidum		0.02 ± 0.02	*
Cenchrus pauciflorus		1.86 ± 0.89 (1.9)	*
Lophochloa phleiodes		0.43 ± 0.27	*
Panicum racemosum	58.97 ± 7.71 (53.79)	42.00 ± 3.00 (42.96)	*
Poa sp.	4.27 ± 1.29 (3.89)	7.36 ± 1.94 (7.53)	*
Stipa sp.		1.96 ± 1.22 (1.82)	*
Forbs			
Achyrocline satureioides	1.22 ± 1.22 (1.11)	8.70 ± 3.75 (8.9)	*
Calystelgia soldanella		0.35 ± 0.24	*
Compuesta 1		1.89 ± 1.83 (1.93)	*
Gamochaeta spicata		0.08 ± 0.06	*
Gnaphalium leucopeplum	4.41 ± 3.14 (4.02)	0.41 ± 0.41	*
Grindelia aegialitis	0.70 ± 0.45		*
Hydrocotyle bonariensis	35.91 ± 12.63 (32.75)	30.86 ± 6.69 (31.56)	*
Medicago minima		0.69 ± 0.48	*
Oenothera mollisima	4.15 ± 2.99 (3.78)	1.35 ± 0.55	ns
BIOMASS			
Total	109.63 ± 11.01	97.76 ± 9.12	ns
Above	82.74 ± 7.27	71.51 ± 6.68	ns
Below	26.90 ± 9.95	26.25 ± 5.95	ns
Grasses	63.24 ± 7.82	53.44 ± 5.62	*
Forbs	46.39 ± 12.72	44.32 ± 7.00	ns
Litter	0.92 ± 0.66	9.17 ± 1.20	*
DIVERSITY			
Richness	7 species	14 species	
H′	0.5044	0.6644	*
H′ max	0.845	1.176	
J′	0.597	0.565	

ANOVA F 0.05, 1, 38 = 4.104
t 0.05 (2) 1.95 = 1.97

Material and methods

The study area is located 10 km south of Necochea, Buenos Aires, Argentina. It consists of a 4–10 km wide coastal dune fringe which slopes into the inland natural grassland. Sand dunes reach altitudes ranging from 30 to 50 m above sea level, and extend 200 to 2 000 m (FRENGUELLI 1928). The grassland where *C. australis* density averages 16 individuals/ha exhibits a vegetation cover of about 20%, with dominant plants including *Poa* sp., *Panicum racemosum* and *Calistelgia soldanella* (MALIZIA et al. 1991). The site was exposed to slight grazing by cattle.

Bioenergetics constraints restrict *Ctenomys australis* to occupy sandy and deep soils with poor cover vegetation (BUSCH 1989; MALIZIA et al. 1991). Excavation activities in deep soils can be verified only by soil material that tuco-tucos bring to the surface at the openings of their tunnel system. Moreover, in

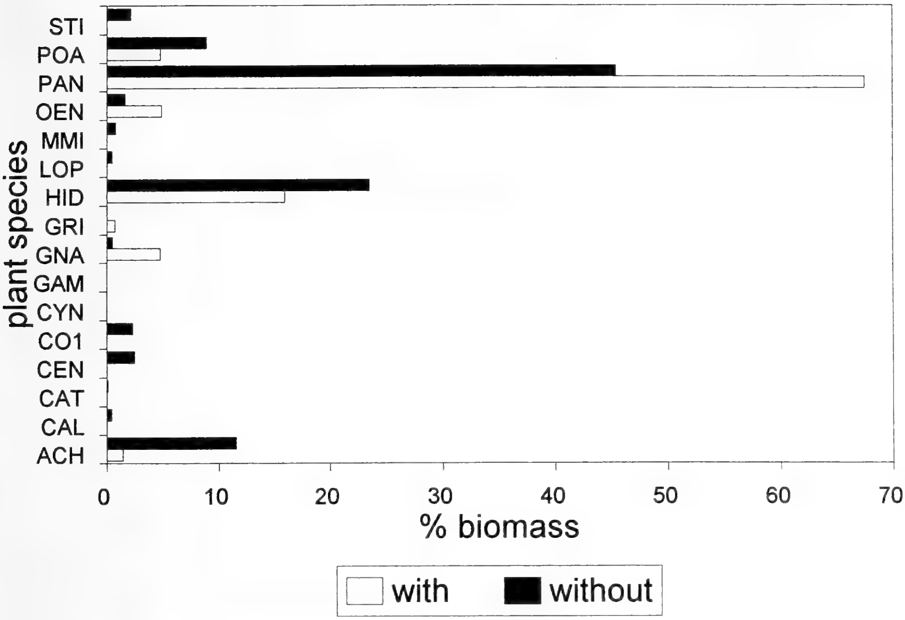

Fig. 1. Percentage of above ground biomass in areas with and without burrows of *Ctenomys australis* for each species. STI *Stipa* sp., POA *Poa* sp., PAN *Panicum racemosum*, OEN *Oenothera mollisima*, MMI *Medicago minima*, LOP *Lophocloa phleiodes*, HID *Hydrocotyle bonariensis*, GRI *Grindelia aegialitis*, GNA *Gnaphalium leucopeplum*, GAM *Gamochaeta spicata*, CYN *Cynodon dactylon*, CO1 Compuesta 1, CEN *Cenchrus pauciflorus*, CAT *Catapodium rigidum*, CAL *Calistelgia soldanella*, ACH *Achyrocline satureioides*.

shallower soils (at the edge of *C. australis* distribution), the resultant burrow is rather superficial, so that it is possible to identify removed earth (mounds) along much of this stretch of land.

Two scales of analysis were defined: macrospatial, in which vegetation of patches with and without burrows is compared; and microspatial, where vegetation associated to mound and intermound areas is compared.

A) Macrospatial: Two 10 × 10 m experimental plots were established in sand dunes where presence of *C. australis* was verified. All above- and below-ground plant material (to a depth of 20 cm) was collected in ten 1 m^2 squares located randomly in the plots. Similar procedure was applied in areas exhibiting no signs of *C. australis* activity to be used as control. No obvious differences were apparent among these areas other than the presence or absence of burrows of tuco-tucos.

B) Microspatial: Two 10 × 10 m experimental plots were established in sand dunes fixed by vegetation. Within each plot, ten 1 m^2 squares were located randomly, choosing the mound nearest to that point. All plant material was collected as indicated above. Similar procedure was applied in control plots where squares were located by randomly selecting the nearest point not occupied by a mound.

The study was conducted during early summer of 1992 when grassland condition improved the chance of detecting tuco-tuco effects. All vegetation samples (80 × 1 m^2 squares) were separated by species in above- and below-ground plant fractions, oven dried at 70 °C for 72 h and weighed to estimate plant biomass. Species richness (S) and diversity (H′) were calculated from this biomass data.

Statistical differences were evaluated by one way ANOVA, and Hutcheson t-test (Zar 1984) was performed to contrast species richness. Log transformations (log x + 1) were performed on all biomass data to normalize the variance structure.

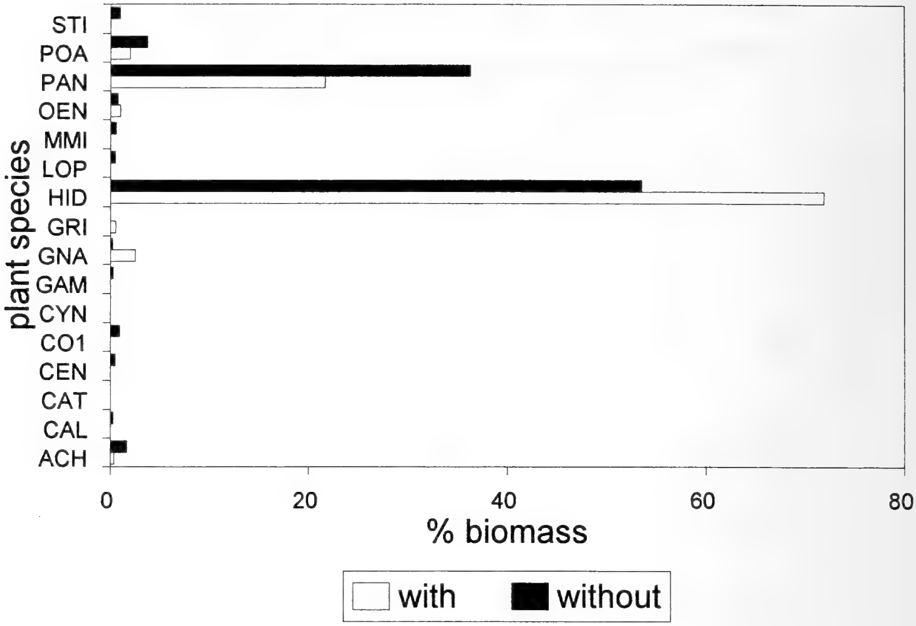

Fig. 2. Percentage of below ground biomass in areas with and without burrows of *Ctenomys australis* for each species. STI *Stipa* sp., POA *Poa* sp., PAN *Panicum racemosum*, OEN *Oenothera mollisima*, MMI *Medicago minima*, LOP *Lophocloa phleiodes*, HID *Hydrocotyle bonariensis*, GRI *Grindelia aegialitis*, GNA *Gnaphalium leucopeplum*, GAM *Gamochaeta spicata*, CYN *Cynodon dactylon*, CO1 Compuesta 1, CEN *Cenchrus pauciflorus*, CAT *Catapodium rigidum*, CAL *Calistelgia soldanella*, ACH *Achyrocline satureioides.*

Results

A) Macrospatial scale

There were no differences in total, above and below-ground plant biomass in areas with and without *C. australis*. However, in this latter areas, litter biomass was higher (Tab. 1). With respect to grassland composition, areas with *C. australis* had significantly higher grass biomass than areas without tuco-tucos (Tab. 1). Although *Panicum racemosum* was the most abundant plant species and the one that contributes most heavily to grass biomass, its biomass was significantly different in areas with and without tuco-tucos. Furthermore, this plant species was more abundant and practically the only grass in areas with *C. australis*. Areas without tuco-tucos were, on the other hand, inhabited by five other species, three of which (*Cenchrus pauciflorus*, *Poa* sp., *Stipa* sp.) represented each more than 1% of the total biomass. All these latter species showed statistically significant differences in biomass between areas (Tab. 1).

There were no differences for total forb biomass (Tab. 1) between areas. Although *Hydrocotyle bonariensis* was the most representative species in both areas, it was significantly more abundant in areas with tuco-tucos. In these latter areas it was present with other four species, three of which (*Achyrocline satureioides*, *Gnaphalium leucopeplum*, *Oenothera mollisima*) contributed each with more than 1% of the total biomass. In areas without *C. australis*, *H. bonariensis* was present together with seven other species, but only

Table 2. Comparisons of dry biomass of vegetation in absolute values (g/m^2), species richness and diversity (H) in mound and intermound areas. Data are shown as X ± SE with percentage of total biomass in parenthesis (%). Percentage values lower than 1% are not given.
*$P < 0.05$

SPECIES	Mound Areas	Intermound Areas	
Grasses			
Cynodon dactylon	0.002 ± 0.002		*
Lagurus ovatus		0.02 ± 0.02	*
Lophochloa phleiodes	0.21 ± 0.07	0.28 ± 0.21	ns
Panicum racemosum	78.02 ± 12.06 (60.33)	145.24 ± 18.79 (64.05)	*
Poa sp.	6.36 ± 1.15 (4.92)	9.58 ± 1.59 (4.22)	*
Stipa sp.	0.05 ± 0.02	0.073 ± 0.05	*
Forbs			
Achyrocline satureioides	1.53 ± 1.27 (1.18)	20.00 ± 10.72 (8.82)	*
Adesmia incana	0.36 ± 0.26	0.28 ± 0.22	ns
Ambrosia tenuifolia	2.43 ± 1.22 (1.88)	8.14 ± 2.83 (3.58)	*
Calystelgia soldanella		0.01 ± 0.01	*
Compuesta 1	1.65 ± 1.33 (1.27)	1.38 ± 1.40	ns
Gamochaeta spicata		0.016 ± 0.01	*
Gnaphalium leucopeplum		1.52 ± 1.52	*
Hydrocotyle bonariensis	1.34 ± 0.83	2.19 ± 0.67	*
Medicago lupulina	0.17 ± 0.17	1.04 ± 1.00	*
Medicago minima	1.94 ± 0.72 (1.50)	1.77 ± 0.98	ns
Oenothera mollisima	1.63 ± 3.42 (8.99)	8.58 ± 3.60 (3.78)	ns
Solidago chilensis	23.61 ± 8.28 (18.26)	26.60 ± 7.67 (11.73)	ns
BIOMASS			
Total	129.32 ± 14.02	226.74 ± 20.75	*
Above	90.38 ± 8.92	166.25 ± 15.94	*
Below	38.94 ± 5.61	60.53 ± 5.89	*
Grasses	84.64 ± 14.57	155.19 ± 5.89	*
Forbs	44.64 ± 6.92	71.54 ± 11.98	*
Litter	14.94 ± 20.2	26.08 ± 3.30	ns
DIVERSITY			
Richness	14 species	17 species	
H′	0.569	0.573	ns
H′ max	1.146	1.230	
J′	0.496	0.465	

ANOVA $F_{0.05, 1, 38} = 4.104$
$t_{0.05\,(2)\,1.95} = 1.97$

two comprising each one more than 1% of total biomass. With the exception of *O. mollisima*, all forbs presented significant differences in biomass for the analysed areas. *G. leucopeplum* and *Grindelia aegialitis* were more abundant in areas with tuco-tucos and the other ones in areas without tuco-tucos (Tab. 1).

P. racemosum and *H. bonariensis* together represented 87 and 75% of plant biomass in areas with and without tuco-tucos, respectively (Tab. 1). The former contributed principally with above-ground biomass ($F = 812.23$, $P < 0.05$ and $F = 413.29$, $P < 0.05$ in areas with and without *C. australis*, respectively). Whereas below-ground biomass appears to be more representative than above-ground biomass for *H. bonariensis*, there were no statistically significant differences in each type of area (F = 0.12, P > 0.05 and F = 0.42, P > 0.05). Furthermore, as shown in figures 1 and 2, presence of *C. australis* favours above ground biomass development in detriment to below ground biomass for *P. racemosum*, whereas the contrary situation was found for *H. bonariensis*.

The plant community, characterized by species richness and diversity indices, showed interesting differences. Areas without *C. australis* showed twofold number of species compared with areas with tuco-tucos and also a significantly higher species diversity (Tab. 1).

B) Microspatial scale

All categories of plant biomass analysed, except litter, were higher in intermound areas (Tab. 2). Within grasses, only *P. racemosum* and *Poa* sp. showed significant differences between areas, contributing each one with more than 1% of total plant biomass (Tab. 2). The same results were found for the forbs *Achiroclyne saturoides* and *Solidago chilensis* (Tab. 2). *P. racemosum* and *S. chilensis* were the most conspicuous species, representing 78 and 76% of total biomass for mounds and intermounds, respectively. Here also *P. racemosum* contributes differentially with above-ground biomass in mound and intermound sites (F = 151.45, P < 0.05; F = 134.59, P < 0.05). The latter species presented similar abundance of both plant fractions (F = 0.34, P > 0.05, F = 0.73, P > 0.05). Furthermore,

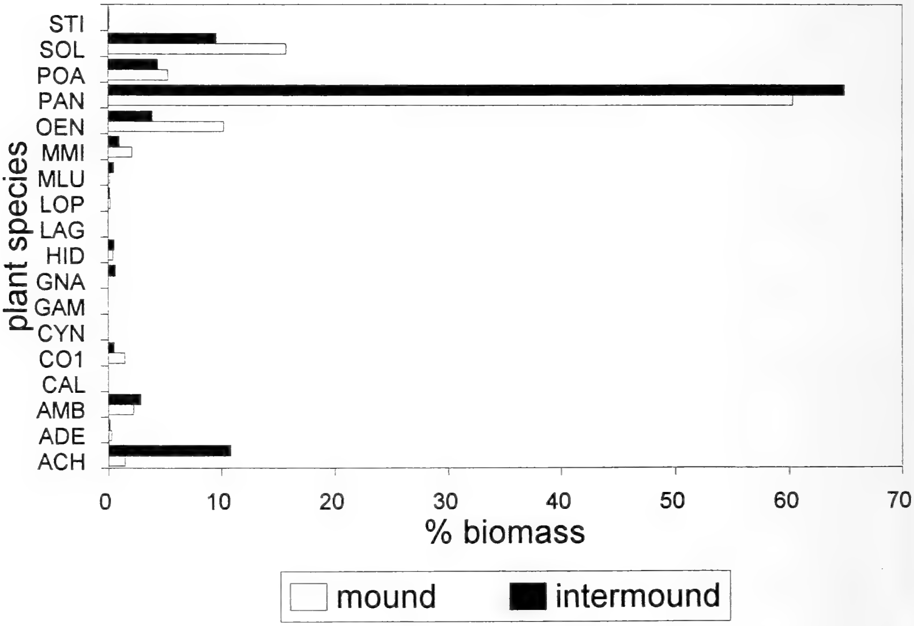

Fig. 3. Percentage of above ground biomass in mound and intermound areas for each species. STI *Stipa* sp., SOL *Solidago chilensis*, POA *Poa* sp., PAN *Panicum racemosum*, OEN *Oenothera mollisima*, MMI *Medicago minima*, MLU *Medicago lupulina*, LOP *Lophocloa phleiodes*, LAG *Lagurus ovatus*, HID *Hydrocotyle bonariensis*, GNA *Gnaphalium leucopeplum*, GAM *Gamochaeta spicata*, CYN *Cynodon dactylon*, CO1 Compuesta 1, CEN *Cenchrus pauciflorus*, CAL *Calistelgia soldanella*, AMB *Ambrosia tenuifolia*, ADE *Adesmia incana*, ACH *Achyrocline satureioides*.

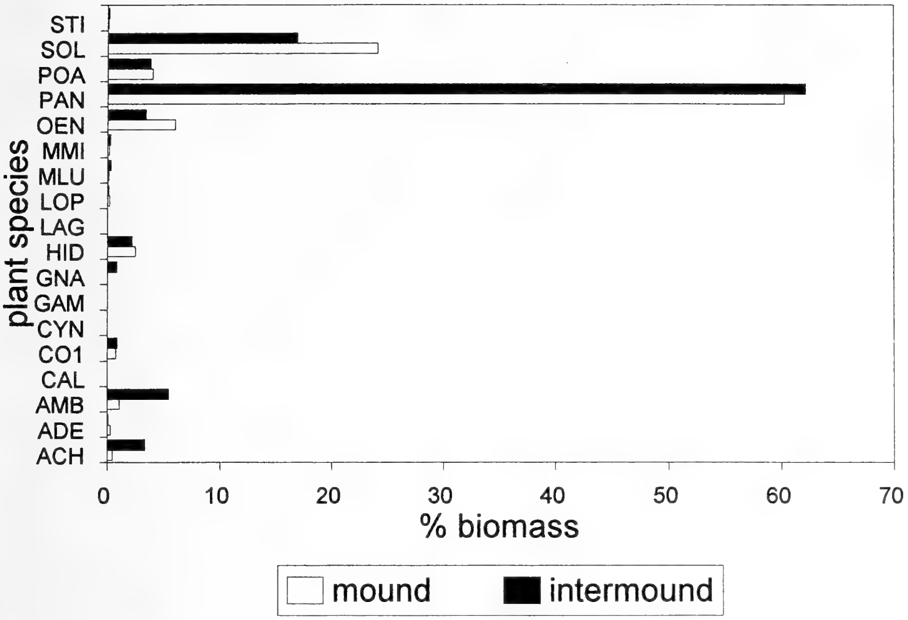

Fig. 4. Percentage of below ground biomass in mound and intermound areas for each species. STI *Stipa* sp., SOL *Solidago chilensis*, POA *Poa* sp., PAN *Panicum racemosum*, OEN *Oenothera mollisima*, MMI *Medicago minima*, MLU *Medicago lupulina*, LOP *Lophocloa phleiodes*, LAG *Lagurus ovatus*, HID Hydrocotyle bonariensis, GNA *Gnaphalium leucopeplum*, GAM *Gamochaeta spicata*, CYN *Cynodon dactylon*, CO1 Compuesta 1, CEN *Cenchrus pauciflorus*, CAL *Calistelgia soldanella*, AMB *Ambrosia tenuifolia*, ADE *Adesmia incana*, ACH *Achyrocline satureioides*.

below and above ground plant biomass per species showed the same pattern in mound and intermound areas (Figs. 3, 4).

Neither species richness nor diversity values between site types showed statistically significant differences.

Discussion

Vegetation is critical in the stabilization of dunes and also promotes their growth, by providing a trap for wind-blown sand. In the coastal dunes of Buenos Aires province, the perennial grass, *Panicum racemosum*, is the first colonizer. This grass only grows well when it is being continually covered by fresh wind-blown sand. Other important early colonizers are *Poa lanuginosa*, *Hydrocotyle bonariensis*, *Calistelgia soldanella* and *Adesmia incana*, but if for any reason, sand is exposed to the wind and loose grains blown away, the *Poa* and *Adesmia* community is replaced by the dune grass *Panicum racemosum*. With increasing stability, soil development and protection from salt spray, the dunes are invaded by species of European origin, such as *Erodium cicutarium*, *Poa annua*, *Cynodon dactylon* and specially *Medicago minima* (Cabrera 1941).

Tuco-tucos mound-building activity results in barren areas open to wind erosion that impinge on plant community and arrests the succession on the earlier pioneer stages. Thus, areas with tuco-tucos have lower plant diversity and half the number of species than those without tuco-tucos. Furthermore, the pioneer perennial grass, *Panicum racemosum*, is the dominant plant in dunes inhabited by tuco-tucos.

Spencer et al. (1985) noted changes in abundance and composition of certain plants near pocket gopher burrows because of differential consumption resulting from dietary preferences. *C. australis* proved to be a herbivore generalist as it consumed almost all plant species available in the grassland (Comparatore et al. 1995). As a consequence, differences in dune community composition cannot be attributed to competitive release mediated by selective feeding.

Feeding and burrowing activities by mole rats and pocket gophers not only reduced locally overlying vegetation, but also enhanced plant biomass directly adjacent to the disturbance, producing a sharp edge effect (Reichman and Smith 1985; Reichman and Jarvis 1989). Moreover, Reichman et al. (1993) revealed a pattern of biomass extending from disturbances, suggestive of a competition-induced wave. At Necochea dunes, total average biomass was not different for areas with and without tuco-tucos, but was higher in intermound than in mound patches suggesting that mound-building activity by tuco-tucos enhanced plant growth near mounds.

Other studies have demonstrated that as a consequence of burrowing activities, high soil turnover promotes the development of favorable conditions for the recruitment of bulbs of geophytes. This mechanism may account for the maintenance of the coexistence of geophytes and mole rats (Lovegrove and Jarvis 1986) and this plant species and coruros (Contreras and Gutiérrez 1991).

Panicum racemosum and *Hydrocotyle bonariensis*, the dominant plant species in this study, are geophytes without bulbs. Their dominance in unstable areas with tuco-tucos may be associated to the fact of being continually covered by fresh wind-blown sand that favors its development.

In conclusion, *Ctenomys australis* alters plant community composition and keeps succession on pioneer stages without altering total biomass. As an overall effect, dune development is arrested and its stabilization is restrained. In consequence, mound-building activities maintain suitable habitats for *C. australis* according to its energetic and thermoregulatory restrictions.

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Zusammenfassung

Einfluß des unterirdisch lebenden Nagetieres Ctenomys australis (Tuco-tuco) in einer Sanddünen-Landschaft

Um den Einfluß des Nagers *Ctenomys australis* (Tuco-tuco) an der Landschaftsgestaltung zu bestimmen, wurden die Pflanzengesellschaften von Sanddünen mit und ohne unterirdischen Gangsystemen dieser Säuger untersucht. Die Biomasse von Pflanzen wurde ober- und unterirdisch bestimmt. Verglichen wurden Biomasse, Artenreichtum und Diversität der Pflanzengesellschaften in Gebieten mit und ohne Bauten (macrospatial scale), sowie auf Bauhügeln und dazwischen (microspatial scale).

Die totale Pflanzenbiomasse unterschied sich in Gebieten mit und ohne *C. australis* nicht. In Gebieten ohne Tuco-tucos fanden sich doppelt so viele Arten und eine signifkant höhere Artendiversität. Keine signifikanten Unterschiede waren bei Flächen zwischen den Hügeln und direkt auf den Hügeln zu erkennen, obwohl die Pflanzenbiomasse zwischen den Erdhügeln größer war.

Die Ergebnisse zeigen, daß *C. australis* die Zusammensetzung der Pflanzengemeinschaft verändert und die Sukkzession in Pionierstadien hält, ohne dabei die totale Biomasse zu verändern. Als Gesamteffekt läßt sich also sowohl eine Hemmung der Dünenentwicklung als auch ihre Stabilisation beobachten.

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On mammals from the People's Democratic Republic of Laos, mainly from Sekong Province and Hongsa Special Zone

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Abstract

Mammal data and material were collected during a short stay in the People's Democratic Republic of Laos in the winter of 1993–1994. Most data are from the southern Sekong Province and the northwestern Hongsa Special Zone, from where practically nothing has been previously reported. Many localities are new, and add to our knowledge of species distributions. Of particular interest are *Megaerops niphanae* and *Taphozous saccolaimus*, which are reported from Laos for the first time; some new localities for *Pygathrix nemaeus*; two new records of *Prionodon pardicolor*; reports on *Panthera tigris* and *Nemorhaedus sumatraensis*; and records of *Leopoldamys edwardsi* and *L. sabanus*, *Maxomys moi*, *Berylmys bowersii* which is new for the Sekong Province region, and *Niviventer* cf. *tenaster* which is new for Laos.

Introduction

The mammal fauna of the People's Democratic Republic of Laos (further abbreviated as Laos) is not well known. No systematic collecting has been carried out. Osgood (1932) described several collections of mammals including specimens from 25 localities in Laos, representing some 90 species. Another valuable collection had been brought together by the Société Royale des Sciences Naturelles du Laos in Vientiane. It served as the basis for a number of systematic and zoogeographic accounts by J. Deuve and M. Deuve in the Bulletin of the Société (1963 a–b; 1964 a–d), culminating in the comprehensive work "Les mammiferès de Laos" (J. Deuve 1972). The collection of mammals and other animals and the library of the mentioned Société are believed to have been destroyed (Mr. Jean Deuwe, pers. comm. 1994). Other important studies on mammals from Laos are those by Phillips (1967), Chazee (1990), Salter (1993), Duckworth (1994), Evans et al. (1994), and Schaller and Rabinowitz (1995).

The present study contains taxonomic and geographic mammal data recently assembled in Laos by the author, as member of a team researching the use of non-timber forest products (Beer et al. 1994). The research was commissioned by the Dutch development cooperation organization Novib. The team stayed in Sekong Province from 3. 12. 1993 to 23. 1. 1994, and in Hongsa Special Zone from 31. 1 to 15. 2. 1994. Most observations in the present study are on mammals from Sekong Province, a number refers to Hongsa Special Zone, and a few to other localities.

Material and methods

Data on the occurrence of species and some material of hunted specimens have been collected during several dozen village interviews. Other material has been seen, and in some cases bought, in the markets of Sekong town, Saravane, Attapeu, Vientiane and Hongsa town, and some at an odd market stall along Hong Khou Vieng in Vientiane. Altogether 111 specimens representing 44 species have been deposited in the Institute for Systematics and Population Biology – Zoölogisch Museum (ZMA) of the University of Amsterdam, the Netherlands. The study also includes notes on species which were not collected, and on six specimens of four bat species from Laos received by the institute in 1983. The identifications are the author's, except for *Niviventer* cf. *tenaster*, which have been identified by Dr. G. G. Musser, while Dr. J. Fooden commented on a first analysis of the *Macaca* material. For identifications several handbooks for the region were consulted, notably Peenen et al. (1969), Deuve

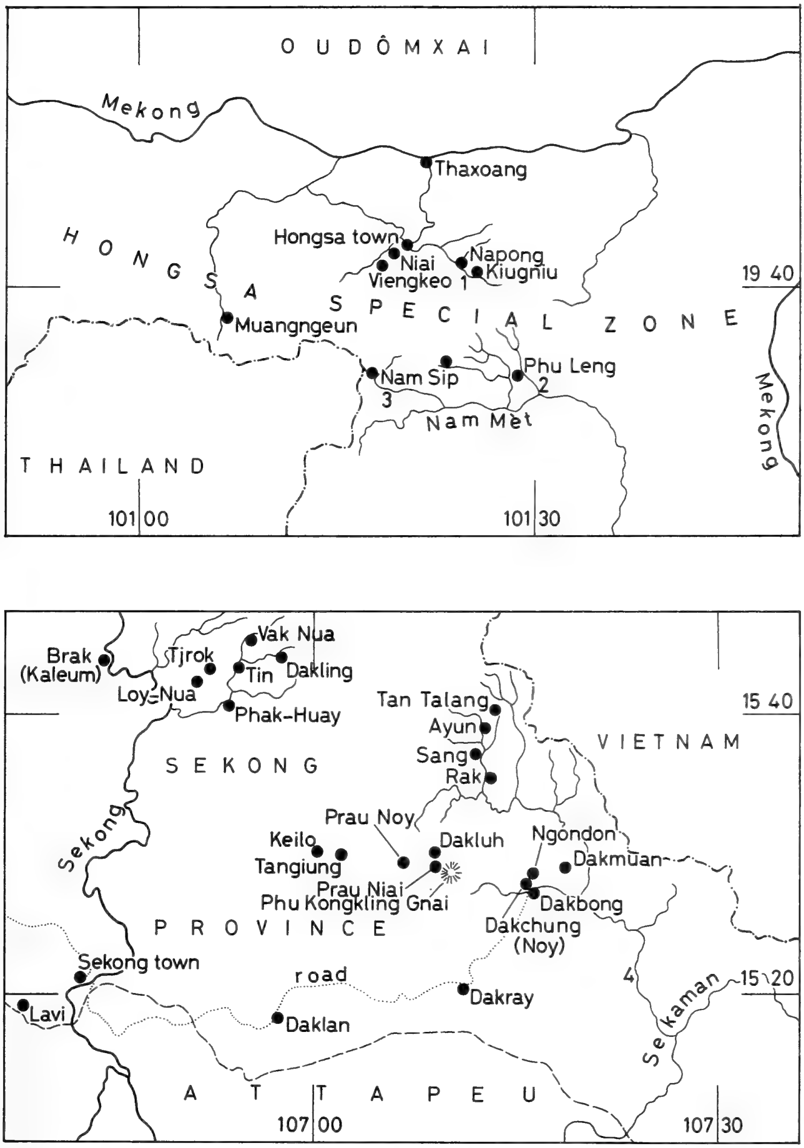

Fig. 1. Maps of the areas visited in Hongsa Special Zone, northwest Laos (above), and in Sekong Province, southeast Laos (below). Localities of some of the smaller villages have been approximated. The names of some smaller rivers are:
1: Nam Ken; 2: Huay Chuang; 3: Nam Sip; 4: Nam Poay Ô.

(1972), LEKAGUL and MCNEELY (1988) and CORBET and HILL (1992). Generalized distribution maps including Laos have been published by LEKAGUL and MCNEELY (1988) and CORBET and HILL (1992). A number of localities are mapped (Fig. 1); not all could be traced with accuracy. Given measurements are in mm, and weights in g. Measurements have been abbreviated as follows: Bimalar width – BMW; upper tooth row – C*–M*; ear length – E; forearm length – FAL; greatest skull length (incisors excluded) – GSL; head and body length – HB; hindfoot length (claws included) – HF; interorbital width – IOW; palatal length – PL; post-rostrum length – PRL; rostrum length – RL; tail length (with/without tuft) – T; total length (with/without tail tuft) – TL; weight – W; zygomatic width – ZW. Bimalar width, rostrum length and post-rostrum length in primates have been measured as indicated by FOODEN (1969).

Results and discussion

Order Pholidota

Manis javanica Desmarest, 1822
Scales and nails of three Sunda pangolins caught near Tan Talang in 8. 1993 were offered for sale, in Dakchung (Noy) on 13. 12. 1993. Some of these were bought (ZMA 24.755). A live specimen from Dakrai was offered for sale in the same place on 14. 12. 1993. Of this specimen some pictures were taken. Another live specimen was offered for sale in the market of Sekong town on 21. 1. 1994. Villagers reported on the occurrence of pangolins (Sunda pangolins according to the map in CORBET and HILL 1992) near Ayun, Dakdan, Daklu, Prau Niai, Sang, Tangiung and Tjrok, all in Sekong Province.

Order Scandentia

Tupaia belangeri (Wagner, 1841)
A specimen shot near Hongsa town was offered for sale in the market of that town on 1. 2. 1994 (ZMA 24.702; TL: 390/360, T: 175/143, HF: 43.6, E: 19.1, W: 168). During our stay several other specimens of this species were seen in the same market.

Order Insectivora

Hylomys suillus Müller, 1841
Villagers reported on what probably belongs to this species at Dakdan and Rak, both in Sekong Province.

Order Chiroptera

Rousettus leschenaultii (Desmarest, 1820)
One specimen was collected by L. J. K. KLEIJN and K. POST on 15. 12. 1983 at Nam Ngum (ZMA 22.073). Two specimens from near Sekong town were offered for sale in the market of that town on 11.1, and another on 23. 1. 1993 (ZMA 24.840–42). A series of male *Rousettus* from Pha Deng, between Hongsa town and Muangngeun, offered for sale in the market of Hongsa town on 12. 2. 1994 also represented this species (ZMA 24.843–56; FAL 11 adult ♂♂: 76.6–85.0; W ditto: 80–98). On 18. 1. 1994, two specimens of *Rousettus*, probably of this species, were seen flying in broad daylight from a bamboo forest at the roadside a few km west of Tjrok in Sekong Province. Other specimens probably of this species were seen on 25. 11. 1993 at a roadside stall in Vientiane (origin: Vangviang), on 31. 1. 1994 in the market of Luangprabang (originating from a cave at the Mekong nearby), and on 20. 2. 1994 at the Vientiane day-market (origin unknown).

Cynopterus sphinx (Vahl, 1797)
Two specimens of this species were bought at Hongsa town market on 8. 2. 1994, originating from a forest east of the town, and two others on 14. 2. 1994, originating from Pha

Deng, a red rock formation at a few km from the town in the direction of Muangngeun (ZMA 24.836–39). Specimens probably belonging to this species were seen on 25. 11. 1993 at a roadside stall in Vientiane (origin: Vangviang).

Megaerops niphanae Yenbutra and Felten, 1983
Two ♀♀ were bought at Hongsa town market on 8. 2. 1994. They had been caught in a forest east of the town (ZMA 24.834–35) and are the first records of this species from Laos. Some measurements are (subadult ZMA 24.834, adult 24.835): FAL: 56.5, 58.0; E: 17.7, 18.8; W: 28, 27. The adult specimen was lactating. The subadult had a nycteribid fly, *Leptocyclopodia f. ferrarii* (Rondani, 1878), possibly a straggler from the preceding species.

Eonycteris spelaea (Dobson, 1871)
One immature specimen from a forest east of Hongsa town was bought in the market of this town on 8. 2. 1994 (ZMA 24.833).

Taphozous saccolaimus Temminck, 1838
Three ♂♂, with FAL: 76.7, 74.3 and 74.0 respectively, were collected by L. J. K. Kleijn and K. Post at Nam Ngum on 15. December 1982 (ZMA 22.069–22.071). This species has not previously been reported from Laos. According to Corbet and Hill (1992), it differs from the other large *Taphozous* of the region, *T. theobaldi* Dobson, 1872, in a number of cranial and other characters, clearly separating the two. One of these characters, the form of the frontal region (concave in *theobaldi*, and not so in *saccolaimus*), appears not to hold true in this case. In specimen 22.069 (the only with extracted skull), the frontal region is inflated anteriorly but distinctly concave between the eyes.

According to Salter (1993) *theobaldi* would be mentioned for central and southern Laos by Lekagul and McNeely (1988) and Corbet and Hill (1992). This is not correct. Lekagul and McNeely, (1988) mentioned Indochina as part of its distribution, and include a large part of Laos in their generalized distribution map. These maps have been compiled mostly from literature reports (Dr. J. A. McNeely, pers. comm. 1994) but I have not been able to trace the source for the occurrence of this species in Laos. Corbet and Hill (1992) do not mention or map *theobaldi* for Laos; localities in both Thailand and Vietnam on their map approach the extreme south of Laos.

Rhinolophus pusillus Temminck, 1834
A ♂ of this species was netted by L. J. K. Kleijn and K. Post at Nam Ngum on 15. 12. 1982 (ZMA 22.154).

Pipistrellus tenuis (Temminck, 1840)
L. J. K. Kleijn and K. Post collected a ♂, FAL: 30.1, at Thalet near Nam Ngum on 25. 8. 1982 (ZMA 22.170).

Order Primates

Nycticebus pygmaeus Bonhote, 1907
A specimen was caught at Dakmuan about 6 km east of Dakchung (Noy) during the night of 13./14. 2. 1994 and offered for sale in the latter town the next morning. It was bought by the author, photographed, and released in a forest near Dakbong. Duckworth (1994) mentioned this species from the proposed protected areas Xe Piane and Phou Xang He, and has a study in press on his field sightings of the Pygmy loris in Laos (Duckworth 1995).

Nycticebus species
The nearby occurrence of slow loris was reported in the villages of Dakdan, Daklu, Prau

Niai, Sang, Tangiung and Tjrok in Sekong Province, and in the villages Napong/Nam Ken, Huay Tjuang and Huay Sali in Hongsa Special Zone.

