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Homing ability of the common vampire bat (*Desmodus rotundus*)

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Abstract

A total of 446 common vampire bats (*Desmodus rotundus*) was released from their home roosts at distances between 10 and 100 km apart. The homing performance varied between < 10 and 60 km. No bats returned when they were released at a distance of 100 km from their home roost. Male homing performance (23%) was superior to that of females (8%). Conversely, the proportion of females settling down in the release area (76%) was larger than that of males (42%). The data suggest that homing ability is closely related to the terrain area of vampire acquaintance or "familiar area".

Key words: *Desmodus rotundus*, homing ability, sex differences

Introduction

Studies on the homing ability of the common vampire bat (*Desmodus rotundus*) have resulted in contradictory statements. Ruschi (1951) sustains that most of the vampire bats are able to return to their home roost from distances of up to 120 km during the release night. This would indicate that the homing ability of the vampire bat is equal to that of migratory bats from the northern hemisphere (Cockrum 1956; Mueller and Emlen 1957; Davis 1966). Nevertheless, observations made on fewer individuals (Young 1971) and two incidental observations (Schmidt et al. 1971; Greenhall et al. 1983), suggest that vampire bat-homing performance is less efficient.

The aim of this study was to re-investigate homing abilities of the common vampire bat in northern Argentina.

Material and methods

The study was carried out between 1988 and 1992 in cattle-raising ecosystems of the Provinces (States) of Misiones (ca. 27°S, 55°W) and Formosa (ca. 25°S, 60°W) in northern Argentina. In an effort to avoid contributing to the spread of paralytic rabies, trials were made in areas within a radius of more than 300 km where this illness did not occur (Delpietro and Russo 1996; Delpietro et al. 1997).

Bats were captured after noon inside their original home roost using manual nets. They were kept in individual paper bags and transported by car to the release point where they were 1 banded. Then, when there was total darkness they were released by opening the bags and allowing each one to fly at its own volition. The bats were released only on nights free of rain or strong winds and when the moon was hidden over most of the time. In all the trials the release point was located south of the home (with a tolerance 20° E or W) and in similar ecological areas (Fig. 1). We only used adult bats,

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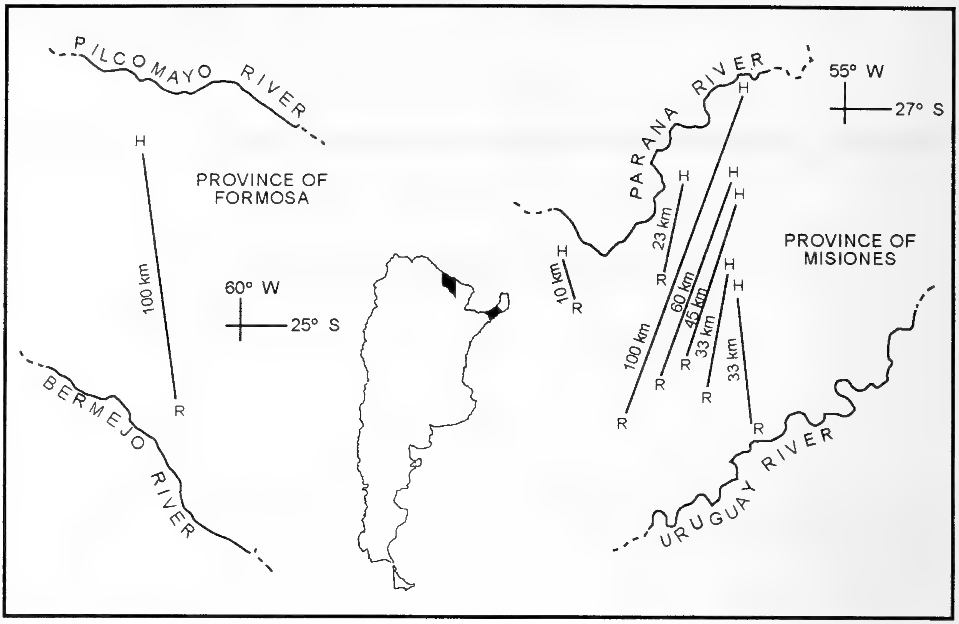

Fig. 1. Homing trials of vampire bats in the provinces of Misiones and Formosa, northern Argentina

but discarding females with a small baby clinging to the nipple and pregnant bats with a palpable fetus larger than 2 cm. A total of 226 males and 240 females was released at different distances ranging between 10 and 100 km (Tab. 1). Nine bats had been banded 7 years before as adults.

Consequently, these individuals were 8 years old when tested (old bats). Mean longevity of vampire bats was estimated to be 2.6 years (Linhart 1973) or 3.4 years (Lord et al. 1976).

In order to obtain information on the vampire bat return time, their home roosts were revisited the day after release (immediate returns), 1 day later (early returns), 1 month later (delayed returns), and 5 to 8 times over a 2 year period (late returns). Also, when we knew the existence of other vampire bat roosts in the home roost area (the roosts located less than 3 km from the original one), we revisited them 4 to 6 times during the 2 years after the release. When we knew the existence of other vampire bat roosts in the release area (the roosts located less than 3 km from the release point), we revisited them 1 month after the release date and 4 to 6 times more over 2 years time. We also registered the bats recaptured far away from the original home roost or the home roost area (strayed bats).

Results

The absolute maximum homing performance was 60 km observed in only 1 of the 69 bats released at that distance. The maximum performance in an immediate return was 33 km. No bats returned when they were released 100 km distance from their home roost (Tab. 1).

A total of 73 bats returned: 71 were recaptured in their home roost and two in the home roost area; male homing performance (23%) was superior to that of females (8%), ($\chi^2 = 14.69$, $p < 0.001$). According to the time of returns, only 8 were immediate (three old bats), 33 early, 21 delayed (one old bat), and 11 late (Tab. 1). The average of immediate returns of the old bats (33%) was higher compared with the entire sample (1.7%) ($\chi^2 = 28.75$, $p \ll 0.001$). In the five trials with home roosts inside the release area we

Table 1. Homing trials of vampire bats in northern Argentina
* = Some were old bat (> 8 years)
·· = Two of these were recaptured in the home roost area
NL = No vampire home roost was located.

Release distance km	Males / females						
			Time of return				Abiding in the release area
	Tested	returned	< 1day	< 2days	< 1month	< 2years	
10	6/4	5/3	*4/1	1/2	0/0	0/0	1/1
23	18/15	7/4	*2/0	2/2	1/2	2/0	0/5
33	62/36	18/4	0/1*	8/1	5/2	··5/0	21/27
33	54/54	19/8	0/0	12/4	*6/3	1/1	NL
45	13/21	3/1	0/0	0/0	1/1	2/0	NL
60	33/36	1/0	0/0	1/0	0/0	0/0	20/32
100	24/30	0/0	0/0	0/0	0/0	0/0	18/27
100	16/44	0/0	0/0	0/0	0/0	0/0	NL
Total	226/240	53/20	6/2	24/9	13/8	10/1	60/92

tested 143 males and 121 females (Tab. 1). We recaptured 60 males (42%) and 92 females (76%) abiding in the release area ($\chi^2 = 8.33$, $p < 0.01$). These bats were not observed again in their original home roost or in the home roost area. Five strayed bats were recaptured. One male and two females from the 45 km trial were recaptured 2 months after release in a roost 24 km distant from their original home roost and 45° skewed from the straight homeward direction (one of those females continued living > 6 years in that roost). Another female belonging to the same trial group was recaptured 5 years after its release in a roost placed 56 km from its home roost and 120° skewed from the straight homeward direction. One male belonging to the 23 km trial group, was recaptured in a cattle-raising field with a mist net 14 months later placed 52 km from their original home roost and 110° skewed from the straight homeward direction. 236 bats were not recaptured at all (lost bats).

Discussion

The data indicate that homing performance of the common vampire bat varies from < 10 km up to no returns being recorded at distances 60–100 km. These results slightly surpass those observed by Young (1971), Schmidt et al. (1971), and Greenhall et al. (1983). In general terms, however they may be considered coincident, since smaller differences may result from larger numbers of trials with greater numbers of bats involved. Our data are also similar to those observed in other new world Phyllostomidae, as e.g. the great fruit-eating bat (*Artibeus lituratus*, Lopez-Forment et al. 1971) and the greater spear-nosed bat (*Phyllostomus hastatus*, Williams and Williams 1967, 1970). Very clearly, however, our results differ from those reported by Ruschi (1951).

The decrease in bat returns increasing with release distances, the diversity of homing performance and its sexual difference, the high proportion of bats abiding in the release area, the strayed bats and the lost ones, strongly suggest that homing in the vampire bat is closely related to the terrain of its acquaintance or "familiar area" (Griffo 1961; Davis 1966). This is not surprising when keeping in mind that an adaptive response cannot be expected in this sense. Vampire bats are not migratory animals (Crespo et al. 1961) and under natural conditions they normally are not displaced from the "familiar area". As a flying animal the bat is safe from floods and only scarcely affected by winds since bats fly near the ground (Dalquest 1955; Villa 1966) and rarely venture far into open areas with no environmental protection (Crespo et al. 1961; Delpietro 1989).

The distances of the immediate returns suggest the maximum extend that the familiar area of the bats can reach, since random returns from these distances during observation time do not appear very likely. On the other hand, the distances of early and delayed returns may point to the fact that some bats may recognize still more extended familiar areas. It is possible that these bats have found a familiar area by scattering radially or wandering at random (Murie 1963; Davis 1966). The late returns and the strayed bats suggest that some of the bats acted that way after being freed.

The diversity of individual vampire bat-homing performance may be related to age (Linhart 1973; Lord et al. 1976), and thus experience as well as learning (Schmidt et al. 1982; Delpietro et al. 1992). Thus, the older bats may have better knowledge of extended "familiar areas" than younger bats.

The higher homing performance of males on average as well as the higher proportion of females settling down in the release area, could indicate that males recognize a larger familiar area than females. Sexual differences in homing performance were observed in other bats (Davis 1966) and in terrestrial mammals (Broadbooks 1970), and this was attributed to the differences in the size of the "familiar area" of each sex. The capacity of the vampire bat to change home range and settle down in the release area can be a selective advantage generated by other situations not related to homing, such as overpopulation, food or refuge shortage, or habitat destruction. In this way, after filling of the Yaciretá (ca. 27°30′S, 56°30′W) and Itaipú (ca. 25°30′S, 54°40′W) dams, we observed that the vampires displaced by the flood settled down in the surroundings of the new lakes. This increased the vampire population density in those areas and produced an increase of predation to livestock and the beginning of predation on humans.

The recapture of most of the homed bats in their original home roost confirms previous observations about vampire bat home loyalty (Schmidt et al. 1978; Delpietro et al. 1992).

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Zusammenfassung

Heimfindevermögen des Gemeinen Vampirs (Desmodus rotundus)

Insgesamt wurden 446 Individuen des Gemeinen Vampirs (*Desmodus rotundus*) in 10 bis 100 km Entfernung vom heimatlichen Ruheplatz freigelassen. Das Heimfindeverhalten variierte bei Strecken zwischen 10 und 60 km. Tiere, welche in 100 km Entfernung freigelassen wurden, kehrten nicht zum ursprünglichen Ruheplatz zurück. Das Heimkehrvermögen der männlichen (23% der Tiere kehrten heim) war besser als das bei Weibchen (8%). Andererseits siedelten sich 76% der weiblichen Tiere im Freilassungsgebiet an, doch geschah dies nur bei 42% der Männchen. Die Befunde lassen darauf schließen, daß das Heimfindevermögen in enger Beziehung zur Vertrautheit mit dem Freilassungsgebiet steht.

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Multiple paternity in the bank vole (*Clethrionomys glareolus*): field and experimental data

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Abstract

The frequency of multiple paternity was estimated in the natural populations of *Clethrionomys glareolus* in northeastern Poland, using enzyme electrophoresis. The percentage of multiply sired litters, those detected and undetected was 35.5 %. A laboratory experiment showed that 30 out of 44 bank vole females mated with two males during one copulatory series (consisting of mounts, intromissions, and ejaculations). Females showed clear preference to finish interrupted copulatory series with the second male, although the interruption of copulatory series did not reduce the chances of pregnancy under laboratory conditions. After the entire copulatory series, all females became non-receptive to any males. We found that under laboratory conditions the number of offspring fathered by the first male did not differ significantly from the number of offspring fathered by the second male. Thus, there are no differences in males' mating success with respect to the mating order in *C. glareolus*. Multiple paternity seems to be a result of social and spatial structure of bank vole populations. It probably evolved as a mechanism to prevent inbreeding.

Key words: *Clethrionomys glareous*, multiple paternity, mating systems, allozymes

Introduction

Animal mating systems have been extensively studied for the last few decades (Parker 1970; Smith 1984; Davies 1991; Arnold and Duvall 1994). Many studies based on protein electrophoresis or DNA fingerprinting showed the occurrence of multiple paternity in a broad variety of animal taxa (Smith 1984; Kawata 1988; Burke 1989; Birkhead and Møller 1992; Gullberg et al. 1997). Multiple paternity can occur when a single female mates with several males within a single estrus period. Such female promiscuity was found in many mammals (Smith 1984; Ginsberg and Huck 1989; Tegelström et al. 1991; Gomendio and Roldan 1993; Boellstorff et al. 1994; Clapham and Palsbøll 1997). Mating systems are regarded as outcomes of the behavior of individuals competing to maximize their reproductive success (Emlen and Oring 1977). The spatial organization and social behavior of small rodents, as in other mammals, have important consequences for mating systems (Ims 1987; Davies 1991).

The bank vole (*Clethrionomys glareolus* Schreber, 1780) is one of the most abundant Palearctic rodent species and its social and spatial structure have been extensively studied (Mazurkiewicz 1971, 1983; Gliwicz and Rajska-Jurgiel 1983; Bondrup-Nielsen and Karlsson 1985). Females will not mature unless they occupy an exclusive territory (Bujalska 1970). Thus, the mature females of the bank vole have mutually exclusive home

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ranges (Bujalska 1990; Gliwicz 1991). Furthermore, the female descendants of one particular female move on to territories as close to the place of birth as possible (Viitala 1977). This results in a kind of family clan system. On the other hand, the spacing systems found in male voles reflect the male reproductive behaviour for obtaining access to the maximum number of fertilizable females (Ims 1987). Home ranges of adult bank vole males are larger than female territories. The degree of home range overlap is high among mature males and male ranges encompass home ranges of several mature females (Bujalska 1970; Gliwicz 1991). Unlike females, only 10 % of the male voles settle close to their natal site as reproductive adults (Ims and Andreassen 1991).

There is a clear dominance hierarchy among males in *C. glareolus* (Viitala and Hoffmeyer 1985). Females can discriminate males according to their social rank by odor cue recognition (Hoffmeyer 1982; Rozenfeld and Rasmont 1991). Horne and Ylönen (1996) showed that postpartum estrus females strongly preferred dominant males for mating, when the female encountered two males: the dominant and the subdominant. However, the authors found that, when the two males were equal in their social status, the females did not show any clear preference for either of the males. Thus, the bank vole females were not simply inclined to mate with a single male, but could be behaviorally receptive to at least two males simultaneously (Horne and Ylönen 1996). Such mating behavior of bank vole females reflects a promiscuous mating system (Gliwicz 1988) and may imply multiple paternity in this species.

Kawata (1988) found multiple paternity in *Clethrionomys rufocanus*, a behaviorally similar species to *C. glareolus*. Sikorski and Wójcik (1990) did not find multiple paternity in a natural population of the bank vole, but they were not able to rule it out. Thus, we decided to re-examine the occurrence of multiple paternity in this species. Firstly, we evaluated the observed frequency of multiple paternity and the paternal exclusion probability in natural populations of the bank vole. Secondly, we estimated males' mating success with respect to the mating order and the frequency of females' multiple matings under laboratory conditions. It is not possible to observe all behavioral events of voles in the wild. Thus, observations of single and multiple matings in the laboratory may allow some conclusions concerning the circumstances of multiple matings under natural conditions.

Material and methods

Bank voles were collected over the years 1996–1997 in four populations in spring and in one population in spring and summer, in northeastern Poland. Trapping was done during two weeks in every population studied. Number of pregnant females caught in a population ranged from 1 to 19. The total sample consisted of 31 pregnant females (27 in spring and 4 in summer) which brought young (31 litters) in the laboratory. Additionally, 50 immature females and 50 males were captured in autumn 1996 and overwintered in separate cages. They were used for the breeding experiment in spring 1997. Dominance hierarchy among males was not established, as every male was kept in its own cage. Individuals were marked by toe-clipping. Toes were immediately frozen at –85 °C and then prepared as homogenates for genotype screening at phosphoglucomutase-3 locus (Pgm-3). This technique allows to investigate individuals' genotypes at Pgm-3 locus without killing the animals. The tissue samples were run on cellulose acetate plates and stained according to Searle (1985). PGM-3 migrates to the most cathodal zone of the PGM system (Searle 1985). Alleles were designated by letters from A (the slowest migrating band) to F according to the relative mobility of corresponding bands on the gel.

The genotypes at Pgm-3 locus of wild-caught pregnant females and their laboratory-born offspring were analysed for multiple paternity. Multiple paternity was indicated when more than two different paternal alleles were found in one litter. It should be noted, however, that using a single locus with 6 alleles will underestimate the frequency of multiple paternity in the wild. Furthermore, the analysis of wild-captured females' genotypes and their laboratory-born offspring does not give the possibility to establish the genotypes of the fathers. Thus, there is no data concerning the number of young fathered by the first and second male in the wild. We estimated the observed frequency of multiple paternity in five bank vole populations studied. Next, we corrected the frequencies of detected multiple paternity by the expected paternal exclusion probability (P), i. e. the probability of detecting an incorrectly assigned parent. Probability P was calculated using the method described by BRUFORD et al. (1992). Calculation of probability P was based on frequencies of six alleles at the Pgm-3 locus in the same five bank vole populations (BORKOWSKA 1999). Next, we used the following formulae to estimated the number and percentage of multiply sired litters (MSL, %MSL; those detected and undetected) in each population and over entire sample: MSL = D/P, and %MSL = MSL/T, where D is the number of observed multiply sired litters, P is the paternal exclusion probability and T is the number of litters tested (GOWATY and BRIDGES 1991).

The laboratory experiment was conducted to establish males' mating success with respect to the mating order and to estimate the frequency of multiple matings by females. Matings occurred between 8.00 and 12.00 hrs in wire-topped plastic cages (50 × 40 × 30 cm) containing sawdust. Females in natural estrus and adult males were used. Genotypes at Pgm-3 locus of all voles were known and males were characterized by mutually exclusive genotypes.

Firstly, we established under what conditions an estrus female was behaviorally receptive to two different males. A female was introduced into the cage 30 min before the first male. Pairs that mated within 20 minutes of the introduction of the male were observed until the achievement of satiety criterion of 45 minutes without intromissions (MILLIGAN 1979). Then, the first male was removed and the second male was put into the female's cage. Female and second male were observed for copulation. All the females (27) that mated with the first male until the achievement of satiety criterion formed group A of the experiment.

In the second part of the experiment the first mating male was removed from a female's cage after its one ejaculation. MILLIGAN (1979) noted, there were two ejaculations during whole copulatory series in the bank vole. Thus, the first male had to be removed after its one ejaculation to enable the second male to perform an ejaculation. One to five minutes elapsed between the removal of the first male and females' exposure to the second one. Females that did not perform whole copulatory series with the first males and refused to mate with second males (group B 1) were kept with second males in a cage for 24 hours. Females that continued interrupted copulatory series with the second male were assigned as group B 2. All females that mated with one or two males were observed for 21 days for pregnancy and offspring.

The genotypes at the Pgm-3 locus in young were examined to establish the number of offspring fathered by the first and second male. Differences in males' mating success were tested using Mann-Whitney test (STATISTICA StatSoft Inc. 1995). Chi-square test was used to test females' preferences to mate with a single male or two different males. Differences in the number of litters among three groups of females (group A, B 1, B 2) were tested using Fisher exact test (STATISTICA StatSoft Inc. 1995).

Results

The analysis of Pgm-3 genotypes in 31 wild-captured females of *C. glareolus* and their offspring revealed that multiple paternity had occurred in at least 7 litters (Tab. 1). This was indicated by the presence of more than two different paternal alleles among the offspring. Multiple paternity was found in every population studied: population 1 – in two out 15 litters in spring and in one of four litters in summer; population 2 – in one of three litters in spring; population 3 and 4 (both) – in one of four litters in spring and population 5 – in one litter studied in spring. The observed average frequency of litters fathered by more than one male in the five populations all together was 22 % (7 out of 31 litters). The percentage of multiply sired litters (%MSL; those detected and undetected) varied from 21.0 % (in population 1) to 33.3 % (in population 2). Percentage of MSL in the full sample was 35.5 % (Tab. 2).

During the first part of the laboratory experiment we found that a whole copulatory series with the first male (consisting of mounts, intromissions, and two ejaculations) lasted about 50 minutes. Thereafter, all the females from group A (n = 27) became non-receptive and they refused to mate with the second male. In the second part of the experiment

Table 1. The genotypes of females and their offspring at Pgm-3 locus and paternal alleles found in litters of wild-caught *Clethrionomys glareolus* from NE Poland.

No.	Mother	Offspring								Paternal alleles
		1	2	3	4	5	6	7	8	
1.	DE	BD	BD	CD	CD	DE	CE	CE	CE	B, C; D or E
2.	DD	BD	DD	DD	DD	DD	DD	DE		B, D, E
3.	DE	BE	BE	BD	CE	DD	EE			B, C, D, E
4.	BD	DD	DD	DD	DE	DE	AB			A, D, E
5.	CE	EE	EE	CE	CE	DE	BC			B, D; E or C
6.	DE	EE	EE	BE	BE	CD				B, C, E
7.	EE	EE	EE	EE	BE	DE				B, D, E

Table 2. Number and percentage of multiply sired litters (MSL, %MSL) in five populations of the bank vole from NE Poland. T – number of litters tested, D – number of observed detections, P – the probability of detecting an incorrectly assigned parent, * 'Full sample' indicates values computed over the entire sample of five populations.

Population	T	D	P	No. of MSL	%MSL
1	19	3	0.7522	4.0	21.0
2	3	1	0.6972	1.0	33.3
3	4	1	0.7041	1.0	25.0
4	4	1	0.7590	1.0	25.0
5	1	1	0.7657	1.0	–
Full sample*	31	7	0.6125	11.0	35.5

44 estrus females mated with the first male. When the first male was removed after its one ejaculation and the second male was introduced to the female, animals smelled each other for 5–10 minutes. Then, 30 females (group B 2) continued the interrupted copulatory series with a new sire. Fourteen females refused to mate with the second male (group B 1). Thus, estrus females showed clear preference to finish interrupted copulatory series ($\chi^2 = 3.94$, $p = 0.047$). One of the females which refused copulation (group B 1) was killed by the second male overnight.

Seven out of 27 females (26 %) that performed whole copulatory series with a single male bore young. Eleven females (37 %) from the group B 2 had offspring and only one out of 13 females (8 %) that had interrupted copulation with first male (group B 1) bore young. However, there were no statistically significant differences in the number of litters between females from group A and group B 1 (Fisher exact test, $p = 0.2477$) and group A and group B 2 (Fisher exact test, $p = 0.3619$). The Fisher exact test did not show any significant difference between groups B 1 and B 2 in the number of litters ($p = 0.1188$), either.

The analysis of 11 females that mated with two different males and had offspring, revealed that in four litters pups were fathered by two different males. In one case offspring was fathered by the first male only, and in six litters the second-mating male was the father of all the pups (Tab. 3). The number of offspring fathered by the first male did not differ significantly from the number of offspring fathered by the second one ($U = 32.50$, $p = 0.0628$, Mann-Whitney test).

Table 3. The number of offspring fathered by the first and the second male of *C. glareolus* born during the laboratory experiment.

Litter	First male	Second male
1.	2	4
2.	4	1
3.	3	2
4.	3	1
5.	5	0
6.	0	5
7.	0	5
8.	0	4
9.	0	4
10.	0	4
11.	0	3

Discussion

Multiple paternity seems to be a common phenomenon in natural populations of the bank vole. Litters fathered by more than one male occurred in all populations studied, both in spring and summer. Sikorski and Wójcik (1990) did not find multiple paternity in the bank vole because they studied only two loci with two alleles and one locus with three alleles. Six alleles at phosphoglucomutase-3 locus (Pgm-3) were found in the bank vole populations from NE Poland (Borkowska 1999). It allowed us to prove for the first time the occurrence of multiple paternity in *C. glareolus*. The average frequency of observed multiple paternity was 22 % in the bank vole populations studied. A very similar frequency of multiply sired litters (21 %) was found using enzyme electrophoresis in an experimental field population of *Clethrionomys rufocanus* (Kawata 1988). However, multiple paternity may not always be detected in natural populations, even using the highly variable Pgm-3 locus. This occurs when a female mates with two males possessing identical Pgm-3 genotypes, or males have one Pgm-3 allele in common. Thus, the frequency of detected multiple paternity in *C. glareolus* seems to be underestimated. The percentage of multiply sired litters detected and undetected (%MSL = 35.5 %) seems to be a more realistic approximation of multiple paternity frequency in natural populations. This means that at least one out of three females successfully mated with more than one male within a single estrus period. More advanced methods of DNA fingerprinting (Gockel et al. 1997) would certainly yield the most precise estimate of the proportion of multiply sired litters in the wild. The basic demonstration of multiple paternity for *Clethrionomys glareolus* in natural populations and under laboratory conditions is convincing, in spite of the fact that we used enzyme electrophoresis. Furthermore, we showed that 30 out of 44 bank vole females trapped in nature mated with two males in the laboratory. This gives the 68 % frequency of multiple matings. However, the estimation of frequency of multiple matings under laboratory experiment does not take into account factors such as population density or other demographic factors.

The existence ot multiple paternity in *C. glareolus* is closely associated with the social and spatial structure of the population. Bank vole females are able to discriminate males according to their social status and strongly prefer dominant males as mating partners (Horne and Ylönen 1996). A dominant male of *C. glareolus* copulates with an estrus female until she becomes non-receptive and then he leaves her to resume searching. According to our study, a female becomes non-receptive after a whole copulatory series and will not mate with another male. We conclude that mate guarding in the bank vole is restricted to the time of copulation only. However, dominant males cannot monopolize all the females within their area. This is caused by the spatial distribution of individuals in the bank vole populations. The home ranges of males overlap extensively and home ranges of adult females may adjoin or overlap, on average with 13.0 males of *C. glareolus* (Sikorski and Wójcik 1990; Gliwicz 1991). Thus, a female may copulate with a subordinate male. If such mating is interrupted by the dominant male, a female will probably finish the copulatory series with him. Therefore, multiple paternity occurred when one male could not deter other males from an estrus female.

In our study we showed that interruption of copulatory series did not reduce the chances of pregnancy under laboratory conditions. It means that one ejaculation may guarantee fertilization of the ova. Why did 68 % of bank vole females continue copulatory series with the second male in the experiment? There are a few hypotheses which may explain the evolution of multiple matings by the bank vole females. Ginsberg and Huck (1989) suggested that golden hamster females mate multiply avoiding the reduction in fecundity as a consequence of mating with recently mated, sperm-depleted males. Moreover, Kawata (1988) noted that males of *C. rufocanus* could not successfully mate with more than one female within a day. Bank vole females might tend to mate with several males when males are available thus avoiding temporary male sperm depletion.

On the other hand, mixed-female behaviour probably evolved in the bank vole. Brown (1997) suggested that females may mate with one male first ensuring fertilization and with a subsequent male to improve offspring quality. This will result in genetic diversification of the brood. Bank vole females that occupy adjoining territories are closely related, because mature daughters establish their home ranges in the vicinity of their mother's range (Viitala and Ylönen 1993). In such a case, a promiscuous mating system with multiple paternity seems to be an important mechanism to prevent inbreeding. Furthermore, females may benefit directly by multiple matings. Copulation with the second male may be less costly than resisting (Reynolds 1996). Females' refusal to mate with the second male may lead to male harassment. Killing of the female by the second male during laboratory experiment indicates that this may also happen in nature. However, male aggression towards females was rare, as it happened in only one out of 14 cases when females refused to mate.

Mating with every estrus female that males meet appears to be advantageous for males, even if they mate as the second. In our laboratory experiment both males had equal chances of siring offspring ($U = 32.50$, ns). However, we were not able to ascertain it in natural populations because we did not know the genotypes of putative fathers. In mammals no differences were found in males' mating success in respect to the mating order when two males mated with a single female close in time (Ginsberg and Huck 1989). In our experiment spermatozoa from both males were potentially capable of fertilizing the ova at the time of ovulation, so that both males could father the offspring. Furthermore, a copulatory plug is an insufficient barrier to prevent further copulation in the bank vole. This is because the copulatory plug from a previous ejaculation was normally lost from the vagina during the initial intromissions of the next ejaculatory series (Milligan 1979). In our study the second mating males fathered all pups in six out of 11 litters. However, the tendency for the second males to father more young than the first one was statistically insignificant. It should be noted, that due to the small sample size and the necessity of using a non-parametric test, our analysis of the laboratory data has quite low statistical power.

We showed that despite the strong female preference to mate with the dominant male (Horne and Ylönen 1996), multiple paternity occurred in natural populations of the bank vole. It seems to be constrained by social and spatial structures of the populations. It would be of interest to discern whether the frequency of multiple paternity in natural populations is related to other ecological factors such as population density, age structure, and sex ratio. We conclude that multiple paternity may also occur in Microtine rodents, showing spatial and social structure of the populations similar to the bank vole (Bondrup-Nielsen and Karlsson 1985). Our laboratory results suggest that multiple paternity probably evolved to prevent inbreeding in bank vole populations.

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Zusammenfassung

Multiple Vaterschaften und Fortpflanzungssysteme bei der Rötelmaus (Clethrionomys glareolus)

Mittels Enzymelektrophorese wurde die Häufigkeit multipler Vaterschaften in natiirlichen Populationen der Rötelmaus (*Clethrionomys glareolus*) aus Nordostpolen bestimmt. Der Anteil von Würfen mit mehreren Vätern betrug 35,5 %. Ein Laborexperiment zeigte, daß sich während eines Kopulationsablaufes (bestehend aus Aufreiten, Eindringen und Ejakulation) 30 von 44 Rötelmausweibchen mit zwei Männchen paarten. Die Weibchen zeigten eine klare Präferenz, unterbrochene Kopulationsabläufe mit dem zweiten Männchen zu Ende zu führen, obwohl unter Laborbedingungen die Störung eines Kopulationsablaufes die Chancen einer Schwangerschaft nicht reduzierte. Nach dem gesamten Kopulationsablauf wurden die Weibchen gegenüber jeglichen anderen Männchen unempfänglich. Unter Laborbedingungen unterschied sich die Zahl der vom ersten Vater stammenden Nachkommen. Somit hat die Reihenfolge der Begattung bei *C. glareolus* keinen nachweisbaren Einfluß auf den Reproduktionserfolg der Männchen. Die Paarung mit mehreren Männchen mag für Weibchen aufgrund der Vermeidung gelegentlicher Spermadefizienzen oder der Vermeidung von Belästigungen durch Männchen nach dem Kopulationsablauf von Vorteil sein. Die Paarung mit dem ersten Männchen stellt für das Weibchen eine Befruchtung sicher, während der Beitrag weiterer Männchen die Fitness der Nachkommenschaft steigern könnte. Das Auftreten mehrfache Vaterschaften scheint eine Folge der sozialen und räumlichem Struktur von Rötelmauspopulationen zu sein und ist vielleicht im Zuge der Etablierung von Mechanismen zur Inzuchtvermeidung entstanden.

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Metabolism and thermoregulation in root voles (*Microtus oeconomus*) from the Qinghai-Tibet Plateau

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Abstract

Metabolic rate and the role of evaporative water loss in thermoregulation were studied in root voles (*Microtus oeconomus*) from the Qinghai-Tibet Plateau. The thermoneutral zone is 28–32.5 °C. Mean basal metabolic rate is 3.29 ml O_2 g^{-1} h^{-1}, higher than predicted values based on body mass. Total thermal conductance is 0.279 ml O_2 g^{-1} h^{-1} $°C^{-1}$, slightly higher than predicted values based on body mass. Evaporative water loss plays an important role in temperature regulation. All these characteristics have important adaptive significance for root voles to cope with their extreme environments. Cold and high altitude are the important factors to affect both metabolism and insulation. From an evolutionary point of view, long-time cold is perhaps the main selective force faced by root voles in their environment of the Qinghai-Tibet Plateau.

Key words: *Microtus oeconomus*, metabolism, thermoregulation

Introduction

Many studies have concerned the ecophysiology of microtine rodent species and found that high metabolic rates are significant characteristics for these animals (Wunder 1985). However, only little information is available for species living at high altitude. Thus, we chose root voles (*Microtus oeconomus*) which have a very wide geographical range, and inhabit vast areas of the northern parts of the Euro-Asiatic continent (Gebczynska 1970), for physiological investigations. Root voles live in the *Potentilla fruticosa* shrub of alpine meadows on the Qinghai-Tibet Plateau. They are herbivorous, burrowing, winter active, and facing the two extreme environmental factors of cold and hypoxia. Therefore, the aim of this study was to investigate and characterize metabolic parameters of this species.

Material and methods

Animals

Animals were live-trapped at the Haibei Alpine Meadow Ecosystem Research Station of the Chinese Academy of Sciences, in the Menyuan County, Qinghai Province (37°29′ – 37°45′N, 101°12′–101°33′E). The altitude is about 3200–3500 m above sea level. The temperature range between day and night is great (minimum –2.6 °C to maximum 23.7 °C in July and from –35.2 °C to 6.1 °C in January). Comparing summer with winter, the differ-

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ences of mean ambient temperature, mean maximum temperature, and mean minimum temperature were 21.9 °C, 17.8 °C, and 24.6 °C, respectively, during the years from 1980 to 1990. The plant growing period is short, only about 130–140 days. Average annual precipitation is 580 mm and mean wind speed is 3.1 m s^{-1}. Most snowfall occurs from September to June. The principal vegetation types are alpine shrub and alpine meadow. *M. oeconomus* were trapped in *Potentilla fruticosa* shrub in October 1992. The experiments were carried out in November 1992. Eight individuals (four males and four females) were used, of which the body mass was 24.0 g ± 1.0 (SE).

Metabolic investigations

Metabolic rates were measured by using open flow respirometry with a Beckman OM-14 oxygen analyzer. Animals were tested in 0.5 l plastic chambers, equipped with air inlet and outlet ports. Metabolism chambers were kept in a temperature-controlled small room, and dry air from flow meters (Made by Shanghai Instrumental Co.) entered the chambers at 400 ml min^{-1}. Air flowed through columns of soda lime and drierite for removal of CO_2 and H_2O before entering the oxygen analyzer.

Resting metabolic rate (RMR) was measured over the temperature range from 15 °C to 37.5 °C, as the lowest oxygen consumption sustained for 5 min of a quiescent, unanesthetized animal during 90 min in the respirometer. Measurements were carried out during daytime in darkened chambers. For reasons of stabilizing and becoming familiar with the chambers, the animals were in the metabolism chambers for 60 min, before oxygen consumption was recorded.

Metabolic rates were computed according to the method of Depocas and Hart (1957) and Hill (1972). The equation was as follows:

$$\mathrm{MR} = \frac{\mathrm{F}(\mathrm{F}_{\mathrm{I}_{\mathrm{O}_2}} - \mathrm{F}_{\mathrm{E}_{\mathrm{O}_2}})}{\mathrm{M}(1 - \mathrm{F}_{\mathrm{E}_{\mathrm{O}_2}})}$$

where MR is metabolic rate in ml O_2 g^{-1} h^{-1}; F is flow rate at standard temperature and pressure conditions in ml min^{-1}; F_{IO_2} is the fractional oxygen concentration of inlet air; F_{EO_2} is the fractional oxygen concentration in outlet air; and M is body mass in g.

Each measurement lasted for 60 to 90 min. The animals were not fed 4 hours before the investigation in order to minimize the specific dynamic action of food.

Evaporative water loss

When metabolic rate reached low readings, "U" shaped tubes packed with pre-weighed dry silica gel (to ± 0.1 mg) were connected to the outlet ports of the chamber for a further 30 min. The increase in weight of the U-tube over this time was taken as the evaporative loss (EWL) rate (Deavers and Hudson 1981). The data of animals that urinated during the experiments were discarded.

All results were expressed as mean ± SEM, and regression analysis was used to analyze the relationship of energetic parameters with T_a.

Results

Oxygen consumption below the thermal neutral zone (TNZ)

Oxygen consumption increased with decreasing T_a below the TNZ (Fig. 1); the relationship between resting metabolic rates (RMR) and T_a (from 15 °C to 28 °C) is described by the equation:

$$\mathrm{RMR}\ (\mathrm{ml}\ \mathrm{O_2}\ \mathrm{g}^{-1}\ \mathrm{h}^{-1}) = 9.011–0.200\ \mathrm{T_a}\ (r = -0.986,\ p < 0.01)$$

The slope of the equation between RMR and T_a was regarded as the total thermal conductance and it is proportional to heat loss from the body by radiation, conductance, convection, and evaporation. For the root vole this is 0.20 ml O_2 g^{-1} h^{-1} $°C^{-1}$. Using the

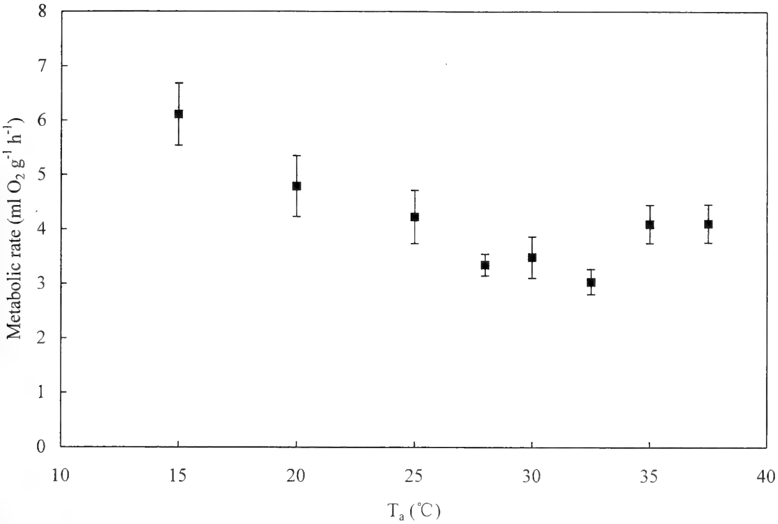

Fig. 1. Relationship of metabolic rates (ml O_2 g^{-1} h^{-1}) to ambient temperature (Ta) in root voles. Bars indicate ± 1 SEM.