Macaca species
Five species of macaque are known to occur in Laos (FOODEN 1971, 1975, 1982 a, 1986, 1990; CORBET and HILL 1992; SALTER 1993): *Macaca mulatta* (Zimmermann, 1780), *M. f. fascicularis* (Raffles, 1821), *M. arctoides* I. Geoffroy, 1831, *M. a. assamensis* Mc Clelland, 1840, and *M. nemestrina leonina* (Blyth, 1863). Our interviews yielded many indications of the presence of macaques: at the villages of Kunsei, Dakdan, Sang, Rak, Dakbol, Daklu, Tangiung, Prau Niai, Loy-Nua, Dakling, Tin, Vak Nua, and Tjrok in Sekong Province, and at Napong/Nam Ken and Phu Leng in Hongsa Special Zone. Many stories were heard relating crop raiding by groups of 10 to 100 monkeys, which must be macaques, and hunting such groups. A captive juvenile macaque was observed at Dakchung (Noy) and another at Tin. An adult was seen high above the ground in a bamboo forest along the Sekong River, between Loy Nua and Brak. Two captive young adults and a juvenile were observed in Hongsa town. As we did not know the species well and had only general literature with us, we did not always note all the data necessary for identification. Retrospective identification of species described in interviews or even of specimens observed has not been attempted. Efforts to identify five skulls – mostly incomplete – from Phu Tjé, Dakling and Vak Nua, purchased from hunters, offer more perspective.

Taxonomy of macaques is based for a large part on characters other than skull form and measurements (FA 1989). FOODEN (1991) mentioned glans penis morphology as the most important basis for modern macaque classification. Descriptions and illustrations of skulls of the individual species mentioned have been published by FOODEN (1975, 1982 a, 1988, 1990, 1991), FOODEN et al. (1985), and LEKAGUL and MCNEELY (1988), but there is no true comparative account. Therefore, distributional data (FOODEN 1971, 1975, 1982 a, 1982 b, 1986, 1990; FOODEN et al. 1985; DUCKWORTH et al. 1993, 1994; TIMMINS et al. 1993) has also been taken into account in assigning the skulls to species.

Macaca fascicularis (Raffles, 1821)
A skull of a ♂ shot in 12.1993 on Phu Tjé, a mountain near Tangiung with an altitude probably between 1 100 and 1 500 m (ZMA 24.916), and a skull of an immature ♂ shot in 1993 near Dakling, altitude c. 750 m (ZMA 24.917), are assigned to this species. In Dakling, people told that a hundred specimens are being killed each year (but these may include specimens of the next two species). If compared with the larger skulls described below, the malar bones in *fascicularis* are narrower, the palatum does not extend behind the tooth rows, and the tooth rows are more strongly curved. Measurements of the adult: GSL: ≥131, C^1–M^3: 44.7, ZW: 85.4. According to FOODEN (1971), the specimens are from the *mulatta* range, although the dividing-line between this species and the narrowly related *fasciculata* in this region appears to be tentative and less fixed than suggested by CORBET and HILL (1992). The present author had first thought to class the skulls as *mulatta*, but Dr. J. FOODEN commented (pers. comm. 21. 11. 1994) that the GSL of the adult specimen seems too large for *mulatta* at this lattitude, where it is less than 120 in all specimens known to him, and where GSL in *fasciculata* apparently exceeds that in *mulatta*.

Macaca assamensis assamensis McClelland, 1840
A skull of an animal shot in 1993 near Dakling (ZMA 24.827) and a skull of one shot in 1993 near Vak Nua (ZMA 24.828) have been assigned to this species. The skulls are considered adult and male by dental wear and large canines or their alveoles. Some measurements are (24.827/24.828): GSL: 146.0/145.0; RL: 62.1/61.5; PRL: 94.1/93.5; BMW: 80.1/78.7; and ZW: 96.4/99.4. The present author had grouped these skulls as exceptionally

large specimens together with the next under *nemestrina* but Dr. J. FOODEN rather associates them with *assamensis*: "The evidence is somewhat ambiguous, but GSL and ZW seem to ally these specimens more closely with *M. a. assamensis* than with *M. nemestrina leonina*" (pers. comm. 21. 11. 1994). CORBET and HILL (1992) do not indicate *assamensis* for the Sekong Province region, but FOODEN (1982 a) identified *assamensis* from Mhuang Tateng in southern Laos.

Macaca nemestrina leonina (Blyth, 1863)
A skull of a specimen shot in 1993 near Dakling (ZMA 24. 826) is assigned to this subspecies. Dr. J. FOODEN agrees with this placement (pers. comm. 21. 11. 1994). Some measurements are: GSL: 140.8; RL: 57.7; PRL: 91.5; BMW: 84.6; and ZW: 102.4. Some differences between this specimen and the ones assigned to *assamensis* are apparent: while in *nemestrina* GSL is smaller, ZW is larger, and hence its relative ZW. Also, its BMW is larger than in *assamensis*, and thus its relative BMW. Another difference is that the nasal opening in the present specimen of *nemestrina* is pointed anteriorly, while it is broad in the specimens of *assamensis*. The distribution of *nemestrina* as given by FOODEN (1975), extended by CORBET and HILL (1992), renders it perfectly likely that the species occurs in Sekong Province.

Semnopithecus cristatus (Raffles, 1821)
One skull without mandible and with incomplete dentition was purchased from a hunter who had shot the animal at Phu Tjé near Tangiung, in 12.1993, and is assigned to this species (ZMA 24.918). Other Laotian species of this genus do not occur as far south as Sekong Province (see FOODEN 1976, rather than CORBET and HILL 1992). Some measurements are: GSL: ≥107, RL: 27.2, PL: 32.2, ZW: 67.1, BMW: 63.9. DUCKWORTH et al. (1994) report observations of *Semnopithecus* monkeys of the "*cristatus* group" from Xe Piane.

Pygathrix nemaeus (Linnaeus, 1771)
The Douc langur is represented by a damaged skull and mandible, from a forest near Ayun where the animal was shot in 9.1993 (ZMA 24.888) and by a damaged skull without mandible and with incomplete dentition of an animal shot in 1993 at about 20 km east of Dakling (ZMA 24.919). Some measurements are (ZMA 24.888/ZMA 24.919): GSL: ≥117.4/≥119.7; RL: 39.0/39.1; C^1–M^3 (alveoles): 39.2/36.2; PL: –/42.3; ZW: c. 84/84.0; BMW: 79.6/76.0. The Dakling specimen differs from the Ayun specimen and from a specimen in the Nationaal Natuurhistorisch Museum in Leiden in its ZW, measuring 8.2 in the former, and 4.1 in the Ayun specimen. This seems too large for individual variation but the material is very limited and other explanations must wait.

In several villages the monkey with the red arms was specifically mentioned. Near Sang it had disappeared long ago, in Tangiung it was called rare, and near Prau Niai (the only village which claimed not to hunt), Loy-Nua, and Tjrok it was still found. Near Loy-Nua people mentioned groups numbering between 5 and 9 animals.

Hylobatidae

SALTER (1993) mentions five species of *Hylobates* Illiger, 1811 for Laos. Of these, *H. gabriellae* Thomas, 1909 occurs in southern Laos east of the Mekong, thus in Sekong Province, and *H. lar* (Linnaeus, 1771) in the north, west of the Mekong, thus in Hongsa Special Zone. We collected no material of gibbons, but many stories indicated their presence and on one occasion we heard one call. Gibbon characters frequently mentioned in interviews include their lack of a tail, their arboreal habits, and their being harmless to crops. They were reported by the villagers of Dakdan, Rak, Dakbol, Tangiung (but there they had vanished), Prau Niai, Loy-Nua, Dakling, Vak Nua and Tjrok in Sekong Province, and at Napong/Nam Ken in Hongsa Special Zone, where gibbons were last observed 20 years ago. We heard a specimen call near Tin, on 17. 1. 1994. Several of the reports from Sekong Province mentioned that ♂♂ are black and ♀♀ red (Tangiung, Prau Niai, Loy Nua, Dakling), possibly indicating *Hylobates gabriellae*. The villagers of Dakling believe that ♀♀ are rare; in a group of seven gibbons there would be only one ♀. Their explanation is that ♀♀ kill female offspring. As a consequence, groups of ♂♂ would steal ♀♀. Deuve (1972) recorded the mentioned species, as a subspecies of *H. concolor* (Harlan, 1826), from Sekong Province (then southeast Saravane Province). Duckworth et al. (1993) and Timmins et al. (1993) provisionally identified gibbons from Phou Xang He and Dong Hua Sao as *H. concolor*, which in the taxonomy used by them includes *H. gabriellae*. In Dakdan the people mentioned a whitish-grey species and in Rak the colour was like that of "ling" (normally a macaque). In Napong/Nam Ken people remembered two forms: one black with white in its face, and one greyish white, which may indicate *H. leucogenys* Ogilby, 1840 and *H. lar*, respectively. A captive specimen of *H. leucogenys* was seen at Hotel Phousy in Luangprabang. Deuve (1972) recorded this species, as subspecies of *H. concolor*, for Luangprabang Province.

Order Carnivora

Cuon alpinus (Pallas, 1811)

The Asian wild dog, red dog, or dhole (in French chien rouge or, quite confusingly, renard – the true fox is known from North Vietnam) occurs near Daklan, Ngondon, Daklu, Tangiung, and Loy-Nua in Sekong Province, and near Hongsa town (8–9 km from the town), Napong, Huay Tjuang, Huay Sali, Nam Sip and in the Muangngeun District in Hongsa Special Zone. A skull of an animal shot in August 1993 at Phu Tjé near Tangiung was obtained at that village (ZMA 24.798). Near Dakdan it is said to be rare and to hunt wild boar. In the District of Kaleum it is said to hunt in groups of 15–20 and to kill and eat goats "till the last one". In the Hongsa District, where it is considered an enemy of goats, pigs and cows, it was mentioned to us at Napong, Huay Tjuang, Huay Sali, and Muangngeun. In the region of Huay Tjuang a group of 20–30 would attack villages once or twice a year. At Huay Sali it was said to be numerous and to approach villages mainly in November and December when, in 1993, it killed six pigs. It is also known to hunt barking deer.

Salter (1993) suggests that some of the village reports on dholes may actually refer to feral domestic dogs.

Canis aureus Linnaeus, 1758

Although the golden jackal is believed to occur only in the northwest of Laos by Lekagul and McNeely (1988) and Corbet and Hill (1992), Deuve (1972) also mentioned reports from the road Savannakhet-Sépone. It was also reported to be present in Daklan village and the District Kaleum in Sekong Province. The Kaleum District Committee told us that the species, called loup in French, hunts in packs of two or three, and kills many chickens. In the Hongsa District we were told that the loup, "a bit smaller than our domestic dog" is an enemy of goats and is known to occur at a distance of 8–9 km around Hongsa town and near Phu Nkut (not located) and Phu Leng. However, according to the Chief of Forestry of the subdistrict Hongsa, Mr. Pinh, who knows the sound of the jackal from Huei Sai in Bokeo Province, it does not occur near Napong, at a few km from Hongsa town. Again, confusion with feral domestic dogs, or even with *Cuon alpinus*, cannot be excluded. Other team members saw two captive specimens of what they believed to represent this species in Vientiane.

Ursus thibetanus Cuvier, 1823
The Asiatic black bear possibly occurs near Prau Niai and Vak-Nua in Sekong province. People there claimed two species of black bear, the larger of which eats mais, sugar cane and bananas. A specimen of *Ursus thibetanus* is held in Hotel Phousy at Luangprabang in a very small cage. In Hongsa Special Zone there were several reports on the species' presence. At Napong people spoke of two species of bear. At Huay Tjuang we met with a men who had been severely wounded and handicapped by a large black bear ("as big as, or bigger than, man"; the other species was said to be much smaller), which was attacking the mais crop. At Nam Sip the small species was said to be more numerous than the large one. In the region, hunting of bears for traditional medicinal purposes appears to occur. Gall bladders but also all other parts of the bears were sold to Thailand. In the District of Muangngeun the species, called meuy, was reported to attack mais crops. While most of these reports must refer to the Asiatic black bear, confusion with the next species – especially by people who know only one species – can never be excluded. Furthermore, we were sometimes told of a third species: *Arctictis binturong* (Raffles, 1821) considered by some to be a bear while others sometimes added that it was not a real bear.

Ursus malayanus (Raffles, 1821)
The sun bear was reported by the villages of Tangiung, Prau Niai, and Vak-Nua in Sekong Province, and Napong, Huay Tjuang and Nam Sip in Hongsa Special Zone. Two skins of this bear were seen at the Morning Market in Vientiane on 27. 1. 1994. The sun bear is hunted by some not only for the traditional medicinal market but also as a competitor for honey.

Arctonyx collaris Cuvier, 1825
The hog-badger was reported, as mu lung, by the villagers of Huay Tjuang in Hongsa Special Zone, where it may be numerous in the region.

? *Melogale personata* Geoffroy, 1831
An animal reported by the villagers of Tangiung in Sekong Province as mu lung, not being longer than 40 cm and having a very strong odour when eaten, probably represents this species rather than the preceding.

? *Lutra lutra* (Linnaeus, 1758)
Deuve (1972) reported the coarse-coated otter from the central provinces. According to Lekagul and McNeely (1988) it occurs only in the north and along the eastern border, but Corbet and Hill (1992) indicate that it would occur throughout the country. Salter (1993) quoted a report claiming the species to be rare in the region. It is not possible to identify reported otters as belonging to this or to the next, smooth-coated species *Lutrogale perspicillata* (I. Geoffroy, 1826), which is larger, with larger feet, a more velvety coat, and a sharp throat demarcation (Foster-Turley et al. 1990). Reports from the villages of Dakdan and Daklu, and from the Kaleum District in the Province of Sekong may refer to *Lutra lutra*.

? *Lutrogale perspicillata* (I. Geoffroy, 1826)
Reports on otters from Napong and Huay Tjuang in Hongsa Special Zone may refer to this species. A stuffed specimen was seen in the Vientiane Morning Market on 27. 1. 1994.

Aonyx cinerea (Illiger, 1815)
This small, dark otter was reported by the people of Dakdan, Ayun, Daklu, and Tjrok in Sekong Province. In Ayun, a poorly preserved skin could be examined. According to the owner, skins fetch high prices in Vietnam.

Viverra zibetha Linnaeus, 1758
Descriptions by villagers of Napong and Huay Tjuang, both in Hongsa Special Zone, of a species called njin hang kan (niai) or njin hang phu (the nen hang ka of DEUVE 1972) refer to the large Indian civet.

Viverricula indica (Desmarest, 1817)
A live specimen of this species in the village Ban Yai, adjacent to Hongsa town, was shown to us on 14. 2. 1994, a day after its capture near that village.

Prionodon pardicolor Hodgson, 1841
A dead ♂ of the spotted linsang was offered for sale in Dakchun (Noy), near the place where it had been killed on 9. 12. 1993. The skull and skin could be secured (ZMA 24.710 b; TL: 760/735, T: 370/345, HF: 62, E: 34.3, W: >500). A second specimen was offered for sale in the market at Hongsa town on 13.1994. It had been caught near Hongsa town during the first week of February. As it had been cleaned and smoked, the sex could not be determined. Its skull has been preserved (ZMA 24.711 GSL: 70.0, CBL: 68.2, ZW: 36.9, C^1–M^1: 24.2). SCHREIBER et al. (1989) list the species among those Viverridae "known or likely to be threatened" and remarked that this species seems to be rare everywhere in its distribution area. In Thailand, where it occurs in the north, it has not been seen since 1976, and likewise there are no recent records from any other country where it occurs except two from (northeast) India and one from southern China. In Vietnam, however, it may still be common. There, the species is offered in markets from time to time (SCHREIBER et al. 1989). The present records are of double interest: they are from a fourth country, and they suggest that also in Laos the species may still be rather common. (According to SI SOUN PHAN, a Junior Forestry Officer who assisted in cleaning the animal from Dakchun (Noy), animals of this type were offered from time to time in the Sekong town market.)

Paradoxurus hermaphroditus (Pallas, 1777)
The common palm civet was reported by the villages of Napong/Nam Ken and Huay Tjuang, in Hongsa Special Zone. Its occurrence in that region was confirmed by a smoked specimen from Kiugniu offered in Hongsa town market on 10. 2. 1994. The young adult specimen is extremely small (skull: ZMA 24.716; HB: c. 350, T: c. 395, GSL: 83.4, ZW: 43.9). CORBET and HILL (1992) give a GSL range of 90–125; in 7 ZMA specimens from Sumatra this range is 100.0–116.9, and in 7 of unknown origin it is 95.5–119.3.

Paguma larvata (Smith, 1827)
Three incomplete skulls of this species, of specimens shot in 1993, were obtained at Ayun and Tangiung in Sekong Province (ZMA 24.712/13/15). The single Tangiung specimen originated from Phu Tjé. Near Huay Tjuang, in Hongsa Special Zone, the species is frequently seen.

Arctictis binturong (Raffles, 1821)
The binturong was reported by villagers of Tangiung in Sekong Province and Huay Tjuang in Hongsa Special Zone. In both villages the species is considered a honey-eating bear. DEUVE (1972) mentioned the Laotian name chon dam, but in Huay Tjuang the name mi hang koh was used. The people there believe that the binturong never attacks people, that it cannot be killed with a knife, and that to defend itself against bees it greases itself with honey and rolls through sand. At Hotel Phousy in Luangprabang a specimen was held in a small cage.

Herpestes urva (Hodgson, 1836)
In Ayun and Tangiung in Sekong province the people knew an "otter" with dog's paws in-

stead of duck's paws (i.e. without webbed toes), which lives near and in water and eats fish. This probably refers to the crab-eating mongoose, a skull of which was secured at Ayun, near the site where it had been killed in 1993 (ZMA 24.714).

Prionailurus bengalensis (Kerr, 1792)
The leopard cat was well-known at the villages of Dakdan, Tan Talang, Ayun, Tangiung, and Tjrok in Sekong Province, and Napong in Hongsa Special Zone. Two incomplete skulls of animals shot in 1993 were obtained from near Ayun (ZMA 24.756/57). In some villages it was said to be numerous and to prey on domestic chickens.

? *Pardofelis marmorata* (Martin, 1837)
Villagers at Tangiung, Sekong Province, recognized the marbled cat from a picture and told us it lived near their village. This would confirm the distribution as given by LEKAGUL and McNEELY (1988) but contradicts the picture in CORBET and HILL (1992), which indicates a scattered distribution, covering only a part of (northwest) Laos. Confusion with the next species cannot be excluded.

Pardofelis nebulosa (Griffith, 1821)
In Sekong Province, only the Kaleum District Committee claimed the presence of the clouded leopard, which was said to be numerous. At Napong in Hongsa Special Zone the species was known but had since long disappeared. A skin was seen in the Morning Market at Vientiane on 27. 1. 1994 and another, not for sale, in a hotel in Vientiane.

Panthera pardus (Linnaeus, 1758)
At Ngondon and Dakbong in Sekong Province the panther is sometimes encountered. According to the Kaleum District Committee in the same province the species is plentiful in this district. However, its presence was confirmed only at the village of Vak Nua, while near Tjrok it did not occur. Near Napong in Hongsa Special Zone the species was also said to be absent. A skin was seen in the Morning Market at Vientiane on 27. 1. 1994.

Panthera tigris (Linnaeus, 1758)
The reports and stories on the tiger are numerous, both in Sekong Province and in Hongsa Special Zone. As noted by SALTER (1993), it is the most frequently reported livestock predator in rural Laos. It was reported to us in the villages of Daklan, Dakchun (Noy), Ngondon, Dakbong, Kun Sei, Dakdan, Sang, Tan Talang, Rak, Daklu, Tangiung, Prau Niai, Loy Nua, Dakling, Vak-Nua, and Tjrok in Sekong Province, and Napong, Huay Tjuang, Huay Sali, Nam Sip and Muangngeun in Hongsa Special Zone. In Attapeu Province, to which we paid a short visit, we were told that there were many tigers; in 1992 or 1993 one had visited San Sai. In Vak-Nua and Tjrok two species of tiger were distinguished: sua khong is large and yellow with black stripes, and sua lay is medium-sized and reddish with black stripes. The latter was considered the most dangerous one, attacking man and pigs. DEUVE (1972) mentioned both names for the tiger, without differentiation. The only direct field evidence observed by the team was a fresh foot print at Phu Kongkling Gnai (or Phu Kong Kring on other maps) in Sekong Province on 31. 12. 1993. With a greatest width of >13 cm there is no doubt as to its identity (STRIEN 1983). Several pieces of skin were seen in the Morning Market in Vientiane on 27. 1. 1994.

Sekong Province has an area of about 8700 km^2 and a population of about 57,500, i.e. an average of 6.6 inhabitants per km^2. In the Dakchun District, with an unknown area (it is one of four Districts of the Province) and 16,000 inhabitants, there are altogether some 6000 buffaloes, 500 cows and numerous pigs (BEER et al. 1994). According to the District Committee, it is not possible to give a reliable estimate of the number of tigers present in the District. A hundred times every year people of the District address the national

Table 1. Village reports on tiger visits

Village	Frequency	Observations	Livestock lost
Dakchun (Noy)	now and then	yes	
Ngondon	?	1973 (killed)	
Dakbong	monthly	rarely seen; many traces	considerable
Kun Sei	many attacks	many traces	buffaloes, pigs
Dakdan	5 in 1993	traces, no animals	5 buffaloes in 1993
Sang	regularly	seen once	buffaloes, pigs
Tan Talang	not often	none	few buffaloes
Rak	9 in 1993	17 Dec. 1993	9 (out of 30) buffaloes in 1993
Daklu	1 or 2 times per month	?	every month; Nov. 1993: 2 buffaloes
Tangiung	4–6 times per year	not after 1979	buffaloes every 2–3 months
Prau Niai	2–3 times per year	?	2 or 3 animals per year
Kaleum town	5 or 6 per year	?	1961 and 1963: human victims
Loy-Nua	a few times every year	?	some animals every year
Dakling	many times per year	?	many animals
Vak-Nua	?	?	?
Tjrok	not many around	?	pigs
Napong	very rare; 1 or 2 per year	1993	2 buffaloes in 1993
Huay Tjuang	?	?	1993: 11 cows, 5 pigs
Huay Sali	rare; seen in villages nearby	1 on 5–6 February '94	none since 4 year, but some pigs in villages nearby
No Kieng	sometimes	c. 5 February '94	salt licks
Nam Sip	?	?	in 1993 4 buffaloes
Muangngeun	not often	traces	yes

authorities with the request for permission to kill a tiger because of attacks on buffaloes or other livestock. In 7 or 8 cases every year, this permission is granted. As in Laos the tiger is a protected species (see SALTER 1993; BEER et al. 1994), a killed tiger becomes the property of the state, and skin and bones are handed over to the authorities, while the hunter receives 20% of the revenues. Only in Dakling, the villagers protected their buffaloes at night by putting them in enclosures next to the village, using salt as a lure. These enclosures were said to be effective.

The village reports are quite variable. Some data on the frequency of attacks on domestic animals are given in table 1. People connect these frequencies to the tiger's habits of covering large areas. In some cases single tigers were held responsable for attacks on the livestock of 5 or 6 villages in a given area, in others the villagers thought that they were dealing with a group of tigers. The attitude of the people vis-à-vis the tiger was generally quite tolerant. It was obvious that the regional presence of the species did not cause anything like fear in any of the villages. It should be kept in mind, however, that the tiger is a protected species and that we may not have been told the entire story. SALTER (1993) stated that tigers in Laos "are probably shot whenever opportunity permits".

The species is believed to move very cautiously, and is seldom seen or heard. People often assumed that tigers do not harm humans, and avoid direct confrontation whenever possible. According to the people at Tangiung, it prefers to hunt in silent, isolated places. On the other hand, we were told that tigers may approach or even enter villages (Dakbong, Kun Sei, Kaleum town, Loy-Nua, Napong, Huay Tjuang). Mr. KHEN SON, Head of Agriculture and Forestry of Kaleum District reported three cases of tigers killing people, including his uncle, in 1961 and 1963. The only other report of an accident was received from Mr. KHAMPHONE MOKMUANGSAM, Head of Agriculture and Forestry in Attapeu Province. In 1979 two travellers in the Province (precise locality not noted) had been attacked by a tiger, one of which had been eaten. The tiger in question may still be alive. DEUVE (1972) remarked that in Laos tigers rarely attack people, and that in some of these rare cases the tigers must have taken people for deer.

According to most reports, tiger attacks on livestock occur after dark. At Tangiung the people thought that the tiger prefers clear, moonlit nights to hunt. At No Kieng near Huay Sali, on the border between Hongsa Special Zone and Sayaboury Province, tigers come to salt licks (to locate prey?) preferably during waning moon. However, near Huay Tjuang in 1993 a tiger attacked cows on their daily walk to the village, between 14 and 18 h p.m., three times in that year. This tiger may have killed up to 4 cows per attack. In 1993, also during daylight, children of Loy-Nua discovered a tiger near their village which had seized a deer. They started screaming and chased the tiger away, after which adult villagers collected the deer.

To get rid of a tiger which has developed a taste for livestock, it may be chased away or killed. At one village, it was believed that tigers can not be killed, only chased away. On 17. 12. 1993 the villagers there trapped the tiger which had killed many buffaloes in 1993, and hit it four times with javelins before, severely injured, it could escape. To kill a tiger, it can either be shot or trapped and killed afterwards. We were told that the tiger normally comes back to its prey the night after the attack, which allows hunters to find it. However, in Daklu the people told us that tigers do not eat much, and in Tangiung tigers were believed never to return at all when man had set traps near their prey. In Napong a man told us that a tiger would jump on a buffalo's neck and not kill it at once but take it to the place where he intends to eat it.

The tiger has given rise to some mythological beliefs in Laos. In Dakchun (Noy) we were told that there is a secret society of people who are befriended with tigers and maintain telepathic relations with them. The tiger also enjoys the protection of the forest spirits. When the injured tiger mentioned in the preceding lines fled into the forest, followed by its hunters, a large dead forest tree fell down. This was taken as a warning from the forest spirit, and the hunters returned home.

Some man-meets-tiger stories were rather fantastic. They can hardly be meant to be taken literally and probably contain some hidden meaning, like a wish to appear exceptionally brave, or a wish to be associated with the powerful tiger. In Napong, a man who lost two buffaloes to a tiger in 1993, related two such stories. In the first, a tiger enters the village to seize one of the pigs under the house of the speaker, who is in the house and on hearing an unusual sound jumps from the window, to land on the fleeing tiger which, pig in mouth and man on back, runs a few hundred meters before releasing the pig. In the second, a tiger chases a dog owned by the same man, the dog flees to its owner inside his house, the tiger enters the house, is frightened and jumps from the window and flees.

Order Cetacea

Orcaella brevirostris (Gray, 1866)
According to Forestry Officers in Sekong town two Irrawaddy dolphins were shot in the Sekong River near the town in 1990. The local people love the dolphins and normally do not hunt them.

Order Proboscidea

Elephas maximus Linnaeus, 1758
Most reports on the Asian elephant are negative and connect its disappearance with the war. During the war, elephant herds (and other large mammals) have been taken for military troops and bombed. During and after the war modern fire-arms were widely distributed and increasingly used for hunting. The following villages in Sekong Province reported its disappearance: Daklan; Dakchun (Noy), elephants last seen near the village in 1964; Ngondon; Sang; Tangiung (the last 5 to 6 killed in the early 1970s); Dakling, none seen since the war; Vak Nua, none seen since 1960; Tjrok, none seen since 1960. According to the Kaleum District Committee the species has been decimated during the war but does still occur in the district, where they move between the district and Saravane Province. The only village in the district reporting the presence of elephants was Loy-Nua. In Attapeu Province we were told there are still many elephants. In Hongsa Special Zone the species had disappeared from Napong since the war, from Ban Sali since 1973, from Nam Sang near Nam Sip, and from the Muangngeun District. In Ban Sali the people blamed both the war and hunters. Wild elephants kill tame elephants, thus wild elephants are being hunted.

Order Artiodactyla

Sus scrofa Linnaeus, 1758
Nearly all the villages where interviews were held reported on large numbers of wild boars visiting during the rice and maize harvests and causing considerable damage. Palisades are hardly effective and so are the villagers who try to chase them away or hunt them. At best, one or two specimens from the raiding dozens to hundreds are shot. Very large solitary specimens are also known. The species was considered dangerous. Near Daklan it had recently killed a hunting dog. In Kaleum District, Sekong Province, wild boars destroyed the wild stands of the medicinal plant *Smilax glabra*. In Hongsa Special Zone, wild boars from Oudomsay Province cross the Mekong River at night to visit the forests in October/November, when the wild nuts are ripe. A skull was observed at Pah Oh in Sekong Province, and two mandibles were obtained at Kiugniu in Hongsa Special Zone (ZMA 24.700/01).

Tragulus javanicus (Osbeck, 1765)
Two specimens of the lesser Malay mouse-deer were seen in a roadside stall in Vientiane on 25. 1. 1994. They had been trapped at Lak, a village 52 km from Vientiane in the direction of Luangprabang. Another specimen was seen in the market of Hongsa town on 3. 2. 1994.

Cervus unicolor Kerr, 1792
The sambar was reported in nearly all the village interviews. Near villages where hunting was an obvious occupation it tends to become rare. Trophies were seen in many houses and offices. Live specimens were seen in Dakchun (Noy), confiscated by the police at Dakmong on c. 25. 12. 1993, and in the enclosed compound of a house at Attapeu town on 10. 1. 1994. In the market of Sekong a live specimen was offered secretly for sale on 23. 1. 1994. The sale being unlawful, the animal was kept in another place. Reports on the species being harmful to crops were received only in the villages of Loy-Nua and Tjrok in Sekong Province. Elsewhere, its appearance in a cultivation seemed to be welcomed, as an excuse for hunting. In Huay Sali in Hongsa Special Zone, the people emphasized the damage it would cause to protected forests. In Huay Tjuang people told that the marketing of antlers had been an important activity. At present, fish trade has taken its place as such.

Muntiacus muntjak (Zimmermann, 1780)
The Indian muntjac or barking deer was reported in nearly all the village interviews, and appears to be an important item in the rural diet. Trophies of muntjacs are very common. A skull of an animal shot in 1993 at Phu Tjé was obtained at Tangiung and trophies at Dakchun (Noy), also in Sekong Province, and at Huay Sali in Hongsa Special Zone (ZMA 24.799/801). Near Dakdan and Tan Talang, the species had become rare, but elsewhere it was said to abound. Only in Loy-Nua and Vak-Nua in Sekong Province people reported on muntjac damage to rice crops. In Dakchun (Noy), Sekong Province, as well as Huang Tjuay, Hongsa Special Zone, we were told that when a person is preparing a field for planting (by burning the vegetation) and hears the cry of a muntjac, he or she has to quit that field and start anew in another site. In Huang Tjuay people added that this applies only to the first day of preparing, and that the sighting of a snake has the same meaning.

Bos sauveli Urbain, 1937
In only one village we received a report on this species. The 83-year-old chief of Ngondon remembered that there had been a herd of 3 to 4 kouprey in the forest near the village but the species had long disappeared. According to Mr. KHAMPHONE MOKMUANGSAM, Head of Agriculture and Forestry in Attapeu Province, there are sightings now and then of 1 or 2 kouprey in the western part of his province ("Il y en a assez."), but SALTER's (1993) account suggests that none of these sightings have been confirmed so far.

Bos gaurus Smith, 1827
In Sekong Province, the gaur used to occur but has disappeared near Daklan and Ngondon. Some other villages denied its presence: Dakchun (Noy), Dakdan, and Daklu. According to the Kaleum District Committee, a small group of gaur is seen two or three times a year. This was confirmed by reports in Loy-Nua and Tjrok, where the species still occurs. Near Tjrok one specimen out of a group of four or five was accidentally killed six years ago. The people told us that it was very difficult to observe the species. In Hongsa Special Zone, the species had disappeared near Napong and Huay Sali 20 to 30 years ago. However, near Huay Sali, where Mong hunters were blamed to still hunt the species, traces had been seen at Lake Nam Sang near Phu Pha Dai (or Padai?) some months ago.

Near Nam Sip, four specimens had been seen in early January 1994. The villagers of Nam Sip believe that gaur are protected by the spirit of the forest. When one kills a gaur, one may die, except the Mong. They mentioned Lake Nam Sang, as a place where in old times there were many gaur.

Nemorhaedus sumatraensis (Bechstein, 1799)
All serow/goral-like animals reported to us have been identified as this species. Parts of some butchered specimens and many trophies, some including large parts of the skull, have been seen, and several villages provided descriptions, all representing or indicating the larger southern serow and not the smaller Chinese goral, *Nemorhaedus caudatus* (Milne-Edwards, 1867).

The southern serow is found near Daklan, Tan Talang (where the local population was estimated at 12 specimens), on Phu Kongkling Gnai, near Tangiung, Prau Niai, and between Loy-Nua and Tjrok in Sekong Province. It has disappeared from Ngondon. In Hongsa Special Zone it was reported from Phu Kon Wa near Huay Tjuang, Phu Pahin near Huay Sali, and near Nam Sip. One trophy adorning a shop in Dakchun (Noy) but originating from near Daklan was obtained from the shopkeeper (ZMA 24.805).

Despite its legal protection, the species is still heavily hunted in several places. In one village in Sekong Province the remnants of two freshly killed specimens were seen and the same hunters had shot about 20 specimens in 1993 alone. In Tangiung, the people emphasized that they no longer hunted the southern serow, and in Nam Sip they claimed that numbers were increasing since the legal protection.

Southern serow horns can be found everywhere as trophies. They are also used for medicinal purposes, both in Laos and in surrounding countries. They were offered for sale in some villages, in the market of Sekong town (5 specimens on 23. 1. 1994) and in the Morning Market of Vientiane (many specimens on 27. 1. 1994). All were said to have been shot before the legal protection of the species.

In the cave Than Nyeung in Phu Pahin, a mountain near Huay Sali, female Southern serow are believed to gather to bear their young. The mountain is protected and people are not allowed to enter the cave.

Pseudoryx nghetinhensis Vu Van Dung, Pham Mong Giao, Nguyen Ngoc Chinh, Do Tuoc, Arctander and MacKinnon, 1993
Sekong Province being an unknown region it seemed worthwhile to show pictures of this species (the ones published with the original description by Vu Van Dung et al. 1993) during our village interviews in the mountainous east. The species is apparently unknown here. Schaller and Rabinowitz (1995), who recorded the species' occurrence in Laos, made it plausible that its southern limit is far north of Sekong Province.

Order Rodentia

Ratufa bicolor (Sparrman, 1778)
A tail of the black giant squirrel was seen and photographed at Ayun and two skulls of specimens killed in December 1993 at Phu Tjé were obtained at Tangiung (ZMA 24.727/28).

Callosciurus erythraeus (Pallas, 1779)
A ♂ of Pallas's squirrel was offered for sale in Dakchun (Noy) on 8. 12. 1993. A picture was taken of the whole animal, and the skull could be preserved (ZMA 24.720; TL: 475/420, T: 255/200, HF: 51.8, E: 23.7).

Callosciurus finlaysoni (Horsfield, 1823)
A ♂ of the variable squirrel was obtained from a road stall in Vientiane on 25. 1. 1994. It had been killed near Ban Lak, a village 52 km from Vientiane along the road to Luang-

prabang. The specimen represents the reddish brown variety with the underside considerably darker than the upperside. Its skull and skin were preserved; its tail plume is missing (ZMA 24.721; TL: 473, T: 235, HF: 57.0, E: 23.4, W: 331; testes small). Another ♂ was bought in the market of Hongsa town on 11. 2. 1994. It had been killed near that town. It represents the variety with full reddish brown upper and under parts and greyish flanks. Its skin and skull were preserved (ZMA 24.722; TL: 533/448, T: 303/218, HF: 55.4, E: 22.0, W: 295).

Callosciurus inornatus (Gray, 1867)
One ♂ of this squirrel was bought at a road stall in Vientiane on 25. 1. 1994. It had been shot near Ban Lak (see preceding species). Its skin and skull were preserved (ZMA 24.723; TL: 450/404, T: 235/189, HF: 47.4, E: 20.0, W: 260; testes: 15.3×9.1, in scrotum).

Tamiops mcclellandii (Horsfield, 1840)
One adult ♂, 1 adult ♀ and 1 probably subadult ♀ of the Himalayan striped squirrel were obtained in the market of Hongsa town on 7. February. They had been killed near that town, and are preserved in alcohol (ZMA 24.733/35; ♂, ♀, ♀: TL: 255/228, 244/209, 245/218, T: 134/107, 136/101, 134/107, HF: 28.2, 27.7, 27.8, E: 12.8, –, 11.3, W: c. 40, 40, 42). The species' presence near Hongsa is in line with its known distribution (Moore and Tate 1965).

Tamiops rodolphii (Milne-Edwards, 1867)
One of two specimens of the Kampuchean striped squirrel trapped near Dakbong, Sekong Province on 14. December, a probably full-grown ♂, was obtained. It was photographed and preserved in alcohol (ZMA 24.732; TL: 250/220, T: 130/110, HF: 27, E: 13). Moore and Tate (1965) mentioned as nearest localities for this species the Boloven Plateau in Laos and Quangtri Phuoc Mon in Vietnam (107° 10′ E, 16° 35′ N).

Tamiops maritimus (Bonhote, 1900)
One adult ♂ and two adult ♀♀ of this species were bought in the market of Sekong town, near which they had been killed, on 11. 1. 1994. They were preserved in alcohol (ZMA 24.729/31; W: 64, 61, 59). Records of this species from southern Laos are scant, Saravane being the only one mentioned by Moore and Tate (1965).

Dremomys rufigenis (Blanford, 1878)
In Dakchun (Noy), Sekong Province, a ♂ of the red-cheeked squirrel taken near that village was eaten on 8. 12. 1993. The specimen was photographed and its skull secured (ZMA 24.725; TL: 390/350, T: 185/145, HF: 45.3, E: 21.0). Another ♂, killed near Hongsa town, was obtained in the market there on 11. 2. 1994. Its skin and skull were preserved (ZMA 24.726; TL: 404/368, T: 217/181, HF: 50.0, E: 21.0, W: 240).

Menetes berdmorei (Blyth, 1849)
A subadult ♂ of the Indochinese ground squirrel was bought in the market of Hongsa town on 1. 2. 1994. It had been killed near that town and is preserved as ZMA 24.724 (TL: 345/313, T: 175/143, HF: 43.6, E: 19.1, W: 168).

Petaurista philippensis (Elliot, 1839)
A ♂ and a ♀ of this flying squirrel, shot at Huay Vie, a river crossing the road to Dakchun (Noy) 10 km from Sekong town, were offered for sale in the market of Sekong town on 23. 1. 1994. The ♀ was secured and its skin and skull preserved (ZMA 24.736; TL: 105.5/100.7, T: 64.0/59.2, HF: 83.5, E: 44.9, W: 1975).