Newtonian model of cooling to calculate thermal conductance involves two assumptions. First, oxygen consumption should be linearly related to T_a; second, at RMR = 0, the intercept point of RMR and T_a is equal to T_b. In the present study, the intercept of RMR and T_a is 45.1 at RMR = 0, and this is much higher than the actual T_b (38.5 °C) of root voles. McNab (1980 b) suggested that when the extrapolated T_b is larger than the actual T_b it should be corrected by the following equation:

$$C_m = C_f\,(1 + 0.06\,\Delta T_b)$$

where C_m is the minimum thermal conductance, C_f is the slope of the regression equation between RMR and T_a, and ΔTb is the difference between predicted T_b at RMR = 0 and measured T_b. From this equation, C_m is calculated to be 0.279 ml O_2 g^{-1} h^{-1} $°C^{-1}$, which is 37% higher than the value predicted by Herreid and Kessel (1967, $C = 1.0\,W^{-0.50}$) and 42% higher than that predicted by Bradley and Deavers (1980, $C = 0.76\,W^{-0.426}$).

Oxygen consumption within and above the TNZ

The TNZ was 28 °C–32.5 °C. Within the TNZ, BMR was 3.29 ml O_2 g^{-1} h^{-1}, 214% and 189% of the values predicted by Kleiber (1961, $BMR = 3.42\,M^{-0.25}$, where M is the body mass in g) and Hayssen and Lacy (1985, $BMR = 4.98\,M^{-0.33}$, where M is the body mass in g), respectively. Above the TNZ, RMR increased with T_a (Fig. 1).

Evaporative water loss (EWL)

EWL was relatively stable below the TNZ, with an average value of 5.48 mg H_2O g^{-1} h^{-1}. Within and above the TNZ, EWL increased with T_a, and reached a peak of 13.8 mg H_2O g^{-1} h^{-1} at 35 °C. Above 35 °C, EWL declined and the root voles did not survive for more than 1 h (Fig. 2) There was a positive relationship between EWL and T_a from 28 °C to 37.5 °C; this was described by the equation:

$$\text{EWL (mg } H_2O\ g^{-1}\ h^{-1}) = -13.54 + 0.74\,T_a\ (r = 0.86,\ p < 0.05).$$

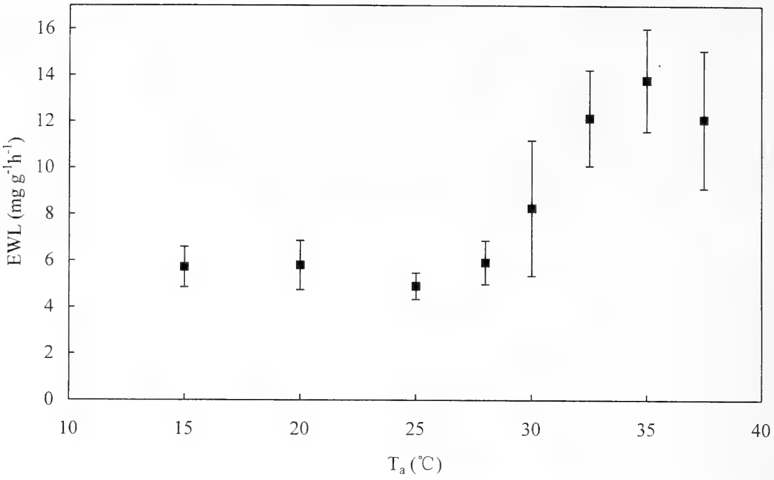

Fig. 2. Relationship of evaporative water loss (EWL, mg g^{-1} h^{-1}) to ambient temperature (Ta) in root voles. Bars indicate ± 1 SEM.

Similarly, within the temperatures of 28 °C–37.5 °C, the ratio EWL/RMR was increased with increasing T_a; the regression equation is:

$$EWL/RMR\ (mg\ H_2O\ ml^{-1}\ O_2) = -1.297 + 0.126\ T_a\ (r = 0.85,\ p < 0.01).$$

Discussion

This study shows that root voles living on the Qinghai-Tibet Plateau had higher values of metabolic rates (214% predicted by Kleiber 1961). Similar results were reported for this species by Jia and Sun (1986, 221% predicted) and Casey et al. (1979, 220% predicted). It seems that the high level of metabolism is characteristics for this species, regardless of whether they are distributed in taiga or on the Qinghai-Tibet Plateau.

Microtine species are generally distributed in boreal high latitude regions, where a high metabolic level is advantageous as an adaptation to the cold. Hypoxia, besides cold, in alpine regions is another important environmental factor. Hays (1989) showed that at high altitudes deer mice (*Peromyscus maniculatus*) have a BMR that is higher than at low altitudes.

BMR may be modified by many factors, such as body size, food habits, activity, climate, and phylogeny (McNab 1986, 1988, 1992) in mammals. For microtine species, their high metabolic rates are thought to be related to cold environments (Packard 1968), poorly digestible food (Wunder 1985; Koteja and Weiner 1993), and intrinsic growth rate of a population (McNab 1980 a). McNab (1992) also suggested that Arvicolids are characterized by a high basal rate of metabolism by general mammalian standards; and Arvicolids that live in cold climates, i. e., at high altitudes and latitudes, have higher basal rates of metabolism than species living in other environments. In alpine meadows, the annual mean temperature is –2 °C, and the mean maximum temperature in summer is only 15.6 °C (Wang and Wang 1996). Root voles here are exposed to cold environments throughout the year. Thus, a high BMR is beneficial to their survival at these high altitudes.

Generally, the thermal conductance of microtine species is lower than predicted values (Wunder 1985). Our study indicated that thermal conductance for root voles is 42% higher than values predicted from body mass (Bradley and Deavers 1980), which provides an effective avenue for heat loss. Slight high thermal conductance could be advantageous for this diurnally active species during the daily high temperature period. Mean maximum temperature of ground-surface may reach 34.9 °C in summer (Wang and Wang 1996).

EWL is very important for thermoregulation in root voles, even at high temperatures. Below the TNZ, the ratio of EWL to metabolic rate remained stable. Within and above the TNZ, the ratio increased sharply with Ta increasing and peaking at 32.5 °C, and then declining. This indicated that within the TNZ increasing rate of evaporative heat loss (EHL) was greater than that of metabolic heat production (HP), so the percentage of EHL to HP increased sharply with increase in T_a. Above the TNZ, the increasing rate of HP was greater than that of EHL, and the percentage of EHL to HP declined. This suggested that root voles have limited ability to cope with high temperatures.

If the EWL in root voles is expressed as the percentage of metabolic heat loss, it is 13% between 15 °C and 25 °C and 33% from 28 °C to 32.5 °C and 39% above. Bradley (cited by Deavers and Hudson 1980) found in seven species of voles that evaporative heat loss was 12% of total heat loss.

In summary, root voles from the Qinghai-Tibet Plateau had higher metabolic rates and slightly higher thermal conductance than predicted. Evaporative water loss plays an important role in thermoregulation, especially at high temperatures. A long period of cold and high altitude, a great temperature fluctuation between day and night, and a relative small temperature fluctuation within a year are perhaps important environmental factors to affect both metabolism and insulation for root voles.

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Zusammenfassung

Stoffwechsel und Temperaturregulation bei Nordischen Wühlmäusen (Microtus oeconomus) vom Qinghai-Tibet Plateau

Stoffwechsel und evaporative Wasserabgabe bei Thermoregulation wurden bei Nordischen Wühlmäusen (*Microtus oeconomus*) vom Qinghai-Tibet Plateau untersucht. Die Thermoneutralzone liegt bei 28–32,5 °C, und der mittlere basale Sauerstoffverbrauch ist mit 3,29 ml O_2 g^{-1} h^{-1} höher als auf der Grundlage des Körpergewichts erwartet. Der gesamte konduktive Wärmeverlust war ebenfalls höher als auf der Basis der Körpermasse zu erwarten war. Der evaporative Wasserverlust spielt eine wichtige Rolle bei der Temperaturregulation. Alle diese Charakteristika haben eine wichtige adaptive Bedeutung für Nordische Wühlmäuse in ihrem Habitat. Aus Sicht evolutiver Adaptation ist sehr wahrscheinlich die lang andauernde Kälte ein Hauptfaktor selektiver Einnischung.

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Age-dependent changes in the stability of the daily activity rythms of laboratory mice

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Abstract

The aim of the present study was to investigate age-dependent changes in the daily activity rhythm of laboratory mice with special reference to its stability and synchronization with the light-dark (LD)-cycle. Attempts were made under laboratory conditions to reverse changes by means of Zeitgeber-strengthening and social factors.

Investigations were carried out on female laboratory mice. Animals were kept under standardized environmental conditions (L : D = 12 : 12; Light-on: 7.00; 100 : 0 lx, T = 21 +/– 2 °C; food and water ad libitum). Locomotor activity was measured by passive infrared detectors. The percentage of total activity per 24 h accounting for the dark period was used as a measure for the synchronization with the LD-cycle. To characterize the stability of the rhythms an ANOVA and a correlation analysis were performed.

The daily activity rhythms were investigated from weaning to death of the animals. Using these results four age groups were chosen for a more detailed analysis (24, 56, 65, and 88 weeks). The total activity per 24 h and the magnitude of the daily changes were found to be statistically lower than in adult mice (24 weeks) only in the oldest group. The percentage of total activity per 24 h accounting for the dark period was already decreased in 56-week-old mice, the stability of the daily patterns in 65-week-old ones. Further investigations were performed simultaneously on adult and presenile mice (24 and 65 weeks old). In an initial experiment the magnitude of the LD-cycle was changed. Following an increase (200 : 0 lx) the interdaily variability decreased to a greater extent in presenile mice. A decrease in the magnitude (5 : 0 lx) caused a higher variability mainly in adult animals. As a result the differences between the age groups were not longer significant. In a second experiment the animals were transferred to groups with 3 individuals. The rhythm stability of presenile mice increased and was not further different from those in adult mice.

The results provide evidence that it is possible to stabilize the circadian system of aged organisms by strengthening of the LD-Zeitgeber and/or additional Zeitgebers.

Key words: *Mus musculus* f. dom., circadian rhythm, age, stability

Introduction

Changes in circadian/daily activity rhythms in aged animals have been frequently described (Aschoff 1994; Turek et al. 1995). These reports concerned characters of rhythm such as the circadian amplitude, the percentage of ultradian components, the period length, and the phase position under entrained conditions. In addition, differences in the phase response to photic and nonphotic stimuli and the resynchronization rate following a Zeitgeber-shift have been obtained.

In our own investigations on laboratory mice we found decreased circadian ampli-

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tudes, while the percentage of ultradian components was elevated. The acrophases were progressively advanced. The rate of resynchronization following Zeitgeber-shift was lower as compared to adult mice. Altogether our results indicated a deteriorating ability of old mice to synchronize their rhythms with periodic environment and its complete loss during the last days before death. The circadian rhythmicity remained as long as the animals realized a certain amount of activity (SCHUH et al. 1991; WEINERT and WEISS 1997; WEINERT and WEINERT 1998).

Established circadian rhythms, their stable synchronization with the periodic environment and physiological phase relationships between different rhythmic functions are characteristics of the internal and external temporal order of adult organisms. As a consequence of the age-dependent changes in the circadian rhythmicity this temporal order is disturbed in old organisms; this in turn may diminish health and performance. The aim of the present investigation was to analyze age-dependent changes in the daily activity rhythm, and to attempt to improve the interdaily stability and the synchronization with the LD-periodicity by means of Zeitgeber-strengthening.

Materials and methods

Experiments were carried out on female laboratory mice of our own outbred stock (Haz:ICR). This has been very well investigated chronobiologically during the last few years (for review, see Weinert and Weinert 1998). Female animals were chosen because most of our former studies were performed on female mice. Also their daily rhythms are more stable compared to male mice (WEINERT 1996). Animals were housed in air-conditioned rooms at an ambient temperature of 21+/–2 °C and a relative humidity of 55–65%. They were exposed to an artificial light-dark (LD) cycle of 12:12 h with light from 07:00 to 19.00 h Central European Time. The mean illumination intensity during light time was 100 lux. Standardized food (Altromin®) an water were available ad libitum. These conditions will further be called "standard conditions".

At an age of 21 days the mice were weaned. Those animals that were investigated at juvenile age were singly housed. The other mice were housed in groups of 10 individuals until two weeks before the experiments started. Then, they were singly housed and exposed to experimental conditions.

To obtain a complete picture of the ontogenetic development of the daily activity rhythm from weaning until the physiological death of the animals, results of several experiments have been summarized. They have all been performed under standard conditions on singly housed mice. Several additional experiments were conducted to fill some gaps of data or to increase the number of animals. On the basis of these results the age groups for the experiments were selected. Adult mice with a stable and well synchronized activity rhythm were chosen as control. In an older group (presenile mice) the activity rhythm was still present but with a deteriorated stability and synchronization (for details, see "Results").

In a first set of experiments the Zeitgeber-strength of the LD-cycle was modified. Compared to standard conditions, the magnitude was decreased (5:0 lx) or increased (200:0 lx). To investigate the influence of social factors two experiments were performed. In the first one, adult and presenile mice were investigated for two weeks individually and thereafter in groups of 3 animals of the same age. In a second experiment, mixed groups with 1 adult and 2 presenile mice or with 2 adult and 1 presenile mouse were studied.

The locomotor activity was recorded continuously using passive infrared motion sensors. They were mounted 5 cm above the cage roof in such a way that they detected motions of the mice in all sectors of the cage. The impulses were stored and partly analysed using the "Chronobiological Kit" (Stanford University). The activity counts were summarized to hourly values, and mean value chronograms of seven consecutive days were calculated for each mouse. The difference between the lowest and the highest values was taken as the magnitude of the oscillation. The activity rhythm was also characterized by the total activity per day (counts/24 h) and the percentage of total activity per 24 h accounted for the dark time. The latter characterizes the synchronization of the daily rhythm with the LD-cycle.

Interdaily variability or stability of the daily activity patterns was investigated by means, of ANO-

VA and correlation analysis (WEINERT 1996). The intra-individual variance was used as a measure for the differences between consecutive days. On the other hand, the coefficient of correlation charcaterized the coincidence between consecutive days.

To verify the obtained differences statistically the Mann-Whithey u-test was used.

Results

The daily activity rhythm was investigated starting immediately after weaning until the death of the mice. Figure 1 shows the mean values of some rhythm characters depending on age. Prominent changes were obtained mainly in juvenile and senile mice. The total activity per 24 h showed a steep increase up to an age of 11–12 weeks and then decreased slightly. From about 24 weeks of age the changes were comparatively small (adult stage). Between the 70th and 80th weeks of age activity decreased to 25% of the value measured in young adults. The magnitude of the daily rhythm changed in the same way as the total activity. Adult mice realized more than 70% of their activity during the dark period. In about one-year-old mice the percentage of total activity per 24 h accounting for the dark period started to decrease. At the beginning, the decrease was slow. About 5 weeks following the steep decrease in the total activity and the magnitude of the activity rhythm, which was observed between the 70th and 80th weeks, the dark period activity decreased considerably. Animals older than 80 weeks realized only about 50% of their total daily activity during the dark period.

Using results depicted in figure 1 four age-groups have been chosen for a more detailed analysis. 24-week-old mice were used as control. Beginning from this age the daily rhythms changed only slightly in the course of several months. 56-week-old mice were chosen because former studies revealed the first age-dependent changes in daily rhythms at an age of one year (WEINERT and SCHUH 1988). Finally, two groups were chosen immediately before (65 weeks) and after (88 weeks) the steep decrease in total activity, rhythm magnitude, and dark-period activity.

The daily patterns of the four age groups are shown in figure 2. They were all bimodal with a main maximum in the dark period and a secondary one following lights-on. The magnitude of the main maximum decreased, whereas the secondary one became more pronounced, becoming higher and broader. Together with the phase advance in the main maximum this caused a shortening of the resting period during the light period. The total activity/24 h decreased with advancing age (Tab. 1). In the younger groups the differences were not yet significant. However, the activity of the oldest animals was only 20–25% from that of adult mice (24 weeks). The daily magnitudes changed similarly. Considerable changes were found for the dark-period activity. It was significantly lower already in 56-week-old animals and decreased further with increasing age. This was a result of the phase advance of the main maximum, but also of the larger secondary maximum.

Age-dependent changes were found also concerning the stability of the daily rhythms (Tab. 1). With increasing age the coefficients of correlation decreased, reflecting a worse coincidence of the activity patterns of consecutive days. ANOVA revealed an increasing percentage of total variance which accounted for the variability between consecutive days. Thus, both analyses confirm a lower stability of the activity rhythm in senile mice, being significantly different from adult mice already in 65-week-old animals.

The experiments investigating possibilities to stabilize the circadian rhythm were carried out simultaneously on adult (24 weeks) and presenile (65 weeks) animals. The 65-week-old mice were chosen, because at this age the stability of the rhythm and its synchronization with the LD-Zeitgeber were already decreased, whereas the activity rhythm itself (shape, daily mean, magnitude) was not yet significantly change.

The differences between the activity patterns of adult and presenile mice obtained un-

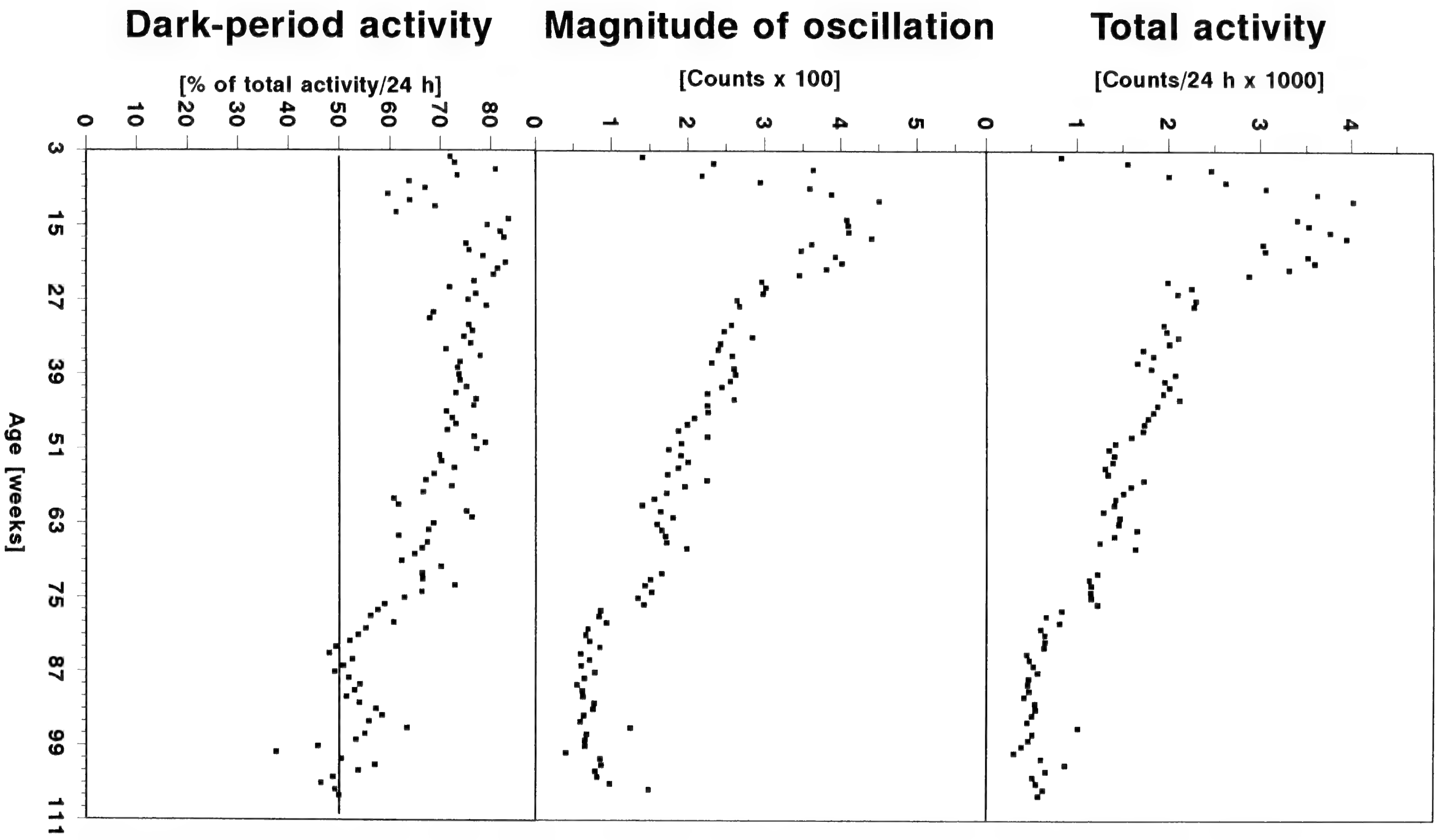

Fig. 1. Changes in some characters of the daily activity rhythm in the course of the postnatal development (weekly mean values of ≥5 female mice, from the 96th weeks of life n = 3).