Mus caroli Bonhote, 1902
Many specimens of this mouse were trapped by children in Dakchun (Noy) on 1. 1. 1994. Eight were preserved in alcohol (ZMA 24.818/25). The species is called nu seeng or nu gee (but it is not sure that these names apply only to this species), and in the Dakchun District it is considered the most serious pest in rice fields.

Rattus nitidus (Hodgson, 1845)
The Himalayan rat is common and often trapped for consumption in the villages in the mountains in eastern Sekong Province. The species is frequently called nu dam (black rat). It often lives commensal with man but is also considered a serious pest in the rice fields. Specimens were obtained in Tan Talung (19. 12. 1993), Tangiung (28. 12. 1993) and Dakchun (Noy) (24. 12. 1993, 1. and 4. 1. 1994) (ZMA 24.746/49, 24.868/74). The black rat was furthermore reported at Dakbol, Prau Niai, Tjrok, all in Sekong Province. Some measurements of adult specimens (a ♂ from Tan Talang and a ♂ and a ♀ from Dakchun) are: TL: 375, 352, 360, T: 180, 164, 172, HF: 41, 39, 38, E: –, 21, 21.7, W: –, 168, 240. The Tan Talang ♂ had large descended testes. In Napong and Huay Sali in Hongsa Special Zone people also mentioned black rats but no specimens were available. This may refer to or include the same species (maps in Lekagul and McNeely 1988; Corbet and Hill 1992).

Bandicota indica (Bechstein, 1800)
Large bandicoot-rats are frequently trapped and consumed or offered for sale in markets. A ♂ from Phu Lak (near Ban Lak, 52 km from Vientiane along the road to Luangprabang), was bought at a roadside stall in Vientiane on 26. 1. 1994 (TL: 432, T: 204, HF: 50, E: 29.9. W: 378. Testes small.) Other specimens were seen at the same stall and in the market of Hongsa town.

Niviventer langbianus (Robinson and Kloss, 1922)
On 2. 1. 1994 an immature ♀ of this rat was caught in a rice field at Dakchun (Noy) (ZMA 24.796; TL: 280, T: 149, HF: 28, E: 17.5, GSL: 33.1, M^1–M^3: 6.0, IOW: 5.5, PL: 16.7, W: 60). On the same day, another immature ♀ was trapped in a rice field at Dakbong (ZMA 24.797; TL: 278, T: 139, HF: 28, E: 19, W: 56). The species is called nu deng (red rat) which name, however, applies to more than one species.

Niviventer cf. *tenaster* (Thomas, 1916)
A ♂ tentatively assigned to this species was collected at Ngondon, Sekong Province on 1. 1. 1994; only the skull could be preserved (ZMA 24.908; TL: 372, T: 212, HF: 34, E: 22, W: 81). Two ♀♀ were obtained on 2. and 3. 1. 1994 at Dakbong, Sekong Province and preserved in alcohol (ZMA 24.905/06; TL: 316/≥286, T: 170/–, HF: 29/32, E: 20/22.5, W: 69/90.5) and a further ♂ was obtained at Dakchun (Noy) on 3. 1. 1994 (ZMA 24.907; TL: 402, T: 228, HF: 33, E: 23, W: 115). All these rats were called nu deng, red rats, and they have been identified as *Niviventer* cf. *tenaster* after consultation with Dr. G. G. Musser, who suggested to await the results of an ongoing revision of the genus for a more definite placement. *Niviventer tenaster* is known from the highlands of Burma and Vietnam but has not previously been recorded from Laos.

Leopoldamys edwardsi (Thomas, 1882)
The genus *Leopoldamys* Ellerman, 1947 is represented in Laos by two species (Musser 1981; Marshall 1988; Corbet and Hill 1992), *edwardsi* and *sabanus*. However, these species are not well defined and in need of taxonomic revision (Musser 1981; Musser and Newcomb 1983). Differences in skull characters or dimensions are not appreciable (Marshall 1988; Musser 1981). Relative tail length, pelage colours, and altitudinal distribution seem to offer some clues. Unfortunately, 3 of our 4 specimens consist of skulls alone. They are assigned to *edwardsi* admittedly on scant grounds only.

Two specimens were presented by the villagers of Tan Talang on 18. 12. 1993. They had been trapped some days previously and were being dried over an open inhouse cooking fire. Their tails were lacking, their pelage was scorched, and their bodies were rotting. Only the skulls could be saved (ZMA 24.744/45). Another skull was obtained at the nearby village of Ayun, from the head of a rat that had been already eaten, on 19. 12. 1993 (ZMA 24.754). Only one of the skulls is of a fully adult specimen (ZMA 24.744; GSL: 59.5). Its dorsal pelage appeared to have been yellowish brown. Although our maps do not indicate these villages, and their exact altitude is not known to me, they are quite high up in a region generally between 1 000 and 2 000 m and potentially harbouring both species (Corbet and Hill 1992). According to Corbet and Hill (1992) *edwardsi* replaces the next species above 1 000 m. This and its presumed fur colour led me to identify this specimen, and the others from this area, as *edwardsi.*

Leopoldamys sabanus (Thomas, 1887)
An adult ♀ of this large long-tailed reddish brown and white rat, trapped at Phu Lak, 52 km from Vientiane along the road to Luangprabang, was bought at a road stall in Vientiane on 26. 1. 1994 (ZMA 24.743). Phu Lak is in a low-lying region (200–500 m). According to the authors mentioned in the above account on *L. edwardsi*, the colours and relative body dimensions (TL: 572, T: 345, HF: 49.0, E: 31.2, W: 321) identify the specimen as *sabanus.*

Maxomys moi (Robinson and Kloss, 1922)
A specimen of this rat was obtained at Ayun on 20. 12. 1994 (ZMA 24.857; TL: 365, T: 185, HF: 37, E: 24, GSL: 42.9, ZW: 19.4, M^1–M^3: 5.8). The species much resembles *M. surifer* (Miller, 1900) which is found all over Laos (Corbet and Hill 1992). *M. moi* and *surifer* show overlap in nearly all measurements, but *moi* differs, among other things, in having "bright, dense and soft pelage as opposed to the duller, spiny pelage of *surifer*" and "usually five plantar pads, as contrasted to six in *surifer*" (Musser et al. 1979).

M. moi is only known from extreme southeastern Laos and adjoining Vietnam (Corbet and Hill 1992; Salter 1993). Salter (1993) suggests that it is found in the – Laotian – triborder area with Kampuchea and Vietnam. If the present specimen is identified correctly, its find extends the known distribution area of the species somewhat further north.

Berylmys bowersii (Anderson, 1879)
A ♂ of this large rat was trapped on the floor of a clear forest near the river Tag, 8 km from Tangiung, Sekong Province, on 28. 12. 1993; its skull and skin were bought from the trapper in Tangiung (ZMA 24.739; TL: 550, T: 285, HF: 58.9, E: ≥32, GSL: 58.0, M^1–M^3 alveoles: 9.2, length diastema: 18.1). The people believed these rats to live in groups and to eat ple non, a kind of nut. But there was no consensus on its Laotian name. It was first called nu wai (rattan rat) but an elderly man said it was nu ploi, and that the rattan rat was still larger. A second ♂ was bought at Dakchun (Noy), also in Sekong Province; it had been trapped at Dakwang, at about 5 km south of Dakchung (Noy) on 4. 1. 1994 (skin and skull: ZMA 24.740; TL: 542, T: 274, HF: 58, E: 33.7, W: 449). These records are the first for southern Laos. They are about halfway the distribution of the genus in North Laos and that in South Vietnam as given by Musser and Newcomb (1983).

Rhizomys sumatrensis (Raffles, 1821)
A skull trophy of the large bamboo rat was obtained at Pah Oh, a village along the road between Sekong town and Dakchung (Noy) on 5. 1. 1994 (ZMA 24.706). It had been taken on 31.12.1993 in an open forest nearby. The species is locally known to eat bamboo and said to be able to destroy whole bushes of it. Another skull was obtained at Vak-Nua on 17. 1. 1994 (ZMA 24.708). The ♂ of a couple taken on 20. 1. 1994 at Davee, a village

on the Lampan river, about a three-hour walk from Sekong town in the direction of Attapeu, was bought in the Sekong town market (ZMA 24.707; TL 520, T 133, HF 68.9, E 23.6, testes 26×16.5). The Laotian name for the large bamboo rat is nu on. The misleading French name in use in Laos for rodents of this type (including the following species) is taupe, in fact the name for insectivorous mammals of the genus *Talpa* Linnaeus, 1758.

Cannomys badius (Hodgson, 1841)
A skull of a specimen dug up at Phu Tjé near Tangiung in July 1993 was obtained at Tangiung (ZMA 24.705). According to the map in Corbet and Hill (1992) this would be the first record for South Laos. An adult ♀ and a juvenile of the lesser bamboo rat were obtained in the forest between Nam Ken and Kiugniu, in Hongsa Special Zone, on 4. 2. 1994 (ZMA 24.703/04; measurements of the adult ♀: TL: 293, T: 69, HF: 35.6, E: 10.7). Live specimens were seen in the Hongsa town market: 9 specimens on 7., 5. on 8., and 4 on 14. 2. 1994. The Laotian name for this species is tun.

Hystrix brachyura Linnaeus, 1758
A damaged skull of this porcupine, caught in 1993 near Ayun, was obtained on 20. 12. 1994 (ZMA 24.710 a). Quills of another specimen were seen at Dakchun (Noy) where they were used in weaving. The species was further reported from Sang, Daklu, Tangiung, and Tjrok in Sekong Province, and from Huay Sali and Nam Sip in Hongsa Special Zone. (In Rak, Prau Niai and Loy-Nua porcupines were known to occur but not specified.) In several villages, people reported that this species, called men, lives in self-dug holes in the forest.

Atherurus macrourus (Linnaeus, 1758)
A head of this species was bought from a hunter who had caught it near Ayun (ZMA 24.709). It was reported in the villages of Dakdan, Sang, Tangiung, and Tjrok in Sekong Province and in Huay Sali and Nam Sip in Hongsa Special Zone. In Sang the species is called to hon. Here and in other villages we were told that the Asiatic brush-tailed porcupine lives in caves, in groups of up to 20 specimens. It eats manioc and gnaws at palisades.

Order Lagomorpha

Lepus peguensis Blyth, 1856
A skull, a mandible and a half mandible of the Burmese hare were obtained at Ayun, all from near that village and caught in 1993 (ZMA 24.802/04). The hunter told us that this species had not always been there. He had seen it since a few years only but emphasized also that it was difficult to observe. It is possible that the species is in the process of spreading into cleared forest areas via cultivated valleys etc.

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Zusammmenfassung

Über Säugetiere aus der Demokratischen Volksrepublik Laos, hauptsächlich der Sekong Provinz und der Hongsa Sonderzone

Säugetiere aus der Demokratischen Volksrepublik Laos, hauptsächlich der Sekong Provinz und der Hongsa Sonderzone wurden im Winter 1993/94 während eines kurzen Aufenthalts in Laos gesammelt. Die meisten Angaben stammen aus der unbekannten südlichen Sekong Provinz und der nordwestlichen Hongsa Sonderzone. Viele Fundorte sind neu für die Wissenschaft und vermehren unsere Kenntnis von der Verbreitung der Arten. Besonders interessant sind *Megaerops niphanae* und *Taphozous saccolaimus*, die zum ersten Mal aus Laos gemeldet werden; einige neue Fundorte von *Pygathrix nemaeus*; zwei neue Funde von *Prionodon pardicolor*; Berichte über *Panthera tigris* und *Nemorhaedus sumatraensis*; und Funde von *Leopoldamys edwardsi* und *L. sabanus*, *Maxomys moi*, *Berylmys bowersii* (neu für die Sekong Provinz) und *Niviventer* cf. *tenaster* (neu für Laos).

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Weitere Ausbreitung des Goldschakals *Canis aureus* L., 1758 in Österreich

Von K. Bauer und F. Suchentrunk

Säugetiersammlung des Naturhistorischen Museums Wien und Forschungsinstitut für Wildtierkunde und Ökologie der Veterinärmedizinischen Universität Wien

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Bis in die 1960er-Jahre war der Goldschakal *Canis aureus* in Europa auf kleine Reliktareale zwischen Nordkaukasus und Kaspischem Meer (nordwärts etwa bis zum Terek) und auf der südlichen Balkanhalbinsel (nordwärts bis SO-Bulgarien, Nord-Mazedonien und Süddalmatien) beschränkt. Nur seltene Irrläufer gelangten zu Ende des 19. und im 20. Jahrhundert nordwärts bis an das Asowsche Meer und in die Große Ungarische Tiefebene. Das nördlichste Vorkommen ist für die „Große Schüttinsel", südöstlich von Bratislava (Slowakische Republik) etwa Mitte dieses Jahrhunderts dokumentiert (Feriancová-Masárová und Hanák 1964). Die verbliebenen Populationen waren meist klein und schienen manchenorts vom Erlöschen bedroht. Nur in Dalmatien gab es etwa ab 1920 einen Vorstoß, der zu dauerhafter Besiedlung Norddalmatiens führte. Um 1970 begann sich die Situation großräumig zu ändern. Auch andere Bestände nahmen wieder zu, und die Art begann sich auszubreiten. Ihr europäisches Areal reicht heute östlich der Balkangebirge durch alle Niederungsgebiete Bulgariens nordwärts bis in die Moldau-Republik und die rumänische Dobrudscha und westlich davon bis Serbien, Binnenland-Kroatien und (seit 1980) Istrien. Als unregelmäßige Wandergäste erschienen Schakale seit den späten 1980er-Jahren in Slowenien, Friaul/NO-Italien, Österreich und (neuerlich) in Ungarn (Demeter und Spassow 1993). Die Ursachen dieser Entwicklung sind vielfältig und beginnen möglicherweise bei weiträumiger Eutrophierung der Agrarlandschaften, wachsendem Wohlstand und ausuferndem Tourismus. Ein ganz entscheidender Faktor ist die weitgehende Ausrottung des Wolfs *Canis lupus*, die dem Schakal nicht nur neue, konkurrenzfreie Räume erschlossen, sondern auch die Überwindung der die Restareale umgrenzenden Gebirge erst möglich gemacht hat (Krystufek und Tvrtkovic 1989, 1990). Die Vorstöße erreichen gegenwärtig Gebiete, in denen die Art vorher noch nie nachgewiesen wurde, Slowenien, Friaul und Österreich.

Über die ersten Feststellungen in Österreich haben Hoi-Leitner und Kraus (1989) berichtet. Um darauf aufmerksam zu machen, daß es nur noch eine Frage der Zeit zu sein scheint, bis der erste Schakal die Bundesrepublik Deutschland erreicht, scheint es wünschenswert, dieses in den Vorarbeiten für eine österreichische Säugetierfauna (Mammalia Austriaca 14) präsentierte Bild auf den neuesten Stand zu bringen.

Vorausschickend sei ergänzt, daß ein von Hoi-Leitner und Kraus (1989) genanntes Belegstück aus Preitenegg an der Koralpe auf der Karte fehlt und in der Dokumentation durch ein Versehen beim Umbruch für Niederösterreich genannt wird. Es handelt sich dabei um den ersten und bisher einzigen Nachweis aus Kärnten. Den 4 von Hoi-Leitner und Kraus (1989) aufgeführten Belegstücken können mittlerweile 4 weitere angeschlossen werden. Außerdem liegen noch zwei glaubhafte Sichtbeobachtungen vor. Die Art wird nach wie vor nur selten richtig erkannt. Eine von Demeter und Spassow (1993) zitierte anonyme Meldung für die Steiermark z. B. bezieht sich auf den ersten im Gebiet erlegten Rotfuchs *Vulpes vulpes* vom Samson-Typ, der wegen seines fremdartigen Aussehens sogar von Fachleuten nicht als Fuchs erkannt wurde, und im ersten oberösterreichischen Belegstück vermuteten Jäger und Zoologen wechselweise einen Wolf oder Coyoten! Alle nachstehend genannten Stücke wurden von uns frisch und/oder im Präparat untersucht, vermessen und mit dem Sammlungsmaterial des Naturhistorischen Museums Wien verglichen. Der Reiz einer „exotischen“ Trophäe ist leider so groß, daß es nur ausnahmsweise gelingt, vollständige Belege für eine öffentliche Sammlung sicherzustellen. Immerhin gelang es, ein von der Gendarmerie geborgenes Verkehrsopfer in das Oberösterreichische Landesmuseum zu übernehmen, und dank dem Verständnis von Eigentümer und Präparatoren konnten zwei weitere Schädel vor dem Einbau in Stopfpräparate bewahrt werden. Neben je einem weiteren Beleg aus Steiermark und Niederösterreich liegen mittlerweile die ersten Nachweise aus Oberösterreich und Salzburg vor (Abb. 1):

1. 48°19′N/14°14′E, 280 m ü. M., Puchenau, PB Urfahr-Umgebung, Oberösterreich. 1 ♂, Verkehrsopfer 18. Januar 1990, Schädel und Dermoplastik im Oberösterreichischen Landesmuseum Linz (Aubrecht 1991).
2. 47°11′N/14°15′E, 880 m ü. M., Winklern bei Oberwölz, PB Murau, Steiermark. 1 ♂, Fallenfang Anfang Februar 1992. Schädel am Forschungsinstitut für Wildtierkunde und Ökologie (FIWI) (Nr. 47/54/92).
3. 48°33′N/15°12′E, 680 m ü. M., Rohrenreith, Gem. Großweißenbach, PB Zwettl, Niederösterreich, 1 ♂, erlegt 20. August 1992. Schädel in der Sammlung des Naturhistorischen Museums Wien (NMW 42 753), Dermoplastik im Besitz des Erlegers W. Lukschuh/Wr. Neustadt (vgl. Anonymus 1993).
4. 47°05′N/13°10′E, 1 000 m ü. M., Paßau am Fuß des Graukogel, Badgastein, PB St. Johann im Pongau, Salzburg. 1 ♂, erlegt 18. Dezember 1992. Schädel (nach Untersuchung am FIWI) als Teil eines Stopfpräparates im Besitz des Erlegers A. Brandtner/Badgastein (vgl. Anonymus 1993).
5. 48°17′N/14°40′E, Asching bei Windhaag (PB Perg), 1 Exempl. unbekannten Geschl., erlegt, Stopfpräp. u. Schädel im Besitz v. F. Fürholzer, Asching; Foto in Zedrosser (1995).
6. 46°57′N/15°51′E, 286 m ü. M., Unterweißenbach, Gniebing-Weißenbach, PB Feldbach, Steiermark, nächtliche Beobachtung von A. Decker aus dem Auto, Oktober 1991.

Alle bisherigen Stücke sind Rüden. Hervorzuheben ist, daß sich das Auftreten keineswegs auf Gunstlagen in den submediterran beeinflußten illyrischen und pannonischen Klimagebieten Österreichs beschränkt. Von den bisher 8 Nachweisen kommen zwei aus eher rauhen am Nördlichen Granitplateau, zwei aus dem montanen Bereich der Koralpe und weitere zwei aus zentralen Alpentälern. Besonders unerwartet ist die Feststellung im kaum von Süden her erreichbaren Gasteinertal. Auch die im Hochwinter erbeuteten Stücke waren in bestem körperlichem Zustand (und mit dichtem, lebhaft goldrotem Fell auch sehr schöne Tiere). Eine klimatische Ausbreitungsgrenze hat *C. aureus* in Mitteleuropa demnach wohl noch nicht erreicht.

Alle bisherigen Nachweise sind Zufallserfolge. In keinem Falle wurde die Art vor Fang oder Erlegung beobachtet oder gespürt. Zwei unserer 8 Funde deuten an, daß Verkehrsopfer kritische Prüfung verdienen. Die von Demeter und Spassov (1993) herausgestellte teilweise Verschmelzung der vorderen und hinteren Zehenballen 3 und 4 tritt keineswegs regelmäßig auf, ist auch nicht artspezifisch und hilft nach unseren Beobachtungen bei der Bestimmung kaum. Das beste Einzelmerkmal vor allem an nicht oder unvollkommen meßbaren Schädeln ist das sehr markant ausgebildete buccale Zingulum von M^{1-2}, das bei Wolf und Hund fehlt oder kaum angedeutet ist (beim Fuchs allerdings ebenfalls vorkommt!). Korrekt abgebildet ist dieses bei Miller (1912).

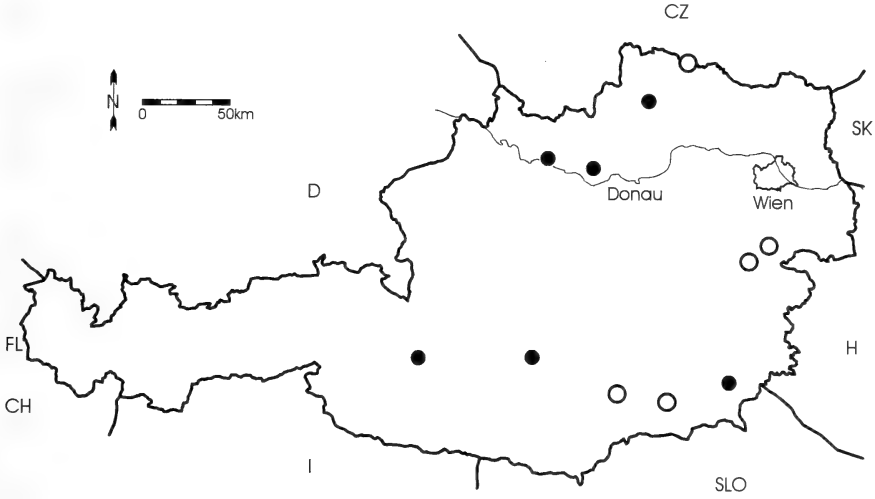

Abb. 1. Vorkommen des Goldschakals in Österreich. Schwarze Kreise: gegenwärtig dokumentierte Nachweise; weiße Kreise: in Hoi-Leitner und Kraus (1989) dokumentierte Belege.

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Unterwasserlaute bei Riesenottern (*Pteronura brasiliensis*)

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Eingang des Ms. 08. 03. 1995
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Die südamerikanischen Riesenotter (*Pteronura brasiliensis*) sind die größten Fischotter der Welt. Sie leben in hochentwickelten Familienverbänden und verständigen sich durch mehrere Laute (Duplaix 1980; Schenck und Staib 1994). Es gibt Kontaktlaute, die einen Zusammenhalt der Gruppe beim Schwimmen und Jagen gewährleisten, Kommandorufe zum Aufbruch, die meist vom ranghohen Weibchen abgegeben werden, Verlassenheitsrufe abhanden gekommener Tiere, Bettelrufe von Jungtieren und Warnlaute, mit denen Gruppenmitglieder alarmiert und Eindringlinge vertrieben werden. Bisher war nicht bekannt, ob Riesenotter auch unter Wasser miteinander kommunizieren. In Carl Hagenbecks Tierpark in Hamburg bot sich die Gelegenheit an dem dort gehaltenen Riesenotterpaar eine erste Untersuchung zur Frage, ob Riesenotter unter Wasser Rufe abgeben, durchzuführen.

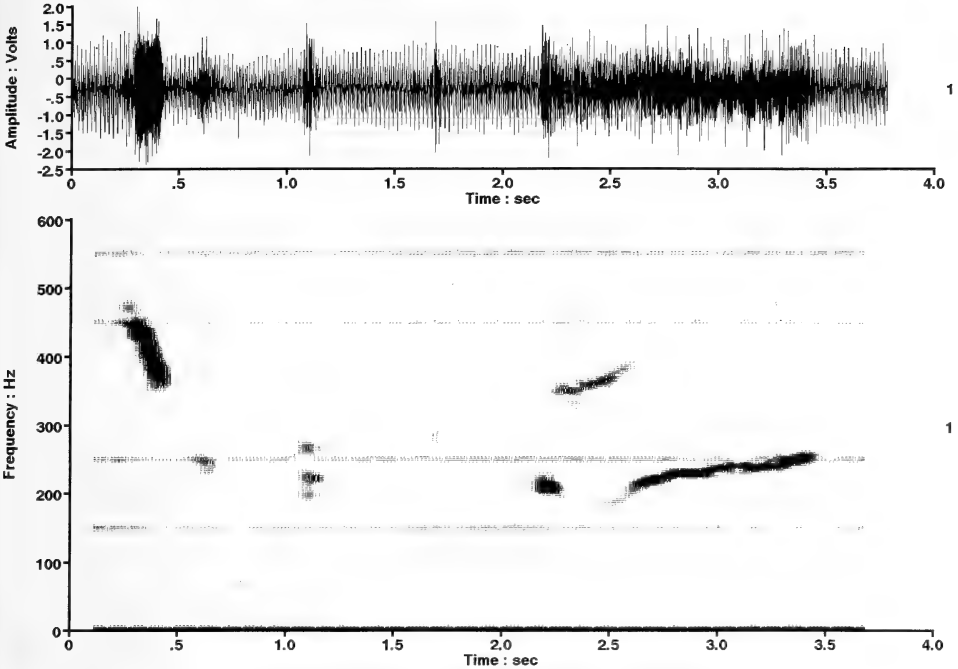
Im Becken des Riesenotterhauses in Carl Hagenbecks Tierpark wurde ein Unterwassermikrophon mit integriertem Vorverstärker (Breitbandhydrophon KE 13 der Firma Allied Signal ELAC Nautik GmbH) installiert. Das Hydrophon wurde in einer Wassertiefe von 0,5 m in der vorderen rechten Ecke des 3 m langen, 2,2 m breiten und 1 m tiefen Beckens befestigt. Zum Schutz vor den Tieren befand sich das Hydrophon in einem 2 m langen PVC-Abflußrohr mit 50 mm Durchmesser. Es wurde in der Höhe der Hydrophonkapsel mit 7-mm-Löchern perforiert. Das Hydrophon wurde im Rohr mit Isolationsschaumstoff gepolstert, um Geräusche durch die Bewegung des Hydrophons und des Kabels zu verhindern. Während der Untersuchung war das Hydrophon an einen Camcorder angeschlossen. Unterwasserlaute wurden auf der Tonspur und das Verhalten der Tiere auf der Videospur zeitgleich aufgenommen.

Das Riesenotterpaar „Ottilie“ und „Kelle“, ein 9jähriges Weibchen und ein 8jähriges Männchen, hatte freien Zugang zum Becken. Die Tiere schwammen während der Aufnahmezeit (24. 3. 1994 von 8.30 Uhr bis 10.00 Uhr und am 29. 3. 1994 von 9.00 Uhr bis 11.00 Uhr) einzeln oder gemeinsam im Wasser.

Die Analyse der Aufzeichnungen fand im Zoologischen Institut und Zoologischen Museum der Universität Hamburg mit den Computerprogrammen RTS 1.2 und SIGNAL 2.2 (Engenering Design 1993) statt.

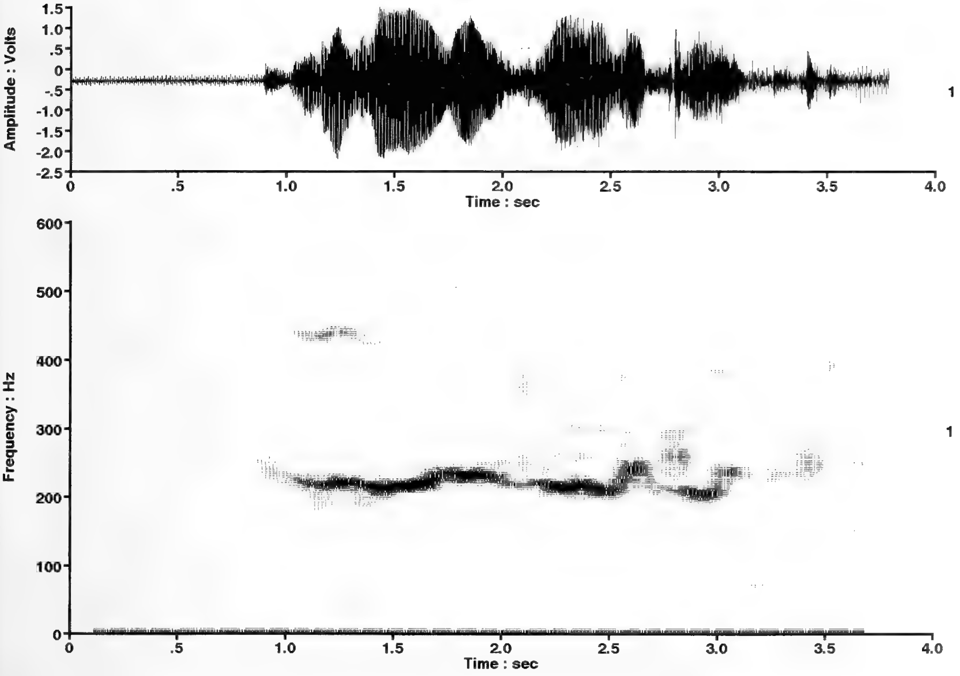
Mit dem Hydrophon wurden Töne aufgezeichnet, die die Tiere sowohl über als auch unter Wasser abgegeben haben. Häufig wurden Laute beim Auftauchen über der Wasseroberfläche ausgestoßen. Mit der gekoppelten Video-Tonaufzeichnung konnte belegt werden, daß sich in sechs Fällen beide Tiere zum Zeitpunkt der Tonaufnahme unter Wasser befanden (Abb. 1 a–c).

Keines der Tiere gab unter Wasser Laute ab, wenn es allein tauchte. Allerdings wurden auch nicht bei jedem gemeinsamen Tauchgang Unterwassertöne ausgestoßen. Auffällig an den Unterwasserlauten ist ihre niedrige Frequenz, die zwischen 200 Hz und 500Hz



DF: 5 Hz DT:204.8 ms T-Inc: 18.9 ms FFT: 512 Wind:HANN
Hi-Filt: OFF Lo:-15 db Hi: -6 db Ampl:LOG Int:MED

Abb. 1 a



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Hi-Filt: OFF Lo:-30 db Hi: -6 db Ampl:LOG Int:MED

Abb. 1 b

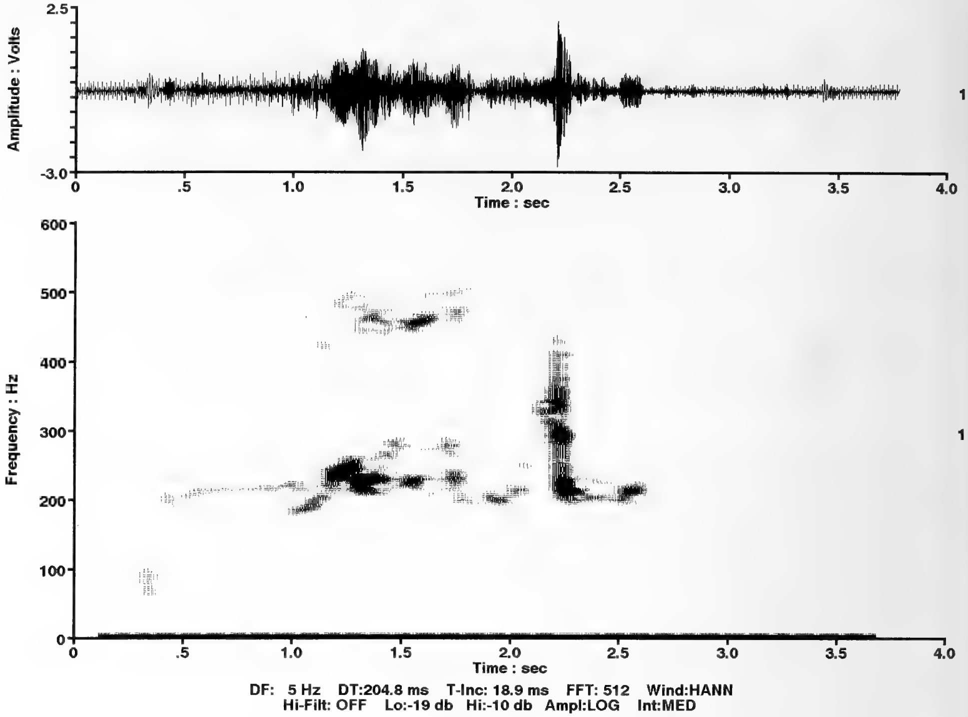

Abb. 1 c

Abb. 1 a–c. Sonagramme der unter Wasser abgegebenen Rufe. Störsignale rühren von einem relativ starken 50 Hz Netzbrummen (als Oktaven in Sonagramm Abb. 1 a zu sehen) und Geräuschen schwappenden Wassers her. a: Der kurze gepreßte Ton (im Sonagramm links) wurde ausgestoßen, als sich beide Tiere unter Wasser befanden. Nach dem Auftauchen stieß das Weibchen an der Wasseroberfläche einen längeren Ruf aus (im Sonagramm rechts); b: Langgestreckter Unterwasserlaut; c: Kurze Rufe unter Wasser mit unterschiedlicher Frequenz.

liegt. Die Laute variieren in ihrer Dauer von wenigen Zehntelsekunden bis zu einer Sekunde.

Die Untersuchung hat gezeigt, daß Riesenotter modulierte, niedrig frequente Laute unter Wasser ausstoßen können, die in der Länge variabel sind.

Riesenotter leben zum Beispiel in Südostperu, einem Gebiet, in dem langjährige Studien an diesen Tieren stattfanden (Schenck und Staib 1994; Staib 1995), in trüben Gewässern. In den Weißwasserflüssen beträgt die Sichttiefe wenige Zentimeter, in den vom Hauptfluß abgetrennten Altarmen, den bevorzugten Aufenthaltsgebieten der Riesenotter, ergaben Messungen mit einer Secchi-Scheibe 16 bis 130 cm. Dort jagen Riesenottergruppen von bis zu zehn Tieren gemeinsam und der Zusammenhalt der Gruppe, selbst bei der Jagd zwischen Schwimmpflanzen und im Sumpfland, ist besonders augenfällig.

In diesen Gewässern kann es den Riesenottern gelingen durch Unterwasserlaute den Gruppenkontakt aufrecht zu halten. Koordinierte Jagd, Schutz der Jungtiere und Alarmierung der Gruppe bei Gefahr kann mit Hilfe von Unterwasserlauten bei aquatisch lebenden Tieren in trüben Gewässern besser erfolgen. Dabei werden niedrig frequente Laute vom Wasser gut übertragen. Auch Fische haben unter den speziellen Bedingungen der Gewässer in den südamerikanischen Tropen vielfältige Lautäußerungen entwickelt, die in Art und Funktion den Paarungsgesängen der Amphibien nahestehen (Schaller 1971).

Die Untersuchungen haben auch gezeigt, daß Laute, die von den Tieren über Wasser abgegeben werden, unter Wasser mit dem Hydrophon aufzuzeichnen sind. Dabei wird möglicherweise der Schall über den Körper der Tiere ins Wasser übertragen. Rufe, die unmittelbar beim Auftauchen über Wasser abgegeben wurden, konnten mit dem Hydrophon besonders deutlich empfangen werden. Dies läßt vermuten, daß die Riesenotter Töne von über Wasser rufenden Gruppenmitgliedern auch unter Wasser hören können. Bei Freilandstudien in Peru konnte oft beobachtet werden, daß einzelne Tiere ohne Unterbrechung laut riefen, während die restliche Gruppe untergetaucht war. Riesenotter sind die einzigen Musteliden, für die die Abgabe von Unterwasserlauten bisher nachgewiesen wurde. Als besonders an das Wasserleben angepaßte Fischotter besitzen Riesenotter damit Fähigkeiten, die nur von Walen und Delphinen bekannt sind (Lewis und Gower 1980; Gewalt 1987).

Danksagung

Die Untersuchungen fanden im Rahmen des Riesenotter-Projekts der Zoologischen Gesellschaft Frankfurt, Hilfe für die bedrohte Tierwelt, und der Wildbiologischen Gesellschaft München e. V. statt. Wir möchten uns bei der Direktion und den Tierpflegern von Carl Hagenbecks Tierpark für die Möglichkeit, die Untersuchungen im Riesenotter-Gehege durchführen zu können, bedanken. Besonderer Dank gebührt auch der Firma Allied Signal ELAC Nautik GmbH, die das Hydrophon für die Untersuchungen zur Verfügung gestellt hat.

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Z. Säugetierkunde **60** (1995) 314–318

Skulls of the Blaauwbok *Hippotragus leucophaeus*

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The recent history of the Blaauwbok, *Hippotragus leucophaeus* (Pallas, 1766), an antelope from the southern tip of Africa which had become extinct by about 1800, was recounted by Mohr (1967), who listed all specimens in museum collections which are plausibly attributable to the species. Klein (1974) attributed subfossil remains, mainly teeth, to *H. leucophaeus*, showing that in the early Holocene it ranged much further east and northwest along the southern African coast. Bosscha Erdbrink (1988) gave notes on the species in the course of discussions on fossil relatives; and Rookmaaker (1992) presented a revised list of specimens attributed to it in the world's museums.

Among the (pathetically few) specimens in collections, there are only two complete skulls: one in the Hunterian Museum, Glasgow (identified as *H. leucophaeus* by the noted palaeontologist Robert Broom in a letter published by Mohr (1967), and one in the Zoological Museum, Amsterdam (identified by Bosscha Erdbrink, 1988). Klein (1974) disputed Mohr's attribution of the Glasgow skull to this species, arguing that it is more probably the skull of the closely related sable antelope, *Hippotragus niger* (Harris, 1838).

The authentication of even one skull of this extinct antelope would be a significant event. We here compare the measurements of the Glasgow and Amsterdam skulls with those of numerous specimens of the two congeneric species.

One of us (CPG) measured specimens in European museums of the two living species of the genus *Hippotragus*: the sable antelope, *H. niger* (Harris, 1838) and the roan antelope, *H. equinus* (Desmarest, 1804). The intended study of geographic variation in these two wide-ranging species has up to now been somewhat delayed; so far only one publication has resulted (Groves 1983).

The measurements taken were as follows:

Greatest skull length; condylobasal length; biorbital width (widest, i. e., on lower orbital rims); maxillary toothrow length (alveolar); maxillary premolar row length (alveolar); mandibular toothrow length (alveolar); mandibular premolar row length (alveolar); length of orbital rim occupied by lacrimal bone; width across horn bases; width of one horn base.

The Amsterdam skull (ZMA 18.623), reputed to be that of a blaauwbok, was measured by CPG in the same manner as the skulls of the two extant species, and a few extra measurements were kindly taken by Dr P. J. H. van Bree (in litt., 29. IV. 77). Measurements of the Glasgow skull were kindly provided by Ms. E. Macartney, Museum Officer of the Hunterian Museum (in litt. 27. IV. 77). All measurements were entered into a datafile by CRW.

H. niger and *H. equinus* skulls were discriminated, sexes separately, using SPSS-DISCRIMINANT ("Direct" method) on the MICOM computer at the Australian National University. The measurements of the putative *H. leucophaeus* skulls were entered as unknowns.

Skulls of *H. niger* and *H. equinus* separated totally using Discriminant Analysis (Fig. 1). Although there is a difference in size – roan are bigger than sable – this was not the main discriminator; instead, in the case of both males and females, premolar row length and biorbital width provided the greatest discrimination, while the horn base measurements provided none (Tab. 1).

When the two putative blaauwbok skulls are considered as males (Fig. 1 a), they turn out to be indistinguishable from sable antelopes. When they are entered into the female analysis, however, the Glasgow skull falls within the sable antelope range, though towards one edge; but the Amsterdam skull falls outside it (Fig. 1 b).

Accordingly, it appears that the Glasgow skull could, as argued by Klein (1974), be that of a sable antelope (although it need not be), while the identity of the Amsterdam skull depends on what sex it is.

As recorded by Bosscha Erdbrink (1988), the Amsterdam skull had previously been identified as female by Dr P. J. H. van Bree "because of its comparatively small size" (p. 144); but Bosscha Erdbrink, basing himself on the strong wear of the upper surface of the horns, considered it as more likely to be a male.

The Amsterdam skull measures 400 mm in greatest length; the Glasgow skull, 396 mm. Adult male skulls of *H. niger* range from 387 to 447 mm (the giant Angolan sub-

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C        |            2      2 I                          1 1 111   1                      |
Y        |            2      2 I                          1 1 111   1                      |
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         |            22222 22222   #           1  1    1 1 111111 111   1                 |
          X---------+---------+---------+---------+---------+---------+---------+---------X
        OUT      -6.0      -4.0      -2.0        .0       2.0       4.0       6.0        OUT
  CLASS   22222222222222222222222222222222222111111111111111111111111111111111111111111111111
CENTROIDS                  2                                   1
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Fig. 1. Discriminant function analysis of *Hippotragus* skulls. (a) Males. (b) Females. Key: 1 = *H. equinus*, 2 = *H. niger*, # = Amsterdam skull, I = Glasgow skull.

Table 1. Correlations between original skull measurements and Discriminant Functions.

	(a) Males	(b) Females
Greatest skull length	0.20921	0.28232
Condylobasal length	0.28118	0.31026
Biorbital width	0.54279	0.47218
Width across horn bases	0.12920	–0.02876
Width of left horn base	–0.08095	–0.07747
Lacrimal on orbit	0.41353	0.14637
Maxillary toothrow	0.37955	0.40722
Maxillary premolars	0.52348	0.52633
Mandibular toothrow	0.51729	0.30903
Mandibular premolars	0.55927	0.30128

species, *H. n. variani*, excepted); only 3, out of 51 measurable skulls, are smaller than the Amsterdam skull, and 2 smaller than the Glasgow skull. Adult female skulls of the same species range from 376 to 444 mm, 4 out of 30 being as small as the Amsterdam and Glasgow skulls or smaller. If they were skulls of *H. niger*, both would therefore be small specimens whichever sex they were. It can be noted that only one skull (a female) of *H. equinus* is as small as 400 mm.

Horn wear resulting in flattening of the anterior surface is more usual in males, but it can be found in both sexes, contra BOSSCHA ERDBRINK (1988). On the other hand, in both *H. niger* and *H. equinus* males' horns are longer and thicker than females. In the present study, the width of a single horn base varies as follows:

H. niger, males 43–60 mm (n = 68), females 37–54 mm (n = 35)
H. equinus, males 45–67 mm (n = 149), females 33–51 mm (n = 85)

There is, therefore, strong sexual dimorphism, but little difference between the two species. The Amsterdam skull's left horn core width is 39, the Glasgow skull's is 36. Both are evidently females on this evidence, and very small ones at that.

There is finally the evidence of horn shape itself. In juveniles and subadults of both sexes of the two living species, the horns curve evenly up and back, and the tips point backward; the horns cease growing in the female, but in the male they continue to elongate, curving down as they do so. The blaauwbok appears to have been the same: the two fully adult males among the four known mounted blaauwbok specimens, the Leiden and Paris specimens (MOHR 1967), both show the typically male downpointing tips, the Leiden one more than the Paris one (which is smaller and perhaps younger), whereas the only known female, the Vienna specimen (MOHR 1967), has back-pointing tips, and the horns also appear to be rather thin. The Amsterdam skull (BOSSCHA ERDBRINK 1988; ROOKMAAKER, 1992) clearly shows the female condition, and the Glasgow skull (MOHR 1967) appears to as well, although only the cores are preserved: both, it should be specified, are fully mature.

Consequently, there can be little doubt but that both Amsterdam and Glasgow skulls are female, and that figure 1 b is relevant. In that diagram, the Amsterdam skull is outside the range of both sable and roan, and by process of elimination would most plausibly be a blaauwbok. Although the Glasgow skull falls within the sable range, it is not too distant from the Amsterdam skull either; we cannot *a priori* exclude the possibility that this could be a blaauwbok as well.

On the basis of the Glasgow skull, ROBERT BROOM distinguished *H. leucophaeus* from its living relatives as having more slender, downpointing premaxillae and a correspondingly downcurved mandibular incisor region, and "the angle made by the nasal with the front of the supra-orbital part of the frontal is less obtuse" (Mohr 1967), although in the photos this angle would seem, if anything, *more* obtuse! Mohr (1967) notes the shortness of the distance along the orbital border which is occupied by the lacrimal bone, and that the horn cores, while long-oval as in *H. niger*, are flattened on their median surfaces rather than on the lateral as in the latter. Does the Amsterdam skull show similar features?

The premaxillae of the Amsterdam skull certainly appear slender, but are by no means as downpointing, nor is the mandibular incisor region as downcurved, as in the Glasgow skull. It is also worth noting that the premaxillae of the Leiden mounted specimen, extracted from the skin, appear slender (no measurements were taken by CPG) but show no signs of being downpointing. The supraorbital slope seems comparable with that of the Glasgow skull, but we are not convinced that this is a consistent character. The horn-core character is the same as in the Glasgow skull, and indeed was the means by which Bosscha Erdbrink (1988) first identified the Amsterdam skull as blaauwbok.

The lacrimal bone in the Glasgow skull occupies only 15 mm of the orbital rim; this is equal to the smallest value in any sable antelope skull (values are higher in roan). In the Amsterdam skull this measurement is 12 mm. There may therefore well be a specific character here.

Mohr (1967) gives the upper premolar row length for the Glasgow skull as 36 mm (left), 35 mm (right), but Klein (1974) doubts this, suggesting that a mistake has occurred and that 46 and 45 mm are more likely. Ms E. Macartney (in litt. to CPG, 27th April, 1977) confirms that this is the case, giving 45 mm for both left and right. There is thus, *contra* Mohr (1967), no difference between the Glasgow skull and *H. niger* in relatlve premolar row length.

We can summarise this discussion as follows: both the Amsterdam and Glasgow skulls are females. Discriminant analysis (*not* based on size) excludes the Amsterdam skull from the ranges of female sable or roan antelopes; the same analysis does not exclude the Glasgow skull from being a sable antelope, but it is placed near the edge of the dispersion, not far from the Amsterdam skull. Both are at the low end of the size range for sable antelope, and show similar distinguishing features: horn coes medially flattened, and lacrimal bone very small. We are convinced they are genuine skulls of the extinct blaauwbok.

Both known blaauwbok skulls are female. This makes comparison with the two living species difficult; but there is enough evidence to state firmly that the species is more closely allied to the sable antelope, *Hippotragus niger*, than to the roan antelope, *H. equinus*. It is perhaps not surprising, then, that blaauwbok and roan antelopes were capable of being sympatric (Klein 1974), while *H. leucophaeus* and *H. niger* constituted a well-differentiated allopatric species pair.

Acknowledgements

We are very grateful to Dr Peter van Bree (Zoological Museum, Amsterdam) and to Ms Ellison Macartney (Hunterian Museum, Glasgow) for information and measurements of the two skulls in question.

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Buchbesprechungen

HARWOOD, J.: **Styles of Scientific Thought – The German Genetics Community 1900–1933.** Chicago and London: The University of Chicago Press 1993. 423 pp., 22 figs., 13 tabs., 27.50 US $. ISBN 0-226-31882-6

This book aims at characterizing research directions and major schools of thought within the German genetics community in the time period from 1900 to 1933. Furthermore it provides a thorough evaluation of differences in scientific approaches, in the organization of research, funding, and teaching, and in the social and cultural background of particular scientists, both within Germany and between Germany and the USA. The author's observations and considerations are presented in nine chapters and a conclusion.

Chapter one provides methodological considerations as to the definition of style in science and its comparison among different countries. Furthermore, a detailed account of German research traditions is given. The latter were characterized by a high interest in morphology and developmental biology, by strong emphasis on a broad education in biology, and by a remarkable resistance against specialization in research and teaching. Chapter two considers the German response to T. H. MORGAN's chromosome theory during the 1920s. While most of the German geneticists (e. g. R. GOLDSCHMIDT, V. HAECKER, A. KÜHN, K. HENKE) felt that the chromosome theory neglected the process of development and were rather interested in developmental genetics and cytoplasmatic inheritance, MORGAN stated it would be "far better to concentrate on more tractable problems such as the structure of the hereditary material and the process of its transmission between generations..." (p. 49). This statement exactly hits what may be considered one of the major differences between research in Germany and the USA elaborated in this book. While most American researchers tended to be "pragmatic", i. e. they attempted to restrict themselves to simple but testable questions, German geneticists were usually willing to address more complex issues, at the inevitable expense of a greater deal of speculation involved in their interpretations. Chapter three concentrates on evolutionary genetics. While in the interwar period many geneticists in the United States were relatively uninterested in evolutionary issues or held overly simplified mutationist or selectionist views, several German geneticists sought to integrate genetic theory with complex patterns of geographical distribution and the fossil record. The author finds it typical that the synthetic theory of evolution was developed by broadly educated biologists (e. g. TH. DOBZHANSKY, J. HUXLEY, B. RENSCH, S. WRIGHT), who were able to bridge the gap between genetic principles and various other biological disciplines. Details on possible reasons for a more specialist and a more generalist approach to genetics in the USA and Germany, respectively, are given in chapter four. For example, whereas in the United States universities regularly expanded by the foundation of new departments, facilitating the establishment of new research disciplines, German universities rather expanded by obtaining additional funds for already existing institutes. Research diversity within the latter was subjected to the constraints set up by the respective chairholders. Due to the payment of extra fees for teaching, in Germany the presentation of basic and general lectures remained the domain of well established professors. By contrast, their American colleagues rather focused on teaching specialities of their interest, leaving basic lectures to junior staff Also with respect to an academic career the organization of the German University actively discouraged specialization. The best strategy for a young geneticist in search of a chair (necessarily in zoology or botany) was to cultivate a broad profile, working on genetic aspects of the major biological problems: development and evolution. Finally, as a result of a much greater dependence on private funds, geneticists in the United States tended to cooperate much more intensively with agricultural institutions than German researchers did.

In chapters five to nine it is shown that the aforementioned differences in research interests did not apply only to geneticists in Germany and the United States, but were, to some extent, also found within the German genetics community. In particular, the careers and research interests of E. BAUR and A. KÜHN are contrasted. The former is considered an early advocate of the chromosome theory and, as a result of his studies on natural populations and selection, a contributor to the evolutionary synthesis. The latter is referred to as a prominent researcher in developmental genetics with a broad interest in various other biological disciplines. Both researchers and various members of their schools are compared in some detail as to broadness of their biological knowledge, their interest in culture, their engagement in policy, and their holistic or pragmatic view of science. This data is then used for sketching some general philosophical and psychological characteristics of researchers holding either a 'comprehensive (holistic)' or a 'pragmatic' view. It is suggested that the pragmatic style of science resulted from an increasing erosion of the traditional ideal of Bildung at the turn of the century. According to an evaluation of the social background, geneticists with a comprehensive view of science typically stemmed from an educated-middle-class milieu whereas those with a pragmatic view were largely from lower- and industrial-middle-class strata. Finally, the author turns from problem choice to theory choice in genetics. The use of social analogies to biological phenomena is briefly reviewed, and their impact on the conception of theories is discussed (e. g. 'monarchist' vs. 'democratic' concepts in the context of cytoplasmatic inheritance). It is argued that, in view of poor empirical evidence, comprehensive thinkers tended to endorse the holistic plasmon theory while pragmatics either adopted a competing atomistic theory or rejected cytoplasmatic inheritance alltogether. In his general conclusion, the author stresses the relevance of the concept derived from research styles in genetics to other disciplines of science.

Apart from providing a rich source of information on the development of genetics in Germany, this excellent book gives a detailed account of the various social, philosophical, and psychological factors involved in the choice of research directions and the development of theories. The issues addressed are far from being merely historical (things have changed only gradually, not in principle), and are highly relevant to everyone interested in biology.

G. B. Hartl, Kiel

Boyd, J. S.; Paterson, C.: **Farbatlas der klinischen Anatomie von Hund und Katze.** Übersetzt aus dem Englischen von M. und B. Schnorr. Stuttgart: Ferdinand Enke Verlag 1995. 192 Seiten, 327 Abb. 148,– DM. ISBN 3-432-26101-2

In diesem großformatigen und auch für den Säugetierkundler informativen Band wird mit photographischen Abbildungen die Anatomie des Hundes ausführlich und die der Katze ergänzend dazu dargestellt. Folgende Körperabschnitte werden behandelt: Kopf und Hals, Wirbelsäule, Schultergliedmaße, Thorax, Bauch- und Beckenhöhle und die Beckengliedmaße; der Abschluß wird von einem Sachverzeichnis gebildet.

Nach Darstellung der Oberflächenanatomie am lebenden Hund, werden in detailreichen Bildern das Skelett und seine Bauelemente vorgestellt, dann folgt die Weichteilanatomie. Vermutlich aufgrund der Tatsache, daß Praktiker mit diesem Farbatlas angesprochen werden sollen, wird teilweise die dem anatomischen Gebrauch entsprechende Terminologie benutzt, teilweise werden aber auch deutsche Begriffe gebraucht. So wird, beispielsweise, in der Abb. 208 einerseits von der „Tunica albuginea" des Hodens gesprochen, doch vom „Körper des Nebenhodens" und nicht vom „Capud epididymidis".

In dem vorliegenden Band werden Muskulatur und Weichteile anhand von unfixierten Frischpräparaten abgebildet. Nach dem Vorwort der schottischen Autoren soll bei Darstellungen, welche von fixiertem Material hergestellt wurden, „Realitätsmangel, verbunden mit dem Verlust der normalen Farbe und Form, ... oft den Wert dieser Publikationen" schmälern, „weil die Präparate häufig wenig Ähnlichkeit mit natürlichen Organen und Geweben haben." Der Referent kann diese Meinung nicht uneingeschränkt teilen, muß aber zugestehen, daß von der Seite der hier angesprochenen chirurgisch arbeitenden Tierärzte und Veterinärpathologen entsprechende Wünsche geäußert werden.

Leider sind einzelne Abbildungen von Muskelpräparationen nicht optimal für die Photographie vorbereitet worden, was wohl an der Tatsache liegt, daß unfixiertes Frischmaterial benutzt wurde: Von der Oberfläche der Präparate nicht entfernte Haare und Gewebebröckchen (beispielsweise in den Abbildungen 113, 206 und anderen) beeinträchtigen den sonst sehr positiven Eindruck, welchen die Abbildungen in diesem Farbatlas machen.

Der Benutzer des vorliegenden Bandes wird an mehreren Details seine Freude haben: Die dargestellte Körperregion ist neben dem Photo auf einer Umrißzeichnung des Hundes so markiert, daß die Orientierung leicht fällt. Zweitens ist positiv die klare Beschriftung mit Ziffern, welche jeweils in einem „Kasten" erklärt werden, zu vermerken. Dies bietet schnellen Überblick auch bei komplexeren Strukturen. (Es ist allerdings zu fragen, ob in nahe beieinander stehenden Abbildungen gleichartiger Knochen von Hund und Katze nicht auch eine gleichartige Numerierung der Details hilfreich wäre. Als Beispiel sei der Axis des Hundes, Abb. 63 B, und der Katze, Abb. 64 B, genannt). Als drittes Positivum sei auf die Ergänzung der anatomischen Abbildungen durch einige Ultraschall-Darstellungen, sowie durch Arteriogramme und mehrere Röntgenbilder hingewiesen.

P. Langer, Gießen

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Allozymic variation and differentiation in moles (Genus *Talpa*, Insectivora) of the Val Bregaglia (Switzerland) and the Val Chiavenna (Italy)

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Abstract

Allozymic variation and differentiation of strictly parapatrically distributed European moles (*Talpa europaea*, n = 44) and Mediterranean moles (*T. caeca*, n = 34) were studied in the Val Bregaglia (Switzerland) and Val Chiavenna (Italy) to estimate interspecific separation and intraspecific gene pool structuring. Tissue samples were screened for allelic variation at 44 putative gene loci using horizontal starch gel electrophoresis. In *T. europaea* four and in *T. caeca* three regional samples separated from one another by water courses were discriminated. The proportion of polymorphic loci was 2.3 per cent in each regional sample, with polymorphisms at the Es-1 locus in *T. europaea* and at the Es-1 and the Es-D loci in *T. caeca*. Expected average heterozygosity ranged from 0.6 to 1.2 per cent in regional samples of *T. europaea* and from 0.9 to 1.2 per cent in *T. caeca*. In *T. caeca* one regional sample showed fixation of a unique allele (Es-D^{143}). This indicated paucity of migration across surrounding water courses. Inbreeding coefficients (F_{IS}) for the Es-1 locus ranged from 0.39 to 1.0 in regional samples. Significant deviations of genotype frequencies for the Es-1 locus due to deficiency of heterozygotes were found in one *T. europaea* and one *T. caeca* regional sample, respectively. The findings are discussed with respect to the parapatric pattern of distribution and the generally low gene pool variability of *Talpa* species found so far.

Introduction

In the Val Bregaglia (Bergell valley, Graubünden, Switzerland) the two mole species *Talpa europaea* and *T. caeca* show strict parapatric distribution. The river "Maira" ("Mera" in Italian) and two of its tributaries (Bondasca, Caroggia) form the parapatric contact line (Maurizio and Hausser 1990, see also Fig. 1). Maurizio and Hausser (1990) hypothesized that competition might be an explanation of this parapatric distribution. However, both species occupy diverse habitats on north and south slopes ranging from the bottom of the valley to an altitude of approximately 1 800 m. These habitats vary greater within each species range along the parapatric contact line than they do across this line. If competition did exert a strong influence on the distribution of the two species, we should note displacement of one species by the other at least in those habitats across the parapatric contact line, where the invading species was more successful.

The parapatric contact line does not appear to correlate with obvious climatic, vegetational or soil changes. This might suggest that the river system itself functions to a certain degree as a migratory barrier for the two species. In each species, the range of regional distribution is also split into several fragments by small mountain creeks (Fig. 1) with possible segregating effects on the intraspecific gene pools. The objective of the present study is to estimate the degree of gene pool structuring within each of the two species in relation to the local water courses. Occurrence of intraspecific gene pool segregation parallel to the creek system would indicate reduced migration across water courses. Thus it would foster the afore-mentioned hypothesis of the significance of the river system for maintenance of allopatry of these two species of moles in the Val Bregaglia.

Material and methods

Specimens of the European mole (*Talpa europaea* L., 1758, n = 44) and the Mediterranean mole (*Talpa caeca* Savi, 1822, n = 34) were collected in the Val Bregaglia, canton Graubünden, south-eastern Switzerland and in Valchiavenna, Province di Sondrio between June 1989–May 1994 (cf. also Maurizio and Hausser 1990). Individuals of both species were taken from different areas separated from one another by rivers and mountain creeks. Four regional samples were distinguished in *T. europaea* and three in *T. caeca*, in accordance with the areal fragmentation by the main water courses (Fig. 1). Regional sample sizes are given in table 1. Tissue samples of heart, kidney and liver were taken from each specimen and maintained at –20 C until processed.

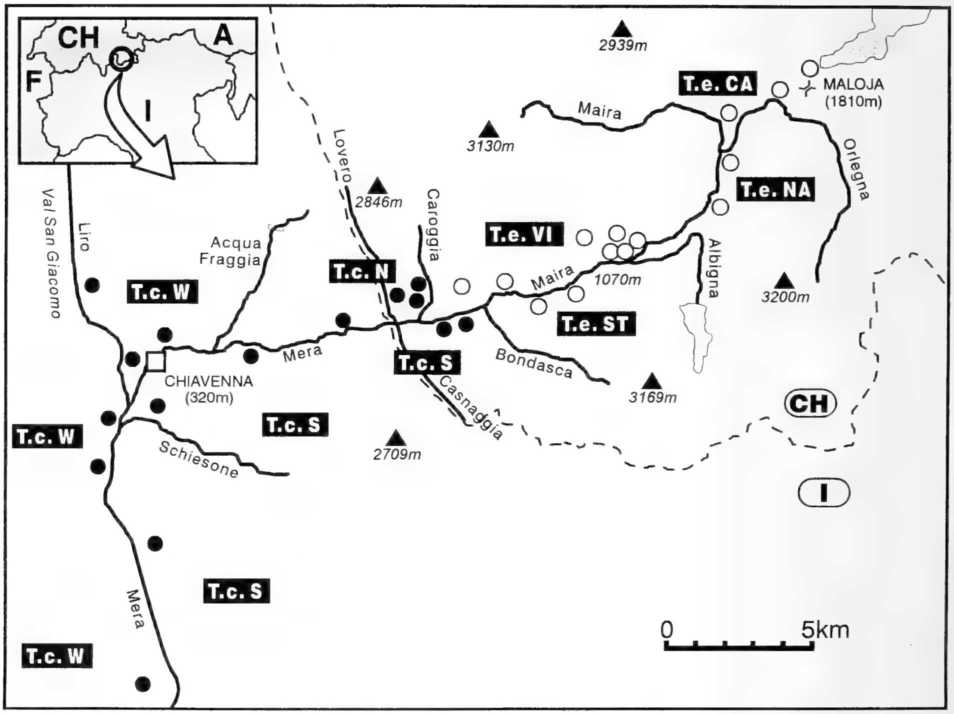

Fig. 1. Study area Val Bregaglia (Kanton Graubünden, Switzerland) and Val Chiavenna (Prov. di Sondrio, Italy). Sampling localities of *Talpa europaea* are indicated by open circles and *T. caeca* by full circles. Sample sizes are one or more individuals per circle. Regional samples for the study of gene pool structuring are as follows. *T. europaea*: *T. e.* CA = Casaccia, *T. e.* NA = Nasciarina, *T. e.* ST = Stampa, *T. e.* VI = Vicosoprano; *T. caeca*: *T. c.* N = North, *T. c.* S = South, *T. c.* W = West. For sample sizes of regional samples, see table 1.

Horizontal starch gel electrophoresis was used to resolve variation in the following 33 isozyme systems encoded by 44 putative gene loci (abbreviation, EC number of enzymes and loci scored in parentheses): α-glycerophosphate dehydrogenase (GDC, EC 1.1.1.8, Gdc), sorbitol dehydrogenase (SDH, EC 1.1.1.14, Sdh), lactate dehydrogenase (LDH, EC 1.1.1.27, Ldh-1, -2), malate dehydrogenase (MOR, EC 1.1.1.37, Mor-1, -2), malic enzyme (MOD, EC 1.1.1.40, Mod-1, -2), isocitrate dehydrogenase (IDH, EC 1.1.1.42, Idh-1, -2), 6-phosphogluconate dehydrogenase, (PGD, EC 1.1.1.44, Pgd), glucose dehydrogenase (GDH, EC 1.1.1.47, Gdh), glucose-6-phosphate dehydrogenase (GPD, EC 1.1.1.49, Gpd), xanthine dehydrogenase (XDH, EC 1.2.3.2, Xdh), glutamate dehydrogenase (GLUD, EC 1.4.1.3, Glud), NADH-diaphorase (DIA, EC 1.6.2.2, Dia-1, -2), catalase (CAT, EC 1.11.1.6, Cat), superoxide dismutase (SOD, EC 1.15.1.1, Sod), purine nucleoside phosphorylase (NP, EC 2.4.2.1, Np), aspartate aminotransferase (AAT, EC 2.6.1.1, Aat-1, -2), hexokinase (HK, EC 2.7.1.1, Hk-1), pyruvate kinase (PK, EC 2.7.1.40, Pk-1), creatine kinase (CK, EC 2.7.3.2, Ck-1, -2), adenylate kinase (AK, EC 2.7.4.3, Ak-1, -2), phosphoglucomutase (PGM, EC 2.7.5.1, Pgm-1), esterases (ES, EC 3.1.1.1, Es-1, Es-D), acid phosphatase (ACP, EC 3.1.3.2, Acp-1), fructose-1,6-diphosphatase (FDP, EC 3.1.3.11, Fdp-1), β-galactosidase (β-GAL, EC 3.2.1.23, β-Gal), peptidases (PEP, EC 3.4.11, Pep-1, -2), guanine deaminase (GDA, EC 3.5.4.3, Gda), adenosine deaminase (ADA, EC 3.5.4.4, Ada-1, -2), aldolase (ALDO, EC 4.1.2.13, Aldo), fumarate hydratase (FH, EC 4.2.1.2, Fh), aconitase (ACO, EC 4.2.1.3, Aco-1), mannose phosphate isomerase (MPI, EC 5.3.1.8, Mpi), glucose phosphate isomerase (GPI, EC 5.3.1.9, Gpi-1).

Tissue preparation, electrophoresis and protein-specific staining were performed as described previously (Hartl and Höger 1986; Grillitsch et al. 1992). Genetic interpretation of band patterns was consistent with the principles outlined by Harris and Hopkinson (1976) and Hillis and Moritz (1990). For resolving allelic variants direct side-by-side comparison of migrating allozymes was carried out including samples of both species on the same gels, respectively. At each variable locus, the corresponding allele of the most common allozyme in *T. europaea* was designated 100 in case of anodal and –100 in case of cathodal migration. All other alleles were numbered as percentages of 100 and –100, respectively. In each specimen the genotypes at polymorphic loci were determined.

The following statistical analyses of population genetics were carried out using the BIOSYS-1 pc package, release 1.7 (Swofford and Selander 1989): allele frequencies, average heterozygosity (H), proportion of polymorphic loci (99% criterion) (P), exact tests of genotypes for deviations from Hardy-Weinberg equilibrium and F-statistics. F_{IS} values for the Es-1 locus were calculated for each regional sample. The same program package was used for calculation of genetic similarity and distance coefficients; Nei's (1978) unbiased D and modified Rogers distances (Wright 1978) were used for cluster analyses employing UPGMA and the distance Wagner procedure by midpoint rooting (Farris 1972). In each species, G-tests (Weber 1980) were carried out to prove homogeneity of allele frequencies at polymorphic loci across regional samples.

Results

Of the 44 loci analysed nine exhibited allelic variation. Seven loci (Mod-2, Pgd, Gpd, Xdh, Np, Aco-1, Mpi) had alleles alternatively fixed in the two species. Variation was detected only at two loci (Es-1, Es-D) in at least one species (Tab. 1). An allelic polymorphism was found only in Es-1 within each regional sample. Es-D showed a fixed allele (Es-D^{143}) in one of the *T. caeca* regional samples (*T. c.* N; cf. Fig. 1, Tab. 1). G-tests for homogeneity of frequencies of Es-1 alleles across regional samples (cf. Tab. 1) revealed heterogeneity in *T. europaea* ($G = 8.02$, $p < 0.05$, d. f. = 3) and homogeneity in *T. caeca* ($G = 2.9$, $p > 0.05$, d. f. = 2). Mean observed/expected heterozygosity (calculated over 44 loci) was 0.003/0.01 for *T. europaea* and 0.005/0.01 for *T. caeca*. The mean proportion of polymorphic loci was 2.3% in both species. Allele frequencies in the *T. europaea* and *T. caeca* regional samples are given in table 1 along with heterozygosity values and rates of polymorphism. Significant deviations of observed genotype frequencies from Hardy-Weinberg expectations at the Es-1 locus were found in one of the *T. e.* regional samples and one of the *T. c.* regional samples (Tab. 1). All these deviations were due to heterozygote deficiency (Tab. 2). The F_{IS} values for the Es-1 locus of each regional sample are given in table 1. The matrices of Nei's (1978) unbiased genetic distances and modified Rogers distances are presented in table 3. A Wagner tree produced by rooting at midpoint of longest path (cophenetic correlation = 1 000) using modified Rogers distances is displayed in figure 2. The UPGMA dendrogram based on Nei's (1978) D genetic distances revealed essentially the same relationships of the concerned gene pools as the Wagner tree.

Table 1. Allele frequencies at variable loci, heterozygosity (H_0 – observed, over 44 loci, H – expected, over 44 loci), proportion of polymorphic loci (P) and inbreeding coefficients (F_{IS}) for the Es-1 locus of the regional samples of *Talpa europaea* and *T. caeca* from the Val Bregaglia and environs. For acronyms of regional samples, see Fig. 1. Significant deviation of genotype frequencies from Hardy-Weinberg expectations are indicated by asterisks with the most common allele at the affected locus (* – $p < 0.05$, ** – $p < 0.001$), n – sample size.

Locus/Allel		regional samples						
		Talpa europaea (T. e.)				*Talpa caeca (T. c.)*		
		T. e. CA	*T. e.* NA	*T. e.* VI	*T. e.* ST	*T. c.* N	*T. c.* S	*T. c.* W
n		10	12	18	4	9	15	10
Mod-2	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	80	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Pgd	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	59	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Gpd	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	93	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Xdh	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	83	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Np	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	64	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Aco-1	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	110	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Mpi	100	1.0	1.0	1.0	1.0	0.0	0.0	0.0
	61	0.0	0.0	0.0	0.0	1.0	1.0	1.0
Es-1	100	0.550	0.542	0.833**	0.750	0.500	0.700	0.750*
	82	0.450	0.458	0.167	0.250	0.500	0.300	0.250
Es-D	100	1.0	1.0	1.0	1.0	0.0	1.0	1.0
	143	0.0	0.0	0.0	0.0	1.0	0.0	0.0
H_0(%)		0.7	0.6	0.0	0.0	0.8	0.5	0.2
H(%)		1.2	1.2	0.6	1.0	1.2	1.0	0.9
P(%)		2.3	2.3	2.3	2.3	2.3	2.3	2.3
F_{IS} (Es-1)		0.39	0.50	1.0	1.0	0.33	0.52	0.73

Table 2. Observed (o) and expected (e) genotype frequencies at the Es-1 locus for all regional samples of *Talpa europaea* (*T. e.*) and *Talpa caeca* (*T. c.*). For acronyms of regional samples, see Fig. 1. For significance of deviations from Hardy-Weinberg expectations see, table 1.

genotype	regional sample						
	Talpa europaea (T. e.)				*Talpa caeca (T. c.)*		
	T. e. CA	*T. e.* NA	*T. e.* VI	*T. e.* ST	*T. c.* N	*T. c.* S	*T. c.* W
	o/e	o/e	o/e	o/e	o/e	o/e	o/e
82/82	3/1.9	4/2.4	3/0.4	1/0.1	3/2.1	3/1.2	2/0.5
82/100	3/5.2	3/6.2	0/5.1	0/1.7	3/4.8	3/6.5	1/3.9
100/100	4/2.9	5/3.4	15/12.4	3/2.1	3/2.1	9/7.2	7/5.5

Table 3. Matrix of genetic distance coefficients. Above diagonal Nei's (1978) unbiased genetic distances and below diagonal modified Rogers distances (Wright 1978) among samples of *Talpa europaea* (*T. e.*) and *T. caeca* (*T. c.*) of the Val Bregaglia and environs. For acronyms, see figure 1.

regional sample	1	2	3	4	5	6	7
1 *T. e.* CA	****	.000	.001	.000	.203	.175	.176
2 *T. e.* NA	.001	****	.002	.000	.203	.176	.176
3 *T. e.* VI	.043	.044	****	.000	.205	.175	.175
4 *T. e.* ST	.030	.031	.013	****	.204	.174	.174
5 *T. c.* N	.426	.426	.429	.428	****	.024	.024
6 *T. c.* S	.400	.400	.399	.399	.154	****	.000
7 *T. c.* W	.400	.400	.399	.399	.155	.008	****

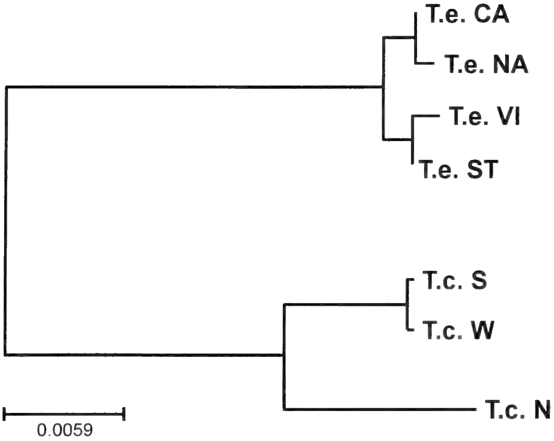

Fig. 2. Wagner dendrogram (midpoint rooting of longest path) using modified Rogers distances (Tab. 3) and displaying differentiation of gene pools of *Talpa europaea* (*T. e.*) and *T. caeca* (*T. c.*) regional samples of the Val Bregaglia (Switzerland) and Valchiavenna (Italy). For acronyms of regional samples, see Fig. 1.

Discussion

In the present study on gene pool structuring of *Talpa europaea* and *T. caeca* of the Val Bregaglia we found indication for reduced or even interrupted gene flow across the river Maira and another water course in both species. This corresponds to the hypothesis of the significance of the river Maira and two of its tributaries for maintenance of parapatry of the two mole species in this region.

Regarding gene flow across rivers and creeks the most striking result was found in *T. caeca* regional samples from north and south of the river Maira. The *T. c.* N. regional sample shows fixation for the Es-D^{143} allele, an allele which has not been found elsewhere in *T. caeca*. Just across the river Maira, south of *T. c.* N, all *T. caeca* individuals harbour the Es-D^{100} allele and no other allele has been detected at this locus in the study area. In *T. caeca* from north of the river Maira the Es-D^{143} allele also does not occur anywhere west of the Aqua Fraggia creek; it occurs, however, on both sides of the Lovero creek. Since we have examined only one individual from the area between Aqua Fraggia and Lovero we cannot exclude introgression of the Es-D^{100} allele in this area by crossing the Aqua Fraggia from west to east.

The Es-D^{143} allele is autapomorphic to the *T. c.N* regional sample and it also does not occur in the other mole species *T. europaea* of the Val Bregaglia. Thus, we interpret this allele as phylogenetically younger than the Es-D^{100} allele. Concerning the origin, aggregation and fixation of the Es-D^{143} allele in the *T. c.* N regional sample, it could be selectively preferred over the Es-D^{100} allele under the particular conditions of habitat of the *T. c.* N regional sample. This is, however, very unlikely because all individuals of *T. europaea* and *T. caeca* with the alternative Es-D^{100} allele live in a variety of habitats reaching from the bottom of the valley to an altitude of approximately 1 800 m. Obviously, this variety of habitats is far greater than that of habitats at the bottom of the valley where both alleles are separated only by the river Maira. Moreover, within the *T. c.* N. regional sample, moles occur also in various habitats, again from the bottom of the valley to an altitude of approximately 1 800 m, but all have exclusively the Es-D^{143} allele. If there was some selection preferring the Es-D^{143} allele, this allele should occur rather in a specific habitat than in a region covering probably as many habitat types as the other regions where the Es-D^{100} allele occurs exclusively. Alternatively, the Es-D^{143} allele could also occur at very low frequencies in other *T. caeca* regional samples and the fixation of it in the *T. c.* N regional sample could be due to a founder effect. Also, the autapomorphic Es-D^{143} allele could have evolved in the *T. c.* N. regional sample and its fixation could be due to genetic drift. Finally, the *T. c.* N. regional sample could represent a relic population of moles which invaded that area in the postglacial phase. Repeated catastrophies (floods, avalanches etc.) could have eradicated all other mole populations in the Val Bregaglia and reinvasions of moles carrying only the Es-D^{100} allele began later on. This would mean that the *T. c.* N. regional sample was an "ancient population" although it carried a phylogenetically younger allele than the other mole populations which immigrated into the Val Bregaglia at a later time.

In view of the remarkably scarce migration that is generally required to prevent genetic divergence under selectively neutral conditions (HARTL 1988), we interpret the occurrence of the Es-D^{143} allele exclusively in *T. c.* N and the absence of the Es-D^{100} allele in this regional sample as resulting from an already longer-lasting lack of migration across the river Maira and probably also across the Aqua Fraggia.

In *T. europaea* of the Val Bregaglia only the Es-1 locus is polymorphic with two alleles. The significant variation of allele frequencies across the regional samples indicates somewhat separated gene pools. In particular, the *T. e.* VI regional sample is separated from the *T. e.* CA and *T. e.* NA regional samples. This indicates reduced gene flow across the river Maira. However, no such reduction of migration obviously occurs across the Orlegna creek, separating the *T. e.* CA and the *T. e.* NA regional samples in the eastern part of the Val Bregaglia. Regarding the situation with the *T. e.* ST regional sample we were not able to finalize our conclusions because of the rather low sample size. Although *T. e.* ST clusters with *T. e.* VI, which would suggest gene flow across the river Maira in this part of the valley, it could equally well be associated with the *T. e.* NA regional sample.