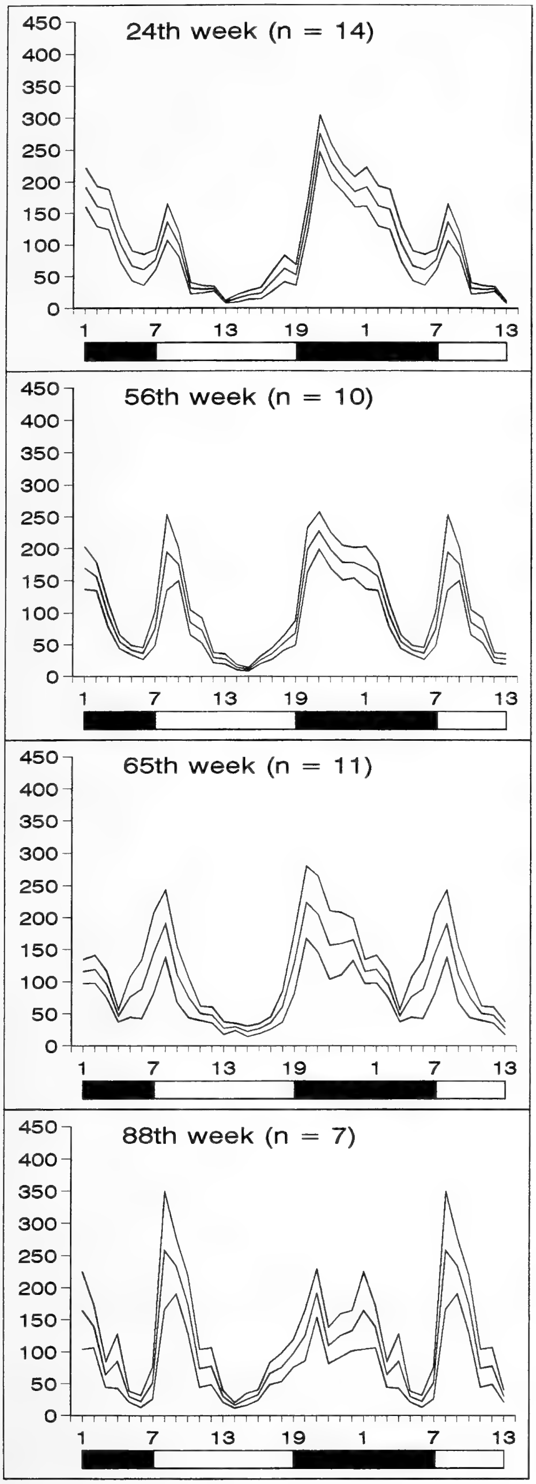

Fig. 2. Daily rhythms of locomotor activity depending on age. Mean values (± SEM) of 7–14 female mice investigated over 7 days. For better visualization $1\,^1/_2$ periods were shown, i. e., the last twelve values of the curves are identical to the first twelve. Abscissa: Time of day, the bars below indicate the lighting regimen. Ordinate: Locomotor activity (deviation from the daily mean in %).

der standard conditions (Fig. 2) were no longer significant following an increase or a decrease in the LD-magnitude (Fig. 3). However, differences have been obtained depending on the LD-magnitude. Under 200 : 0 lx the activity increased steeply following lights-off, whereas under 5 : 0 lx it started to increase already at the end of the light period.

The percentage of total activity accounting for the dark period and the rhythm stability were not significantly different under both LD-magnitudes but increased with increasing light intensity (Tab. 2). Considering the results obtained under standard conditions re-

Table 1. Age-dependent changes of the daily activity rythm. (The data set depicted in Fig. 2 has been used.) Mean values ± SEM (* – for ANOVA and correlation analyses the data of the subsequent week were included.) Bold: Significant different from 24 weeks old mice: [a] – $p \leq 0.05$, [b] – $p \leq 0.01$, [c] – $p \leq 0.001$ (Mann-Whitney u-test)

	24 weeks	56 weeks	65 weeks	88 weeks
Total activity (counts/24)	1 986 ± 168	1 723 ± 202	1 398 ± 382	**463 ± 84**[c]
Magnitude of oscillation (counts/h)	296 ± 26	224 ± 34	170 ± 52	**65 ± 15**[c]
Dark-period activity (% of total activity/24 h)	76.7 ± 1.8	**67.1 ± 3.5**[a]	**61.7 ± 3.4**[b]	**51.8 ± 2.6**[c]
Correlation between consecutive days (r)*	0.62 ± 0.50	0.54 ± 0.03	**0.45 ± 0.04**[a]	**0.42 ± 0.04**[b]
Interdaily veriance (% of total variance)*	41.5 ± 4.6	50.1 ± 3.5	**56.5 ± 3.8**[a]	**62.8 ± 4.6**[b]

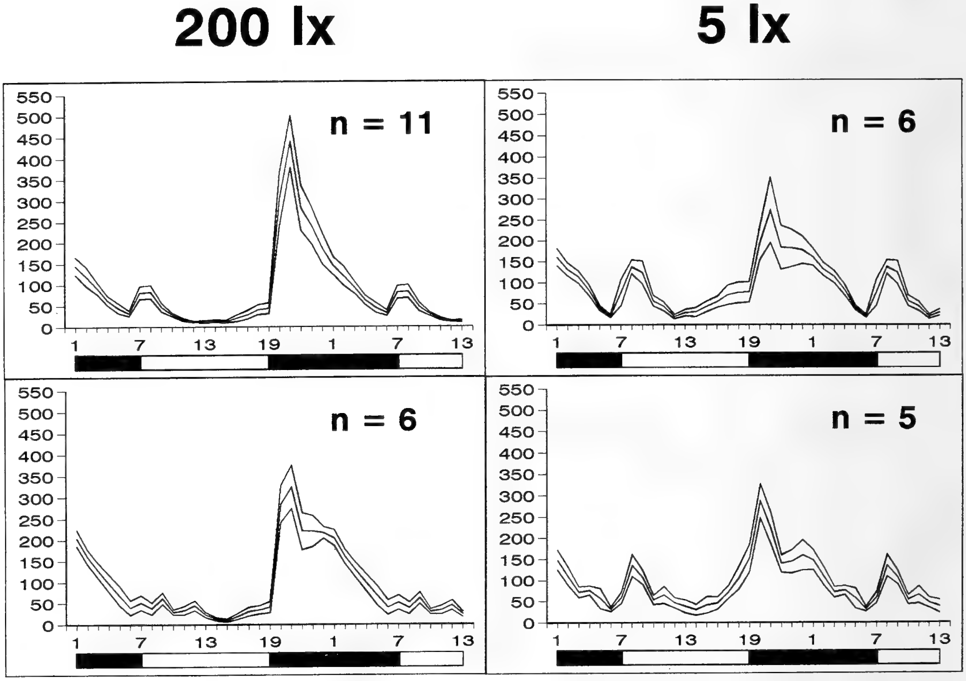

Fig. 3. Daily rhythms of locomotor activity of adult (top) and presenile (bottom) mice under L:D =12 h : 12 h with 200 lx (left side) or 5 lx (right side) during the light period. Mean values (± SEM) of 5 to 11 female mice investigated over 7 days. For better visualization $1\frac{1}{2}$ periods were shown, i. e., the last twelve values of the curves are identical to the first twelve. Abscissa: Time of day, the bars below indicate the lighting regimen. Ordinate: Locomotor activity (deviation from the daily mean in %).

Table 2. Synchronization and stability of the daily activity rythm depending on age and Zeitgeber strength. (The Data sets depicted in Fig. 2 (100 lx) and Fig. 3 (5 and 200 lx) have been analysed. Mean values ± SEM (* – for ANOVA and correlation analyses the data of the subsequent week were included) ** – the same values as in Tab. 1 (all differences between adult (24 weeks old) and presenile (65 weeks old) mice are significant). ^{a} – significantly different from the value under 5 lx ($p \leq 0.05$, Mann-Whitney u-test)

	Age	200 lx	100 lx**	5 lx
Dark-period activity (% of total activity/24 h)	adult presenile	82.1 ± 2.7 83.6 ± 3.4^{a}	76.7 ± 1.8^{a} 61.7 ± 3.4	66.8 ± 2.4 61.8 ± 3.6
Correlation between consecutive days (r)*	adult presenile	0.69 ± 0.04 0.68 ± 0.04^{a}	0.62 ± 0.05^{a} 0.45 ± 0.04	0.43 ± 0.03 0.41 ± 0.05
Interdaily variance (% of total variance)*	adult presenile	36.4 ± 4.3 38.0 ± 5.0^{a}	41.5 ± 4.6^{a} 56.5 ± 3.8	56.7 ± 2.9 61.4 ± 3.0

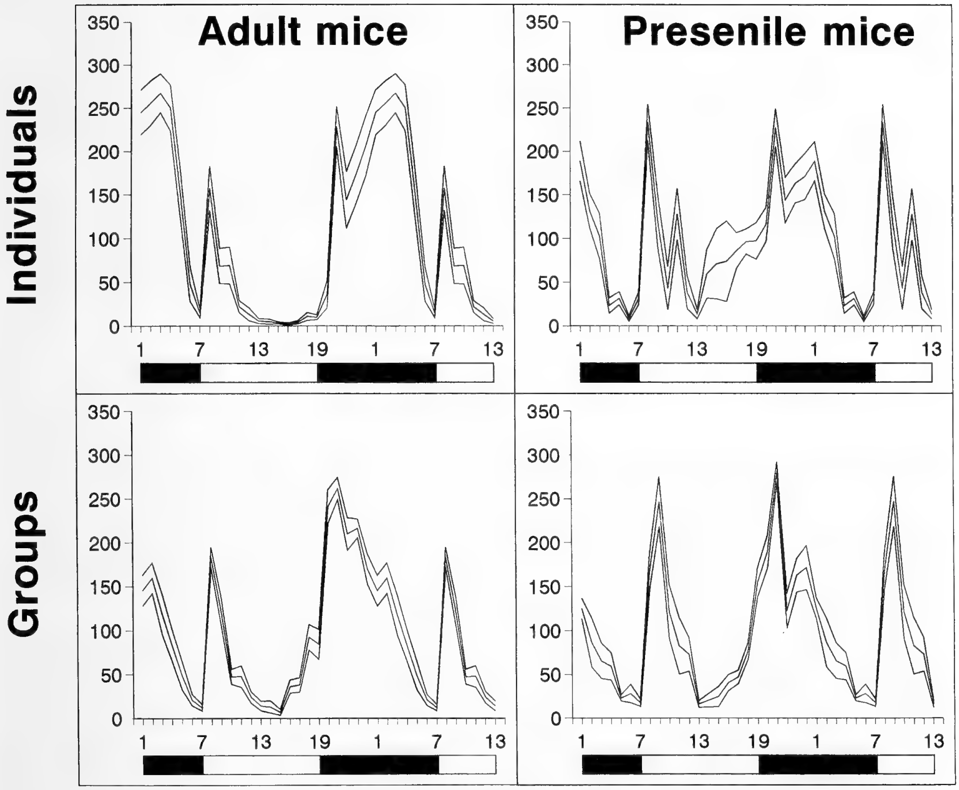

Fig. 4. Representative examples of daily activity rhythms of adult (left side) and presenile (right side) mice housed individually or in groups (n = 3). Mean values (± SEM) over 14 days. For better visualization $1\frac{1}{2}$ periods were shown, i. e., the last twelve values of the curves are identical to the first twelve. Abscissa: Time of day, the bars below indicate the lighting regimen. Ordinate: Locomotor activity (deviation from the daily mean in %)

Table 3. Stability of the daily activity rhythm depending on age and housing conditions. (The same data set as for Fig. 4 has been analysed.) * – results of all investigated mice were summarized; $^{\text{a,bç}}$ – significant differences ($p \leq 0.05$, Mann-Whitney u-test); I – individual mice; G – groups

		Adult mice*	Presenile mice*
Correlation between consecutive days (r)	I	0.62 ± 0.05^{a} (n = 14)	0.45 ± 0.04^{a,b} (n = 11)
	G	0.65 ± 0.03 (n = 6)	0.59 ± 0.03^{b} (n = 6)
Interdaily variance (% of total variance)	I	41.5 ± 4.7^{c} (n = 14)	56.5 ± 3.8^{c} (n = 11)
	G	37.2 ± 4.2 (n = 6)	45.5 ± 3.3 (n = 6)

veals age-dependent differences. The stability and synchronization of the activity rhythm of adult mice were significantly improved under 100 : 0 lx. The coefficient of correlation was higher, the percentage of total variance accountable for intra-individual variance was lower, and the percentage of total activity accountable for the dark period was higher. For presenile mice, the same result was obtained only under the highest LD-magnitude, which indicates a lower susceptibility to light.

Figure 4 shows representative activity rhythms of mice housed singly or in groups. While the patterns of adult mice were similar independent of the housing conditions, the daily pattern of presenile mice was clearer when kept in groups. The stability of the activity rhythm was also influenced by the housing conditions (Tab. 3). The coefficient of correlation was significantly higher, the percentage of total variance accounting for intra-individual variance was significantly lower in individual adult mice as compared to presenile ones. When adult animals were transferred to groups both values remained nearly unchanged. On the contrary, in presenile mice the coefficient of correlation increased and the intra-individual variance decreased significantly. Thus, when animals were kept in groups, the rhythm stability was no longer different with respect to age. Also in mixed groups (2 adult + 1 presenile or 1 adult + 2 presenile animals) the coefficient of correlation and the intra-individual variance were the same as in groups of only adult or only senile mice.

Discussion

The results of the present study are consistent with data in the literature (ASCHOFF 1994; TUREK et al. 1995; VALENTINUZZI et al. 1997) as well as with our own earlier investigations (WEINERT and WEINERT 1998). They showed that with advancing age all characters of the daily activity rhythm change. However, they also showed a decreased rhythm stability and a deteriorated ability to synchronize with external Zeitgebers at comparatively early age when regarding the mean life span of our mice (85 weeks). In contrast, the daily rhythm was present as long as the animals were locomotoric active.

Several reasons might be responsible for the lower rhythm stability and the impaired synchronization in presenile mice. This is mainly due to the high complexity of the circadian system, which includes oscillator(s), mechanisms of external synchronization, and internal coupling. Deterioration in the function of any of these components may result in changes of circadian rhythms in old age. In addition, one must bear in mind that not all changes in the overt rhythm – consisting of endogenous, due to the body clock, and exogenous (masking) components – are caused by changes in the circadian system.

The main component of the circadian pacemaker system is the nucleus suprachiasmaticus (SCN) of the hypothalamus, which consists of a number of mutually synchronized pacemaker cells (MILLER 1998). If the number of functioning neurons decreases with advancing age, and if this were linked to a weaker coupling between them, it is probable that only unstable rhythms could be generated. A lower stability of the free-running activity rhythm was found in old mice (WEINERT and KOMPAUEROVA 1998; WEINERT and WEISS 1997), hamsters (ASCHOFF 1994), and humans (WEVER 1992).

The total number of neurons does not change in the SCN of aging rats (MADEIRA et al. 1995). However, the number of neurons expressing neuropeptides, which are believed to be involved in circadian time-keeping (AVP, VIP), decreased in old rats (LUCASSEN et al. 1995; LI and SATINOFF 1998) and humans (HOFMANN et al. 1996). VAN DER ZEE et al. (1999) found a decrease in the number of AVP-immunopositive cells in aging common voles which coincided with a loss of precision of circadian rhythmicity.

The LD periodicity has been accepted for rodents and other mammalian species as the most potent Zeitgeber, exerting a stable phase control over circadian rhythms. With respect to the problem of impaired synchronization, one might expect a decreased sensitivity of the circadian system to light in old organisms. There is evidence in favour of this supposition. SUTIN et al. (1993), ZHANG et al. (1996) and BENLOUCIF et al. (1997) found a decreased sensitivity to light in rats, hamsters, and mice. The response of immediate early genes (IEG), which are part of the entrainment pathway, was less in the SCN of old animals, as was the phase-shifting effect of the light pulses. There are further studies on hamsters (ASCHOFF 1994; POHL 1984; ROSENBERG et al. 1991) and mice (PROVENCIO et al. 1994; WEINERT and KOMPAUEROVA 1998) investigating only the phase response of the activity rhythm. Despite some inconsistency, all results indicate an altered susceptibility to light with increasing age.

An altered response of the circadian system to photic stimuli in advanced age may be caused by changes in the retina, in the afferent, neuronal pathways to the SCN, or in the SCN itself. With respect to photoreceptors there is currently a debate as to what receptors are relevant for the circadian system (FREEDMAN et al. 1999; PROVENCIO et al. 1994). No differences were found in the retinal innervation of the SCN (ZHANG et al. 1998). Concerning the SCN, CAI and WISE (1996) were able to restore the decreased response to light in old rats by transplantation of fetal SCN tissue.

Finally, analysing the stability and synchronization of daily rhythms one must take into account also non-photic factors. These are effective via motor activity or the associated arousal. Some evidence exists that photic and non-photic events interact to produce entrainment (HASTINGS et al. 1998). The impact of non-photic Zeitgebers is decreased in old animals not only due to their lower activity level but also due to deficits in the monoaminergic neurotransmission (PENEV et al. 1995).

Age-dependent changes initially concern only the stability of the circadian rhythms and their ability to synchronize to the environment. Both are diminished, whereas the rhythms themselves continue to be pronounced. Therefore, it seems possible to treat disturbances. As for old organisms, a decreased susceptibility to external cues, particularly Zeitgebers, becomes characteristic, this might be realized by increasing the strength of the main Zeitgeber and/or additional, synergistic Zeitgebers, as a temperature cycle, a restricted or scheduled feeding regimen, or social Zeitgebers. Another possibility might be to strengthen feedback effects, by increasing the daily amount of motor activity, for example, and to improve the synchronization and stability of circadian rhythms by this means. The LD-cycle, the main Zeitgeber for mammals, may be strengthened by increasing its magnitude. By this means, WITTING et al. (1993) were able to reverse some of the age-related changes in the sleep-wake cycle of rats, particularly the damped amplitude. Similarly, LABYAK et al. (1998) reduced the fragmentation of the activity rhythm, increased the general activity level, and increased its amplitude in old hamsters. The present study on old mice revealed an improvement of the rhythm stability; the percentage of activity during the dark period was increased. All these results might reflect an improved synchronization of the circadian rhythm; however, masking effects due to the high level of illumination during the light phase must be considered as well (ASCHOFF 1988).

In the present study we also found age-dependent differences in the circadian rhythm of activity between mice kept individually or in groups. Whereas in adult animals the rhythm stability was not different regardless of whether the animals were kept in groups or individually, in senile mice, the inter-daily variability decreased significantly when they were transferred to groups, and then did not differ from adult mice. As mice are social animals, the decreased stability of the activity rhythm of animals kept individually might be a consequence of isolation stress, and it is possible that old mice are more susceptible to this condition. Another possible explanation might be that housing animals in groups stabilizes the circadian rhythm by means of social Zeitgebers. However, the problem of whether social factors are effective as Zeitgebers is controversial, and has recently been discussed (GATTERMANN and WEINANDY 1997).