The second important finding of this study concerns the statistically significant deviations of genotye frequencies at the Es-1 locus from the Hardy-Weinberg expectations in two regional samples due to heterozygote deficiency. In the remaining five regional samples we observed the same tendency toward heterozygote deficiency. Although based on low sample sizes, we consider these findings as being reliable, because of the generally rather low population densities of moles in the study area. Thus, the proportion of animals sampled is quite high and this fact increases the reliability of the population genetic estimators. The general uniform excess of homozygous genotypes in all regional samples might either result from respective low effective population sizes and high tendencies toward inbreeding or be due to substructuring of gene pools within regional samples (Wahlund effect). This accords to the above-cited interpretation of little or interrupted migration across water courses.

Values of observed heterozygosity and rates of polymorphism found presently in the moles are very low. They correspond to those of many other subterranean talpids (YATES and GREENBAUM 1982; TOLLIVER et al. 1985; FILIPPUCCI et al. 1987; NEVO et al. 1990; YATES and MOORE 1990). Among others NEVO (1978, 1979) and NEVO et al. (1990) argued that subterranean mammals living in fairly constant and homogeneous environments should harbour lower allozymic variability than above-ground dwelling mammals that are exposed to more fluctuating and unstable environments. TOLLIVER et al. (1985), however, could not confirm this "niche-width hypothesis of genetic diversity" in a series of subterranean and above-ground living insectivores. They suggested that there might be other aspects of the biology of insectivores that contribute to the reduction of their genetic diversity. We found indications for reduced or even interrupted gene flow among regional samples and quite high rates of inbreeding within regional samples of moles. Thus, little genetic exchange between local populations in connection with low effective population sizes and inbreeding could have also contributed to the erosion of allelic variability in the course of the evolutionary history of both species (see also YATES and MOORE 1990). However, we emphasize that NEVO's (NEVO et al. 1990) niche-width hypothesis of low allozymic diversity in subterranean mammals and the present hypothesis are not mutually exclusive.

Despite the very low allozymic variation in both species, distinct separation between the gene pools of the two mole species is presently indicated by seven diagnostic loci. This is in good accordance with previous data of the two species (FILIPPUCCI et al. 1987). Contrary to this pronounced interspecific divergence, absolute genetic differentiation of the four regional samples of *T. europaea* is negligible. Similar results have been found for various *T. europaea* populations from northern Italy (FILIPPUCCI et al. 1987). However, the latter authors found a quite clear separation between *T. europaea* from the Austrian Alps and some populations from northern Italy due to a very high frequency of the Mpi^{108} allele in the Austrian sample and the absence of this allele in all the Italian *T. europaea* samples. In *T. caeca* from Italy, the genetic distance between a population of *T. c. caeca* from Tuscony and one from Abruzzo was low, whereas genetic differentiation between these two populations and one of *T. c. augustana* from Aosta (northwestern Italy) was quite high (FILIPPUCCI et al. 1987). This significant divergence of gene pools of two conventional *T. caeca* subspecies was predominantly due to alternatively fixed alleles at one locus (Gpd). Similarily, the presently found isolation of the *T. c.* N gene pool from those of the two other *T. c.* regional samples in the Val Bregaglia is also due to alternative fixation of alleles at one locus (Es-D). All these findings suggest that the rate of gene pool divergence in both mole species might be occasionally accelerated by random isolation of particular genomic variants and their subsequent fixation due to genetic drift in small populations.

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Zusammenfassung

Allozymvariabilität und -differenzierung bei Maulwürfen (Genus Talpa, Insectivora) aus dem Bergell (Schweiz) und dem Val Chiavenna (Italien).

Untersucht wurden Genpoolvariabilität, -strukturierung und -differenzierung bei zwei Maulwurfarten (*Talpa europaea*, n = 44) und *Talpa caeca*, n = 34), die im Untersuchungsgebiet strikte parapatrische Verbreitung zeigen, anhand der allelischen Variation an 44 hypothetischen Strukturgenloci mittles Stärkegelelektrophorese. Bei *T. europaea* wurden vier und bei *T. caeca* drei regionale, durch Wasserläufe voneinander getrennte, Subpopulationen analysiert. Die Polymorphierate betrug für jede Subpopulation 2,3%. Bei *T. europaea* war nur ein Locus (Es-1) polymorph; bei *T. caeca* lag allelische Variation an zwei Loci (Es-1, Es-D) vor. Die erwarteten durchschnittlichen Heterozygotiewerte waren generell sehr niedrig (*T. europaea*: 0,6–1,2%; *T. caeca*: 0,9–1,2%). Bei *T. caeca* zeigte sich in einer Subpopulation ein fixiertes Allel am Es-D Locus. Die Inzuchtskoeffizienten (F_{IS}) für den Es-1 Locus lagen bei den einzelnen Subpopulationen zwischen 0,39–1,0. Am Es-1 Locus wurden signifikante Abweichungen der Genotypenhäufigkeiten zu Ungunsten der Heterozygoten festgestellt. Die Ergebnisse werden in Hinblick auf das örtliche parapatrische Verbreitungsmuster der Arten und die allgemeine Verarmung der Genpoolvariabilität bei Maulwürfen diskutiert.

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The influence of moonlight on the activity of Little brown bats (*Myotis lucifugus*)

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Abstract

Lunar cycles influence the activity patterns of a variety of organisms including marine fish, rodents, birds, and fruit-eating bats. Lunar light, specifically a full moon, has also been suggested to depress the activity of insectivorous bats, because of increased predation risk or decreased insect prey abundance. These observations are generally anecdotal, however, with few quantitative data to support or refute them. The purpose of our study was to measure activity of little brown bats (*Myotis lucifugus*) in relation to the lunar cycle, and other environmental conditions, (e.g., ambient temperature, cloud cover, and wind strength). If bats are "lunar phobic" for predator avoidance reasons, then activity levels should decrease or shift to more sheltered habitats. We used ultrasonic bat detectors to assess bat activity. Counter to our prediction, the percent moon face illuminated did not significantly predict bat activity levels. There was also no evidence of a habitat shift correlated with lunar light levels. Activity was significantly related only to ambient temperature, a result commonly found in other studies. Our results indicate that insectivorous bats are not lunar phobic, implying they do not experience substantially higher predation risk or lower prey availability during moonlit periods.

Introduction

Exogenous factors such as photoperiod, temperature and light levels often influence biological rhythms in animals. Rhythms influenced by light are said to follow a lunar cycle if the maxima or minima of the rhythmic activity appears once in a lunar month (Saigusa and Hidaka 1978). Many vertebrate animals incorporate a lunar cycle into their activities, including marine fish (Robertson et al. 1990), rodents (Lockard and Owings 1974; Wolfe and Summerlin 1989; Kotler et al. 1991; Daly et al. 1992), nocturnal birds (Mills 1986; Brigham and Barclay 1992), and frugivorous bats in the laboratory (Häussler and Erkert 1978) and under natural conditions (Erkert 1974; Morrison 1978, 1980). Not surprisingly, nocturnal birds and visually orienting bats become more active during the brightest portions of the lunar cycle when visual sensitivity is increased (Martin 1990). All else being equal, foraging by insectivorous bats, which rely on echolocation, should not be effected by lunar light conditions. To date, the few studies done have reached equivocal conclusions (Erkert 1982).

Two hypotheses have been proposed to explain why insectivorous bat activity may be depressed during the bright phase of the lunar cycle. First, there may be a higher risk of predation from visually orienting predators. During moonlit periods, terrestrial animals reduce activity or choose to occupy more cluttered habitats which presumably provide more cover (birds: Imber 1975; Storey and Grimmer 1986; Watanuki 1986; Nelson 1989 and rodents: Kotler 1984; Price et al. 1984; Longland and Price 1991; Dickman 1992).

If bats exhibit "lunar phobia" in response to increased predation risk, then activity levels should decline with increasing levels of moonlight or increase in "safer" habitats (REITH 1982).

The second hypothesis is that flying insect abundance is depressed during the bright part of the lunar cycle. If this is true, then bats may be less active on moonlit nights because it is energetically unfavourable to forage, especially when they can enter torpor to save energy (AUDET and FENTON 1988). In other words, bats may not themselves be lunar phobic, but simply react to a lunar effect on insects.

The objective of this study was to evaluate the hypothesis that activity by little brown bats (*Myotis lucifugus*) is depressed by increasing levels of lunar light. If bats alter activity patterns to avoid visually orienting predators, activity should decline with increased lunar light levels or shift to habitats with more "cover". Records of night roost use suggest that the activity of *M. lucifugus* is not influenced by lunar conditions (ANTHONY et al. 1981), however no direct measurement of foraging activity has been made.

The little brown bat is a small insectivorous bat (6–11 g; VAN ZYLL DE JONG 1985; NAGORSEN and BRIGHAM 1993) which ranges over most of North America. It is the most common species captured in the Cypress Hills (KALCOUNIS and BRIGHAM 1995), although other *Myotis* spp. do occur. *Myotis lucifugus* consumes small (3–10 mm long) flying insects, usually from the orders Coleoptera, Diptera, Ephemeroptera, Homoptera, Isoptera, Lepidoptera, and Trichoptera (FENTON and BARCLAY 1980).

Material and methods

The study was conducted from May–August 1992 in the West Block of the Cypress Hills Provincial Park (49°34′N, 109°53′ W) in southwestern Saskatchewan. Local vegetation is a mixture of forest and grasslands with the forest consisting of white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), and trembling aspen (*Populus tremuloides*). Battle Creek, its tributaries, and small beaver (*Castor canadensis*) ponds are the main water bodies in the area. The area was a particularly suitable location for this study because there are virtually no artificial light sources.

We monitored bat activity at one site in each of three habitat types; over water, over open fields, and in *P. glauca* forests. These habitats represent those regularly used by *M. lucifugus* (KALCOUNIS and BRIGHAM 1995) in the study area. We quantified activity by using ultrasonic bat detectors (Ultrasound Advice, 23 Aberdeen Road, London N5 20G, U.K.) set at 42 kHz, the peak frequency used by *M. lucifugus* (THOMAS et al. 1987). The detectors allowed us to separate bat passes (calls made by commuting bats) from feeding buzzes (calls produced in association with attacks on prey; GRIFFIN et al. 1960). To assess activity over water (slow moving sections of Battle Creek), the detector was angled over the water from the creek bank; in field and forest habitats the detector was pointed directly upwards.

We counted the number of passes or feeding buzzes heard in 5-minute intervals during "true night", i.e., the time between the end of nautical twilight in the evening and the beginning of nautical twilight in the morning when the sun is 12° below the horizon (HAGEN and BOKSENBERG 1990). We monitored activity for at least one hour at the beginning and one hour at the end of true night. We chose these periods since they represent the times when the bats were most active overall (KALCOUNIS and BRIGHAM 1995). Light sources were turned off for at least 2 minutes prior to and during all sampling intervals to minimize any effect of light on insects in the vicinity.

The percentage moon face illuminated (%MFI) was used as an index of lunar light (HAGEN and BOKSENBERG 1990; BRIGHAM and BARCLAY 1992). Bat activity was measured only if the moon was above the horizon, unless %MFI was <5%. Low %MFI moons are rarely above the horizon during true night and these periods were defined as having 0 %MFI. Collecting data during true night periods when %MFI is low is difficult because of the short period of time the moon is up (MARTIN 1990). Times for moonrise and moonset, and the end and beginning of nautical twilight were calculated for the study site by the Dominion Astrophysical Observatory (Victoria, B.C.).

Cloud cover, wind strength, precipitation in the form of rain, and ambient temperature were recorded at the end of each sampling period. Cloud cover and wind strength were rated subjectively on a scale of 0–3, with 0 representing no wind or cloud and 3 meaning 100% cloud cover or very strong winds (>30 km/hr). Precipitation was recorded as yes or no and temperature was measured using a telethermometer located within 5 km of all sampling sites.

Stepwise multiple regression analysis was used to determine if bat activity was related to % MFI and ambient temperature; cloud cover and wind speed did not vary enough to be included in the model. Activity in the three habitat types was analyzed using ANOVA to determine if activity changed with respect to lunar light, classified as (0–25%, 26–50%, 51–75%, 76–100%MFI). Results are presented as means ± 1 SE and a 0.05 rejection criterion was employed for all tests.

Results

We sampled bat activity on 36 nights between 20 June and 28 August (approximately 3 full lunar cycles) for a total of 628 five-minute intervals. This included 440, 142, and 46 intervals in the water, field and forest habitats, respectively. Cloud cover obscured a substantial amount of sky on only 3 nights (cloud cover index >1). Two of these nights were accompanied by moderate temperatures with no rain or wind. Activity occurred in both cases, despite the fact that one night had a low %MFI (0%) and the other had a high %MFI (99%). The third cloudy night was relatively cool (2 °C), with strong winds (wind strength = 2) and rain, and no bat activity occurred.

Overall, activity levels were low and feeding buzzes accounted for <5% of all activity. We therefore combined passes and buzzes for all analysis. Bats were significantly more active in the over water habitat (F = 26.21, df = 2, p < .001), than in the field or forest habitats which is why we concentrated our sampling efforts in that habitat. Ambient temperature was a significant predictor of bat activity ($r^2 = 0.14$, $P < 0.05$; Fig. 1), but %MFI was not (Fig. 2). There was no evidence of an relationship between activity and lunar light levels in any of the 3 habitats (Water: F = 2.55; Field: F = 2.91; Forest: F = 2.23; df = 3 and P > 0.05 in all cases).

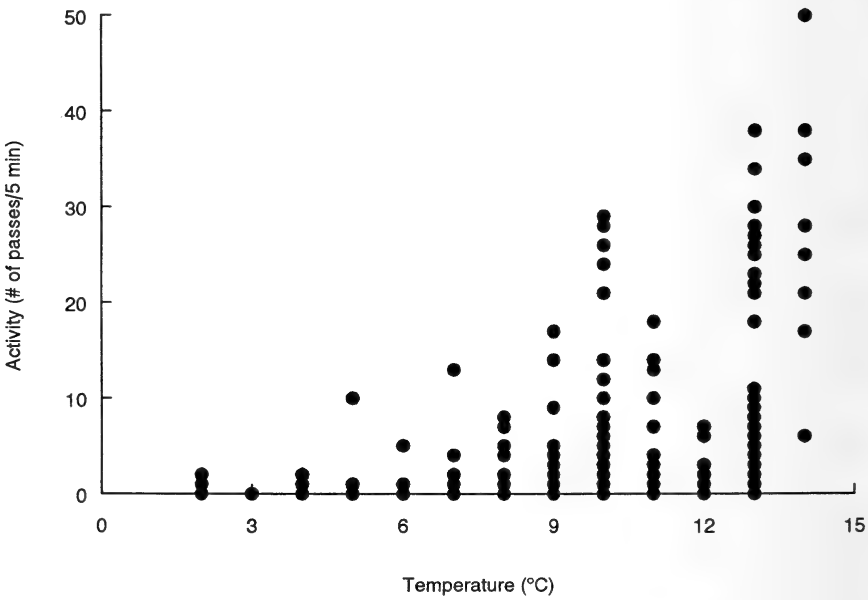

Fig. 1. Bat activity levels (# of bat passes/5 minutes) as a function of ambient temperature (°C) for data from water habitat.

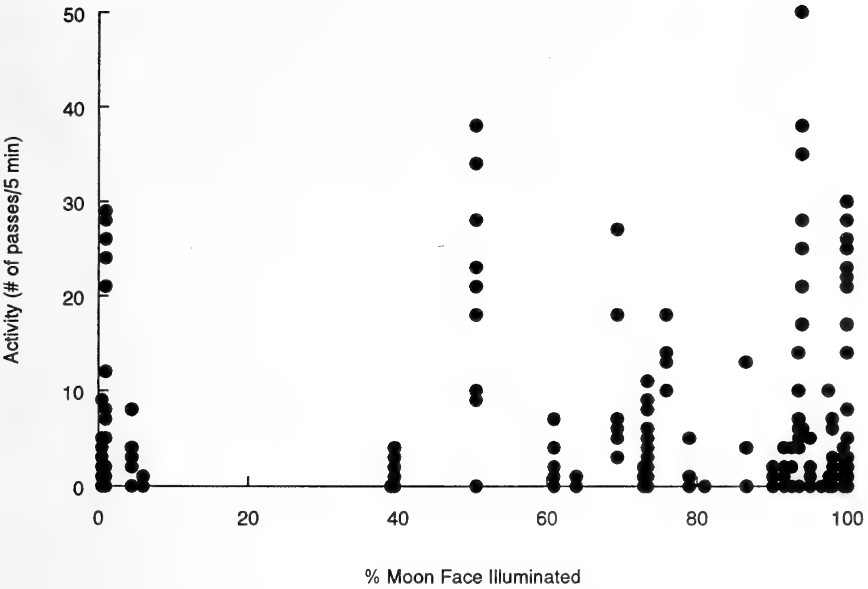

Fig. 2. Bat activity levels (# of bat passes/5 minutes) as a function of percentage of moon face illuminated (%MFI) for data from water habitat.

Discussion

Our results indicate that %MFI is not a significant predictor of *M. lucifugus* activity, although it has been shown to predict activity in other animals such as insectivorous birds (Mills 1986). Erkert (1974) and Morrison (1978; 1980) demonstrated that visually orienting frugivorous bats display lunar phobia, and argued that the behaviour likely evolved in response to increased predation pressure during the brightest portion of the lunar cycle. However, because of the absence of predators, bats in temperate locations may not have evolved such a response. Baker (1962) argued that nocturnal birds of prey (e. g., owls), the most likely predators on bats, are incapable of the flight manoeuvres required to capture bats regularly. This may explain anecdotal reports which indicate lunar effects have no influence on bat activity (Bell 1980; Bradbury and Vehrencamp 1976; Leonard and Fenton 1983; Kronwitter 1988; Wai-Ping and Fenton 1989).

Myotis lucifugus did not demonstrate a habitat shift from open to covered habitats in response to increasing lunar light levels unlike rodents (Daly et al. 1992) and birds (Watanuki 1986). Reith (1982) concluded that *Myotis yumanensis* used shadows more during moonlight conditions, but his data were collected on only 7 nights during one month. Clark et al. (1993) commented that in bright moonlight *Plecotus townsendii* foraged adjacent to vertical surfaces such as trees and cliffs, but presented no quantitative data. At our study site, habitat shifts are known to occur, but apparently for aerodynamic reasons as a result of fluctuations in body mass (Kalcounis and Brigham 1995). However, because activity did not decrease in bright moonlight, the lack of evidence for a habitat shift is not surprising. That activity in the water habitat was higher than the field or forest reinforces the findings of other studies on activity patterns of this species (Fenton and Barclay 1980).

There is considerable debate in the literature as to whether the lunar cycle influences flying insect activity. Evidence for a lunar effect on insect abundance may be due to decreased light trap effectiveness during moonlit periods (Siddorn and Brown 1971). Williams and Singh (1951) used alternative attractants and did find a lunar effect on insect abundance. Conversely, Bidlingmayer (1964), Bowden and Morris (1975), Williams et al. (1956), and Hardwick (1972) found that insect densities either increased or did not change during the period of the full moon. When taken in combination these studies suggest that the effect of the lunar cycle is likely species specific (Brown and Taylor 1971; Taylor 1986), and the effect on overall prey abundance for bats may be negligible which would concur with our activity results.

Ambient temperature was a good predictor of bat activity levels, an idea widely reported in the literature (e. g., O'Farrell and Bradley 1970). Temperature is presumed to have mostly indirect effects on bat activity because low ambient temperatures decrease flying insect activity (Taylor 1963; Mcgeachie 1989; Danthanarayana and Gu 1992).

Cloud cover, strong winds, and precipitation were rare during our sampling, and thus, not important factors influencing activity. The one cloudy night which had no bat activity also had a low ambient temperature. Cloud cover does not appear to affect activity levels of birds (Mills 1986) or bats (Leonhard and Fenton 1983), even for those bats which do exhibit lunar phobia (Morrison 1978).

Although it is likely that we only detected *M. lucifugus* in this study, it is possible that other insectivorous bats were also sampled. Ultrasonic bat detectors provide a simple and inexpensive means for monitoring bat activity without the need for catching, and thus potentially disturbing bats. However, the detectors we used only provide information on an approximate 3 kHz window at one time (Thomas and West 1984), and do not allow for unambiguous species identification. The next step is to use radio-telemetry and directly assess the activity patterns of known individuals with respect to the lunar cycle (e. g., Brigham and Barclay 1992).

To maximize fitness, animals should increase the benefits of activity (which is often associated with feeding) while reducing the costs associated with activity. Since little brown bats do not reduce activity levels during the brightest part of the lunar cycle, we infer that they do not experience significant costs, either in terms of increased predation risks or decreased prey levels, during periods with lunar light.

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Zusammenfassung

Der Einfluß von Mondlicht auf die Aktivität der kleinen braunen Fledermaus Myotis lucifugus.

Die Mondphasen beeinflussen das Aktivitätsmuster einer Reihe von Organismen, u. a. von Meeresfischen, Nagern, Vögeln sowie frugivoren Fledermäusen. Es wird ferner angenommen, daß Mondlicht, insbesondere Vollmond, die Aktivität insektivorer Fledermäuse aufgrund erhöhter Predationsgefahr oder geringerer Verfügbarkeit von Beute vermindert. Die zugrundeliegenden Beobachtungen sind jedoch im Allgemeinen Einzelfälle, und die wenigen vorhandenen quantitativen Daten können die Annahme weder erhärten noch widerlegen. Das Ziel unserer Untersuchung war, das Verhältnis der Aktivität von *Myotis lucifugus* zum Mondzyklus und anderen Umweltbedingungen, z. B. Umgebungstemperatur, Bewölkungsgrad, Windstärke, zu bestimmen. Sind Fledermäuse „mondscheu", um Predatoren zu entgehen, sollte ihre Aktivitätsintensität abnehmen oder sie sollten in geschütztere Habitate ausweichen. Wir verwendeten Ultraschallempfänger, um die Fledermausaktivität zu messen. Entgegen unserer Annahme bestand kein signifikanter Zusammenhang zwischen Mondphase und Fledermausaktivität. Es gab auch keine Anzeichen für einen Habitatswechsel in Abhängigkeit von der Mondphase. Die Aktivität korrelierte einzig mit der Umgebungstemperatur, ein Ergebnis das auch in anderen Untersuchungen häufig gefunden worden ist. Unsere Ergebnisse zeigen, daß insektivore Fledermäuse nicht mondscheu sind und daß sie bei hellem Mondlicht weder stärkerer Predation ausgesetzt sind, noch die Verfügbarkeit von Beute eingeschränkt ist.

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Timing of reproduction in the Red fox, *Vulpes vulpes*

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Abstract

Ovulation date was estimated for 93 female red foxes (*Vulpes vulpes*) collected in central Italy. Three methods were used: ageing embryos, examination of ovarian bodies, and of placental scars. Most females ovulated around 26 February (SD ± 9.5 days). Estimates from different methods gave consistent results. Ovulation date was independent of physical condition and size, but was 5 days earlier in the north of the study area than in the south. The testes of 154 males were also weighed. Male testicular mass decreased after the end of February. Results from this and other studies are consistent with the hypothesis that timing of reproduction in the red fox is constrained by a winter trophic bottleneck in the north, but can be more variable in the south. Small-scale variation in our study area was probably unrelated to food availability.

Introduction

The red fox (*Vulpes vulpes*) is a seasonal breeder. Its reproduction has been studied both in the wild (in North America and in northern Europe) and in fur farms (see Hayssen et al. 1993 for a review). In central and northern Europe, oestrus is later with increasing latitude (i. e. late January to late March at 51°N to 63°N); with 52–53 days of gestation, whelping occurs from mid-March to mid-May (Lloyd and Englund 1973). From the study of Lloyd and Englund (1973), however, no data for northern American red foxes were available. In Scotland, the onset of breeding shows local variation, presumably depending on local food availability (Kolb and Hewson 1980). No interannual variation was recorded (Fairley 1970). Spermatogenesis in males ceases after the female oestrus (e. g. Fairley 1970).

We hypothesised that the onset of breeding in the red fox may be regulated by two different phenomena: (a) in the northern part of its range, where foxes are under nutritional stress during winter (e. g. Lindström 1982), females must postpone the birth season until the increase in environmental productivity. At the same time, a delay of reproduction causes cubs to enter the winter at a younger age. The equilibrium point between the two opposing selective pressures will be positively related to the beginning of productivity pulse (i. e. spring; Geist 1987), which in turn is positively related to latitude; (b) more to the south, where winters are shorter and less rigorous, limiting factors (e. g. food availability and quality in spring or in summer: Cavallini and Lovari 1991; social structure: Lindström 1989) are presumably more variable among areas. Here we can therefore expect a lack of relationship between latitude and onset of breeding at lower latitudes. Data from the southern part of the fox range are therefore important to test these concepts. Unfortunately, no studies have been carried out in Mediterranean environments (except for a recent preliminary report from Spain; Martorell and Gortazar 1993).

Objectives of this study were to: (a) evaluate the seasonality of reproduction in wild red foxes from a Mediterranean region (central Italy), from an area where no data are yet available, (b) compare these results with published results from other areas, and (c) test the above hypothesis on the relation between the timing of ovulation and latitude.

Material and methods

From January to May 1992, during the main fox hunting season, we obtained 330 red foxes (205 M, 125 F) from hunters in the Pisa Province (ca. 43°N, 10–11°E), central Italy. Due to physical damage, sample size was reduced. The area (52 km E–W by 75 km N–S; 2 448 km^2) is mostly flat and intensively cultivated (mainly cereals) in the north, becoming increasingly hilly (up to 800 m a. s. l.) and wooded towards the south. Climate is Mediterranean, with mild winters and dry, hot summers. Foxes were usually collected within 6 hours of death and kept in plastic bags in a refrigerator (≤48 hours, –2 °C) until dissection. Before dissection, foxes were weighed (±0.05 kg) and measured (head and body length; ±0.5 cm). Complete female reproductive tracts (from cervix to ovaries included) were also removed, and the ovulation date estimated by 3 methods:

(1) ageing embryos by mass and crown-rump method (Layne and McKeon 1956; Englund 1970). Length was measured ±0.05 mm, mass ±0.01 g. Dead embryos diagnosed by (a) the presence of placental remnants only; (b) disintegration of the embryo; (c) anaemic and flaccid condition of the embryo compared with others of the same litter (Englund 1970) were excluded. This method is applicable only to embryos ≥28 days from the date of conception. For younger embryos, age was estimated (although less accurately) by measuring the major diameter of the corresponding uterine swelling (Englund 1970). To reduce within-litter variability, we used the average for the entire litter both for younger and older embryos.

(2) Ovarian bodies were examined both macro- and microscopically, and were classified in: (a) primary follicles (characterised by several layers of cells surrounding the ovum); we estimated that these bodies were present about 8 days before ovulation; (b) mature follicles, where the cells surrounding the ovum secrete an oestrogen-rich fluid that fills the cavity (antrum) and surrounds the egg; they develop after the primary follicles, but before ovulation. We therefore estimated that they occur approximately 5 days before ovulation; (c) de Graafian follicles, protruding above the surface of the ovary with the liquor folliculi under pressure; they are present before ovulation (approximately 2 days); (d) after release of the ovum, the follicular cavity fills with blood and lymph, which is gradually replaced by granulosa cells to form the corpus luteum; we called these bodies transition structures, and estimated their occurrence as about 14 days after ovulation (Valtonen 1992; Valtonen and Jalkanen 1993; L. Jalkanen, pers. comm.). When one of the ovaries was damaged, the sample was excluded.

(3) After parturition, placental scars are swollen (Kirkpatrick 1980). We estimated that about 4 days intervened between parturition and sampling (56 days from conception) when traces of blood were still visible in the swollen area. We assumed that 2 days intervened between ovulation and conception, and 52 days between conception and parturition (Hayssen et al. 1993). No adequate reference figures on the macroscopic development of the ovary during ovulation and conception are available in the literature. All our estimates are therefore approximations only.

Mass of testes is higher (about 8 g) during the spermatogenetic period, and vital spermatozoa are found only during the 2 or 3 months of peak testicular mass. When testicular mass decreases, no vital spermatozoa are present in male reproductive tracts (Fairley 1970; Lloyd and Englund 1973; Nelson and Chapman 1982). Both testes (including epididymes) were therefore removed from males and weighed (±0.1 mg). Damaged testes were excluded from the sample. Age was determined by measuring eye lens mass and canine teeth pulpar width, and by counting the incremental annuli in the cementum of canine teeth (Jensen and Nielsen 1968; Cavallini and Santini 1995). The logarithm of the kidney fat index was used to evaluate nutritional status (e. g. LaJeunesse and Peterson 1993; Cavallini 1994).

We used parametric statistical tests (regression analysis) for normally distributed variables (as determined by Lilliefors test, a modified version of the Kolmogorov-Smirnov test; Lilliefors 1967), nonparametric tests (Kruskal-Wallis ANOVA, Mann-Whitney's two-sample test) for the remaining variables.

Results and discussion

Date of ovulation was determined for 93 females. Estimates for different methods ranged from day 54 (swollen placental scars, N = 8) to day 60 (mature follicles, N = 8) from the beginning of the year. Most ovulation dates were determined by embryo ageing (mean date = 54.8 days ±9.6 SD, N = 30) and by immature follicles (57.9 days ± 9.6 SD, N = 24). Difference among methods was not significant (Kruskal-Wallis Test, H = 5.72, p = 0.33, 5 d. f., N = 93). Births were highly synchronised: half of the females ovulated between 22 February and 3 March (median: 25 February; average: 57th day from the beginning of the year ±9.5 SD; range: 2 February–21 March); therefore most births took place around the end of April.

Ovulation date was independent from the age class of the female (Mann-Whitney Test, U = 1 177, p = 0.18, N = 90), from nutritional status (logarithm of the kidney fat index: regression analysis, $r^2 = 0.02$, p = 0.20, N = 80) and from physical dimensions (head and body length: regression analysis, $r^2 = 0.002$, p = 0.69, N = 86). Females from the north of the study area ovulated on average 5 days earlier than those in the south (north: 54.8 days ± 9.5 SD, N = 59; south: 60.2 days ± 8.6 SD, N = 34; Mann-Whitney Test, U = 717.5, p = 0.022).

Mass of testes from 145 foxes was constant from January until the end of February. After mid-March it decreased rather abruptly (Fig. 1).

The different methods used to estimate ovulation date gave consistent results, and therefore can be compared, and each can be used in future studies. Female red foxes in central Italy ovulated around the end of February, and the fertile period for males presumably ended after mid-March. This was substantially later than determined in all other studies conducted at low latitudes, and close to values for northern Sweden (Tab. 1). The relationship between latitude and ovulation date is approximately linear, positive and very strong at northern latitudes (>55°N; $r^2 = 0.900$, p = 0.004, N = 6), as shown in an earlier study (Lloyd and Englund 1973). Below 55°N, this relationship disappears ($r^2 = 0.020$, p = 0.68, N = 11), and the scatter among studies is very large (Fig. 2; about

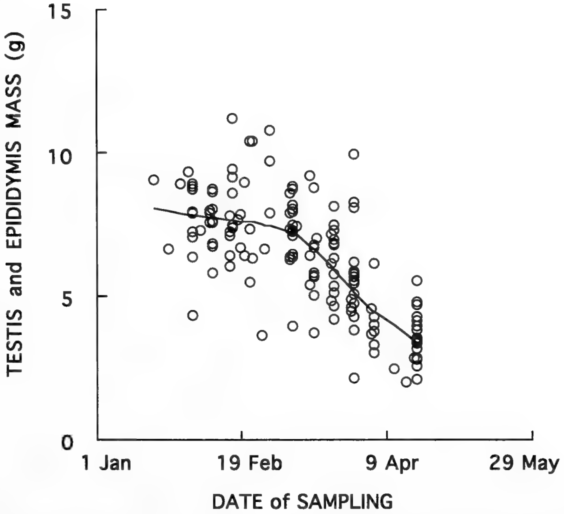

Fig. 1. Decrease of mean testis and epididymis mass with date of death for 145 male red foxes collected between January and May 1992 in the Province of Pisa, central Italy. The curve indicates LOWESS smoothing (Cleveland 1981).

40 days among the fox populations living between 41.5°N and 43.5°N). Within the Mediterranean area, Spanish foxes ovulate about 20 days earlier than Italian foxes (Tab. 1). These results are in accordance with our hypothesis: timing of reproduction of foxes ap-

Table 1. Ovulation date of the red fox (*Vulpes vulpes*) in various areas (in N–S order) compared to the present study

Reference	Area	Ovulation date
LLOYD and ENGLUND (1973)	Jarmtland, Sweden	22 March [a]
LLOYD and ENGLUND (1973)	Varmland, Sweden	5 March [a]
LLOYD and ENGLUND (1973)	Uppland, Sweden	20 February [a]
KOLB and HEWSON (1980)	NE Scotland, U. K.	26 January [b]
KOLB and HEWSON (1980)	W Scotland, U. K.	5 February [b]
LLOYD and ENGLUND (1973)	Skane, Sweden	30 January [a]
LLOYD and ENGLUND (1973)	Wales, U. K.	28 January [a]
LLOYD and ENGLUND (1973)	England, U. K.	22 January [a]
FAIRLEY (1970, 1971)	NE Ireland, U. K.	20 January [b]
ARTOIS et al. (1982)	N France	24 January [b]
ALLEN (1984)	N Dakota, U. S. A.	6 February [b]
SHELDON (1949)	New York, U. S. A.	18 January [b]
STORM et al. 1976	Iowa and Illinois, U. S. A.	2 February [b]
PILS and MARTIN (1978)	Wisconsin, U. S. A.	12 February [b]
MARTORELL and GORTAZAR (1993)	NE Spain	5 February [b]
MCINTOSH (1963)	ACT, Australia	15 July [b]
This study	Pisa, central Italy	26 February [c]

[a] median
[b] recalculated average (approximate)
[c] average

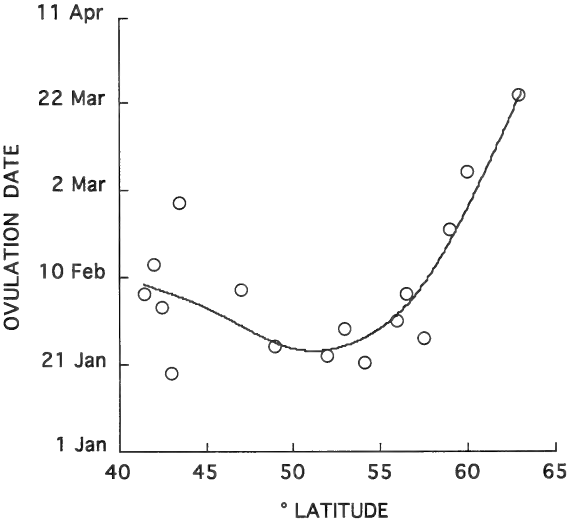

Fig. 2. Relationship between mean (or median, when the mean is unavailable) ovulation date in female red foxes and degrees of latitude North across different studies. The curve indicates distance weighted least squares smoothing (MCLAIN 1974). For references to individual studies, see table 1.

pears strongly constrained by the winter trophic bottleneck in the north (Lindström 1982), but is more variable among localities in the south. The few studies from the southern hemisphere (Australia; 35°30′ S; McIntosh 1963; Ryan 1976) indicate that most oestruses here occurred in mid-July, corresponding to mid-January in the northern hemisphere.

Within our study area, variations in the date of ovulation cannot be attributed to age or physical conditions. In contrast, local variation in timing is small but significant even at such a small scale (<70 km). This result, although surprising, is consistent with the findings of a study in Scotland: cubs in the west were born on average 10 days later than in the northeast (separated by approximately 150 km), probably because the peak in food availability is different in the two areas (Kolb and Hewson 1980). In the Province of Pisa, north-south differences in food consumption are limited to a few secondary food items (Cavallini 1994), so that this is not a likely candidate to explain the difference in ovulation dates within such a small area. Habitat, hunting pressure, external morphology, and female fat levels are different between the north and the south of our study area (Cavallini 1994; Cavallini in Press). The relative influence of these factors on the small-scale timing of reproduction, however, is unclear.

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Zusammenfassung

Zeitliche Abstimmung der Fortpflanzung beim Rotfuchs, Vulpes vulpes.

Das Eisprungdatum wurde für 93 Rotfuchsfähen, die in Zentralitalien gesammelt wurden, geschätzt. Es wurden drei unterschiedliche Methoden eingesetzt, und zwar: Altersbestimmung des Embryos, Untersuchung der Eierstöcke und der Gebärmutternarben. Bei den meisten Weibchen setzte der Eisprung um den 26. Februar ein (SD ± 9.5 Tage). Schätzungen durch die verschiedenen Methoden ergaben konsistente Ergebnisse. Der Eisprung war unabhängig vom Körperzustand und der Körpergröße, setzte aber im Norden des Studiengebietes 5 Tage früher ein als im Süden. Auch die Hoden von 154 Rüden wurden gewogen, und es wurde festgestellt, daß deren Masse nach Ende Februar abnahm. Die Ergebnisse dieser und anderer Studien unterstützen die Annahme, daß die zeitliche Abstimmung der Fortpflanzung beim Rotfuchs durch winterlichen Futtermangel im Norden eingeschränkt wird, im Süden jedoch variabler ist. Unterschiede kleineren Maßstabes in unserem Studiengebiet waren wahrscheinlich mit Futteranwesenheit nicht korreliert.

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Stomach contents of stranded Common Dolphins *Delphinus delphis* from the south-east of Southern Africa

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Abstract

Examined were the stomach contents of common dolphins stranded, both singly and mass, along the south-east coast of southern Africa between 1975 and 1991. Prey are an indication of the prey resources available to predators, during the summer months. Overall, the diet was dominated by cephalopods, particularly the locally abundant squid species *Loligo vulgaris reynaudi*, occurring in 92.9% of the total number of stomachs and constituting 18.6% and 40.3% of the total percentage number and percentage reconstituted mass, respectively. Other important cephalopods were *Sepia officinalis* and *Lycoteuthis diadema.* The fish content of the diet was made up predominantly of three species of clupeoid fish – *Sardinops sagax*, *Etrumeus whiteheadi* and *Engraulis japonicus.* Fish species dominate the diet between 1975 and 1979 but between 1980 and 1989 cephalopod species constitute 89.9% of the total reconstituted mass of prey. Reproductive activities and nutritional demands result in a form of resource partitioning, whereby lactating dolphins and calves have the same dietary preference. The results of the study reflect the summer diet of common dolphins in the region and are compared to the winter diet, as found in the stomach contents of incidentally-caught common dolphins, further north. The diet of the mass-stranded common dolphins stress the important influence that nutritional demands and regionally distinct prey abundance have on the distribution and movements of common dolphins along the south-east coast of southern Africa.