In summary, the present results provide evidence that it is possible to stabilize daily rhythms by means of Zeitgeber strengthening and/or additional Zeitgebers.

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Zusammenfassung

Altersabhängige Änderungen in der Stabilität von Tagesrhythmen der Aktivität bei Labormäusen

Ziel der vorliegenden Untersuchung war die Erfassung altersabhängiger Änderungen des Tagesrhythmus der Aktivität, insbesondere unter dem Aspekt der Stabilität sowie der Synchronisation mit dem Licht-Dunkel (LD) -Wechsel. Desweiteren sollte unter Laborbedingungen versucht werden, altersbedingte Änderungen rückgängig zu machen. Die Untersuchungen erfolgten an einzeln gehaltenen weiblichen Labormäusen in klimatisierten Räumen (T = 21 ± 2 °C, relative Luftfeuchte – 55–65%, Licht-Dunkel-Zyklus von L : D = 12 : 12 h, 100 : 0 lx, Licht von 07 : 00 bis 19.00 h, Futter und Wasser ad libitum). Die lokomotorische Aktivität wurde mit PIR-Bewegungsdetektoren registriert. Die Beurteilung der Stabilität der Tagesmuster erfolgte mittels Varianz- und Korrelationsanalysen.

Tagesrhythmen der Aktivität wurden vom Absetzen (21. Lebenstag) bis zum Alterstod erfaßt. Auf dieser Grundlage wurden vier Altersgruppen (24, 56, 65 und 88 Wochen) ausgewählt und genauer untersucht. Die Tagesmuster waren erst bei der ältesten Gruppe deutlich unterschiedlich. Auch die Gesamtaktivität/24 h sowie die Schwingungsbreite im Tagesgang waren hier signifikant geringer als bei den adulten Mäusen (24 Wochen). Der Anteil der Aktivität in der Dunkelzeit an der Gesamtaktivität/24 h, als ein Maß für die Synchronisation mit dem LD-Wechsel, war bereits bei den 56 Wochen alten Tieren signifikant geringer, die Stabilität der Tagesmuster im Alter von 65 Wochen.

Da sich zunächst nur die Synchronisation sowie die Stabilität verschlechterten, der Rhythmus jedoch erhalten blieb, schien es möglich zu sein, den Rhythmus zu stabilisieren. Diese Untersuchungen erfolgten parallel an 24 und 65 Wochen alten Tieren. Zunächst wurde die Zeitgeberstärke des LD-Wechsels modifiziert. Durch eine Erhöhung der LD-Amplitude auf 200 : 0 lx verminderte sich die Variabilität der Muster aufeinanderfolgender Tage vorwiegend bei den senilen Tieren. Wurde die LD-Amplitude verringert (5 : 0 lx) nahm die Variabilität zu und zwar in stärkerem Maße bei den adulten Tieren. In beiden Fällen bestanden keine Unterschiede zwischen den Altersgruppen mehr. Der Anteil der Aktivität in der Dunkelzeit an der Gesamtaktivität/24 h erhöhte sich mit zunehmender LD-Amplitude vorwiegend bei den senilen Mäusen und verminderte sich bei Verringerung der Amplitude vorwiegend bei den adulten. Eine Stabilisierung des Aktivitätsrhythmus konnte auch durch eine Gruppenhaltung erreicht werden. Bei einzeln gehaltenen senilen Tieren war die Stabilität signifikant geringer als bei adulten. Wurden die Tiere in Gruppen umgesetzt, erhöhte sich die Stabilität bei den senilen Mäusen deutlich und unterschied sich nicht mehr von der adulter.

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Chemical reactors of the mammalian gastro-intestinal tract

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Abstract

This study reviews and defines the classes of chemical reactors known in mammalian gastro-intestinal tracts, describing how they differ from the "ideal reactors" of chemical engineering. Three classes of reactors are present in the mammalian guts: batch reactors, plug-flow reactors and continuous-flow, stirred-tank reactors. These are modified from the ideal types in two ways: firstly, the method of transport of reactants through a reactor; secondly, by continual absorption of products throughout the length of the reactor. To avoid confusion with the reactors of chemical engineering, gut reactors are defined as simple and complex types on the basis of their musculature. There are five types of chemical reactor found in mammalian gastro-intestinal tracts – semi-batch reactors (the caecum of caecum fermenters), simple plug-flow reactors (the small intestine), complex plug-flow reactors (the macropodid forestomach), simple continuous-flow, stirred-tank reactors (the unipartite stomach) and complex continuous-flow, stirred-tank reactors (the haustrated colon of colon fermenters). Application of chemical reactor theory to gut function is an important tool in understanding the relationships between morphology, diet chemistry, and digestive processes in mammals.

Key words: Mammals, gastro-intestinal tracts, modified chemical reactors

Introduction

In 1986, Penry and Jumars used chemical reactor theory to describe the processes of digestion in animals, as the ability to process substrates (from the food) in bulk is the basic requirement of any gastro-intestinal tract (Penry and Jumars 1986). Industrial reactors are designed to optimise the return of products from a particular chemical reaction within given 'economic' constraints (Denbigh and Turner 1971). Digestive processes operate under similar economic constraints, resulting in the optimisation of the return of nutrients to an animal from its diet (Sibly 1981; Penry and Jumars 1986; Hume 1989). The reactors of chemical engineering (called ideal reactors in this review) differ in a number of operating features from those found in the mammalian gastro-intestinal tract. There is a need to clarify these differences and to define the characteristics of mammalian gut reactors (Caton 1997).

The application of chemical reactor theory to gastro-intestinal tract function has provided a means of understanding the complexity of the physiological relationships between an animal and its food (Hume 1989). Application of reactor theory also permits an integrated approach to this problem through the development of mathematical models of digestive processes (Penry and Jumars 1987; Alexander 1991; Martinez Del Rio et al. 1994). Quantifiable predictions of digestive function can then be made with reactor mod-

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	BATCH REACTORS	PLUG-FLOW REACTORS	CONTINUOUS-FLOW STIRRED-TANK REACTORS
Shape:	vat- like.	tubular.	vat-like.
Flow system:	closed (entry and exit port the same).	open.	open.
Flow pattern:	interrupted by down-times for filling and emptying the reactors.	continual and unidirectional, contents travel in unmixed plugs.	continual stirring results in perfect mixing of contents.
Mixing:	continual and perfect while the reactor is filled.	radial, with no or little axial mixing.	continual and perfect.
Concentration of reactants:	high at loading, then gradual decrease with increased holding time.	high at entry, then gradual decrease along the length of the reactor.	reactants diluted immediately on entry.

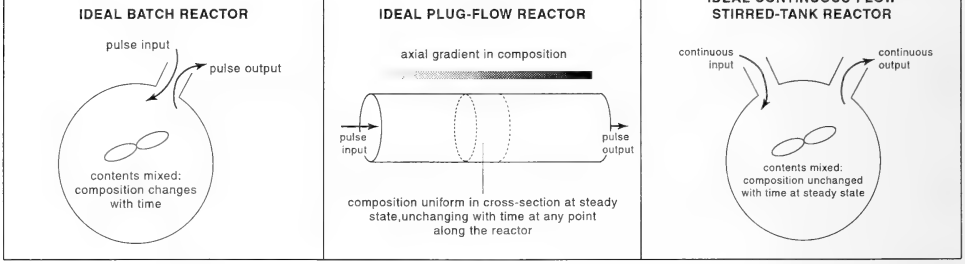

Fig. 1. The three types of idea reactors that have analogues in animal digestive systems (after Stevens and Hume 1995 and Caton 1997). Batch reactors, with a single entry-exit port best describe gut compartments that process digesta in discrete batches, e. g. the mammalian caecum. The vertebrate mid gut functions as a tubular plug flow reactor. Continuous-flow, stirred-tank reactors are vat reactors similar to those seen in the compartments of the ruminant forestomach.

els, using physiological parameters from living animals to predict optimal reactor types and thus the optimal morphology and physiology for processing specific diets (Hume 1989; Martinez Del Rio et al. 1994; Caton 1997).

Chemical engineers use three types of ideal reactor when designing plants for the bulk processing of chemicals – batch reactors, plug-flow reactors and continuous-flow, stirred-tank reactors. Each of these types has performance characteristics that allow optimisation of returns from specific chemical reaction systems, a factor of considerable importance when modeling gut function (Penry and Jumars 1986; Hume 1989; Martinez Del Rio et al. 1994). Functional characteristics, such as flow patterns (including mixing of contents), retention times and performance (reaction rate), are important in determining the suitability of a particular reactor for a given set of reactions (Denbigh and Turner 1971). Before describing gastro-intestinal reactors it is necessary to define the characteristics of ideal reactors, as these provide the basis for understanding the function of the modified reactors of the mammalian gastro-intestinal tract.

Characteristics of Ideal Reactors

Batch reactors are used for processing small quantities of reactants in discrete volumes or batches. All the reactants are introduced into the chamber at the same time (pulse input), and subsequently all products with any unreacted fractions are removed as a pulse output

(Denbigh and Turner 1971) (Fig. 1). In batch reactors reaction periods alternate with "down-time" periods during which the reactor is emptied and then loaded again (Denbigh and Turner 1971). Batch reactors are closed systems with single entry-exit ports (Fig. 1), thus there is no flow in or out during the operating period (Karasov and Diamond 1988; Penry 1993). During the operating or holding time, the contents of an ideal batch reactor are perfectly mixed (homogeneous) and changes in composition occur only with respect to time (Penry and Jumars 1986, 1987). The functioning of the reactor continues either for the time needed to reach thermodynamic equilibrium, or until the reaction is stopped (Denbigh and Turner 1971). Holding time is the most important operating variable with a batch reactor, as the longer the reactants remain in the reactor the greater the extent of their conversion (Penry and Jumars 1986). In these closed systems reaction rates are high initially, gradually slowing as the residence time increases and the reactants are depleted. Holding time in a batch reactor equals both residence time and mean residence time, as there is no throughput flow (Denbigh and Turner 1971). Both holding time and down time are important when considering the efficiency of a batch reactor (Martinez Del Rio et al. 1994). The interruption of the down times effectively limits reactor performance, so that overall production rates are generally low (Denbigh and Turner 1971; Hume 1989). The effect of reactor down time can be compensated for by increasing the volume of the reactor (Hume 1989; Martinez Del Rio et al. 1994), or by the continuous removal of the products as occurs in a semi-batch reactor (Penry 1993).

Plug-flow reactors are usually tubular in shape (Fig. 1), and were defined by Denbigh and Turner (1971) as "... any continuously operating reactor in which there is a steady movement of one or all reactants in a chosen spatial direction (reactants entering at one end of the system and leaving at the other) and in which no attempt is made to induce mixing between the elements of the fluid at different points along the direction of flow." For any cross sectional area of a plug-flow reactor, mass flow rate and fluid properties are uniform. All elements of the fluid (which may be described as travelling in small, self-contained envelopes) spend equal time passing through the reactor, and undergo the same sequence of pressure, temperature and concentration changes. Characteristically, reactants and products do not diffuse between these plugs during their passage through the reactor (Denbigh and Turner 1971). As a result, the reaction must occur to the same extent in each element of the fluid. Plug-flow reactors are thus regarded as miniature batch reactor systems travelling through a tubular reactor (Denbigh and Turner 1971).

By definition, any plug-flow reactor is an open system (Fig. 1), characterised by the uni-directional flow of material between separate entrance and exit ports (Denbigh and Turner 1971; Hume 1989). With this pattern of flow there is no accumulation of reactants within the tubular vessel, and no dilution of reactants on entry to the reactor (Denbigh and Turner 1971). Flow within the reactor is laminar, with negligible diffusion relative to bulk flow resulting in little or no axial mixing (Denbigh and Turner 1971; Martinez Del Rio et al. 1994). For steady state operation in a plug-flow reactor the gradient in the concentration of reactants and products remains constant throughout the length of the reactor (Martinez Del Rio et al. 1994). Increasing the length enhances the performance of plug-flow reactors, with a resultant increase in the degree of radial mixing (Martinez Del Rio et al. 1994).

Reaction rates and the concentration of reactants are highest at the entrance, then gradually decline along the length of a plug-flow reactor (Hume 1989; Martinez Del Rio et al. 1994). Performance of a plug-flow reactor is measured by the fraction of reactant converted to product (measured at the exit), thus through-put time is important in assessing performance (Martinez Del Rio et al. 1994). Residence time distribution, mean residence time and through-put time of material in the effluent fluid are all equal in a plug-flow reactor, and there is no spread of residence times (Denbigh and Turner 1971). Performance is generally high in this type of reactor as function is continuous, with no down time as in a batch reactor (Hume 1989; Martinez Del Rio et al. 1994). In industry, plug-flow reactors are used extensively for catalytic reactions (Denbigh and Turner 1971).

Continuous-flow, stirred-tank reactors are tanks or vats with well-mixed contents, into which "... there is a continuous flow of reacting material, and from which the (partially) reacted material passes continually" (Denbigh and Turner 1971). Continuous-flow, stirred-tank reactors are open systems with separate entry and exit ports (Fig. 1). The characteristics of continuous-flow, stirred-tank reactors include dilution of reactants immediately on entry by contents remaining from previous runs, the constant flow of material through the reactor, and the complete mixing of the contents (Denbigh and Turner 1971). At steady state the composition of the contents of the reactor is spatially homogenous with respect to time (Penry and Jumars 1986). Under these steady state conditions there is no dead space within the reactor and the effluent stream has the same composition as its contents. Increasing the viscosity of the reactants impedes mixing and reduces performance (Denbigh and Turner 1971). Structural baffles built into the wall of a continuous-flow, stirred-tank reactor are used to assist mixing of reactants (Denbigh and Turner 1971).

Residence times of molecules in a continuous-flow, stirred-tank reactor will vary because of the continual mixing. In the ideal reactor with perfect mixing, residence time, mean residence time and throughput time would all be equal (Penry and Jumars 1987). The broader the range of residence times and the faster the flow through the reactor the lower the performance (Denbigh and Turner 1971; Hume 1989). By-pass loss is another important consideration with any continuous-flow, stirred-tank reactor, as there is a significant probability that a given molecule entering the system will pass directly into the outflow. While by-pass loss is the result of stirring, the loss would be greater without mixing due to bulk streaming (Denbigh and Turner 1971). By-pass loss can be overcome by having several continuous-flow, stirred-tank reactors in series, thus achieving a higher overall rate of conversion (Denbigh and Turner 1971).

Comparison of Ideal Reactor Function

Reaction rates in continuous-flow, stirred-tank reactors tend to be lower than in either batch reactors or plug-flow reactors, and continuous-flow, stirred-tank reactors are best suited to comparatively slow liquid-phase reactions (Denbigh and Turner 1971). Greater volumes of reactants must be processed if a continuous-flow, stirred-tank reactor is to give results equivalent to those of the other two (Denbigh and Turner 1971). Overall yield can be raised considerably if several continuous-flow, stirred-tank reactors are used in series (Denbigh and Turner 1971). The advantage of continuous-flow, stirred-tank reactors is that the continual mixing of incoming reactants with the reaction products makes it possible to operate these reactors continually at the lowest point of the reaction rate (Denbigh and Turner 1971). It is found that higher reaction rates are achieved in continuous-flow, stirred-tank reactors with fermentation reactions than with catalytic reactions (Denbigh and Turner 1971).

Gastro-intestinal Reactors

The characteristics of the three classes of ideal chemical reactors are compared in figure 1. Analogues of the three classes of chemical reactor are found in the gastro-intestinal tracts of mammals, in which each type performs a different set of digestive functions (Figs. 2–4). Chemical processing of food macromolecules during digestion involves their hydrolysis to smaller component molecules in the presence of a range of catalysts (enzymes). Digestive processes can be divided into two broad groups on the basis of the source of these enzymes (Stevens and Hume 1995). Catalytic reactions involve endogenous enzymes that are manufactured and secreted by glands of the digestive system. High-quality components of the diet (proteins, lipids, simple sugars and starches) can be digested by endogenous enzymes (Stevens and Hume 1995). Fermentation tends to be slower and is controlled by exogenous enzymes produced by symbiotic micro-organisms living within the gut. Structural polysaccharides from plant material, which cannot be processed by catalysis, are digested by these micro-organisms (Stevens and Hume 1995). Catalytic and fermentation reactions have different processing requirements and produce different end-products (Denbigh and Turner 1971; Penry and Jumars 1987; Hume 1989; Alexander 1991; Martinez Del Rio et al. 1994). A priori, it must follow that:

(1) A reactor cannot perform catalytic and fermentation functions at the same time.
(2) Different types of chemical reactor will be more efficient and thus better suited for different types of organic compounds in the diet.

These factors have important implications for the development of models of gut function in mammals.

Gastro-intestinal reactors differ from ideal reactors in two ways. Firstly, the 'pump' moving the contents through a gut reactor is intrinsic or part of the wall, unlike ideal reactors in which the pump is extrinsic. Movement of gut contents is the result of activity of cells in the two layers of the external muscle coat, or tunica muscularis, of the wall. The movements produced by the muscle cells in these layers is complex, resulting in mixing and in the overall transport of digesta from mouth to anus. The control of this muscular activity is also complex, and dependent upon neural, hormonal and intra-mural factors triggered by the physical and chemical nature of the digesta.

The second difference is the method of removal of the products of the reactions, or nutrients, as they are continually absorbed across the lining of the lumen, the tunica mucosa, into the bloodstream. Removal of products in blood flowing through the mucosal capillaries produces concentration gradients that result in an increased rate of nutrient removal from the lumen of the reactor. This absorption process is important as it facilitates digestion reactions, which are slowed or stopped by increasing concentrations of products in the reactor (Denbigh and Turner 1971). Absorption is a general function of the mucosa of the entire gastro-intestinal tract.

The aims of this review are to define the types of reactors found in mammalian gastro-intestinal tracts, and to describe how they differ from the ideal reactors of chemical engineering. These definitions are based primarily on the results of dissections of mammalian gastro-intestinal tracts, as well as the known physiology of individual gastro-intestinal compartments in mammals, including the results of digesta transit studies (Warner 1981; Stevens and Hume 1995; Caton et al. 1996; Caton 1997).

Materials and method

Gastro-intestinal tracts of a wide range of mammals have been dissected over a period of years; in particular primates (lemurs, monkeys, apes), but also marsupials (both carnivores and herbivores), ruminants (domestic and wild), rodents and lagomorphs. The data collected included descriptions of the gross morphology of the gastro-intestinal tract, with photographs and drawings, and details of the musculature of individual compartment, including the position of the sphincters at compartmental junctions. The length and calibre of individual compartments were measured after careful removal of the mesenteries to avoid stretching the tissues.

Table 1. Comparison of the morphology of gastro-intestinal compartments of mammals.