Introduction

It has been suggested that dietary studies based on the stomach contents of stranded animals may be biased because of illness (Jones 1981) and/or show differences between stranded and non-stranded animals of the same species, because of their passage through coastal waters prior to stranding (Leatherwood et al. 1978; Sekiguchi et al. 1992). However, the usefulness of interpreting cetacean diets from the examination of stomach contents of stranded animals remains equivocal. Ross (1984), in a study of 24 cetacean species, found no bias and concluded that stranded cetaceans provide an accurate indication of the normal diet, at least in the region sampled. The diet of seven incidental common dolphin captures and nine strandings off the south-east coast of southern Africa showed the diet of both samples to be an indication of the local fish fauna. In addition to this, the type of prey dominant in the diet of both stranded and free-ranging common dolphins in this region matched that of common dolphins in the Black Sea (Tomilin 1967); the Pacific (Evans 1976); British waters (Evans 1980); the Mediterranean (Schmidt 1923); the north-east Atlantic (Collet 1981), the south-west (Sekiguchi et al. 1992) and south-east (Young and Cockcroft 1994) coasts of southern Africa.

Common dolphins, from all geographic regions, are generally considered to be opportunistic feeders, consuming seasonally and locally abundant, easily captured, small shoaling prey, associated with the deep scattering layer (Schmidt 1923; Tomilin 1967; Evans 1976; Collet 1981; Pascoe 1986; Evans 1987; Overholtz and Waring 1991; Young and Cockcroft 1994). In this respect, they are similar to other delphinids, whose movements closely parallel that of potential prey – dolphin distribution and diet apparently determined by seasonal and topographic changes in preferred prey abundance (Hui 1979; Evans 1980; Leatherwood et al. 1982; Pascoe 1986; Selzer and Payne 1988).

On the south-east coast of southern Africa, common dolphins inhabit cool temperate waters, south of about 33° latitude, in the austral summer, but large numbers make an extensive northerly migration into warm, more tropical waters during winter. This migration appears to be closely linked to the winter, northward migration of large shoals of South African pilchard (*Sardinops sagax*) known as the 'sardine run' (Cockcroft and Peddemors 1990). The diet of common dolphins off this coast, during the winter months, was reported to be dominated by pelagic, shoaling fish, such as pilchard, anchovy (*Engraulis japonicus*) and red-eye herring (*Etrumeus whiteheadi*) and squids (Cockcroft and Ross 1983; Cockcroft and Peddemors 1990); although Young and Cockcroft (1994) showed there to be a large content of elf (*Pomatomus saltatrix*), maasbanker (*Trachurus delagoa*), mackerel (*Scomber japonicus*) and strepie (*Sarpa salpa*) in the diet during this time. This diet composition is a reflection of those fish species present during the annual migration.

This study examines the diet of common dolphins along the south and south-east coasts of southern Africa, using animals stranded in this region between 1975 and 1992. Regardless of biases inherent in data from stranded animals, these data are often the only data available for certain areas or populations/stocks; and are able to provide an important counter perspective where data for free-ranging animals are also accessible. In this respect, the results of this study will be compared with the diet of common dolphins incidentally captured 1 000 km further north in Natal (Young and Cockcroft 1994).

Common dolphins examined for this study do not fit the classification of Heyning and Perrin (1994). They show a combination of the colour pattern of *Delphinus delphis* and the long rostrum of *D. capensis.* Consequently, the earlier, single species classification of *D. delphis* is used.

Material and methods

A total of 83 common dolphins stranded between Mossel Bay (34°10′ S; 22°08′ E) and Mzamba (31°06′ S; 30°10′ E), Transkei (Fig. 1), between 1970 and 1992. However, only 39 stomachs were available for examination. This number also includes samples from a mass stranding; at Hluleka Nature Reserve (31°37,4′ S; 29°18′ E), Transkei. Morphological measurements and biological samples, wherever possible, were taken for all specimens and are kept at the Port Elizabeth Museum. The methodology used for stomach excision, sorting of stomach contents and prey identification are described in Cockcroft (1990) and Young and Cockcroft (1994). Fish nomenclature follows that of Smith and Heemstra (1986).

The maximum number of left or right otoliths, and upper or lower cephalopod beaks, was used as an indication of the total number of prey in each stomach. Otoliths and beaks were measured across the greatest diameter and across the lower rostral length, respectively. (Lower hood length was used in the case of sepiids (Clarke 1986 a, b). Reconstituted weight and length data were calculated using the appropriate regression or estimate (Cockcroft and Ross 1990; Young and Cockcroft 1994). An index of relative importance (IRI) was calculated for each species such that, IRI = (percentage number + percentage reconstituted weight)×percentage frequency occurrence (Pinkas et al. 1971).

Results

Twenty eight of the 39 stomachs contained solid prey remains. From these, fifteen fish species and four cephalopod species were identified. Cephalopods (particularly *Loligo*

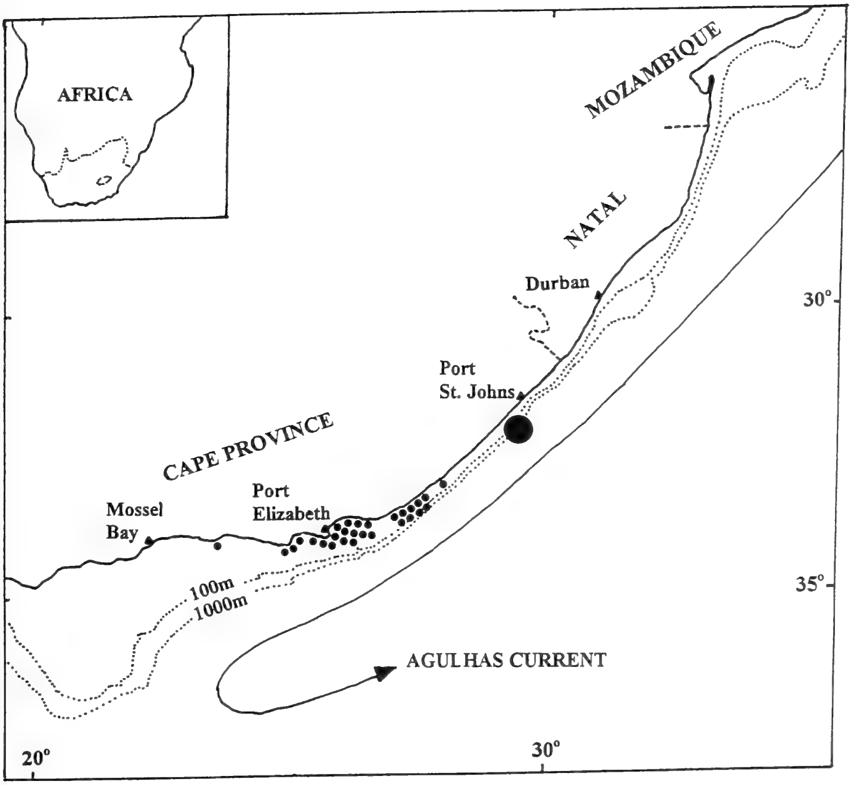

Fig. 1. Map showing the location of common dolphin strandings along the south-east coast of southern Africa (• single stranding; ● mass stranding).

squid) and clupeoid fish prey dominated the diet of stranded common dolphins (Tab. 1). However, there were clear interannual variations (between 1975 and 1991) in the relative importances of the five most important prey according to percentage weight, percentage frequency of occurrence and/or percentage reconstituted mass (Tab. 2).

Between 1975 and 1979 the diet was dominated by pelagic clupeoid fish, whereas cephalopod species dominated the diet between 1980 and 1989. In 1990 and 1991, the diet was again dominated by fish species, similar to that of 1975–1979 (Tab. 2). The ratio of fish to squid in the diet varied with sex-size groups and reproductive state (Fig. 2). Lactating females and calves ate mainly cephalopod prey (*Loligo* squid and cuttlefish, *S. officinalis*), in contrast to mature males, resting and pregnant females, which apparently preferred small, shoaling fish (pilchard and herring). However, the total number of prey species consumed did not differ significantly between sex-size groups ($\chi^2 = 2.29$; df = 5; $P > 0.05$) (Fig. 2).

Though there was a low correlation between dolphin length and actual stomach content weight ($r = 0.12$; $p < 0.05$; $n = 27$), the correlaton between dolphin length and total reconstituted weight of prey in the stomach was significant ($r = 0.34$; $p < 0.05$; $n = 27$). Similarly, although the correlation between dolphin length and the total number of prey items consumed was significant ($r = 0.36$; $p < 0.05$; $n = 28$), that between dolphin length and the number of prey species eaten was not ($r = 0.14$; $p > 0.05$; $n = 28$). Additionally, there was a significant correlation between dolphin length and mean length of prey ($r = 0.45$; $p < 0.05$; $n = 21$).

Table 1. Fish and cephalopod prey consumed by stranded common dolphins along the south-east coast. (A – number; B – percentage number; C – frequency of occurrence; D – percentage frequency of occurrence; E – reconstituted mass; F – percentage reconstituted mass; IRI – Index of Relative Importance, see text) (ND – no data)

SPECIES	A	B	C	D	E	F	IRI
Fish							
Etrumeus whiteheadi	403	22.9	16	57.1	26 668.2	17.5	2 312.5
Sardinops sagax	298	22.6	12	42.9	32 358.4	21.3	1 882.6
Engraulis japonicus	182	10.4	13	46.4	2 962	2	571.1
Unid. myctophid spp.*	116	6.6	3	10.7	9 562.2	6.3	138.1
Merluccius capensis	36	2.1	4	14.3	758.7	0.5	36.4
Pomadasys olivaceum	1	0.1	1	3.6	ND	ND	0.2
Pagellus bellotti	7	0.4	2	7.1	47.6	ND	3.1
Atrobucca nibe	1	0.1	1	3.6	371.3	0.2	1.1
Trachurus delagoa	3	0.2	1	3.6	1 176	0.8	3.4
Unid. trachurid	6	0.3	1	3.6	ND	ND	1.2
Liza sp. 1*	29	1.7	4	14.3	758.7	0.5	36.4
Liza sp. 2*	1	0.1	1	3.6	219.5	0.1	0.7
Sphyraena spp.	1	0.1	1	3.6	16.1	ND	0.2
Trichiurus lepturus	3	0.2	2	7.1	ND	ND	1.2
Scomber japonicus	6	0.3	5	17.9	1 766.5	1.2	26.9
Unidentified fish	10	0.6	3	10.7	ND	ND	6.1
Cephalopods							
Sepia officinalis	43	2.5	7	25	2 650.7	1.7	104.7
Loligo spp.	327	18.6	26	92.9	61 227.7	40.3	5 467.5
Lycoteuthis diadema	184	10.5	7	25	5 771.5	3.8	356.6
Ommastrephes bartrami	1	0.1	1	3.6	18.8	0.1	0.3

* common regression calculated

Table 2. Annual changes in the five most important prey species in the diet of stranded common dolphins between 1975 and 1991 (A – percentage number; B – percentage frequency of occurrence; C – percentage reconstituted mass; IRI – Index of Relative Importance, see text) (ND – no data).

SPECIES	A	B	C	IRI	IRI RANK
1975–1979					
E. whiteheadi	32.8	28.6	36.9	1 992.7	2
S. sagax	19.8	42.9	32.8	2 250.2	1
Myctophid spp.	28.4	28.6	ND	811.3	4
S. officinalis	2.5	42.9	2.8	224.2	5
Loligo spp.	4.7	42.9	16.2	893.6	3
No. stomachs = 7					
1980–1989					
A. nibe	0.5	16.7	3.1	59.7	5
Liza sp. 1	3.7	16.7	6.2	165.2	4
S. officinalis	15.9	50	7.8	1 185.2	2
Loligo spp.	53.4	66.7	77.7	8 740.2	1
L. diadema	17.5	33.3	4.4	727.7	3
No. stomachs = 6					
1990–1991					
E. whiteheadi	23.7	78.6	25.9	3 893.5	2
S. sagax	48.3	64.3	63.5	7 181.1	1
E. japonicus	25.8	78.6	6.9	2 566.6	3
S. japonicus	0.5	21.4	2.2	56.9	4
Loligo spp.	0.8	21.4	1.6	50.2	5
No. stomachs = 14					

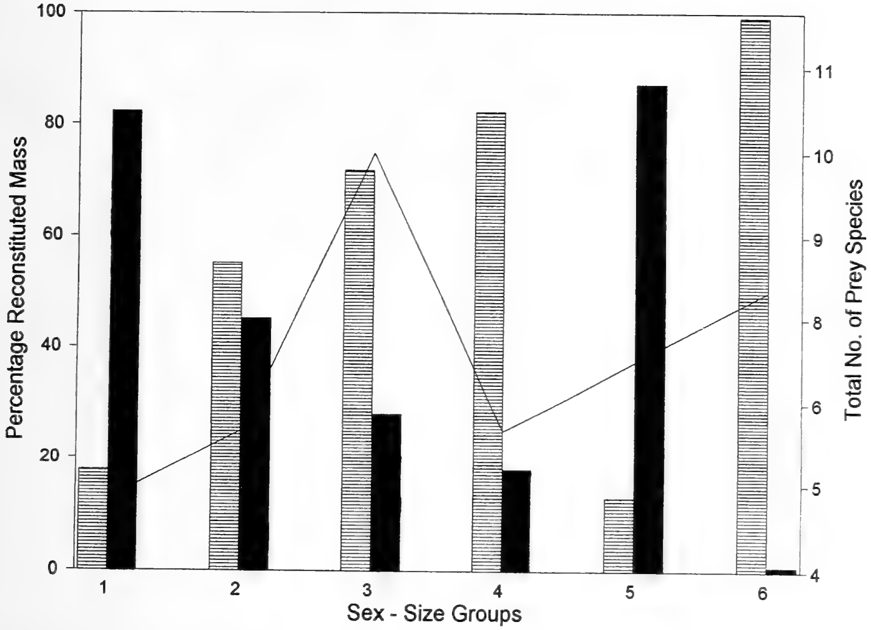

Fig. 2. The proportion of fish (hatched) and cephalopod (solid) prey items (by percentage reconstituted mass) in the diet of different sex-size groups of stranded common dolphins (the solid line indicates the total number of prey species consumed by each group – 1. calves; 2. adolescents; 3. mature males; 4. non-lactating females; 5. lactating females; 6. pregnant females).

Fifteen animals originated from a mass stranding at Hluleka Nature Reserve, Transkei (31°47′ S; 29°18′ E). The total reconstituted prey weight of this sub-sample comprised 26.2% of the total for all stranded common dolphins. Three fish species accounted for 96.8% of the total prey weight for this group, i. e. pilchard, (64.5%), herring (25.8%) and Cape anchovy (6.9%) (Tab. 3). Although anchovy accounted for only a small portion of the reconstituted weight, it was the most frequent prey species, identified from 84.6% of stomachs. *Loligo* squid accounted for only 1% (by reconstituted prey weight) and was found in only two of the 13 stomachs.

Table 3. Fish and cephalopod prey species in the diet of common dolphins mass stranded at Hluleka Nature Reserve, Transkei (A – percentage number; B – percentage frequency of occurrence; C – percentage reconstituted mass; IRI – Index of Relative Importance, see text).

SPECIES	A	B	C	IRI	IRI RANK
Fish					
E. whiteheadi	22.9	76.9	25.8	3 742.2	2
S. sagax	49.5	69.2	64.1	7 858.4	1
E. japonicus	26.4	84.6	6.9	2 823.9	3
S. japonicus	0.5	23.1	2.2	62	4
Cephalopods					
Loligo spp.	0.3	15.4	1.00	20.2	5

No. stomachs = 13

Discussion

The mass-stranded group was found to comprise 13 mature females and 2 males: an adult and an adolescent. Of the 13 females, 11 were pregnant. The dietary composition of these animals was similar to free-ranging common dolphins off Natal (Young and Cockcroft 1994) characterized by an abundance of pilchard and a lack of cephalopod species. In contrast, the stranded common dolphins from the Eastern Cape coast consumed predominantly cephalopod species and a large amount of herring. The reasons for these differences are unclear, but they could reflect regionally disparate prey abundance and availability.

Common dolphins, along the south-east coast are found throughout the year below the 33° latitude (Cockcroft and Peddemors 1990). However, they are only found north of this during the annual winter fish migration, locally known as the 'sardine run'. As the shoals of pilchard, other clupeoids and migratory fish species are followed by predatory fish, sharks, whales and dolphins, the distribution of common dolphins, in particular, undergoes a massive shift norhwards. In this respect, the presence of common dolphins along the Transkei coast (31°47′ S; 29°18′ E), during the austral summer is unusual. The mass stranding took place in December, three months after the end of the 'sardine run', and it is possible that these animals may have been feeding on pilchard, and other clupeoids, returning to the south on the Agulhas current (Davies 1956; Baird 1971; Crawford 1981). However, the size of pilchard in the diet does not suggest this. The mean size of pilchard found in stomachs of mass-stranded animals (21.5 cm) did not differ from those in the stomachs of dolphins stranded elsewhere (22.5 cm), or from the free-ranging animals in Natal (22.5 cm) (Young and Cockcroft 1994).

Results of both the present study and Young and Cockcroft (1994) show that pregnant common dolphins consume a larger proportion of fish than lactating females. The nutritional demands of the mass-stranded group (predominantly pregnant females) may have forced them to move northwards in search of more abundant, energy-rich prey. Lactating females, which depend more on cephalopod prey, probably remained further south where squid resources are more abundant, during summer.

For single-stranded common dolphins the majority of the diet is accounted for by cephalopods, especially *Loligo* spp. *Loligo vulgaris reynaudii* is an abundant, common squid along the continental shelf of the southern and eastern coasts of southern Africa (Augustyn 1989, 1990; Sauer 1993). Comparable to the pelagic schooling fish species which play a major role in the diet of common dolphins from other regions (Tomilin 1967; Collet 1981; Jones 1981; Leatherwood et al. 1982; Ross 1984; Klinowska 1991, Young and Cockcroft 1994), this semi-pelagic species occurs in the coastal waters, during the summer, forming dense "spawning concentrations" in the inshore zone. These seasonally abundant, spawning squid masses, appear to have an important influence on the distribution and diet of common dolphins in the area. Although stranding localities cannot be used as a direct indication of dolphin distribution and the causes of single strandings are unknown, the areas where squid form spawning concentrations along the East Cape coast (Sauer 1993), coincide with the areas where the majority of single strandings occur. Of the 39 animals, all except four, stranded in spring and summer, coinciding with those months in which dense concentrations of spawning squid form. It is uncertain whether the higher number of common dolphin strandings can be directly related to their close proximity to the shore, making them more susceptible to stranding; or is merely an indication of a larger number of dolphins in the area, due to an abundance of prey.

Besides the large number of cephalopods in the diet, the stomach contents can also be used as an indication of the fish fauna along the coast. Of the dominant clupeoid component, round herring, which is abundant and widespread along the east coast, throughout the year, makes up the largest percentage. The distribution of pilchard, herring and anchovy is reported to be significant and almost continuous along the South African south-east coast; and the respective biomasses are of approximately the same proportions as that found in the diet (Armstrong et al. 1991). However, the biomass of pilchard and round-herring is reduced in winter, when a portion of the stock moves northwards during the 'sardine run' (Smale 1983; Armstrong et al. 1991).

Common dolphin diet has undergone various fluctuations between 1975 and 1991, the most dramatic change coinciding with increased commercial squid catches during the late 1980's, reaching a peak of 10000 tons in 1989, whereafter, commercial catches declined markedly (Sauer 1993). This temporal pattern in prey abundance is reflected in common dolphin diet during this time.

Although only four common dolphins stranded in the winter months, specifically May, the diet of these animals does not differ significantly from strandings in spring and summer. The winter diet consists of an abundance of cephalopod species. Fish species found in the winter diet include herring, pilchard and myctophids.

The few winter samples give no evidence of a reduction in squid content in the diet, and possibly even an increase in cephalopod consumption. It is possible that those common dolphins which remain in southern waters during winter increase the proportion of squid in the diet to compensate for the reduced clupeoid abundance.

The prey spectrum consumed by all sex-size groups is narrow and most categories feed on similar prey. All adolescent and mature animals (excepting lactating females) fed primarily on fish, whereas calves and lactating females ate mainly cephalopods. Lactating spotted dolphins (*Stenella attenuata*) consumed a larger proportion of fish during lactation, attributed to higher nutritional demands (Bernard and Hohn 1989). Although fish tend to have higher energy contents than cephalopods, the most influential factor governing this dietary change may be the production of milk. Calves stranded in the Eastern Cape were younger than those captured in Natal, and therefore still dependent on the mother for milk and maternal care, reflected by a close dietary relationship. The similarities in diet may also indicate that common dolphins may teach and assist young calves to feed, as reported for bottlenose dolphins (Cockcroft and Ross 1990).

Energy stores may be severely depleted following the energetically expensive period of calving, maternal care and early weaning in Eastern Cape waters. The winter 'sardine run' presents an ideal opportunity for both the final weaning of calves from milk to the energy-rich solid foods necessary for growth and the mother's replenishment of depleted energy stores.

In Natal, free-ranging common dolphins appear to make use of resource partitioning to a greater extent than do those in the Eastern Cape (Young and Cockcroft 1994). This difference may be related to the nature of feeding activity in the two regions. The highly seasonal influx of prey, together with huge schools of common dolphins (Cockcroft and Peddemors 1990), during the 'sardine run' may result in concentrated, high-density feeding. Nursery groups may serve not only to reduce the costs of maternal care but also to protect the calves from potential predators during feeding activity (Young and Cockcroft 1994). Lactating females are then able to remain within the main feeding group, making optimum use of the available prey.

These data confirm that common dolphins are opportunists, making use of those prey species most abundant and readily available, on a temporal and regional scale. The diet of the mass-stranded common dolphins provides an interesting example of the effect that reproductive-related nutritional demands and regionally disparate prey resources have on the distribution and movements of common dolphins in the region. The different diet and feeding biology regimes of stranded and incidentally-caught dolphins (Young and Cockcroft 1994) can be attributed primarily to seasonally distinct prey abundance and distribution and reproductive-associated nutritional demands.

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Zusammenfassung

Mageninhalt gestrandeter Gemeiner Tümmler Delphinus delphis von der Südostküste des südlichen Afrika

Untersucht wurden die Mageninhalte von Gemeinen Tümmlern, die einzeln und in Massen, an der Südost-Küste von Südafrika zwischen 1975 und 1991 gestrandet waren. Die Beute lieferte Hinweise auf die Nahrungsressourcen, die während der Sommermonate zur Verfügung stehen. Cephalopoden dominierten die Nahrung, insbesondere die lokal häufige Art *Loligo vulgaris reynaudii*, die in 92.9% aller Mägen vorkam, 18.6% aller gezählten Beute ausmachte, sowie 40.3% Gewichtsanteil erreichte. Andere Cephalopoden von Bedeutung waren *Sepia officinalis* und *Lycotheuthis diadema.* Die wichtigsten drei Fischarten waren die Clupeiden *Sardinops sagax*, *Etrumeus whiteheadi* und *Engraulis japonicus.* Fische dominierten die Nahrungszusammensetzung zwischen 1975 und 1979, jedoch in den Jahren von 1980 bis 1989 machten Cephalopoden 89.9% Gewichtsanteil aus. Fortpflanzungsaktivitäten und Nahrungsbedarf führen zu einer Aufteilung der Beute, mit dem Resultat, daß säugende Weibchen und Kälber die gleiche Nahrung bevorzugen. Die Ergebnisse der Sommernahrung dieser Studie werden mit der Winternahrung von Gemeinen Tümmlern verglichen, die weiter im Norden in Netze geraten sind. Die Ergebnisse von Massenstrandungen machen deutlich, wie stark Nahrungsbedürfnisse und regionale Beutevorkommen die Verteilung und Wanderungen von Gemeinen Tümmlern entlang der Südost-Küste von Südafrika beeinflussen.

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Evidence of pre-mating reproductive isolation in two populations of the Vlei rat *Otomys irroratus*: experiments of intra- and interpopulation male-female encounters

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Abstract

Studied was the male-female interaction of representatives of two allopatric *Otomys irroratus* populations (Kamberg and Karkloof) in 40 intrapopulation and 34 interpopulation encounters. The study aimed to: (1) establish the existence of population-specific courtship behaviour during intrapopulation encounters; and (2) ascertain whether or not differences in courtship behaviour rendered males and females incompatible during interpopulation encounters. During intrapopulation encounters, Kamberg males and females were less aggressive and more amicable than their Karkloof counterparts, and Karkloof males performed more sexual acts than Kamberg males. These behavioural differences apparently reflect the social organization and mating behaviour of each population. Compared to intrapopulation pairings, interpopulation pairings displayed more exploratory behaviour, fewer sexual acts, more aggression, less amicability, and later development of essentially amicable interaction. It is possible that population-specific olfactory, visual and tactile cues resulted in highly aggressive interpopulation encounters. Aggression may function as a pre-mating reproductive isolating mechanism between the Kamberg and Karkloof populations should they meet in nature.

Introduction

Pre-mating reproductive isolating mechanisms prevent interbreeding between males and females of closely-related species. The most effective pre-mating isolating mechanisms are ethological ones (Dobzhansky et al. 1968), particularly courtship behaviour (Koepfer 1987). Species-specific courtship behaviour permit conspecific males and females to recognize only one another as potential mates, thereby ensuring positive assortative mating (Beiles et al. 1984).

Mutual recognition between conspecific mates during courtship is normally mediated by means of male-female signals and responses, which may be referred to as the specific-mate-recognition system (i. e. SMRS; Paterson 1980, 1985). The signal-response chain comprises all behaviour patterns leading to copulation (McFarland 1987), and includes several modalities of communication (e. g. odour, postural changes; Carter and Brand 1986; Koepfer 1987; Dempster et al. 1992).

Previous experiments on mate recognition in two allopatric populations (from Kamberg and Karkloof) of the vlei rat *Otomys irroratus* has revealed preference for mates of the same population or their odours (Pillay et al. 1995). It was predicted that population-specific courtship behaviour, and olfactory cues in particular, influenced mate recognition in Kamberg and Karkloof *O. irroratus*.

The present study aimed to investigate male-female interactions in intrapopulation encounters to establish the existence of population-specific courtship in Kamberg and Karkloof *O. irroratus.* An additional aim of the study was to ascertain whether or not differences in the courtship behaviour (i. e. differences in SMRSs) rendered representatives of these two populations behaviourally incompatible during interpopulation encounters. Such incompatibility would indicate the existence of pre-mating barriers to reproduction.

Material and methods

Animals used in the study were either live-trapped at Kamberg (29°23′S, 29°42′E) and Karkloof (29°17′S, 30°11′E) in the KwaZulu-Natal Midlands, South Africa, or laboratory reared descendants (F1) of wild-caught parents.

Details of the maintenance of animals in captivity and the conditions under which the present study was conducted are provided elsewhere (Pillay et al. 1992). Male-female interaction of 20 of each of Kamberg and Karkloof intrapopulation pairs and a total of 34 interpopulation pairs was studied in neutral arena encounters. Interpopulation pairings, specified below as male × female, were bi-directional (Plllay et al. 1992), comprising 18 Kamberg × Karkloof and 16 Karkloof × Kamberg pairs.

Encounters were staged in asbestos enclosures 90 × 90 × 60 cm, furnished with coarse wood shavings. Between encounters, wood shavings were changed after the enclosures were washed with water and a 50% ethyl alcohol solution to remove odours of the previous occupants.

Prior to observations, an enclosure was divided into two parts with a wire mesh partition. A female in pro-oestrus, ascertained by means of vaginal smears, and a male were placed on either side of the partition at 18.00 h. Following a familiarization period of approximately 14 h (i. e. approximately 08.00 h the next day, when females usually displayed oestrus), the partition was removed and the first 20 min of interaction video-recorded. Testing coincided with the period of maximum diurnal activity, from 07.00 h to 09.00 h. Recordings were made under fluorescent white light, using a Hitachi KP-141 CCTV camera and a Hitachi VTL-30ED time-lapse video cassette recorder.

Pillay (1990) showed that male-female interactions in staged encounters involving three *O. irroratus* populations differed at both the intra- and interpopulation level even after two weeks of pairing. Consequently, additional video recordings of the interactions of each pair in the present study were made every two days from the day of pairing (designated Day 0), for 12 days. Recordings under incandescent red lights were conducted during the dark phase of the light cycle from 00.00 h to 01.00 h, which represented the period of maximum nocturnal activity.

All animals were sexually experienced. Members of a pair had never previously met in the laboratory. Each male was used in two encounters – one intrapopulation and one interpopulation encounter. Females were used only once.

Analysis of video recordings made during the first 20 min of interaction entailed first encoding 18 male and 15 female behaviour patterns. Thereafter, all behavioural acts occurring in each 10-s interval of the 20 min observation period were recorded. Acts were identified when animals changed their behaviour (after Dempster et al. 1992).

The frequencies of all behaviour patterns of males and females of each pairing were calculated. Mean frequencies were obtained for each sex in respect of intrapopulation or interpopulation pairings.

During the nocturnal sampling (i. e. recordings every second night for 12 nights), the occurrence of only agonistic and amicable behaviour patterns in each pair were recorded, and mean percentages were calculated for intra- and interpopulation pairings. Other behaviour patterns (e. g. exploratory, sexual behaviour) were not considered because the frequency of their occurrence was too small to warrant analysis.

Results obtained from diurnal and nocturnal recordings were treated separately because of the different time scales involved (i. e. 20 min and on 7 nights). Data from diurnal experiments were tested for significance using the Mann-Whitney U test (Sokal and Rohlf 1987); significant differences were accepted at $P < 0.05$. Data obtained from the nocturnal study illustrated trends that were sufficiently clear to obviate the need for statistical analysis.

Results

Behaviour patterns identified in encounters are presented in table 1. All acts were displayed by both sexes, although follow-mounting and presenting were sex-specific activities (Tab. 1).

Table 1. Behaviour patterns identified in encounters. Those behaviour patterns that were combined to allow comparison between diurnal intrapopulation and interpopulation encounters are indicated as subsets A – D; see text.

Explore arena
Self-groom
Mark
Watch
Inactive
Naso-nasal contact

A) Agonistic
Aggressive approach
Chase
Upright sparring
Submissive flee

B) Amicable
Amicable approach
Groom invitation
Allogroom
Huddle

C) Follow-mount (males only)
Naso-anal contact
Follow
Attempted mount
Mount

D) Present (females only)
Move away
Dart
Present and lordosis

Interpopulation same-sex comparisons of the frequencies of behaviour patterns recorded in intrapopulation encounters revealed significant differences in respect of six male and four female acts. These acts represented mainly agonistic and amicable behaviour. Compared to their Karkloof counterparts, Kamberg males were involved in significantly less upright sparring ($\bar{x} \pm 2$ SE: 2.4 ± 1.4 vs 6.8 ± 2.0), and displayed significantly higher levels of amicable approach (19.8 ± 2.0 vs 14.9 ± 2.8), allogroom (4.5 ± 1.0 vs 1.4 ± 1.3), and huddle (14.2 ± 4.7 vs 5.3 ± 2.7) behaviour patterns. In contrast, Karkloof males performed significantly more following (10.5 ± 3.0 vs 6.6 ± 2.5) and attempted mounting (12.7 ± 2.0 vs 8.5 ± 1.3) acts than Kamberg males. Kamberg, compared to Karkloof, females displayed significantly less flee behaviour (4.3 ± 1.5 vs 7.5 ± 0.9), and were involved in significantly more grooming invitation (5.2 ± 2.4 vs 2.0 ± 1.2), allogrooming (6.0 ± 3.2 vs 1.4 ± 1.3) and huddling (14.2 ± 4.7 vs 5.3 ± 31.3) activities.

Mean frequencies of behaviour patterns recorded during diurnal interpopulation and intrapopulation encounters are compared in respect of males in figure 1 and females in figure 2. Preliminary examination of the data indicated a low frequency of some behavioural patterns during interpopulation encounters. These acts were therefore combined with other motivationally similar acts (see Tab. 1) in figures 1 and 2.

Both sexes spent a large proportion of time at opposite ends of the arena, and hence the frequency of inactive behaviour was higher than that of other behaviour patterns (Fig. 1, 2). Significantly higher levels of aggression and significantly lower levels of amicability were recorded in interpopulation than in intrapopulation encounters. There was a marked decrease in sexual activity during interpopulation encounters, as exemplified by fewer follow-mount acts by males and fewer presenting acts by females. Interestingly, exploratory behaviour by all animals was significantly lower during inter- than intrapopulation encounters (Fig. 1, 2).

Mean percentages of nocturnal interaction devoted to agonistic and amicable behaviour are plotted against time in figure 3. Males of nine Kamberg × Karkloof pairs and four Karkloof × Kamberg pairs attacked and seriously wounded their partners during the first two days of encounters. These pairs were separated, resulting in reduced sample sizes for the interpopulation pairings from Day 2 onwards (Fig. 3).

For every pairing, levels of agonistic interaction were highest soon after animals were paired, and none of the pairs immediately displayed high levels of amicability (i. e. Day 0; Fig. 3). It is evident in all cases that levels of agonistic interaction decreased during encounters, with a corresponding increase in levels of amicability. The most important fea-

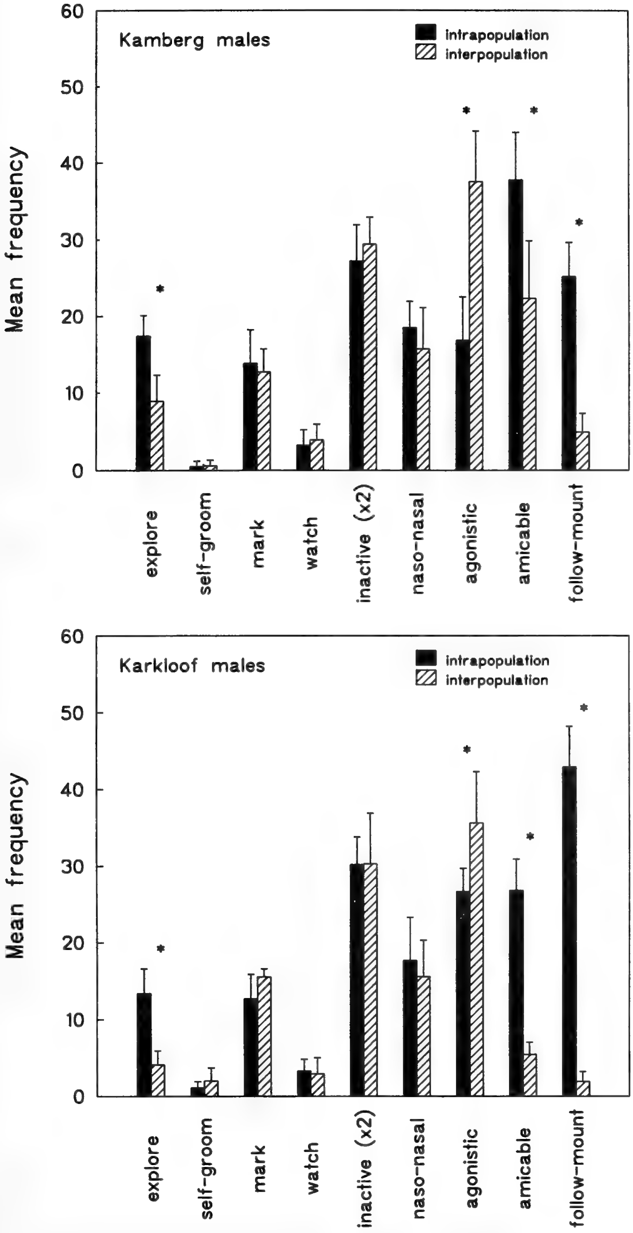

Fig. 1. Comparison of mean frequencies of behaviour patterns of males during the first 20 min of intrapopulation and interpopulation encounters. Inactive (×2) = twice the frequency value indicated. Error bars = 2 SE of the mean. * = values which differed at the 5% significance level, Mann-Whitney U test.

ture illustrated in figure 3 is the variation in the time taken to the point of intersection of the curves representing agonistic and amicable interaction. Kamberg pairs displayed equal levels of amicable and agonistic interaction sooner than any other pairing (i. e. before Day 2), while the Karkloof pairs reached this stage just before Day 3. The curves re-

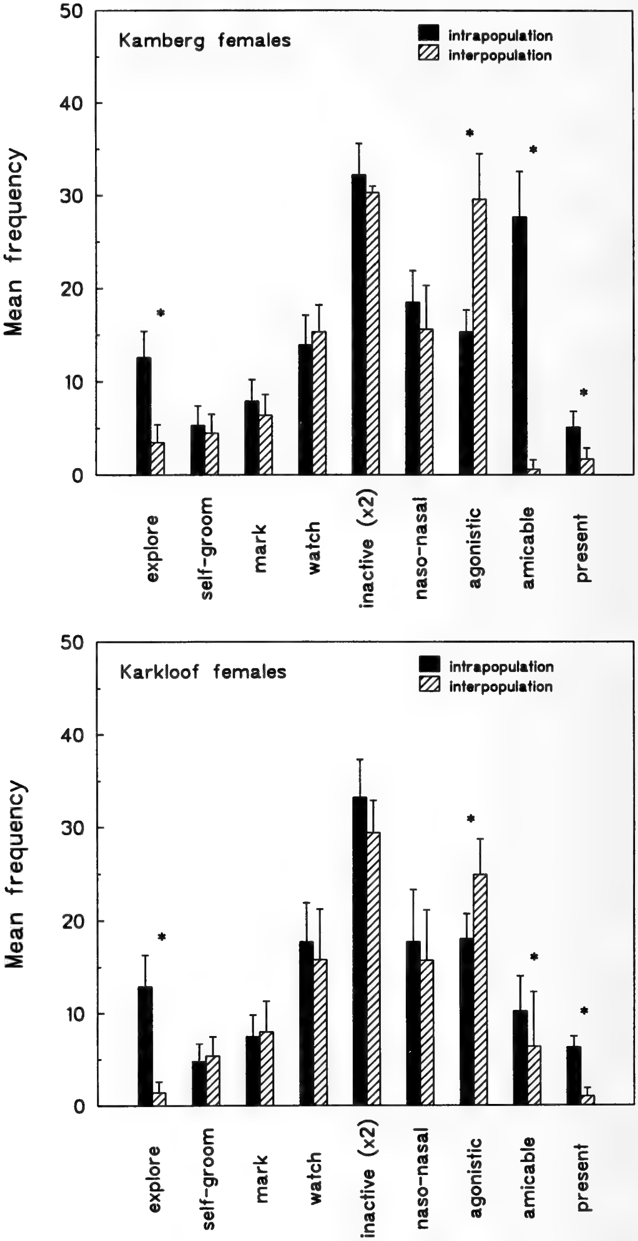

Fig. 2. Comparison of mean frequencies of behaviour patterns of females during the first 20 min of intrapopulation and interpopulation encounters. Inactive (×2) = twice the frequency value indicated. Error bars = 2 SE of the mean. * = values which differed at the 5% significance level, Mann-Whitney U test.

presenting agonistic and amicable interaction of the interpopulation pairings intersected at approximately Day 6, and by Day 12 higher levels of agonistic interaction were recorded in interpopulation than in intrapopulation encounters (Fig. 3).