Compartment	Simple Morphology	Complex Morphology
Stomach	Unipartite; globular to pyriform. Regions – fundus, body, pyloric segment. Mucosal glands secrete mucus, hydrochlorid acid, pepsin. Tunica muscularis – three layers of muscle cells, outer longitudinal, inner circular separated by an oblique layer	Pluripartite; shape variable Regions – forestomach and hindstomach which may be subdivided into smaller compartments. Mucosal glands secrete mucus (forestomach); hydrochloric acid, pepsin and mucus (hindstomach). Tunica muscularis complex – three layers of muscle cells, outer longitudinal, inner circular separated by an oblique layer; longitudinal layer may be divided into 2 discrete bands (taeniae).
Pyloro-duodenal junction – annular pyloric sphincter encircles the lumen; formed by a thickening of the circular muscle coat.		
Small intestine	Elongated tube, relatively uniform calibre; length variable. Regions – duodenum, jejuno-ileum. Accessory glands secrete into duodenum; tubular glands in the mucosa secrete mucus and enzymes. Tunica muscularis – outer longitudinal layer, inner circular layer.	No complex morphology.
Ileo-caecal or ileo-colic junction – annular sphincter encicles the lumen of the terminal ileum; formed by thickening of the circular muscle coat.		
Caecum	Elongate or bag-like diverticulum; variable length. Tubular mucosal glands secrete mucus. Tunica muscularis – outer longitudinal layer, inner circular layer.	Elongate or bag-like diverticulum; variable length. Tubular mucosal glands secrete mucus. Tunica muscularis – outer longitudinal layer, inner circular layer; longitudinal layer divided into 2–4 discrete bands (taeniae)
Caeco-colic junction – annular sphincter encircling the lumen may separate these hindgut compartments; formed by thickening of the circular muscle coat.		
Colon	Elongated tube, relatively uniform calibre; length variable. Regions – proximal colon, distal colon and rectum. Tubular glands in the mucosa secrete mucus. Tunica muscularis – outer longitudinal layer, inner circular layer.	Elongated tube, calibre variable especially of proximal colon; length variable. Regions – proximal colon, distal colon and rectum. Tubular glands in the mucosa secrete mucus and enzymes. Tunica muscularis – outer longitudinal layer, inner circular layer; longitudinal layer divided into 2–4 discrete bands (taeniae)

Results

The results of the study of the morphology of the compartments of the mammalian gastro-intestinal tract are summarized in table 1. The division of compartmental morphology into simple and complex is a reflection of the function of a particular compartment. In general, the chemical functions of compartments with simple morphology are digestion by endogenous enzymes and absorption. Compartments with complex morphologies are fermentation chambers containing micro-organisms capable of digesting non-starch polysaccharides from plant cell walls and insect exoskeletons. Mammals with guts adapted to processing non-starch polysaccharides generally have a single fermentation chamber in their gastro-intestinal tracts. These compartments are easily recognized by their greater capacity and specialized musculature (Tab. 1). The patterns of mammalian gastro-intestinal morphology characteristic of different digestive patterns are outlined in table 2.

Table 2. Patterns of mammalian gastro-intestinal morphology associated with different digestive patterns.

Digestive Pattern	Gastro-intestinal Compartment Morphology			
	stomach	small intestine	caecum	colon
Carnivore	simple	simple	small – simple, or vestigial	simple
Insectivore	simple	simple	simple; size variable	simple
Herbivores				
1. forestomach fermenters	complex forestomach; simple hindstomach	simple	simple; size variable	simple
2. caecum fermenters	simple	simple	enlarged; simple or complex morphology	simple
3. colon fermenters	simple	simple	variable size; simple or complex morphology	proximal colon capacious and complex

Discussion

Compartmentalisation of the gastro-intestinal tract

Unlike most industrial reactors, mammal gastro-intestinal tracts are multi-reaction systems involving parallel or sequential reactions (Petersen 1965). This presents certain design problems or constraints (Martinez Del Rio et al. 1994) which are largely overcome through increasing the total length of the gastro-intestinal tract and the division of the tract into morphologically and functionally distinct compartments.

Compartmentalisation of the gastro-intestinal tract separates catalytic and fermentation reactions. Functional separation also occurs at the molecular level as the result of enzyme specificity (Petersen 1965). This functional separation also includes absorption of the products of these reactions (nutrients) via different routes (Karasov and Diamond 1988; Stevens and Hume 1995). The chemical composition of an animal's diet dictates the type of digestive reaction required. This in turn dictates the type of reactor found in the gastro-intestinal tract. The optimal reactor for catalytic reactions is a plug-flow reactor, for fermentation reactions a continuous-flow, stirred-tank reactor. Batch reactors can be used for either type of reaction, but not at the same time (Denbigh and Turner 1971; Caton 1997). This separation of catalytic and fermentation reactions in the gastro-intestinal tract is the result of differences in operating requirements for the three classes of chemical reactors (Tab. 1). Separation of catalytic and fermentation reactions has the additional advantage of protecting symbiotic micro-organisms from the action of endogenous enzymes.

The optimal reactor types for processing a given diet are dependent upon the reactants and the reaction conditions, as the performance of reactors varies considerably (Denbigh and Turner 1971; Martinez Del Rio et al. 1994). Digesta passage studies based on inert markers, the equivalents of the tracer experiments of chemical engineering, are used to measure gut reactor performance (Hume 1989; Martinez Del Rio et al. 1994). In batch reactors conversion or performance is a function of holding time and down time (time taken for loading and emptying the reactor) (Martinez Del Rio et al. 1994). Down time is eliminated by continuous flow of reactants through both batch reactors and continuous-flow, stirred-tank reactors. The dilution of reactants immediately on entry into a continuous-flow, stirred-tank reactor increases the time required for conversion of a similar amount of reactants in a continuous-flow, stirred-tank reactor than in a plug-flow reactor. Batch reactors also operate at higher levels of reactant concentrations than continuous-flow, stirred-tank reactors for the same reactor-feed conditions, at least initially. However, the ability of continuous-flow, stirred-tank reactors to operate continuously at lower concentrations is an important feature in their application, as the reaction rate is the same throughout the reactor due to mixing (Denbigh and Turner 1971; Martinez Del Rio et al. 1994). With highly digestible dietary components, plug-flow reactors out-perform both batch reactors and continuous-flow, stirred-tank reactors achieving the same extent of conversion in less time (Denbigh and Turner 1971). The combination of different reactors found in mammalian gastro-intestinal tracts gives them flexibility to process a diverse range of dietary materials (Penry and Jumars 1986; Alexander 1991).

Mammals with their long, complicated gastro-intestinal tracts provide examples of the modification of the basic (ideal) reactor types. These modifications reflect different digestive patterns (Hume 1989; Caton 1997). Herbivores and omnivores, which eat large quantities of structural polysaccharides, rely on fermentation to a greater extent than carnivores (Stevens and Hume 1995). Their complex gastro-intestinal tracts separate the catalytic processing of high-quality dietary components from the fermentation of structural polysaccharides. Chemical reactor models provide the conceptual and mathematical basis for making comparisons of compartmental function and morphology (Penry and Jumars 1986; Caton 1997).

Characteristics of gastro-intestinal reactors

The chemical reactors found in mammalian gastro-intestinal tracts are modified from the ideal types as the walls of the compartments function as both conduits and pumps, unlike industrial reactors in which these two functions are separate (Denbigh and Turner 1971; Weems 1987). In industrial reactors products are removed at precisely determined intervals along the reactor or at the exit port (Denbigh and Turner 1971). In the gastro-intestinal tract, however, there is continual removal of reaction products by absorption through the wall, while undigested residues pass either to the next reactor or are eliminated to the environment (Weems 1987; Stevens and Hume 1995).

These modified reactors are associated with the different functions of a particular compartment of the tract (usually catalysis versus fermentation) that reflect evolutionary changes that enable mammals to exploit new dietary niches, e. g. from insectivory to herbivory (Caton 1997). These changes involved alterations to existing structures enabling them to perform new tasks, rather than adding new compartments to the gastro-intestinal tract. The distinctions between the classes of gut reactors are often not as clear as those seen in the ideal three types, with the result that the modified reactors are hybrids (Hume 1989). Martinez Del Rio et al. (1994) considered that the three classes of ideal chemical reactor are points on a continuum, noting that: “A long series of CSTRs [continuous-flow stirred-tank reactors] behaves like a PFR [plug-flow reactor] and the behaviour of a plug-flow reactor with intense recycling resembles that of a CSTR”. Denbigh and Turner (1971) made a similar point when they wrote that the radial mixing of the contents in plug-flow reactors resulted in their functioning as a series of small batch reactors. Chemical reactor theory provides a mathematical basis for comparing the functions of the gut reactors with the performances of the ideal types (Penry and Jumars 1987).

The modified plug-flow reactor of the macropodid forestomach was the first gut reactor recognised as differing from the ideal (Dellow and Hume 1982) (Tab. 3). Penry (1993) considered the mammalian caecum to be a semi-batch reactor, as there is continual absorption of products from the lumen and continual filling, but discontinuous emptying. Comparison of morphology, function, and digesta flow patterns of the various gastro-intestinal tract compartments with the characteristics of ideal chemical reactors indicates that gut reactors can be divided into simple and complex types (Tabs. 1 and 4). The musculature is of particular importance in defining gut reactor type (Caton 1997).

Semi-batch reactors are the only form of batch reactor found in the mammalian gastro-intestinal tract (Penry 1993). They are usually sites of fermentation containing large populations of micro-organisms (Stevens and Hume 1995). The ruminant forestomach has the morphological and functional characteristics of a semi-batch reactor (Tab. 3). The caecum is also a semi-batch reactor, enabling mammals to process plant structural polysaccharides, exudates and chitin from arthropod exoskeletons (Hume and Sakaguchi 1991; Caton et al. 1996; Caton 1997) (Fig. 2). Continual removal of products results in increased reaction rates in semi-batch reactors (Penry 1993). The flow of reactants between

Table 3. Terms used by various authors in descriptions of the modified chemical reactors of the mammalian gastro-intestinal tract compared with those discussed in this study.

Batch reactors	Plug-flow reactors	Continuous-flow, stirred-tank Reactors	Source
IDEAL caecum	IDEAL small intestine	IDEAL simple stomachs, ruminant forestomach	Penry and Jumars (1987)
IDEAL possibly the caecum	IDEAL small intestine	IDEAL simple stomachs, ruminant forestomach	Hume (1989)
	MODIFIED macropodid forestomach		
	IDEAL small intestine	IDEAL ruminant forestomach; haustrated proximal colon	Alexander (1994)
SEMI-BR caecum			Penry (1993)
SEMI-BR caecum	SIMPLE small intestine	SIMPLE reticulum of ruminants	This Study
	COMPLEX macropodid forestomach	COMPLEX haustrated proximal colon with the caecum	

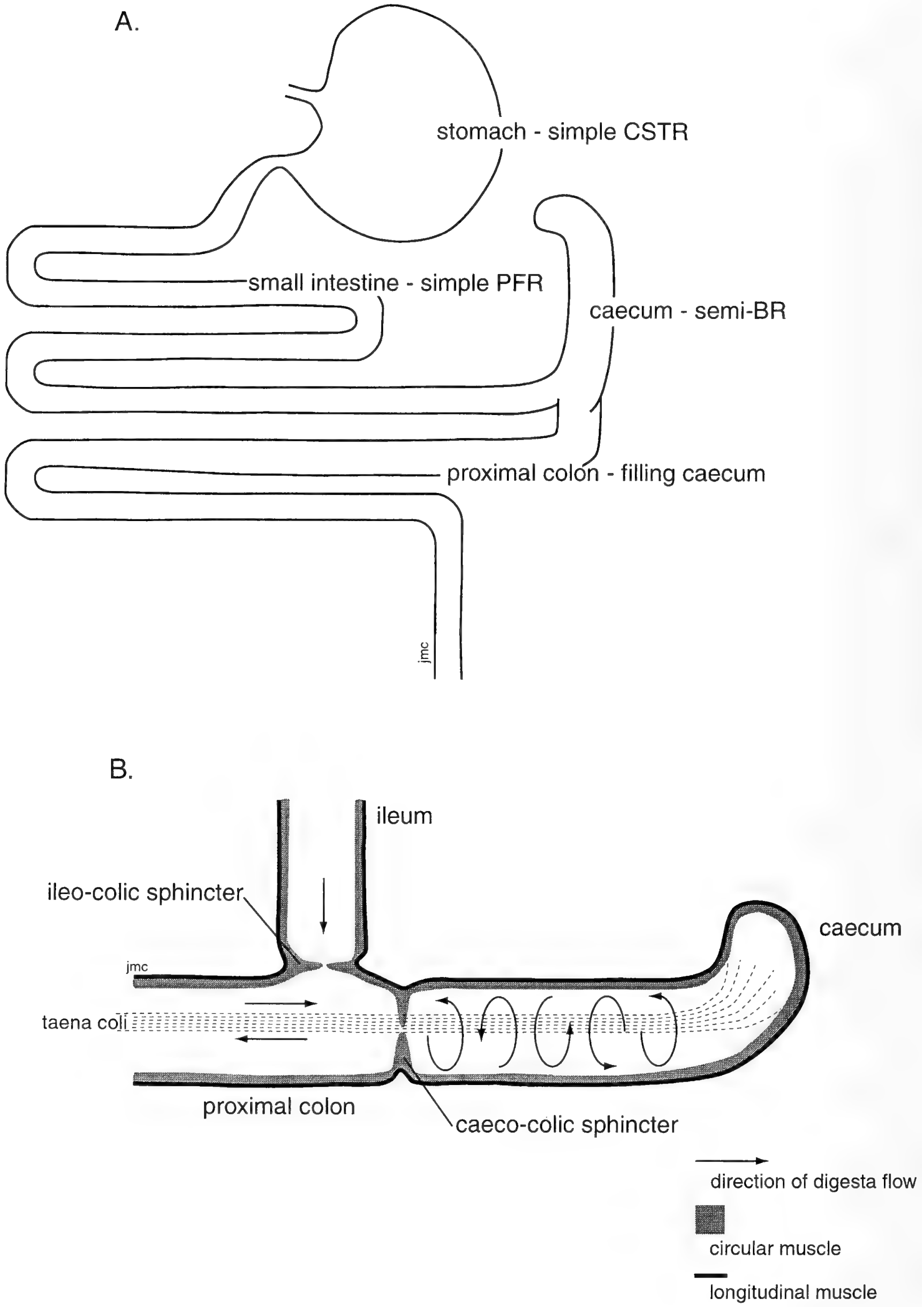

Fig. 2. The gastro-intestinal tract (A) of the common marmoset (*Callithrix jacchus*), with details of the caecum (B), which functions as a semi-batch reactor. The caeco-colic sphincter would remain closed during fermentation of batches of digesta. The contents of the caecum are mixed by contractions of the circular muscle layer of the tunica muscularis and by contraction of fibres of the single taenia coli. Abbreviations: CSTR, continuous-flow, stirred-tank reactor; PFR, plug flow reactor; semi-BR, semi-batch reactor.

Table 4. Comparison of the functional characteristics of the modified reactors of the mammalian gastro-intestinal tract. Calculations of surface area-to-volume ratios based on data from Chivers and Hladik (1980).

Reactor Characteristics	Semi-batch	Plug-flow		Continuous-flow, stirred-tank	
		simple	complex	simple	complex
Shape	vat-like	tubular (smooth-walled)	tubular and haustrated	vat-like	tubular and haustrated
Flow system	closed	open	open	open	open
Flow pattern	not interrupted by down-times as continuous absorption of products	continuous and unidirectional	continuous and unidirectional	continual stirring with perfect mixing of contents	contents are moved back and forth by alternating peristalsis and antiperistalsis.
Mixing	continual and perfect while the reactor is filled	radial with no axial mixing	radial in individual haustra, with localised axial mixing in the individual haustra.	continual and perfect	contents mixing by alternating peristalsis and antiperistalsis, also by localised mixing movements of individual haustra
Concentration of reactants	high at loading, then gradual decrease with increased holding-time	higher at the reactor entry than at the exit	higher at the reactor entry than at the exit	reactants diluted immediately on entry to the reactor	reactants diluted immediately on entry to the reactor
Absorption	continual absorption of products through the walls	continual absorption of products throughout the reactor	continual absorption of products throughout the reactor	continual absorption of products throughout the reactor	continual absorption of products throughout the reactor
Digestive process	fermentation of soluble polysaccharides, e. g. the marmoset caecum	catalytic digestion, e. g. the mammalian small intestine	fermentation of plant cell walls, e. g. macropodid forestomach	1. catalytic digestion, e. g. the unipartite mammalian stomach 2. fermentation of plant cell walls, e. g. ruminant reticulum	fermentation of structural polysaccharides, e. g. catarrhine, pig and equine proximal colons

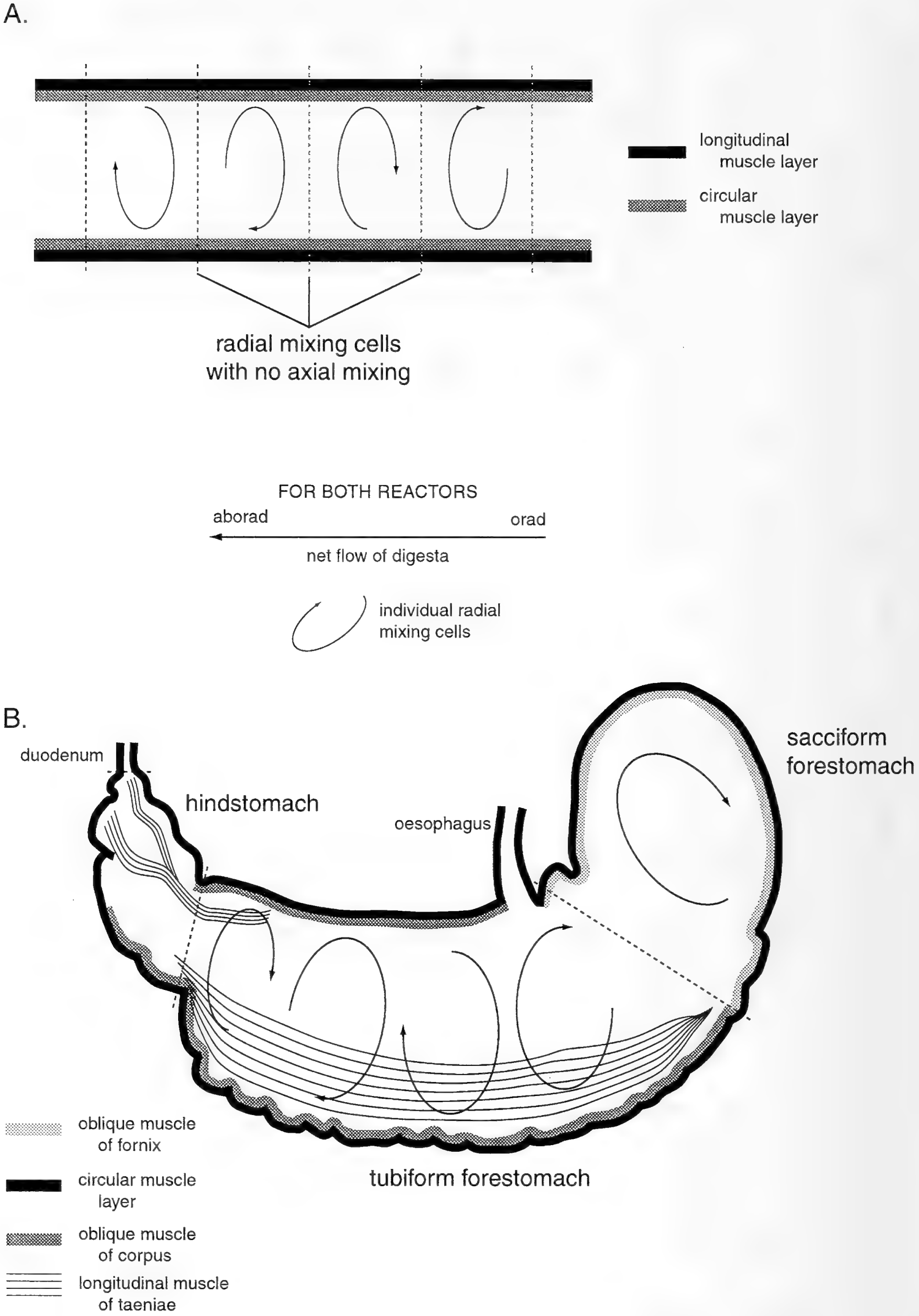

Fig. 3. Characteristics of plug-flow reactors of mammalian gastro-intestinal tracts. The small intestine (A) is a simple plug-flow reactor and its structure and function is constant throughout the phylum. The forestomachs of the herbivorous Macropodidae (kangaroos and wallabies) function as complex plug-flow reactors. (Drawing of the macropodid forestomach after LANGER 1988).

the caecum and colon is regulated by the caeco-colic sphincter, which is both the entry and the exit port (Tab. 3; Fig. 2 B). Taeniae and haustra, which facilitate mixing of the contents, are frequently present in these semi-batch reactors.