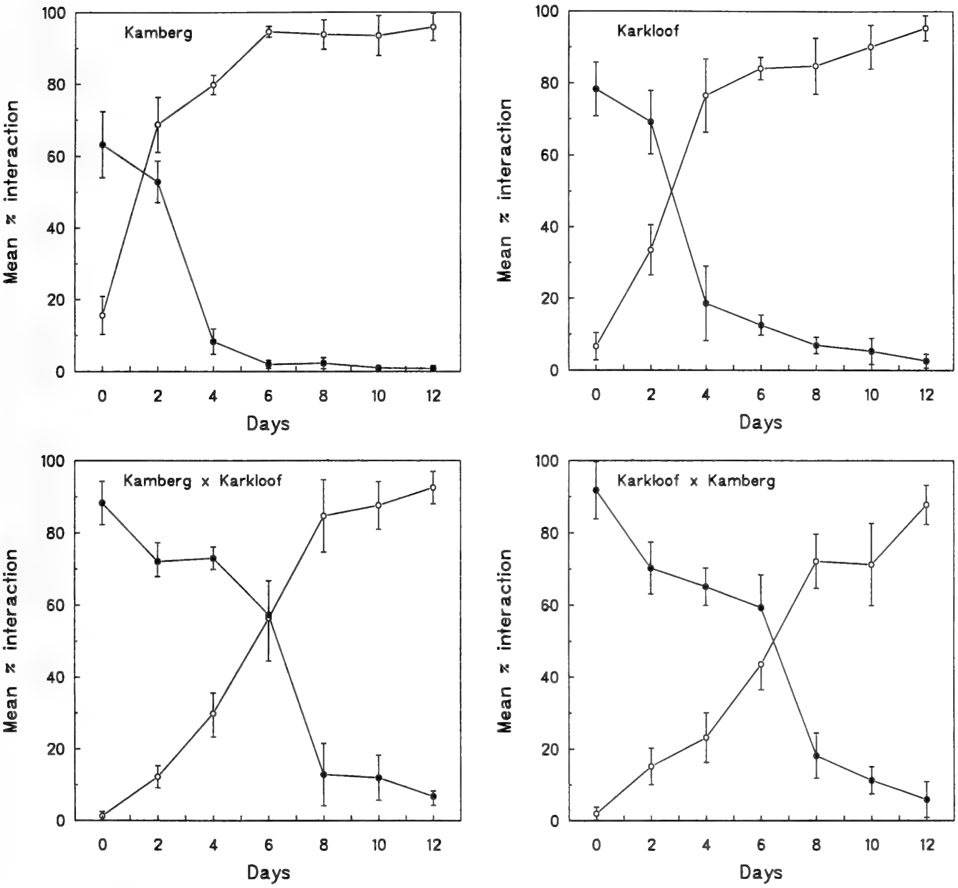

Fig. 3. Mean percentage nocturnal agonistic (filled circles) and amicable (open circles) interaction for the intrapopulation and interpopulation pairings indicated. Error bars = 2 SE above and/or below the mean. Sample size = 20 each for the intrapopulation pairings. Sample size for Kamberg × Karkloof and Karkloof × Kamberg pairs = respectively 18 and 16 on Day 0, and 9 and 12 from Day 2 to 12.

Discussion

The results obtained in this study demonstrate the existence of population-specific courtship behaviour. In addition, it appears that recognition as potential mates by members of the Karkloof, Kamberg × Karkloof and Karkloof × Kamberg pairs was comparatively delayed. Possible explanations of this conclusion as regards intrapopulation and interpopulation encounters are provided below.

Intrapopulation pairings

The differences in the interactions of Kamberg and Karkloof intrapopulation pairs may have been due to underlying disparities in population-specific social organization and mating behaviour.

The social organization of the Karkloof population (Pillay 1993) appears to be similar to that of other *O. irroratus* populations (Davis 1973; Willan 1982; Brown 1988). Breeding females are intrasexually aggressive and appear to be intrasexually highly territorial, while males have intrasexually overlapping home ranges and have dominance hierarchies. The home ranges of males overlap those of females. In contrast, Kamberg males are intrasexually highly aggressive, and they appear to defend their territories from other males (Pillay 1993). There is a high degree of social tolerance among Kamberg females, whose territories may overlap (Pillay 1993).

On the basis of the social organization of both populations, it has been hypothesized that the mating systems of Kamberg and Karkloof populations are polygynous and promiscuous respectively (Pillay 1993): Kamberg males apparently have exclusive access to several females, while Karkloof males compete for access to receptive females.

Females of species which are involved in promiscuous matings would tend to meet males (i. e. potential mates) comparatively frequently, and selection would be predicted to favour reduced attractiveness of males to females (Alder et al. 1981). Females would respond aggressively to male solicitation; increased female aggression may function as a mate choice mechanism based on male quality (Ferkin 1987). At the same time, male-male competition for receptive females would be intense, and the most successful males would be those which rapidly achieve copulation with receptive females (Alder et al. 1981).

In polygynous species, males maintain intrasexually exclusive territories which they would have previously established by means of male-male competition (Shapiro and Dewsbury 1986). In order to ensure mating with a genetically-fit male, females simply mate with the male within whose territory they occur (Emlen 1976; Shapiro and Dewsbury 1986). Therefore, these females may be less discriminating during mate choice than promiscuously-mating females, potentially resulting in reduced aggression and higher amicability during the courtship of polygynous species.

Interpopulation pairings

The results of the interpopulation encounters support the prediction that both Kamberg and Karkloof individuals discriminate between mates from the same and the other population. Increased sexual activity and reduced aggression in intra- relative to interspecific encounters were apparently indicative of mate recognition in *Gerbillurus* species (Dempster et al. 1992).

The somewhat reduced exploratory behaviour observed in interpopulation pairings may have been the result of pairs engaging in increased agonistic interaction. Similarly, male-female interactions involving *Microtus pennsylvanicus* and *M. pinetorum* (Cranford and Derting 1983) indicated that, unlike intraspecific pairs, interspecific pairs favoured aggressive and contact-orientated behaviour over exploratory activity.

Failure to recognize specific auditory, olfactory, tactile and/or visual cues may result in high levels of aggression during interspecific encounters of closely-related rodent species, and may lead to delayed recognition between potential mates (Bauer 1956; Godfrey 1958; Scott 1966; Koepfer 1987). Consequently, differences in behaviour between intra- and interpopulation Kamberg and Karkloof pairings, as exemplified by increased aggression during interpopulation pairings, may be directly attributable to contrasting courtship behaviour, and, in particular, population-specific modes of communication.

Kamberg and Karkloof individuals preferred odours of same-population mates in olfactory discrimination experiments (PILLAY et al. 1995), demonstrating that olfactory cues are important in mate recognition. In the present study, the importance of olfactory cues in courtship was indicated by high frequencies of naso-nasal and naso-anal contact in all encounters.

Except for inactive behaviour and possibly exploratory behaviour, all other behaviour patterns observed in encounters constituted tactile and visual signals (DAVIS 1972; WILLAN 1982; PILLAY 1990). Hence, tactile and visual communication appear to be important in the courtship behaviour of both populations.

As in previous studies of mate recognition involving Kamberg and Karkloof populations (PILLAY 1993; PILLAY et al. 1995), the results of the present study indicate the existence of population-specific courtship behaviour. Differences in courtship behaviour (i. e. an important SMRS) are clearly reflected in interpopulation encounters where underlying differences in population-specific olfactory, tactile and visual cues apparently resulted in high levels of agonistic interaction during interpopulation encounters. The role of aggression as a pre-mating reproductive isolating mechanism has been identified in chromosomal races of *Spalax ehrenbergi* (NEVO et al. 1986) and in populations of *Mus musculus* (CORTI et al. 1989). Aggression may function also as a pre-mating barrier to breeding between Kamberg and Karkloof individuals should the populations meet in nature.

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Zusammenfassung

Hinweise für einen Isolationsmechanismus der Reproduktion in der Vorpaarungszeit bei zwei Populationen der Ohrenratte Otomys irroratus: Experimente zu Begegnungen der Geschlechter innerhalb und zwischen Populationen

Untersucht wurden Interaktionen zwischen Männchen und Weibchen von Individuen aus zwei Populationen der allopatrischen Ohrenratte *Otomys irroratus* (Kamberg- und Karkloof-Population). 40 Zusammentreffen von Individuen gleicher Population und 34 von Angehörigen verschiedener Populationen konnten durchgeführt werden. Während der Zusammentreffen von Tieren gleicher Population waren Kamberg-Männchen und -Weibchen friedlicher und weniger aggressiv als die Karkloof-Tiere, und Karkloof-Männchen zeigten ein stärkeres Sexualverhalten als die Kamberg-Männchen. Diese unterschiedlichen Verhaltensweisen spiegeln möglicherweise eigene Sozialstrukturen und Besonderheiten im Paarungsverhalten der jeweiligen Population wider.

Verglichen mit Paarungen von Individuen gleicher Populationen zeigten die Tiere bei Paarungen von Angehörigen verschiedener Populationen verstärktes Erkundungsverhalten sowie geringeres Sexual-, stärkeres Aggressions- und weniger Demutsverhalten und gleichzeitig eine verzögerte Entwicklung von Demutsverhalten. Es ist möglich, daß populationsspezifische olfaktorische, visuelle und taktile Besonderheiten zu diesen aggressiven Begegnungen zwischen den Populationen führten. Im Falle, daß sich Individuen der Kamberg- und der Karkloof-Populationen in freier Wildbahn begegnen, könnten sich in der Vorpaarungszeit die Aggressionen als Isolationsmechanismen auswirken.

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Morphometric and immunological relationships among some Greek *Mus* L. populations (Mammalia, Rodentia, Muridae)

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Abstract

One hundred and ninety nine individuals of the wild house mouse were collected from twelve mainland and insular Greek localities and investigated both morphometrically and immunologically. This study expands information on the phylogenetic relationships of the two known *Mus* taxa occurring in mainland Greece and clarifies the systematic position of some insular populations from the Aegean and Ionian areas. The clear morphometric distinction of *Mus musculus domesticus* from *Mus macedonicus* was confirmed and reevaluated on the basis of the statistical analysis of sixteen body and cranial characters as well as on the two discriminant ratios already established (body and zygomatic coefficients, as described in the text). Also, a diagnostic key has been constructed using stepwise discriminant analysis which gives mean values of 0.523 for *M. musculus domesticus* and –3.197 for *M. macedonicus*. The albumin immunological distance between these two taxa was 6 ID units, corresponding to a time divergence of about 1–1.2 million years between them. Contrary to the traditional opinion that Crete and some other Aegean islands are inhabited by the distinct taxon *M. musculus praetextus*, the results of our Canonical Analysis and MANOVA tests indicated a considerable morphological overlap of all the insular mice populations studied. Only the single form *M. musculus domesticus* appears to be present. This opinion is also corroborated by our immunological data. Paleontological evidence and the probable evolutionary history of *Mus* in the southern Aegean area are also briefly discussed.

Introduction

According to Auffray et al. (1990 a, c) five taxa of house mice occur in mainland Europe and the circum – Mediterranean region. Greece is regarded as being inhabited by two of these taxa which are morphologically, biochemically and ecologically distinct (Bonhomme et al. 1978; Thaler et al. 1981; Orsini et al. 1983; Bonhomme et al. 1983, 1984). These are (a) *Mus musculus domesticus* Schwarz and Schwarz, 1943 (also referred to as *M. domesticus* by Marshall and Sage 1981; Sage et al. 1986), a relatively long-tailed species that may be either commensal and feral, and (b) *Mus macedonicus* Petrov and Ruzic, 1983 (formerly known as *M. musculus spicilegus, M. abbotti* or *M. spretoides*), a relatively short-tailed and exclusively feral species. Earlier studies (Schwarz and Schwarz 1943; Zimmermann 1953; Ondrias 1966; Reichstein 1978; Engels 1980, 1983) suggested the occurrence of two additional taxa in the Greek area: *M. m. brevirostris* Waterhouse, 1837, a commensal form supposedly widely distributed both on the mainland and islands, and *M. m. praetextus* Brants, 1927, described as a feral insular form distributed on Crete and other Aegean islands (*M. m. praetextus* has also been reported from Cyprus, Sicily and other Mediterranean islands and from northern Africa and the Middle-East). These latter two taxa have been described mainly on the basis of fur color. However, their taxonomic validity has been disputed by Selander and Yang (1969), Britton and Thaler (1978), Sage (1981) and Britton-Davidian (1990) on the basis of biochemical data. These authors argue that neither form differs genetically from *M. m. domesticus* and thus should not be considered as distinct taxa.

Despite the clarification of relationships among the European *Mus* taxa during the last fifteen years, the taxonomic status of the Greek populations (especially the insular ones) is unclear. The material from Greece used in the few studies carried out during that time period is both quantitatively limited, geographically restricted and insufficiently analyzed. In this study we present data on the morphometric variation and the albumin immunological differentiation of some Greek *Mus* populations, inhabiting an area of the Mediterranean basin which is thought to be an important site in the route of European colonization by *Mus* (Auffray et al. 1990 c).

Material and methods

Morphometric study

A total of 199 adult mice, live trapped at the localities shown in figure 1, were studied morphologically. Mice of the Macedonian sample were identified as *M. macedonicus* according to morphological, ecological and zoogeographical data already known for the short-tailed mice of southern Balkans (Marshall and Sage 1981; Orsini et al. 1983; Kratochvil 1986; Vohralik and Sofianidou 1987; Auffray et al. 1990 a; Gerasimov et al. 1990). Also, animals of the Patra sample were classified as *M. m. domesticus* according to available data (Fraguedakis-Tsolis et al. 1986; Giagia et al. 1987; Fraguedakis-Tsolis 1992). All specimens (skins and skulls) are deposited in the collections of the Zoological Museum of Patra University. Sixteen morphometric measurements corresponding to four external and 12 skull characters were analyzed: Head + body length (HB), tail length (TL), ear length (EL), hind foot length (HFL), condylobasal length (CBL), basilar length (BL), diastema length (DL), palatal length (PL), nasal length (NL), mandibular length (ML), distance between the incisor and the third molar of the upper jaw (I–M^3), zygomatic width (ZW), upper molar series length (UMSL), lower molar series length (LMSL), width of the anterior part of the malar process (dorsal ramus) (A), width of the upper part of the zygomatic arch (B). Also two ratios were analyzed separately. These are head + body length/tail length (H + B/TL) and A/B (zygomatic coefficient, ZC). All linear measurements were taken with a Preisser Digi-Met. digital vernier caliper with an approximation of 0.01 mm. External characters were measured with a rule to the nearest mm. For the definition of these measurements we followed Niethammer and Krapp (1978) and Darviche and Orsini (1982).

For comparitive purposes three additional samples were considered. The first was from Antikythira, which consisted of six specimens (collected by us), for which the complete set of measurements was obtained. The other two were (a) from Cyprus, originally classified as *M. m. praetextus* and (b) from Germany and Yugoslavia, originally classified as *M. m. domesticus* (both described in Reichstein 1978). The two latter samples each consisted of 14 specimens, and included seven variables that we measured (H + B, TL, HFL, EL, CBL, DL, ZW).

Canonical (Discriminant) Analysis was used to represent the multivariate structure of the data. Multivariate Analysis of Variance (MANOVA) was used to detect differences between populations. P-values given in this study correspond to the Wilk's criterion, however all other MANOVA criteria (Pillai trace, Hotteling-Lawley trace or Roy's ϑ) gave similar results. For all multivariate methods presented in this study the reader can find useful references in Morrison 1976 or Reyment et al. 1984.

The SYSTAT statistical package, with its SYGRAPH module (Wilkinson 1988) was used for all the analyses and graphs presented in this study.

Immunological study

For the determination of albumin immunological differences among the *Mus* samples tested, reciprocal experiments of the micro-complement fixation (MC'F) quantitative tests were carried out, according to the method of Champion et al. (1974). These differences are expressed in immunological distance units (D units) which are generally believed to be a reliable measure of amino acid sequence differences

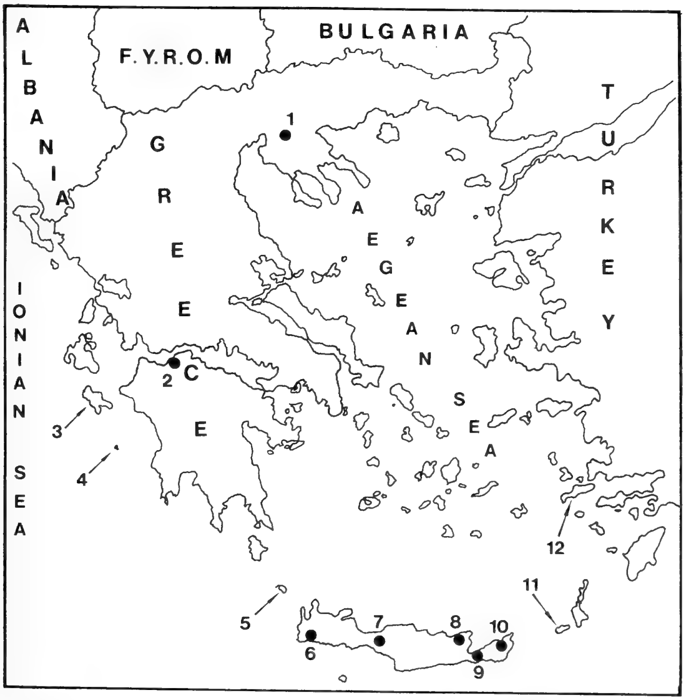

Fig. 1. Map of Greece indicating the *Mus* sampling localities. 1: Langadikia, Macedonia. 2: Patra, Peloponnese, 3, 4: Zakynthos and Strofades islands (Ionian Sea). 5: Antikythira island. 6: Paleochora. 7: Spili. 8: Milatos. 9: Between Ierapetra and Ag. Nikolaos. 10: Sitia (localities 6–10 are on Crete island). 11, 12: Kasos and Kos islands (Dodecanisa archipelago, Aegean Sea). All mice collected were of the feral ecotype except those of Patra which were of both the commensal and feral ones.

between the albumins of the taxa being compared. As representative material of the two known Greek taxa, *M. m. domesticus* and *M. macedonicus*, mice from Patra ($n = 30$) and Langadikia ($n = 18$) were used, respectively. In addition, mice from Crete ($n = 30$) were also tested, since we considered their taxonomic position ambiguous.

The pooled individual sera of each of the three samples were subjected to successive chromatography through Sephadex G-150 and DEAE cellulose columns in order to isolate and purify the serum albumin. Three New Zealand rabbits were immunized against each sample albumin, and the resulting antisera were titrated using the MC'F procedure and pooled in an inverse proportion to their titers (Prager and Wilson 1971). For more details see also Nikoletopoulos et al. (1992).

The computing of the immunological distances derived from the results of the MC'F experiments was made using the formula given by Champion et al. (1974). Since each one-way MC'F experiment for each pair of samples was carried out three times, the mean and standard deviation were calculated. The final immunological distance value of each sample pair was the mean of the two one-way means of the reciprocal experiments. In the case of reciprocal MC'F tests it was also necessary to estimate the parameter σ which expresses the percent standard deviation from reciprocity (Beverley and Wilson 1982).

Results

Morphometric study

A preliminary analysis of the raw data indicated that there was no significant sexual dimorphism in any sample (MANOVA, $p > 0.05$). Also, since there were no significant dif-

Table 1. Mean, standard deviation (SD) and coefficient of variation (CV) of measurements (in mm) of the five populations studied. For abreviation of measurements see Material and methods.

	Patra (n = 116)			Crete (n = 24)			Macedonia (n = 28)			Dodecanisa (n = 9)			Ionian (n = 22)		
	mean	sd	cv	mean	sd	cv	mean	sd	cv	mean	sd	cv	mean	sd	cv
H + B	76.3	8.6	11.3%	84.8	5.6	6.6%	85.0	4.1	4.8%	76.3	4.3	5.6%	73.9	7.6	10.3%
TL	76.8	8.0	10.4%	81.0	6.7	8.2%	69.6	4.9	7.0%	81.9	4.8	5.9%	76.9	5.2	6.7%
HFL	17.3	1.1	6.4%	17.3	1.3	7.3%	17.1	0.8	4.6%	17.5	1.0	5.8%	17.6	1.6	9.0%
EL	13.8	1.5	10.6%	13.7	1.4	10.4%	12.9	0.7	5.6%	13.7	0.8	6.0%	13.7	1.9	13.8%
CBL	19.3	1.2	6.4%	21.0	0.8	3.9%	21.4	0.6	2.6%	19.6	0.6	2.8%	19.6	1.0	5.0%
BL	16.2	1.1	6.6%	17.5	0.7	4.1%	17.7	0.6	3.2%	16.6	0.7	4.0%	16.2	0.9	5.8%
PL	9.2	0.6	6.4%	10.0	0.4	4.0%	10.0	0.4	4.0%	8.9	0.7	7.3%	9.2	0.5	5.9%
NL	7.4	0.7	9.5%	8.3	0.6	6.8%	8.3	0.4	4.9%	7.8	0.4	4.6%	7.7	0.5	6.4%
DL	5.2	0.4	8.3%	5.5	0.3	5.8%	5.9	0.3	4.4%	5.2	0.3	6.3%	5.2	0.3	6.0%
I-M^3	8.0	0.5	6.4%	8.5	0.3	3.8%	8.9	0.4	4.3%	8.1	0.3	4.0%	7.9	0.4	4.7%
ZW	10.7	0.6	5.1%	11.5	0.4	3.8%	11.9	0.3	2.8%	11.0	0.2	2.1%	10.9	0.5	4.3%
ML	10.1	0.6	6.1%	11.0	0.5	4.1%	11.4	0.4	3.3%	10.6	0.5	4.9%	10.6	0.6	5.3%
UMSL	3.4	0.2	5.9%	3.8	0.2	5.6%	3.9	0.2	3.9%	3.4	0.2	7.1%	3.4	0.2	6.4%
LMSL	3.0	0.2	5.7%	3.3	0.2	5.2%	9.4	0.2	1.7%	3.1	0.3	9.8%	3.0	0.2	5.0%
A	0.5	0.1	17.0%	0.5	0.1	14.0%	0.7	0.1	19.2%	0.5	0.1	17.6%	0.5	0.1	16.3%
B	0.9	0.1	13.6%	1.0	0.1	12.1%	0.9	0.1	12.8%	0.8	0.1	9.5%	0.8	0.1	12.0%
H + B/TL	1.0	0.1	8.3%	1.1	0.1	8.8%	1.2	0.1	6.3%	0.9	0.1	6.2%	1.0	0.1	7.2%
ZC	0.5	0.2	19.9%	0.5	0.1	15.9%	0.9	0.2	19.5%	0.6	0.1	18.2%	0.6	0.1	16.2%

Table 2. Pairwise squared Mahalanobis distances. All pairwise T^2 comparisons are significant ($p < 0.001$), except that between Ionian and Dodecanisa ($p = 0.044$).

	Patra	Crete	Macedonia	Dodecanisa	Ionian
Patra	0				
Crete	7.25	0			
Macedonia	22.97	11.68	0		
Dodecanisa	8.55	13.71	31.81	0	
Ionian	4.79	7.19	22.42	6.47	0

ferences in body measurements between the mice from each of the respective sample pairs, the samples from Kasos and Kos and those from Zakynthos and Strofades were pooled. This procedure yielded two samples large enough for reliable comparisons. Thus, subsequent analyses were carried out on the following five samples: 1) Patra (*M. m. domesticus*), 2) Crete, 3) Kasos and Kos (collectively referred to as Dodecanisa), 4) Zakynthos and Strofades (collectively referred to as Ionian) and 5) Langadikia (referred to as Macedonia – *M. macedonicus*).

The basic statistics of the 16 variables and the two ratios for these five groups are presented in table 1. The variables A and B were excluded from further analysis, since they showed large intra-population variability.

Multivariate analysis: Our data were subjected to a five group Canonical Analysis. The MANOVA results were significant (Wilk's $\Lambda = 0.107$, $F = 9.78$, $df = 56{,}706$ and $p < 0.0001$). Pairwise Mahalanobis distances are given in table 2. All pairwise contrasts were significant except that between Ionian and Dodecanisa. It should be stressed that the comparisons Patra vs Dodecanisa and Patra vs Ionian were only significant because of the ML variable. Therefore, one may consider these three populations as belonging to the same taxon.

The plot of the first two Canonical Variates is given in figure 2. There is a considerable overlap between these populations, except for the first and most significant axis which clearly discriminates Macedonia from all the others. The third and fourth Canonical Variates reveal no differences between any of the populations.

In the bivariate plot of the log-transformed ratios (Fig. 3) it can be seen that Patra, Ionian, Dodecanisa and Crete are indistinguishable, and that they differ from Macedonia. A univariate ANOVA on the two ratios gave $F = 44.1$ ($p < 0.0001$) and $F = 39.9$ ($p < 0.0001$), respectively, while in both cases Tukey's HSD-test grouped together Patra, Crete, Ionian and Dodecanisa, which all differ from Macedonia ($p < 0.0001$). The discriminant functions obtained from the Canonical Analysis were applied to the Antikythira specimens, and five out of six were classified into Crete and the last one into Ionian.

The H + B/TL ratio was higher for the Cyprus sample (1.12 ± 0.06) than for those from Crete and Antikythira, and this difference is significant (t-test, $P < 0.01$). On the basis of the restricted set of the seven linear characters Cyprus is different from Crete (MANOVA, $p < 0.008$), but this difference is only due to the smaller TL values exhibited in the former sample. The calculation of Mahalanobis' distances between Cyprus and the Greek populations shows that the smallest distances are between Cyprus and Antikythira, as well as between Cyprus and Crete, while Cyprus is well separated from Dodecanisa, Macedonia, Patra and Ionian. Our statistical treatment of REICHSTEIN's (1978) raw data showed no significant differences between *M. m. domesticus* and *M. m. praetextus* (MANOVA, $p = 0.185$), except for the TL variable which again had smaller values in individuals from Cyprus.

For a comparison at the species level between *M. m. domesticus* and *M. macedonicus* we summarize the statistics of the two ratios calculated from our material and that of other studies (Tab. 3).

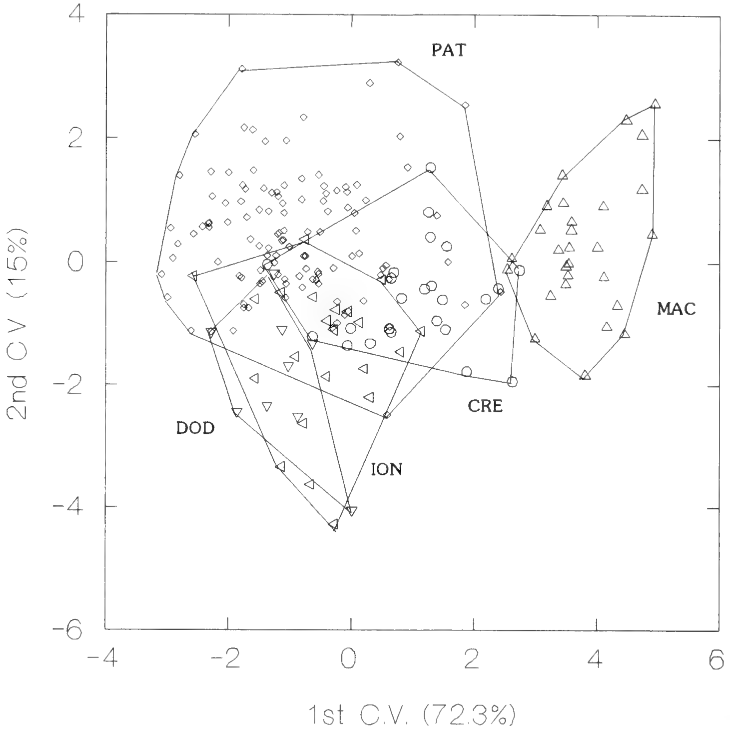

Fig. 2. First and second Canonical Variate plot with the borders of each population sample. PAT: Patra, CRE: Crete, MAC: Macedonia, DOD: Dodecanisa and ION: Ionian.

Immunological study

The average titre and slope values for the three *Mus* antisera used in this work are 3,167 (4,000, 2,900 and 2,600) and 385 (400, 395 and 360), respectively. These values lie within the range given in the literature for some rodent taxa (Nikoletopoulos et al. 1992). The immunological distance data computed from the results of the reciprocal MC'F tests are presented in table 4. The percentage standard deviation from reciprocity derived from our results took a value $\sigma = 6.4\%$ which is considered a satisfactorily low value lying within the limits of σ-values reported in similar studies (Ellis and Maxson 1980; Fuller et al. 1984; Nikoletopoulos et al. 1992; Fraguedakis-Tsolis et al. 1993).

The final values of immunological distances between each pair of taxa that we compared were:

M. m. domesticus – *M. macedonicus*:	$(5.9 + 6.2)/2 = 6.05$ ID units
M. m. domesticus – Cretan *Mus*:	$(0.5 + 0.2)/2 = 0.35$ ID units
M. macedonicus – Cretan *Mus*:	$(5.8 + 6.6)/2 = 6.20$ ID units

Thus we see that the Cretan *Mus* are essentially indistinguishable from *M. m. domesticus* on immunological criteria and both of these taxa differ by approximately 6 ID units from *M. macedonicus.*

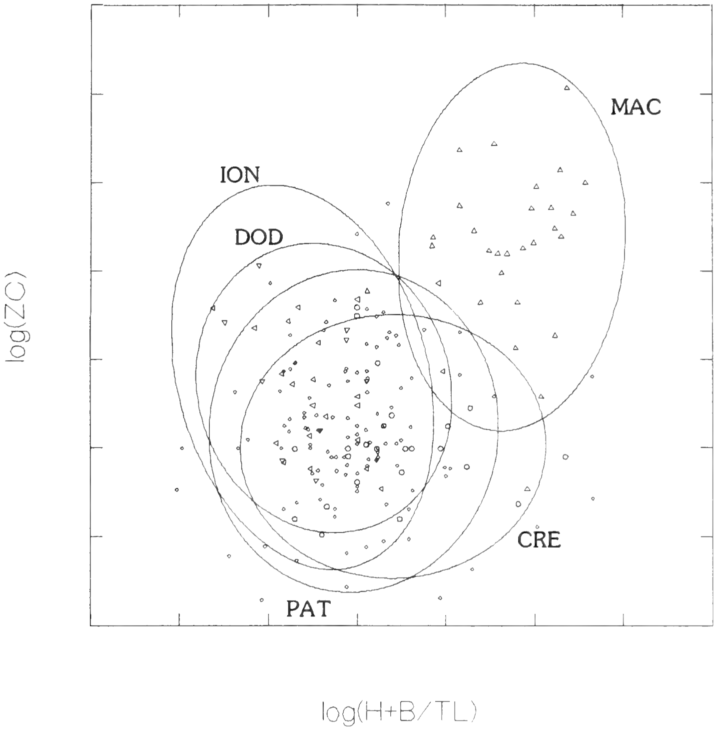

Fig. 3. Bivariate plot of the log-transformed ratios values with 90%-concentration ellipses for each population sample. PAT: Patra, CRE: Crete, MAC: Macedonia, DOD: Dodecanisa and ION: Ionian.

Table 3. Comparison of our and bibliographic data concerning the two discriminant morphometric ratios.

Ratios	Taxa	Data from								
		ORSINI et al. (1983)			AUFFRAY et al. (1990 b)			This study		
		n	x	SD	n	x	SD	n	x	SD
H + B/TL	*M. m.*	35	1.49	0.10	14	1.28	0.08	28	1.23	0.08
	M. m. d.	15	1.07	0.03	13	1.03	0.03	171	0.99	0.08
ZC	*M. m.*	45	0.74	0.10	47	0.80	0.10	28	0.86	0.17
	M. m. d.	22	0.47	0.05	52	0.52	0.07	116	0.53	0.11

M. m.: Mus macedonicus, M. m. d.: Mus musculus domesticus

Discussion

Both morphological and immunological differences found between individuals from Macedonia and Patra confirm the widely accepted distinction between *M. macedonicus* and *M. m. domesticus.* Actually, the immunological distance of 6 D units found between them indicates a rather substantial genetic differentiation of their albumins in comparison to

Table 4. Mean values (range and standard deviation in parenthesis) of the one-way albumin immunological distances (in ID units) computed from the results of the three repeating MC'F experiments for each pair of the three *Mus* samples tested.

Sample	Anti- *M. m. domesticus*	Anti- *M. macedonicus*	Anti- Cretan *Mus*
M. m. domesticus	0	6.2 (6.0–6.6, 0.32)	0.2 (0.1–0.4, 0.17)
M. macedonicus	5.9 (5.8–6.1, 0.17)	0	6.6 (6.3–6.9, 0.31)
Cretan *Mus*	0.5 (0.4–0.6, 0.10)	5.8 (5.5–6.0, 0.26)	0

that reported for other cases of congeneric rodent taxa (ELLIS and MAXSON 1980; NIKOLETOPOULOS et al. 1992). In a previous study (NIKOLETOPOULOS et al. 1992). In a previous study (NIKOLETOPOULOS et al. 1992) we have already proposed an evolutionary rate for the rodent albumin, equal to 100 amino acid substitutions per 16–20 million years. According to this rate the lineages leading to *M. macedonicus* and *M. m. domesticus* must have separated about one million years ago (Lower-Middle Pleistocene). The oldest known fossils of *M. macedonicus* in Israel have been dated to only 0.12 million years (AUFFRAY et al. 1988) but paleontological and morphometric data (THALER 1986) and data on DNA-DNA hybridization (CATZEFLIS et al. 1987) indicate that *M. spretus* (the feral mouse of SW Europe and N Africa) and *M. m. domesticus* diverged 1–3 million years ago. Combining all this information we conclude that both feral mice taxa of the circum-Mediterranean area may have evolved at about the same time; these speciation events possibly took place in south Asia, the area of origin of *Mus* from where mice spread westwards to the Middle East and Europe (for a review on the evolutionary history of *Mus* see AUFFRAY et al. 1990 c).

The value of the two ratios, H + B/TL and ZC, for the discrimination of *M. macedonicus* and *M. m. domesticus* has already been established from studies on Bulgarian and Israeli populations (AUFFRAY et al. 1988, 1990 b; GERASIMOV et al. 1990). Data on these ratios coming from a mixed Greek-Bulgarian sample (containing only a few specimens from Greece) were given by ORSINI et al. (1983), but this study support the usefulness of these ratios in a more ample Greek material. It is clear that our values for H + B/TL and ZC are lower and higher, respectively, than those from the literature, but both of them are surprisingly close to values obtained for mice from Israel. AUFFRAY et al. (1990 b) commenting in the relatively longer tail of *M. macedonicus* from Israel in comparison to its European conspecifics, attributed this difference to the warmer climatic conditions of Middle-East, as expected from Allen's rule. However, our results for both species studied cause us to question this idea, since the Greek climate is generally cooler than that of Israel. So, in the absence of a really adequate data set, we believe that variation in tail length in *M. m. domesticus* and *M. macedonicus* are more likely due to random intraspecific variation than to climatic factors.

As well as making use of morphological ratios to discriminate *M. m. domesticus* and *M. macedonicus*, we also constructed a discriminant diagnostic key between these taxa (see GERASIMOV et al. 1990). From stepwise discriminant analysis, the equation $y = 1.262 \times \log TL - 0.574 \times \log CBL - 0.261 \times \log LMSL - 0.447 \times \log DL - 0.352 \times \log(H + B)$ provides means of 0.523 for *M. m. domesticus* and -3.197 for *M. macedonicus.*

Since no differences were found between the mice of Patra and the Ionian islands, the mice of the latter sample are thought to belong to the same taxon *M. m. domesticus.* It should be noted that the occurrence and the taxonomic status of the Strofades mice was completely unknown until our study. Regarding the Zakynthos island the previous information was controversial. Ondrias (1966) believed that this island is inhabited by *M. musculus spicilegus* (that is, *M. macedonicus* according to the current taxonomic nomenclature), while later studies (Fraguedakis-Tsolis et al. 1986; Giagia et al. 1995) revealed that only *M. m. domesticus* exists on this island.

Contrary to the older opinion classifying the Cretan *Mus* into the distinct subspecies *M. m. praetextus*, the results of the present study do not strongly support such a differentiation. So, although the MANOVA results were significant, the homogeneous character of the Cretan mice as compared to the heterogeneity of the Patra sample (reasonably being ascribed to the smaller sample size –24 vs. 116 individuals) plays an important role in tests of significance. Moreover, there is no difference between Patra and Crete mice in terms of morphological ratios that express the "shape" of the individuals.