Gastro-intestinal plug-flow reactors are elongated tubular compartments that can be divided into two types, simple and complex, depending on their morphology and function (Tab. 1). The flow of reactants is unidirectional. Digesta are released into the plug-flow reactors in discrete batches through well-developed sphincters (MALAGELADA et al. 1984; MALAGELADA and AZPIROZ 1989; STEVENS and HUME 1995). The performance of the simple plug-flow reactor is closest to that of the ideal plug-flow reactor, differing from it in the continual absorption of digestion products and the motility of the wall (WEEMS 1987; STEVENS and HUME 1995). The small intestine, which is the major site of catalysis in the mammalian gastro-intestinal tract, is a simple plug-flow reactor (Fig. 3 A). The tunica muscularis in the small intestines of all mammals consists of an outer longitudinal coat (adjacent to the serosa) with a circular coat inside that (Fig. 3 A).

Complex plug-flow reactors, or modified plug-flow reactors (Tab. 4), are adapted for fermentation through morphological changes, especially in the tunica muscularis (Fig. 3 B). These modifications result in longer retention times, increased axial mixing of the contents of the compartment and maintenance of suitable environmental conditions for cellulolytic micro-organisms (DELLOW and HUME 1982; DELLOW et al. 1983). The macropodid forestomach is an example of a complex plug-flow reactor (STEVENS and HUME 1995; CATON 1997) (Fig. 3 B).

The most important diagnostic features of plug-flow reactors, whether simple or complex, are their length, radial mixing and the unidirectional flow of reactants (Tab. 4). Increasing the length of plug-flow reactors increases their operational efficiency, as well as providing a greater surface area for the absorption of nutrients (DENBIGH and TURNER 1971; CHIVERS and HLADIK 1980).

Simple continuous-flow, stirred-tank reactors are rare in mammalian gastro-intestinal tracts. The best examples are sac-like simple unipartite stomachs (Fig. 4), and the sacciform forestomach of some mammalian herbivores (LANGER 1988; HUME 1989) (Tab. 1).

The capacious proximal segment of the hindgut, which is modified for fermentation in herbivores and omnivores, is a complex continuous-flow, stirred-tank reactor (CATON 1997) (Fig. 4 A). Complex continuous-flow, stirred-tank reactors are tubular in shape, like complex plug-flow reactors, and are sites of fermentation. They are hybrid reactors that have characteristics of both ideal plug-flow reactors and continuous-flow, stirred-tank reactors (Tab. 4; Fig. 4 C). Enlargement of the reactor by increasing the calibre of a compartment and haustration of the wall by longitudinal muscle bands or taeniae increases the amount of radial mixing. Alternating bouts of peristalsis and antiperistalsis facilitate axial mixing. The determination of the functional category of a complex reactor depends on the pattern of flow of digesta (e. g. unidirectional in a complex plug-flow reactor) and the amount of axial mixing that occurs (e. g. limited in a complex plug-flow reactor) (Tab. 4; Figs. 3 and 4).

Retention mechanisms in gastro-intestinal reactors

Mechanisms that delay and alter the pattern of digesta flow through compartments are common in the gastro-intestinal tracts of mammals. Retention mechanisms are of three general types:

(1) Functional mechanisms that work throughout a specified compartment, e. g. alternating periods of peristalsis and antiperistalsis in the human colon (CHRISTENSEN 1989) assist in mixing the contents and delay the emptying of this complex continuous-flow, stirred-tank reactor

(2) Sphincters within gastro-intestinal tract compartments regulate the volume and rate of

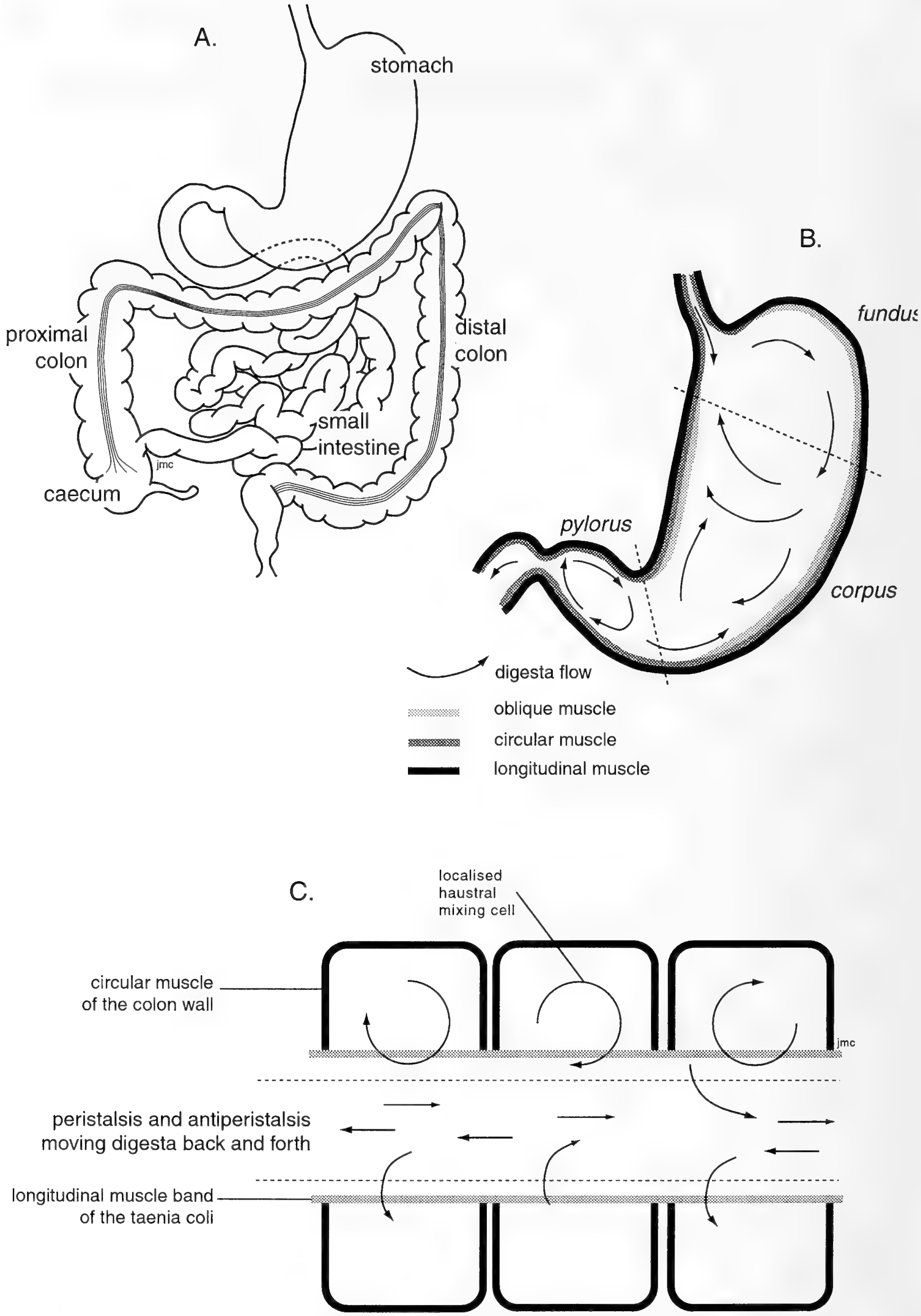

Fig. 4. Continuous-flow, stirred-tank reactors in the human gastro-intestinal tract (A). The Human stomach (B) functions as a simple continuous-flow, stirred-tank reactor for the preliminary processsing of digesta. The proximal colon and caecum (C) are a complex continuous-flow, stirred-tank reactor in which structural polysaccharides are processed by microbial fermentation.

aboral flow from one compartment to the next (Björnhag 1994; Stevens and Hume 1995). Sphincters also control the aboral flow of digesta through the gastro-intestinal tract (Papasova 1989).

(3) Specialised mophological features for directing digesta orally are evident in the hindguts of lagomorphs and certain rodents (Stevens and Hume 1995). Well-developed rugae (mucosal folds) are found in the stomachs of many mammals (Langer 1988; Stevens and Hume 1995; Caton 1997); these are 'baffles', increasing mixing of the contents of a compartment as well as delaying its transit.

These retention mechanisms are most often found in fermentation compartments. They improve the performance of continuous-flow, stirred-tank reactors by reducing by-pass loss and increasing retention times (thereby increasing the time available for the reaction to take place, which results in greater efficiency of fermentation compartments and increases the mixing capabilities of a particular compartment).

Conclusions

The application of chemical reactor theory to gut function has proved to be an important tool in the understanding of the complexity of the relationships between gut morphology, diet chemistry and food processing in the gastro-intestinal tract of mammals (Hume 1989; Caton 1997). The mathematical models developed have enabled physiologists to make detailed descriptions of the optimal reactor arrangements for processing specific diets, and thus to compare the digestive patterns of different species (Alexander 1991; Martinez Del Rio et al. 1994).

The widespread acceptance and use of chemical reactor theory in mammalian digestive physiology has necessitated the clarification and definition of the specific characteristics of gut reactors, which are the analogues of industrial reactors. The system of classification of mammalian gut reactors proposed here is based on both their structure and function (Caton 1997). Catalytic reactors, such as the human stomach and the small intestine, have simple morphologies. Fermentation compartments tend to have complex musculature, which facilitates the mixing and retention of digesta (Caton 1997). To avoid confusion with ideal reactors, gut reactors are defined as either simple or complex on the basis of their structure and functional characteristics.

The gastro-intestinal tract of mammals has the same basic morphology across taxa, despite phyletic and dietary differences (Stevens and Hume 1995). It is essentially a tubular structure that is divided into four compartments, stomach, small intestine, caecum and colon, each of which is adapted for either catalysis or fermentation (Chivers and Hladik 1980; Caton 1997). Ingesta are transported to the stomach via the oesophagus, where they are stored and prepared for sustained release into the tubular small intestine. The digesta then enter the hindgut, which consists of a blind diverticulum (the caecum) and tubular colon. Digestive wastes are voided into the environment via the anus. These morphologically distinct compartments perform different functions. The evolution of compartmentalisation of the mammalian tract separates catalytic and fermentation processes. This has resulted in greater flexibility in the processing of a range of dietary components and an increased ability to process larger amounts of ingesta per unit time. The importance of catalysis or fermentation in the digestive pattern of a particular species of mammal is reflected in the relative size of a compartment or reactor in which the processing of the significant dietary component occurs (Chivers and Hladik 1980; Stevens and Hume 1995; Caton 1997). The gastro-intestinal tract is more complex in plant-eaters as they rely to a much greater extent on fermentation than flesh-eaters (Stevens and Hume 1995).

The optimal reactor class for catalysis is the plug-flow reactor, if reaction rates are high (Denbigh and Turner 1971). The small intestine fits the criteria for this type of reactor (Tab. 3; Fig. 3), i. e. it is a long narrow tube; the concentration of reactants is highest at the entrance to the reactor, where they are mixed with the catalysts (endogenous enzymes). There is limited axial mixing due to controlled segmental motility (peristalsis). The small intestine is always present in mammals irrespective of diet, but is relatively longer in mammals that eat high-quality diets (Chivers and Hladik 1980).

Continuous-flow, stirred-tank reactors are the optimal reactor class for fermentation (Denbigh and Turner 1971). Characteristically, they have a vat-like structure with well-mixed contents and longer retention times to allow for slower reaction rates (Tab. 4; Fig. 4). Simple continuous-flow, stirred-tank reactors, which approach this ideal type, are found only in the stomach, either singly as in camivores and proximal hindgut fermenters, or in series as in the complex stomachs of herbivores (Langer 1988). This arrangement of simple continuous-flow, stirred-tank reactors in series increases the efficiency of processing as it reduces by-pass loss (Denbigh and Turner 1971; Alexander 1994). Ruminants, camelids, peccaries and sloths are the main groups exhibiting this type of gastric morphology (Langer 1988; Stevens and Hume 1995). The other two groups of forestomach fermenters, macropodids and colobines, have tubiform forestomachs. The macropodid forestomach functions as a modified plug-flow reactor (Dellow 1979; Hume 1989) (Fig. 4). The function of the colobine stomach is more complex than that of macropodids, consisting of a continuous-flow, stirred-tank reactor in series with a plug-flow reactor (Caton 1997).

The morphology of the hindgut is modified in herbivores in which it is the major site of fermentation. The caecum acts either as a semi-batch reactor during fermentation (Penry 1993), or as an extension of the colon (Elliott and Barclay-Smith 1904; Björnhag 1994). The tubular colon in these mammals is wide and haustrated for mixing and slowing the transit of contents (Chivers and Hladik 1980; Clemens and Phillips 1980; Caton 1997). Comparison of the characteristics of the functional morphology of the hindgut with those of ideal reactors is important in determining the types of reactors present in this region.

The differences in mammalian gut morphology and reactor classes represent adaptations to diets with different processing requirements (Hume 1989; Alexander 1994). Strict herbivores and strict carnivores are dietary specialists representing the two ends of a dietary continuum. Omnivores, with their adaptations for processing mixed diets of variable chemical composition, have more flexible digestive abilities, enabling them to exploit a wide range of diets under variable environmental conditions.

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Zusammenfassung

Überblick über die Typen des Gastrointestinaltraktes von Säugetieren unter Berücksichtigung der „chemical reactor“-Theorie

Penry und Jumars (1986) nutzen als erste die Theorie der “chemical reactors” zur Modellierung der Wirkungsweise des Verdauungstraktes bei Säugetieren. Weil diese Theorie, in welcher der Verdauungsprozeß in Form eines mathematischen Modells dargestellt wird, es ermöglicht, die komplexen physiologischen Beziehungen zwischen Säugetier und seinem Futter besser zu verstehen, fand sie breite Zustimmung. Daten, welche im Rahmen physiologischer Untersuchungen an lebenden Säugern ermittelt wurden, können mit Hilfe der „chemical reactor“-Theorie das Verständnis der komplexen Beziehungen zwischen Morphologie, chemischer Zusammensetzung der Nahrung und Verdauungsprozessen bei Säugetieren erleichtern.

Im Verdauungstrakt der Säuger treten mehrere Reaktortypen auf. Gegenüber den „idealen“ technischen Reaktionsgefäßen sind jene im Verdauungstrakt der Mammalia abgewandelt. Im Verdauungstrakt und im technischen System unterscheiden sich die Entfernung der Reaktionsprodukte aus dem Reaktor, aber auch die dort stattfindenden Mischungs- und Transportprozesse. Zur Vermeidung von Verwechslungen mit chemotechnischen Reaktortypen wird hier eine neue Klassifikation für die Reaktoren des Verdauungstraktes vorgeschlagen. Diese Klassifikation beruht auf Form- und Funktionsdifferenzen in den verschiedenen Abschnitten des Verdauungstraktes. Die im Gastrointestinaltrakt der Säugetiere auftretenden Reaktortypen ermöglichen die Anpassung an unterschiedliche Futterarten, welche unterschiedlichen Verdauungsprozessen unterworfen werden.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Variability in measurements of microchiropteran bats caused by different investigators

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The forearm length is a standard measurement taken in studies of microchiropteran bats. It has been used in taxonomic revisions (e. g. Kitchener and Caputi 1985; Kitchener et al. 1986, 1987), for the differentiation of closely related bat species during field studies (e. g. Hall and Richards 1979; Reardon and Flavel 1991; Parnaby 1992; Queale 1997) and to investigate differences between populations of individual species (e. g. Kitchener and Caputi 1985; Tidemann 1986; Lumsden and Bennett 1995), in determining age and growth rates (e. g. Kunz and Anthony 1982; Anthony 1988), body condition (e. g. Ransome 1990; Herr 1998), and sexual dimorphism (e. g. Myers 1978; Best 1988; Jones and Kokurewicz 1994; Lumsden and Bennett 1995). In most ecological studies measurements are taken on live animals under field conditions, thereby increasing the potential for error. Errors could be due to variation in measurements taken by a single investigator or due to differences between investigators. Bilateral differences in the length of the forearm of individual bats are another source of variation. This study investigates the variability of forearm measurements of bats caused by different investigators as well as differences in left and right forearm lengths of individuals.

Measurements were taken on 31 little forest bats (*Vespadelus vulturnus*) and 13 Gould's wattled bats (*Chalinolobus gouldii*) caught in Chiltern State Forest, north-eastern Victoria (36°09′S 146°39′E) in February 1996. The sample included both males and females, adults and sub-adults. The authors (Investigators 1–3) used their own Vernier calipers to measure the forearm lengths of the bats under field conditions. Each measured the left and right forearm of each bat twice. Measurements were made to the nearest 0.1 mm. The data were recorded separately for each investigator by three additional people.

The results were analysed using one-way and two-way ANOVAs. All data were normally distributed with equal variances. Although there were several outliers in the data, ANOVAs conducted with and without these outliers were found not to influence the results significantly. To assess variability among investigators, their first measurements were compared, whilst treating the measurements of left and right forearms as independent values.

There were no significant differences among the mean measurements taken by the three investigators for either species (Tab. 1), with variation between investigators less than 0.5 mm. Using the first measurement of each forearm (all investigators combined),

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Table 1. Means and standard deviations of the first measurement made by three investigators (1, 2, 3) of each forearm of the 44 microchiropteran bats. All measurements in mm. Results of one-way ANOVAs are also presented.

Forearm	Investigator			F-ratio ANOVA	P
	1	2	3		
V. vulturnus (n = 31)					
Left forearm	27.8 ± 0.8	27.9 ± 0.7	28.1 ± 0.8	1.29	N.S.
Right forearm	28.0 ± 0.8	28.0 ± 0.8	28.1 ± 0.8	0.16	N.S.
Mean (both forearms)	27.9 ± 0.8	27.9 ± 0.7	28.1 ± 0.8	1.11	N.S.
C. gouldii (n = 13)					
Left forearm	45.5 ± 1.4	45.4 ± 1.4	45.8 ± 1.3	0.29	N.S.
Right forearm	45.7 ± 1.3	45.5 ± 1.4	45.9 ± 1.5	0.35	N.S.
Mean (both forearms)	45.6 ± 1.3	45.4 ± 1.4	45.8 ± 1.3	0.66	N.S.

Table 2. Mean absolute differences (in mm) between the first and second measurement of each forearm measured by the three investigators (measurements from both forearms have been combined).

Species	Investigator	N	Mean absolute difference	S. D.	Mean forearm	Mean difference (percentage of forearm)
V. vulturnus	1	62	0.23	0.31	27.9	0.8%
	2	62	0.09	0.09	27.9	0.3%
	3	62	0.16	0.19	28.1	0.6%
	Combined	186	0.16	0.22	28.0	0.6%
C. gouldii	1	26	0.31	0.31	45.6	0.7%
	2	26	0.15	0.16	45.4	0.3%
	3	26	0.15	0.12	45.8	0.3%
	Combined	78	0.20	0.23	45.6	0.4%

the 95% confidence intervals of forearm length were calculated to be ± 0.1 mm for *V. vulturnus* and ± 0.3 mm for *C. gouldii*. The mean absolute difference between measurements of individual bats taken by different investigators was 0.3 ± 0.3 mm for *V. vulturnus* and 0.4 ± 0.3 mm for *C. gouldii*.