The addition of further island mice (Dodecanisa) from an area close to Crete and known as a part of the *M. m. praetextus* range (Ondrias 1966), offered more information about the relationships of "*praetextus*" mice to *M. m. domesticus.* In fact, as it appears from the Mahalanobis' distances, Dodecanisa mice are morphometrically closer to the more geographically distant *M. m. domesticus* from Patra and the Ionian islands than to the nearby Cretan animals. The morphometric similarity between *M. m. domesticus* and mice assigned to *M. m. praetextus* is also evident from our statistical comparison of raw data cited by Reichstein (1978) (see the "Results" section). Moreover, the co-evaluation of the data taken from the analysis of the Antikythira sample (the existence of *Mus* on this island is reported in this study for the first time) contributes to a smoothing out of differences among all samples, if we except that of *M. macedonicus.*

Conclusively, we can say that all of our morphometric data converge to the view that only the Macedonian sample is morphometrically distinct. The small differences revealed among the remaining samples are insufficient to classify them into more than one taxa. This is also corroborated by the extremely low immunological distance between *M. m. domesticus* and the Cretan *Mus.*

Correlating all the above mentioned findings we conclude that the Patra and all insular populations studied should belong to *M. m. domesticus.* This is in accordance with the conclusions of Britton-Davidian (1990) who biochemically proved that *M. m. praetextus* from Algeria, Tunisia and Israel is not a valid taxon and should be included within *M. m. domesticus.*

Paleontological evidence shows the occurrence of *Mus* in the area of Greece since the Middle Pleistocene (Van de Weerd 1973; Storch 1975; Mayhew 1977). Auffray et al. (1990 c) have stressed that at the end of Pleistocene Crete was possibly the only European area inhabited by *Mus*, namely the taxon *M. minotaurus* fossil material of which was found in the uppermost Pleistocene deposits of Crete (Mayhew 1977). *M. m. domesticus* appeared in the Middle-East Mediterranean coasts about 12,000 years ago, and in its progression into Europe it colonized Greece during the Late Holocene, about 8500–8000 years ago (Auffray et al. 1990 c). If the endemic *M. minotaurus* continued to exist on Crete during Holocene time, then the present–day Cretan mice constitute the result of an interaction between the older, local *Mus* form and *M. m. domesticus* which was unintentionally dispersed by man from the mainland to all the Greek islands, including Crete. It could be speculated that this interaction led to a subsequent competitive exclusion of the possibly more susceptible *M. minotaurus* or to its extinction through introgression events. Such evolutionary processes could be responsible for the final production of an island mouse form very similar to the mainland *M. m. domesticus.*

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Zusammenfassung

Morphologische und immunologische Beziehungen zwischen einigen griechischen Mus L. Populationen (Mammalia, Rodentia, Muridae).

Einige Populationen freilebender Hausmäuse aus Griechenland wurden morphologisch und immunologisch untersucht. Ziel der Studie war es, neue Informationen über die beiden vom Festland bekannten Taxa der Gattung *Mus* zu gewinnen und ihre phylogenetischen Beziehungen zu einigen Inselpopulationen zu klären. Die morphologisch klare Trennung von *Mus musculus domesticus* und *Mus macedonicus* konnte bestätigt werden. Der albuminimmunologische Abstand ID zwischen diesen beiden Taxa betrug 6 Einheiten, was eine Trennungszeit von 1–1,2 Millionen Jahren bedeuten würde. Unsere Resultate stützen nicht die verbreitete Auffassung, dass auf Kreta und anderen Inseln der Ägäis das Taxon *M. musculus praetextus* vorkommt. Die untersuchten insulären Hausmäuse unterschieden sich nicht von *M. musculus domesticus* und sollten daher als solche klassifiziert werden. Paläontologische Daten und die vermutliche Evolutionsgeschichte der Hausmäuse in der südlichen Ägäis werden ebenfalls besprochen.

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Observations of Muskoxen (*Ovibos moschatus*) in Central East Greenland

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Abstract

Muskoxen (*Ovibos moschatus*) were counted in eastern Greenland both from a ship as well as during extensive aerial surveys conducted along the coasts between approximately 70° N and 76°20′ N during the ARK X/2 cruise of RV "Polarstern" from 22 August to 25 September 1994. A total of 820 muskoxen were observed. Highest densities were found on the large islands and in the eastern areas between 72° N and 74° N, and in the western parts of the Scoresby Sund fjord complex. Muskoxen have not to date been systematically counted in the latter area. The surveys confirmed earlier findings that muskoxen are scarce north of 74° N, whereas the population between 72° and 74° N appeared to have remained stable since 1982. Overall, calves born in the current year constituted at least 10.5% of the total population, indicating that 1994 was a year of good productivity.

Introduction

Muskoxen (*Ovibos moschatus*) are found in eastern Greenland between Scoresby Sund (approximately 70° N) and Nyeboes Land (82° N). The core of their distribution is, however, between Scoresby Sund and Ardencaple Fjord; figure 1 (Boertmann et al. 1992). They are thought to number between 9 500 and 12 500 in total, with highest densities in Jameson Land (Boertmann et al. 1992).

Although several studies have been conducted to determine the abundance of muskoxen in parts of their range in eastern Greenland (cf. Boertmann et al. 1992; Boertmann and Forchhammer 1992), only few studies have covered large areas systematically. Aerial surveys were conducted during spring between 1981 and 1990 to determine numbers of muskoxen on the peninsula of Jameson Land (e. g. Aastrup 1990; Aastrup and Mosbech 1988, 1993). In the spring of 1988 an aerial reconnaissance was flown over the coastal areas between Kong Oscars Fjord and Jøkel Bugt (78° N) to determine distribution and numbers of muskoxen (Bay and Boertmann 1988). In 1982 and 1984 Sittler (1988) counted muskoxen between 72° N and 74° N from rubber dinghies, terrestrial vantage points and, to a limited extent, also from a helicopter. Based on intensive helicopter reconnaissance and land-based observations, Stemmerik (1987) presented numbers of muskoxen in the Traill Ø, Geographical Society Ø and Ymer Ø areas.

During the ARK X/2 cruise of RV "Polarstern" to the central parts of eastern Greenland (17 August–7 October 1994) a study of the distribution and abundance of polar bears (*Ursus maritimus*) was conducted jointly by the Greenland Institute of Natural Resources and the Norwegian Polar Institute. During this study, which involved aerial surveys conducted over the coastal areas between Scoresby Sund and southern Dove Bugt (approximately 76°20′ N) to search for "land locked" polar bears, all observations of other wildlife were also recorded. Here we present information on the distribution, numbers and calving rate of muskoxen in central east Greenland in August and September 1994.

Material and methods

Between 22 August and 25 September 1994, a total of 39.6 hours of flying were spent surveying areas between approximately 70° N and 76°20′ N in eastern Greenland (Fig. 1).

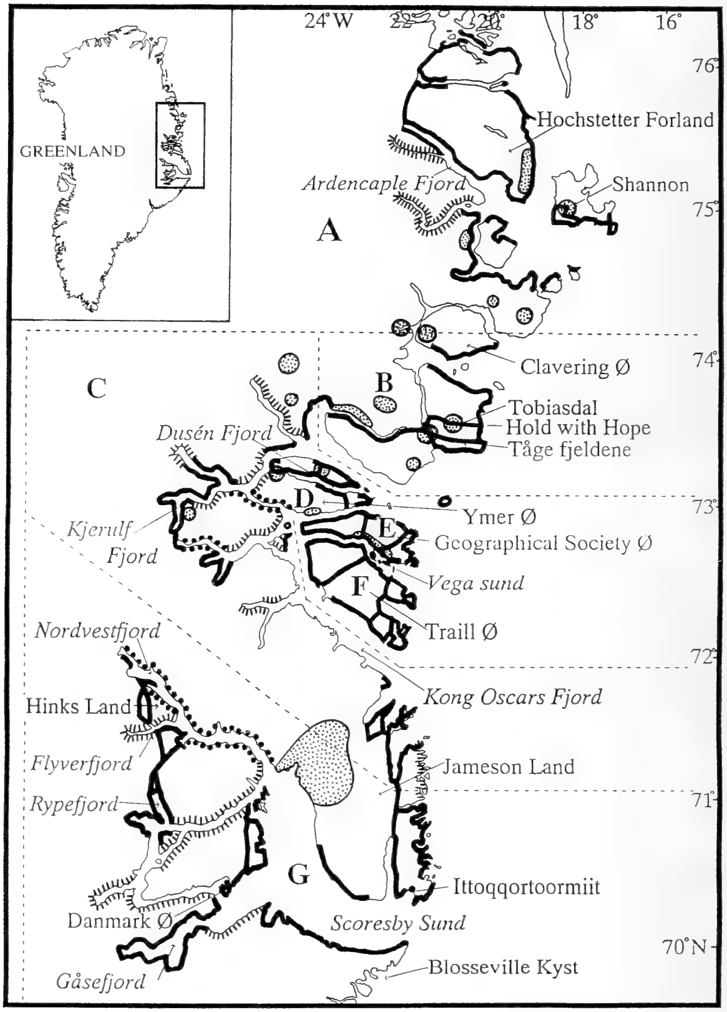

Fig. 1. Areas covered during ship-based and aerial surveys for muskoxen in the central parts of eastern Greenland, 22 August–25 September 1994. Legend: Thick lines = areas surveyed from aircraft; dotted line = surveyed from ship; - - - - - - - - - - = Borders of sub-areas; ////// = Areas where the mountain slopes are considered to be too steep to represent suitable muskox habitat; Stippled areas = wintering habitat according to Boertmann and Forchhammer (1992). Black dot = settlement of Ittoqqortoormiit/ Scoresbysund.

For analyses, the survey area was subsequently divided into a northern sub-area (A), central sub-areas (B to F), and a southern sub-area G (Fig. 1). Sub-areas B and C are continental: B is close to the Greenland Sea and has less steep mountain slopes than sub-area C which has alpine landscape dominated by deep fjords that in many places have very steep slopes. Sub-areas D, E and F represent the three major islands (Ymer Ø, Geographical Society Ø and Traill Ø) between 72° and 74° N. Sub-area G is the Scoresby Sund fjord complex. The hours allocated for surveying the different areas and the linear km flown are presented in table 1.

Table 1. Number of flying hours, linear distance (km) flown and observations of muskoxen per lin. km. flown over different areas of central east Greenland, 22 August–25 September 1994.

	Areas			Total
	North A	Central B C D E F	South G	
Hours	5.25	25.0	9.35	39.6
Linear km	972	4 600	1 725	7 297
N	34	472	314	820
N/linear km	0.035	0.103	0.182	

Aerial surveys were carried out over land with the flight track usually being placed between 200 and 500 m from the shore line, depending on the topography. This allowed one observer to scan the beaches and low-land, and the other observer to search the hills and mountain slopes up to about 300 m a. s. l. and out to a distance of approximately 1 000 m.

A B-105 helicopter equipped with a radar altimeter and a GPS navigation system was used. The surveys were flown between approximately 60 and 150 m (200 and 500 feet) altitude, depending on tracking conditions and topography. Indicated air-speeds varied between 167 km/h and 185 km/h (90 and 100 knots), but were usually 185 km/h. All observations of wildlife made by the front left and the rear right observer were recorded on data-sheets. The two observers kept the same position in the helicopter during all surveys. Muskoxen were only classified as either non-calves or 0-year-old calves, respectively. No attempt was made to approach the muskoxen to identify further group size or age and sex composition.

For the majority of the survey period, "Polarstern" cruised in the fjords between Gåsefjord (approximately 70° N) and Ardencaple Fjord. During cruising, the mountain slopes of some of the narrow fjords were searched from the crow's nest (25 m a. s. l.) using binoculars (8 and 10×50 Zeiss) and a KOWA SN-1 monocular telescope (20×) (Fig 1).

Although some areas were surveyed more than once, potential double-countings have been excluded from the presentation of results.

Results

Weather conditions were very good during all flights, usually with a 0 octas cloud covering. Starting on 31 August the northward facing mountain slopes were covered with new snow down to sea level. After a few days the slopes facing southward were free of snow below about 300 m. During the remainder of the study period, temperatures were usually below freezing, with periodical snowfall. This, presumably, implies that the muskoxen were attaining their winter distribution during the survey period.

Observations on muskoxen are indicated in figure 2. A total of 820 animals was observed. Of these, only five animals (= three groups) were observed from the ship. Areas of concentration were: Hold with Hope (Tobias Dal and Tågefjeldene), the northern coasts of Dusén Fjord and Vega Sund, Kjerulf Fjord, Hinks Land and Rypefjord. Generally, the muskoxen were found in snow-free areas with relatively lush vegetation. An exception was a part of Hinks Land, where some animals were observed between 300 and 1 200 m al-

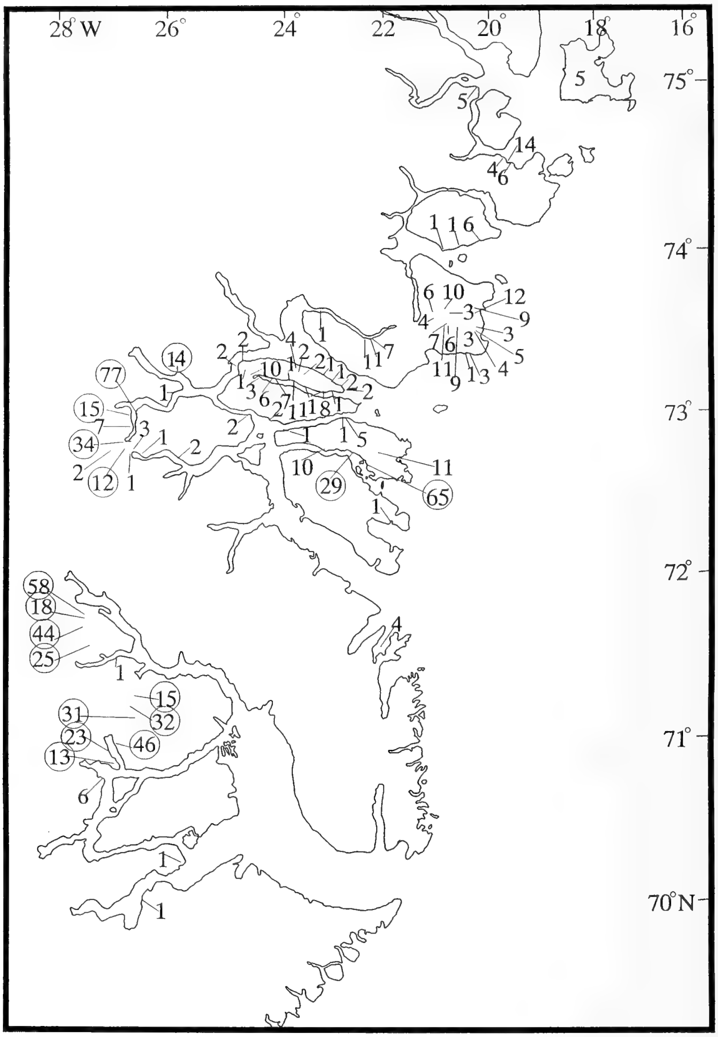

Fig. 2. Numbers of muskoxen observed during ship-based and aerial surveys in the central parts of eastern Greenland, 22 August–25 September 1994. In some cases (encircled) where densities were high, the groups have been pooled in the figure.

titude in areas covered with new snow. Tracks indicated that these animals apparently were in the process of moving across the mountain top from Nordvestfjord to the head of Flyverfjord. Counts of muskoxen in the different sub-areas are shown in table 2. Few muskoxen were seen in sub-area A (0.035 ind./linear km), whereas in the central areas (B–F) densities were nearly three times higher (0.103 ind./km). Highest densities (0.182 ind./km) were recorded in the western parts of the Scoresby Sund fjord complex (sub-area G), in areas where muskoxen have not previously been counted systematically.

The southernmost muskox recorded in this study was a single adult on the southern coast of Gåsefjord (70°10′ N–27°10′ W).

When all areas were combined, the proportion of calves averaged 10.5% of all observed muskoxen (68 calves/645 total). Overall, the mean group size was 3.4 (SD = 2.9; range: 1–17; n = 220; Tab. 2).

Table 2. Total numbers, percentage of calves born in the current year to totals, and mean group size of muskoxen recorded during surveys in central east Greenland, 22 August–25 September 1994. For comparison, estimates of number of animals provided by Sittler (1988) and Stemmerik (1987) are presented.

	Sub-areas	Period	Observations							Sittler		Stem-merik
			Total	% Calves	Group size							
					Mean	SD	Range	N		1982	1984	1986
A	North of 74°20′ N	Aug 22–24	34	8.8	6.8	4.1	4–12	5		–	–	–
B	Clavering Ø – Hold with Hope	Aug 29	114	18.3	5.0	3.5	1–12	23		68	129	–
C	Mainland – west	Sep 1–16	175*	2.9*	2.4	1.7	1–8	46		169	83	–
D	Ymer Ø	Aug 29–Sep 9	60	10.0	2.9	2.6	1–10	21		99	78	137+
E	Geogr. Society Ø	Sep 1–17	122	11.4	4.1	4.0	1–17	30		84	53	63+
F	Traill Ø	Sep 1–17	1	0	1.0	–	–	1		23	23	95
G	Scoresby Sund	Sep 20–25	314	8.3	3.3	2.5	1–12	94		–	–	–
	Total		820	10.5*	3.4	2.9	1–17	220		443	366	295+

* Two congregations of a total of about 60 animals in Kjerulf Fjord (area C) were scattered over too large an area to allow closer inspection, and they are therefore not included in the calculations of age category, group size and overall ratio of calves born in the current year to non-calves.

Discussion

Boertmann and Forchhammer (1992) indicated that the southern limit of muskoxen in eastern Greenland is Danmark Ø. However, we observed muskoxen in Gåsefjord. During this survey Gåsefjord had lush vegetation on the northern and western shores, and also in some places on the southern shore. This indicates that this fjord is part of the muskoxen's normal range, as also reported by Vibe (1967) and Pedersen (1974). However, according to hunters from the settlements of Scoresby Sund, muskoxen are scarce in Gåsefjord (J. Brønlund, settlement of Ittoqqorttoormiit/Scoresbysund, pers. commn. 1995). Stray animals may even occur along the Blosseville Kyst, south of the entrance to Scoresby Sund (Vibe 1967). For example, 3–4 muskoxen were shot on Steward Ø (69°50′ N–22°30′ W) in the late 1960s (J. Brønlund pers. commn. 1995).

Boertmann and Forchhammer (1992) presented estimates of the number of muskoxen based on a variety of sources. From these data, which are heterogeneous in terms of survey techniques, survey platform used, and season, Boertmann and Forchhammer (1992) attempted to derive estimates of abundance for different areas. A comparison between the counts listed by Boertmann and Forchhammer (1992) for Ymer Ø, Geographical Society Ø and Traill Ø from the mid-1980s and our data indicates that there has been no major decline, except on Traill Ø, where, despite relative good coverage, only one muskox was recorded. The surveys of the northern area support indications of a decline in numbers on Shannon and Hochstetter Forland, as reported by Boertmann and Forchhammer (1992). The lack of observations of muskoxen in the vicinity of settlements at the entrance to Scoresby Sund also confirms a statement by Boertmann and Forchhammer (1992) that the muskoxen avoid these areas. Due to their basic heterogeneity, the data presented by Boertmann and Forchhammer (1992) are, however, difficult to interpret and are not readily comparable with data obtained during surveys which covered larger areas systematically within a relatively short period of time (i. e. Sittler 1988 and this study). Although the methods used by Sittler (1988) differed from those used in the present study, our surveys covered almost all the high concentration areas between 72° and 74° N identified by Sittler (1988). For those parts of the muskoxen's range where the same areas were surveyed systematically in 1982 and 1984 (Sittler 1988) and in 1986 (Stemmerik 1987) it appears that the populations have remained stable; with the exception of Traill Ø.

There is reason to believe that the population estimates are negatively biased, even in areas where we are confident that the surveys represented a good picture of the situation (good coverage, excellent survey conditions) as, for example, on Ymer Ø, Geographical Society Ø and Traill Ø. During aerial surveys conducted in late winter in Jameson Land, 25–30% of all muskoxen within a distance of about 1 000 m of the flight track were not observed by any of the observers (Aastrup and Mosbech 1993). Similar to Aastrup and Mosbech (1993) we may have missed an unknown proportion of muskoxen actually present within about 1 000 m from the flight track.

The surveys indicate that muskoxen can move relatively long distances (or out of the study area) within a short period of time. Kjerulf Fjord was surveyed under good survey conditions on 5 and 13 September, respectively. During the first survey, a total of 143 muskoxen was observed, whereas during the second survey only 34 animals were seen. Thus, surveys such as this one, which attempt to cover extensive areas during short periods of time, can be problematic in that it might be difficult to determine what proportion of the population is actually assessed.

Presuming that the muskoxen more or less occupied their wintering habitats, this survey represents a relatively good coverage of the area north of 72° N. However, we did not survey an important muskox wintering area on southwestern Jameson Land, where an estimated 3 000–3 600 animals are found (Boertmann et al. 1992).

In this study, the number of calves observed represented 10.5% of muskoxen observed. This appears to be the level of calf productivity in a stable muskox population (Freeman 1971; Ferns 1977). Ferns (1977) listed annual calf percentage recorded during the period 1954–1974 in the areas between 71° N and 74° N (eastern Greenland) ranging between 1.5% and 25%. The average "calf crop" was 11.7% per year (Ferns 1977). Average calf percentage recorded by Stemmerik (1987) on the large islands between 72° and 73°30′ N in eastern Greenland was 9.2. Calf percentage observed on Ellesmere Island ranged between 7 and 15% (Freemann 1971; Ferns 1977).

The calf to non-calf ratio obtained in this study is assumed to be reliable. There were, however, conditions that may have negatively biased the calf counts. We did not purposely approach groups for inspection, and therefore calves may have been missed in some distant groups. This may have also been the case where the animals moved into tight groups. However, the animals were usually counted before they had had a chance to form their characteristic tight defense position as a response to the noise of the helicopter. Therefore we cannot preclude that the estimated calf percentage was negatively biased, although the percentage obtained by Stemmerik (1987) using other methods of observations indicate that it is not.

The mean group size of 3.4 recorded in the present study does not differ significantly ($P > 0.05$) from the mean group size of 5.7 (1961) and 3.6 (1974) reported by Ferns (1977).

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Zusammenfassung

Beobachtungen von Moschusochsen (Ovibos moschatus) im zentralen Ost-Grönland

Zählungen von Moschusochsen (*Ovibus moschatus*) wurden im östlichen Grönland sowohl vom Schiff aus als auch während ausgedehnter Flugerkundungen entlang der Küste zwischen etwa 70° N und 76°20′ N durchgeführt. Diese Erkundungen fanden während der Expedition ARK X/2 von FS „Polarstern" vom 20. August bis zum 25. September 1994 statt. Ingesamt wurden 820 Moschusochsen beobachtet. Die größten Populationsdichten wurden auf den großen Inseln, in den östlichen, Gebieten zwischen 72° N und 74° N sowie in den westlichen Teilen des Fjordsystems am Scoreby Sund gefunden. Im letzteren Gebiet sind Moschusochsen nie zuvor systematisch gezählt worden. Die Untersuchungen bestätigen die frühere Erkenntnis, daß Moschusochsen nördlich von 74° selten sind, während die Population zwischen 72° N und 74° N seit 1982 stabil geblieben zu sein scheint. Insgesamt machten die Kälber des Jahres mindestens 10.5% der Gesamtpopulation aus, was zeigt, daß 1994 ein Jahr guter Reproduktion war.

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MITTEILUNGEN DER GESELLSCHAFT

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 25. September 1995 im Großen Hörsaal des Fachbereichs Erziehungswissenschaften der Universität Göttingen.

Der 1. Vorsitzende, Herr Schmidt, eröffnet die Versammlung um 16.30 Uhr

1. Die Tagesordnung wird angenommen.
2. Der Geschäftsführer, Herr Erkert, verliest den Bericht über das Jahr 1994. Die 68. Hauptversammlung der Gesellschaft fand auf Einladung von Frau Spitzenberger vom 25.–29. September 1994 in Wien statt. Schwerpunktthemen waren „Holozäne und spätpleistozäne Säugetierfauna“, „Akustische Kommunikation und Gehör“, „Systematik und Ökologie ost- und südosteuropäischer Säugetiere“. Mit rund 200 Teilnehmern, 37 Vorträgen und 43 Postern war die Veranstaltung sehr erfolgreich. Zum Gelingen beigetragen haben ferner die Führung durch den Tiergarten Schönbrunn und die Exkursion an den Neusiedler See. Herr Erkert dankt den Veranstaltern sowie Herrn Dr. Pechlaner und den übrigen Organisatoren für die Ausrichtung der gelungenen Tagung.

   Herr Tembrock, Berlin, wurde zum Ehrenmitglied ernannt. Der Fritz-Frank-Förderpreis ging an Herrn Dr. Ulrich Zöphel, Halle, für seine Arbeit „Populations- und ethoökologische Untersuchungen an der Steppenwühlmaus (*Microtus brandti* Radde, 1861) in der Mongolei.“ Die Posterpreise wurden gewonnen von M. Preleutner, H. Gossow und G. Rabender, Wien; U. Hecker-Bisping und H. Bierlein, Heidelberg; C. Würth und U. Hecker-Bisping, Heidelberg.

   Die Zeitschrift für Säugetierkunde erschien in 6 Heften mit insgesamt 384 Seiten. Sie enthielt 42 größere Originalarbeiten, 7 wissenschaftliche Kurzmitteilungen sowie einige Mitteilungen der Gesellschaft. Herr Erkert schildert, welche Vorarbeiten nötig waren (erweiterte Vorstandssitzung am 14. 4. 1994 in Berlin, außerordentliche Mitgliederversammlung am 16. 6. 1994 in Bonn und zahlreiche Verhandlungen), um zum 31. 12. 1994 den Verlagsvertrag mit dem Gustav-Fischer-Verlag abzuschließen. Der neue Vertrag stellt eine deutliche Verbesserung gegenüber dem alten dar, weil in ihm die Rechte der Deutschen Gesellschaft für Säugetierkunde erheblich klarer formuliert sind.

   Die Mitgliederzahl hatte sich bis Ende 1994 auf 605 verringert. Durch den Tod verlor die Gesellschaft folgende Mitglieder:

   Prof. Dr. Christian Vogel, Göttingen,
   Prof. Dr. Agatha Gijzen, Merksem,
   Dr. Uwe Dietrich, Berlin,
   Dr. Hans Kumerloeve, Gräfeling.

3. Herr Erkert erläutert den von Frau Kühnrich abgefaßten detaillierten Kassenbericht und dankt der Schatzmeisterin für ihre sorgfältige Arbeit.
4. Die Herren Bohlken und Schliemann haben die Kontounterlagen der Gesellschaft in Hamburg geprüft und für korrekt befunden.

5. Die Anträge auf Entlastung des Schatzmeisters und des Vorstandes werden bei Enthaltung des Vorstandes angenommen.
6. Die Herren Bohlken und Schliemann werden bei einer Enthaltung als Kassenprüfer für das Geschäftsjahr 1995 gewählt. Beide sind mit der Wahl einverstanden.
7. Der Vorstand schlägt vor, die Mitgliedsbeiträge für 1996 unverändert zu lassen (DM 100,– Vollmitglieder, DM 65,– Studenten, DM 10,– Ehepartner). Dies wird einstimmig angenommen.
8. Die Mitgliederversammlung nimmt die Einladung der Herren Kruska und Hartl an, die 70. Jahrestagung vom 22.–26. September 1996 in Kiel abzuhalten. Als Schwerpunktthemen sind vorgesehen „Evolution und Domestikation", „Populationsökologie" sowie „Säugetierschutz".

   Per Akklamation wird angenommen, daß Herr Fischer für 1997 nach Jena eingeladen hat.
9. Die Mitgliederversammlung nimmt zur Kenntnis, daß die Proceedings der vom IZW Berlin für 1996 geplanten Tagung (1st Symposion on Physiology and Ethology of Wild and Zoo Animals) voraussichtlich als Sonderheft der ZfS erscheinen werden.

   Per Akklamation beauftragen die Mitglieder mehrheitlich Herrn Uhr mit der Gründung einer Arbeitsgemeinschaft zum Thema Domestikation.

   Herr Heidecke trägt die Aktivitäten der Bibergruppe vor.

   Herr Ganslosser berichtet, daß die Arbeitsgemeinschaft Tiergartenbiologie am 11. und 12. Dezember 1995 erneut in Erlangen tagen wird.

   Das Positionspapier der Tierschutzkommission sowie eine Stellungnahme der Artenschutzkommission zum Thema „Markierung freilebender Tiere" lösen eine intensive Diskussion aus. Einigkeit besteht darüber, daß das Markieren wildlebender Tiere kein Tierversuch im Sinne des Tierschutzgesetzes ist. Herr Schröpfer wird beauftragt, rechtzeitig zur Kieler Tagung eine detaillierte Stellungnahme vorzulegen mit dem Ziel, die Mitgliederversammlung 1996 darüber abstimmen zu lassen.
10. Der Beschluß, ob die Deutsche Gesellschaft für Säugetierkunde aus der „Union deutscher biologischer Gesellschaften" austreten soll, wird vertagt.

Die Sitzung endet um 19.00 Uhr.

Prof. Dr. U. Schmidt	Prof. Dr. H. Erkert	Dr. H. Frädrich
1. Vorsitzender	Geschäftsführer	Schriftführer

Z. Säugetierkunde **60** (1995) 382–384

Buchbesprechungen

MacDonald, D.; Barrett, P.: **Collins Field Guide. Mammals of Britain and Europe.** Harper Collins Publisher, London, Glasgow 1993. 312 pp. £ 14.99
ISBN 0-00-219779-0

In the last few years, over a dozen field guides dealing with European mammals have been published. Another one has now been added to that list. Almost all of them are structured like ornithological field guides: a major part with illustrations presenting the species in an attractive way is integrated into the text. Mammals living in the wild cannot be observed in the field like birds: they live hidden, are mostly active at night and over 50% of the species are smaller than a squirrel, that is to say, almost unobservable. Consequently, this volume is not a field guide in the sense that mammals can be determined in nature with its help. Illustrations were contributed by Priscilla Barrett in her well-known and excellent quality that can hardly be excelled as far as their clearness and delineation of the species-specificity is concerned. It is indeed a pleasure to look at the represented mammals. However, the voles are a bit too identical. The eyes of the *Pitymys* species are too big, e. g. in comparison to the size of their ears. The reader who intends to use the illustrations for a determination should have read the introduction carefully. It would have been better to have marked the characteristics of the species on the illustrations with arrows or other signs. Without these hints this guide only serves specialists.

The representations of field signs such as paw prints, droppings, skeletons and skulls are so small that they are almost useless for a determination of collected materials.

The fox is represented with a hunted squirrel which might be attractive as far as the art of presentation is concerned, but it is certainly one of the most rare kinds of preys and could lead to false conclusions for inexperienced observers. A similar case is the vignette of a fish-eating *A. terrestris.* In the case of the roe deer, a tail is mentioned in the caption, but this tail cannot be seen outside the contour of the body.

The nasalia as a differentiating feature between *C. fiber* and *C. canadensis* cannot be used as represented here. In the case of *C. fiber* they reach between the frontals, whereas in the case of *C. canadensis* they are clearly convex on the side and do not reach the frontals.

The illustrations drawn expressively for the differentiation of swimming rodents do not give the typical swimming positions, both in the case of the beaver and the muskrat. The sacral region of the swimming muskrat, for example, should be seen above water. Unfortunately, the chapter dealing with the group of whales has been divided into two parts by the section with the colour plates. Some inserted vignette drawings are supposed to show differences, others do not, which leads to confusion. Instead of using the correct term 'semiaquatic', the indicated species of carnivores and rodents are falsely designed as aquatic. Furthermore, the group of grass voles does not exist. *Sylvaemus* does not indicate a genus, but a subgenus. It is also unsuitable to group both *A. agrarius* and *Sicista* among the striped mice.

The text is inappropriately and uncommonly long for a field guide and gives many details that often require literature references. As the author himself emphasizes, many details were taken from the literature. However, the quantity of information for the different species is not well-balanced: *V. vulpes*, a species on which the author has worked intensively, is dealt with for over 4 pages; the same amount given to *R. norvegicus* and *M. musculus.* Other species such as *N. noctula, S. scrofa* and *P. vitulina* are described less extensively. The dental formula for *V. vulpes*, it is not clear: In the upper yaw Canidae have only three instead of four premolars and three instead of two molars. For the determination of *P. (Microtus) subterraneus* not only the M^3 should be given as a diagnostic feature, but also M_1. It is doubtful whether *M. socialis* and *M. guentheri* represent one species because of the different karyotypes. Spanish varieties of the *M.s.* do not exist, since they occur in Europe only in some parts of Greece.

The list of species is structured according to the orders and not tabularly, it is therefore absolutely unmethodical. The scientific names are missing here. In the descriptions of the species only the English common names are given.

Unfortunately, the French and German names are not added, which can lead to false designations (e. g. field mouse, field vole). The scientific names are cited without the year and designator. The author tries to explain the scientific names which is often impossible with artificial names.

In spite of all these remarks this volume offers a great amount of useful information. For the first time, a key is given for the identification of bat calls by using a bat detector.

With this presentation we have a reference book in which much short information about mammal species can be found. Together with its extensive glossary (e. g. fitness, hormones, invertebrates), this is a guide in mammalian species biology. It can be warmly recommended to the reader searching for such information and it should also be kept in mind that the twin volume "A natural history" will appear shortly.

R. Schröpfer, Osnabrück

Storch, V.; Welsch, U.: **Kurzes Lehrbuch der Zoologie.** Stuttgart, Jena, New York: Gustav Fischer 1994. 593 S., 284 Abb. Kart. DM 62,–, ISBN 3-437-20507-2.

Das bewährte ‚Kurze Lehrbuch der Zoologie' liegt nunmehr in der siebenten, neubearbeiteten Auflage vor. Es bietet dem Studierenden der Zoologie einen reichhaltigen ersten Überblick über das Fachgebiet, wobei die sachkundigen Ausführungen durch eine Vielzahl hervorragender Abbildungen ergänzt werden.

Dem in zwei Teile (A: Allgemeine Zoologie, B: Systematische Zoologie) gegliederten Unterrichtswerk ist ein Abriß der Geschichte der Zoologie vorangestellt. Der Abschnitt über Allgemeine Zoologie beginnt mit dem Aufbau und dem Stoffwechsel der Zelle und gibt anschließend einen Überblick über die Gewebetypen und deren Funktionen. Sinneszellen und Sinnesorgane sind der Inhalt des 3. Kapitels, gefolgt von einer Darstellung der Nervensysteme und einer kurzen Einführung in die Grundlagen der Ethologie. Die Kapitel 6 bis 12 umfassen alle wichtigen Teilgebiete der Physiologie. Danach leitet der Abschnitt über Vererbung zu einer kurzgefaßten Darstellung der Evolution über, und die Kapitel 15 über Ökologie und 16 über Tiergeographie beenden den der Allgemeinen Zoologie gewidmeten Teil des Buches. In der Systematischen Zoologie wird ein Überblick über die Baupläne und die taxonomische Untergliederung der Stämme des Tierreiches gegeben. Letztere reicht bei den Säugern generell bis zur Ordnung und in Einzelbeispielen bis zur Ebene der Gattung.

Insgesamt besticht das Buch durch seinen logischen Aufbau sowie durch die Klarheit der Darstellung und der Sprache. Kritisch zu bemerken wäre, daß durch die Abhandlung der Baupläne und der Klassifikation von Tieren in Verbindung mit einer hauptsächlich am Ablauf und weniger an den Mechanismen orientierten Darstellung der Evolution dem Studienanfänger ein eher typologisches Bild der Stammesgeschichte vermittelt wird. Die umfangreichen Entwicklungen in den Fachgebieten der molekularen Genetik, der Morphometrik und der Soziobiologie während der letzten zwanzig Jahre finden, abgesehen von einem kurzen Abschnitt über Gentechnologie, kaum einen Niederschlag. So beschränkt sich auf Seite 333 die Beschreibung des Einsatzes molekularer Methoden in der Systematik immer noch auf die Sequenzierung von Proteinen, während etwa den DNA-Techniken wegen der ‚größeren Variationen' in diesem Molekül ein untergeordneter Stellenwert eingeräumt wird. In dem als Gesamtwerk sehr empfehlenswerten ‚Kurzen Lehrbuch der Zoologie' könnte meines Erachtens durch einen kurzen Abschnitt mit neueren Arbeitstechniken und Ergebnissen im Bereich der Mikroevolution der biologischen Variation mehr Ausdruck gegeben werden. Hier fänden auch Ausführungen über die Domestikation einen bezugsreicheren Platz als lediglich im Zusammenhang mit Tierzucht im Kapitel über die Vererbung.

G. B. Hartl, Kiel

Cole, T. C. H.: **Taschenwörterbuch der Zoologie. A Pocket Dictionary of Zoology.**
Stuttgart, New York: Georg Thieme Verlag 1995. 261 S. Flexibles Taschenbuch, DM 36,–.
ISBN 3-13-101961-1

Bei dem vorliegenden Band handelt es sich um ein deutsch-englisches und englisch-deutsches Spezialwörterbuch der Zoologie im Taschenbuchformat. Der Autor, ein Mitarbeiter der Biologischen Fakultät der Europa-Abteilung der Universität von Maryland, USA, faßt den Begriff „Zoologie/zoology“ erfreulich weit. Nicht nur Begriffe der allgemeinen und speziellen Zoologie werden genannt, auch Termini aus Nachbargebieten sind zu finden: Die „A-Bande“ der mikroskopischen Anatomie der quergestreiften Muskulatur, der „Gleichgewichtszustand“, „Knochenmehl“, „Cenozoic“, „pouch“ oder „spotted fever“ sind aufgelistet und übersetzt. Auf lange Erklärungen wird verzichtet, wenn nötig wird allerdings ein klärender Begriff in Klammern beigefügt. Die britische und die amerkanische Schreibweise sind berücksichtigt, z. B.: „Cainozoic Era/Cenozoic/Cenozoic Era“.

Das vorliegende Werk hat einen sehr hohen Gebrauchswert. Es gehört auf den Arbeitstisch all jener deutsch- und englischsprachigen Zoologen und Vertreter verwandter Wissenschaften, welche Fachliteratur in der jeweiligen Fremdsprache lesen oder sich in ihr fachlich korrekt ausdrücken wollen!

P. Langer, Gießen

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b) From books:

HERRE, W.; RÖHRS, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.

c) From reference books:

NIETHAMMER, J. (1982): *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Handbuch der Säugetiere Europas. Ed. by J. NIETHAMMER und F. KRAPP. Wiesbaden: Akad. Verlagsges. Vol. 2/I, 7–28.

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