The influence of the different investigators and the sides (left and right forearm) were compared using the first measurements of each forearm. There were no significant differences between the mean length of the left and right forearms, nor between the mean forearm length. However, in three of the 31 *V. vulturnus* measured, the right and left forearms were significantly different, with all six pairs of measurements outside the 95% confidence limit. In all cases the right forearm was larger than the left, with mean differences of 1.7 ± 0.5, 1.0 ± 0.3, and 0.7 ± 0.2 mm.

The mean absolute differences between first and second measurements of each forearm taken by the three investigators were compared. This mean difference is presented as a percentage of the forearm length for comparison between species (Tab. 2). The differences between repeated forearm measurements were proportionally higher for the smaller species *V. vulturnus* with 16.1% of the differences outside the 95% confidence interval, compared to 3.8% for *C. gouldii*. These differences were markedly higher for Investigator 1, with 25.0% of the differences between repeated measurements outside the 95% confidence interval, compared to 3.4% and 9.1% for Investigators 2 and 3, respectively.

Although there was no significant difference in the mean value of measurements taken by the three investigators, there was considerable variability between sets of repeated measurements, with variability of the measurements of one investigator being greater than the variability among the investigators. Measurement variability was not uniform among investigators. For example, Investigator 1 showed the greatest difference between the first and second measurements of *V. vulturnus* at 1.5 mm, while this difference was 0.4 mm for Investigator 2 and 1.0 mm for Investigator 3.

This study found that measurements taken by single investigators are more reliable than those collected by multiple investigators. This variability needs to be considered when measurements made by two or more investigators are compared. Further, researchers need to take their own inconsistencies into consideration when using morphometrics to identify closely-related species or to compare populations. Within south-eastern Australia, the lengths of the forearm of several pairs of sympatric bat species (e. g. *Scotorepens orion* and *S. balstoni*, *V. darlingtoni* and *V. pumilis*, and *Nyctophilus timoriensis* and *N. gouldi*) are used as a diagnostic character in taxonomic keys often relying on differences of 1 mm (PARNABY 1992). Such differentiation between species requires careful measuring, preferably with duplicate measurements.

Although differences in the lengths of left and right forearms of bats have been recognised previously (unpubl. data), this study has demonstrated that such differences often may be due to measurement errors. While there was no significant difference between the left and right forearms of the population, three individual *V. vulturnus* showed a significantly larger right forearm than left. Clearly, when repeated measurements are being used, for example, for growth studies, all measurements should be taken from the same side of the bat.

Variability of measurements caused by the use of different techniques among researchers could be reduced by the adoption of measuring standards. We suggest measuring to the end of the radius of the bat's right forearm. If the data are being recorded by a second person, the recorder should repeat the measurement back to the measurer, to reduce recording errors. It is further recommended that bat forearms are measured to the nearest 0.1 mm, but that statistical comparisons suggesting differences between means of less than 0.2 mm for the smaller species (proportionately greater for the larger species) are treated with some caution.

The precision of investigators can be verified by comparing duplicate measurements or by comparing forearm measurements obtained by different investigators (as described by BARRETT et al. 1989). The 95% CIs of all first measurements reported in this study (± 0.1 mm and ± 0.3 mm) would suggest that duplicate measurements of the forearm of individual *V. vulturnus* and *C. gouldii* should be less than 0.2 mm and 0.6 mm, respectively.

To overcome variability between investigators, comparisons of measurements could be used to generate confidence intervals of means, although this would only be practical in a limited geographical region and would need to be repeated and checked at regular intervals (ROGERS 1984; BARRETT et al. 1989). Where such an approach is not possible, measurement variability should be determined and considered in statistical analyses of morphometrics.

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Habitat isolation and genetic divergence of bank vole populations

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In a previous study (PAILLAT and BUTET 1996), we demonstrated that bank vole, *Clethrionomys glareolus* (SCHREBER, 1780) populations in agricultural landscapes exhibited signs of extinction in relation to the size and the connectivity of hedge fragments as already shown in small woodlots by APELDOORN et al. (1992). These processes could have effects on the genetic structure of populations and may enable identification of landscape parameters that control their dynamics. This has already been studied in several small mammal populations (MERRIAM et al. 1989; BAUCHAU and LE BOULENGÉ 1991; KOZAKIEWICZ and KONOPKA 1991; HANSKI and KUITUNEN 1986; GEBCZYNSKI and RATKIEWICZ 1998) and we carried out preliminary investigations to test if such an effect can occur at the landscape scale from populations of different isolation context.

Bank voles were collected by live trapping in April 1996 at three stations of the Mont-Saint-Michel Bay (north Brittany, France) and were analysed by using enzymatic and epigenetic methods. The first station (BOC) is a woodlot (0.65 ha) within a dense hedge network landscape ("bocage") providing good conditions for dispersal of bank voles. The two other stations (POLD A and POLD B) are hedges situated in an adjacent intensive agricultural landscape on reclaimed areas ("polders"). They are small linear woody elements (0.11 and 0.17 ha), 3 km away from each other, and weakly connected with other woody elements of the network. Eight voles were collected in a woodlot situated 55 km away from the study area as a control sample for enzymatic study.

Homogenates of either liver, kidney, and heart of 30 bank voles (10 from each station) were assayed using horizontal starch-gel electrophoresis. Fourteen enzyme systems were chosen for screening (locus and EC number): (ADH; 1.1.1.1), (GPD; 1.1.1.49), (IDH; 1.1.1.42), (MDH; 1.1.1.37), (PGD; 1.1.1.44), (LDH; 1.1.1.27), (ME; 1.1.1.40), (SOD; 1.15.1.1), (PGM; 2.7.5.1), (AAT; 2.6.1.1), (ADA; 3.5.4.4), (ALP; 3.1.3.1), (ES; 3.1.1.1), (GPI; 5.3.1.9).

On the basis of OTTO (1978), SIKORSKI and BERNSHTEIN (1984), and VASIL'EV et al. (1996), the frequency of 11 uni- and bilateral non-metric traits (binary) were scored from 53 bank vole skulls (21 from BOC, 20 from POLD A and 12 from POLD B) (Fig. 1, Tab. 1). These traits are not correlated to each other and with age or sex of voles.

Epigenetic differentiation was assessed by calculating the mean measure of divergence (MMD) between each pair of populations as described in detail by SJØVOLD (1977). Statistical significance of differences between populations was observed when the value of MMD was greater than double of the standard deviation of MMD. The measure of uniqueness (MU) was also calculated for each population, as the sum of all MMD used in comparing the population. For each population and in each skull variant the inter-indivi-

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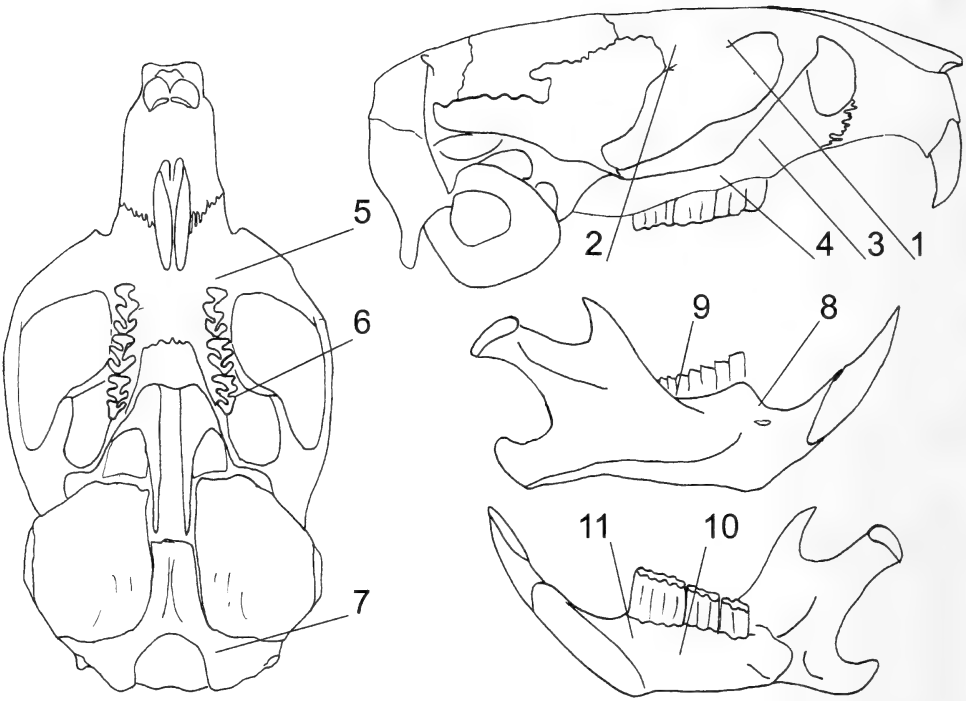

Fig. 1. Location of the 11 non-metrics traits scored in the bank vole skulls (number legends are detailed in table 1).

Table 1. Percentage frequencies of the 11 skull variants analysed (n = sample size).

Skull variants	Populations		
	BOC n = 21	POLD A n = 20	POLD B n = 12
1. Anterofrontal foramen double	71.1	45.1	58.1
2. Frontal foramen double	12.6	10.7	5.6
3. Foramen maxillare II present	66.4	91.7	78.3
4. Foramen maxillare III present	66.4	54.9	90.4
5. Foramen maxillare I present	45.3	18.1	33.8
6. Fourth M^3 buccal angle present	33.7	10.7	10.0
7. Foramen hypoglossi double	47.7	23.0	33.8
8. Foramen mentale II present	50.0	30.4	54.0
9. Dentary foramen present	52.3	67.2	82.3
10. Internal foramen mentale III present	73.4	47.5	78.3
11. Internal foramen mentale I present	28.9	25.5	17.7

dual variation was calculated as the standard deviation of the dichotomized character state values. The mean over the standard deviations of all variants (IV) served as an index of population-specific inter-individual variability (HARTL et al. 1993).

A total of 26 presumptive loci was identified by the electrophoretic study. All the loci were monomorphic and we neither observed variation in the gene loci of individuals of the three bank vole populations studied nor in the "control" group. Only epigenetic ana-

Table 2. Phenetic distances (MMD) between populations and populations uniqueness (MU). Standard deviations of MMD are given in parentheses.

	POLD A	POLD B	MU
BOC	0.145* (0.0218)	0.0916* (0.0257)	0.2366
POLD A		0.1156* (0.0261)	0.2606
POLD B			0.2072

* = statistically significant divergence

lysis revealed differences. Observation of the matrix of phenetic distances between corresponding pairs of populations always showed significant differences between populations and the three measures of uniqueness were approximately similar (Tab. 2).

The distribution of skull variant frequencies in table 1 differed clearly from one population to another. Thus, the percentage of skull variant frequencies for frequency interval [40–60] were 36.4, 27.3, and 18.2 in BOC, POLD A, and POLD B respectively while they were 9.1, 36.4, and 45.5 for intervals [0–20] and [80–100]. These results indicate highly variable traits in the woodlot population from the bocage, whereas the two polder populations show more fixed traits. In the same way, IV values were higher in the bocage ($\bar{x} = 0.48$) than in the polder ($\bar{x} = 0.41$ and 0.42) (Krustal-Wallis Test, $P < 0.05$).

Fluctuation of heterozygosity can be linked to season and/or age, degradation, and patchiness of the forest communities (Fedyk and Gebczynski 1980; Leitner and Hartl 1988; Gebczynski et al. 1993; Gebczynski and Ratkiewicz 1998). Genetic divergences among bank vole populations over short geographic distances were observed by Leitner and Hartl (1988). However, in our fine-scale study, a total loss of heterozygosity was found both in samples and "control" groups. The small sample size (although consistent with population size) and the number of loci (although polymorphic in other studies), are perhaps partly responsible of the low heterozygosity obtained (Nei 1978), but we think that electrophoretic methods are probably inefficient to distinguish biochemical variation at our study scale.

The results with epigenetic techniques are in line with other fine scale studies on bank voles (Kozakiewicz and Konopka 1991; Sikorski and Bernshtein 1984). The three populations are genetically distinct and the analysis of the distribution of skull variant frequencies and IV values suggest that isolated populations from hedges have lost variability of their characters. Connectivity favours trait variability by promoting "rescue effects", favouring interpatch dispersal and reducing amplitude of fluctuation (Farhig and Merriam 1985; Henein and Merriam 1990). Inversely, like Kozakiewicz and Konopka (1991), we conclude that bank vole populations inhabiting small isolated habitats are subject to severe falls of density and extinction/recolonisation processes leading to the fixing of traits through "bottleneck" and founder effects.

Relationships between biochemical genetic and epigenetic variability are not clear (Hartl et al. 1993) but, in our fine-scale study, the epigenetic method appears better adapted to reveal intragenetic variation in patchy populations which can be tied to connectivity in the landscape.

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Infrared video-monitoring of mammals at a fauna underpass

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Fauna passages have been built to provide safe crossover sites for wildlife. Some authors have examined wildlife use of different kinds of passages (Olbrich 1984; Madsen 1996; Foster and Humphrey 1995; Broekhuizen and Derckx 1996; Rodriguez et al. 1996, 1997), but few have directly observed the behaviour of animals entering or leaving fauna passages. The only species observed at fauna passages, to our knowledge, are the North American mule deer (*Odocoileus hemionus*; Reed 1981; Reed et al. 1975; Ward 1982) and mountain goat (*Oreamnus americanus*; Singer 1978; Pedevillano and Wright 1987).

In our study the entrance of a 155 m long underpass was surveilled. The entrance of the underpass is shaped like a half circle, and is 13 m wide and 7.5 m high. The underpass is placed under highway E45 between Aarhus and Randers in Jutland, Denmark. On this site an 18 m high dam is built across a 500 m wide valley, and a small stream runs through the valley, traversing the dam in the middle of the underpass. On each side of the stream is a 4–4.5 m wide dry bank.

Along the highway is a 1.75 m high fence on each side. The length of each of the fences is approximately 2 km, in both directions 1 km from the underpass.

The equipment used in surveillance included two infrared lamps, a light-sensitive camera, with zoom optic, and pan/tilt head, which were placed at a distance of 50 m from the entrance of the underpass. It was connected to a monitor, video cassette recorder, and remote control, which was placed in a vehicle a further 100 m away, uphill, behind a group of trees. Power was supplied by a generator.

The underpass was surveilled for two periods each lasting 30 days; April 10 to May 11, 1997 and August 4 to September 3, 1997. During the 60 nights the underpass was surveilled for 495 hours.

During surveillance the camera was pointed towards the entrance of the underpass so that mammals leaving or entering could be seen and visually followed. All observations of mammals were recorded on video tape for further analysis.

Besides the infrared video surveillance, tracks of mammals were registered in sand layers at both ends of the underpass on each side of the stream. Every morning the sand layers were investigated for tracks and then prepared for new tracks by raking. Criteria described by Bang and Dahlstrøm (1989) were used for identifcation of tracks.

During the two periods of surveillance a total of 122 red foxes (*Vulpes vulpes*), 16 badgers (*Meles meles*), 18 stone martens (*Martes foina*) and 20 roe deers (*Capreolus capreolus*) was observed passing through the underpass. The total number of mammals passing through was higher in April–May than in August–September (Tab. 1).

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Table 1. Observed mammals passing through the underpass, compared to the number of tracks in the sand layers in the same periods. The percentage of observed mammals of the total number of mammals that passed through the underpass is shown in the right column.

	April–May			August–September		
	Observed	Tracks	Percent	Observed	Tracks	Percent
Red fox	74	100	74	48	61	79
Badger	0	0	–	16	22	73
Stone marten	11	31	35	7	10	70
Roe deer	11	25	44	9	16	56
Total	96	156	62	80	109	73

The number of individual carnivores using the underpass was estimated, based on fur and behaviour, to be at least three different foxes, three different badgers, and only one or possibly two different stone martens. When individuals of the three species of carnivores entered or left the underpass they seldomly changed behaviour or velocity. When changes did occur it was almost always in accordance with territorial marking behaviour or smelling of markings from other animals. Foxes were observed marking at the entrance of the underpass 13 times (of 122 passages), badgers four times (of 16 passages) and stone martens six times (of 18 passages). When carnivores passed through the underpass there were no specific distances to the stream or to the wall of the underpass.

It was possible to observe the mammals the first 50 m in the underpass. The velocity of the foxes at the outmost 50 m of the underpass in April–May (mean velocity = 2.6 m/sec., N = 17) was significantly higher than in August–September (mean velocity = 1.4 m/s, N = 22; Mann-Whitney test, U = 327, critical value = 246, $p < 0.05$). Because of insufficient observations it was not possible to compare the velocities of badger and stone marten.

Only one male roe deer identified by its antlers was observed passing through the underpass. In many cases the roe deer travelled along the same path from the underpass to a forest 80 m away. So it was possible to measure the velocity of the roe deer in the underpass (the first 50 m) and outside the underpass. The roe deer travelled at significantly higher velocity in the underpass (mean velocity = 2.1 m/s, N = 9) than outside (mean velocity = 1.2 m/s, N = 10; Mann-Whitney test, U = 78.5, critical value = 66, $p < 0.05$). In the underpass, the roe deer always kept a distance of about 3.5 m to the wall and 0.5 m to the stream. At the entrance, the roe deer often changed its manner of walking. It often stopped, looked around or lowered the head. In the underpass, the roe deer seldomly changed the manner of walking. In April–May, the roe deer often galloped into or out of the underpass. This did not happen in August–September.

Apart from the single roe deer that used the underpass, five adult roe deer (3 males and 2 females) and three roe deer kids were observed in the area. Only one female roe deer with one kid was observed close to the entrance of the underpass. This occurred three times, but the two individuals only looked into the underpass without entering it.

At least three brown hares (*Lepus europaeus*) were observed in the area. Brown hares were only observed entering the underpass twice, and in both cases the brown hares showed reluctant behaviour, turned around, and ran out very rapidly.

Carnivores (except small mustelids) use different kinds of fauna passages usually without difficulties (Broekhuizen and Derckx 1996; Bekker et al. 1995). Therefore, no change in behaviour could be expected at the underpass for species such as fox, badger, and stone marten. The observed individuals of these three species did not seem to be influenced by the underpass. When the animals came close to the underpass, they went through with very few exceptions. These few exceptions could in most cases be explained by the presence of other mammals or perhapes as a reaction to the infrared light. The reason that the foxes moved faster in the underpass in April–May than in August–September is possibly a result of the breeding season.

Apparently the roe deer habituated to the underpass during summer. Galloping through the underpass was only observed in April–May. The reason is probably that the roe deer used the underpass all summer in connection with territorial defence, and so it is likely that the roe deer habituated to the underpass.

According to Olbrich (1984) the openness has to be approximately 0.75 before roe deer are willing to use an underpass. The studied underpass had an opening of 0.5 and thus it appears that the underpass is too narrow for roe deer. This might explain why only one roe deer used the underpass.

The studied underpass was of sufficient size for fox, badger, and stone marten. Based on our results, underpasses have to be very large, and with an opening of 0.5–0.75 before roe deer in general will use them. If all species are to be catered for, it will be necessary to build larger underpasses or other types of passages.

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In Kooperation
74. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde
und
48. Jahrestagung der Vereniging voor Zoogdierkunde en Zoogdierbescherming
vom 24.–28. September 2000 in Groningen

Einladung

Die 74. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde findet von Sonntag, dem 24. September bis Donnerstag, dem 28. September 2000 gemeinsam mit der 48. Jahrestagung der niederländischen Gesellschaft für Säugetierkunde VZZ im ‚Het Tehuis'-Zentrum in Groningen statt.

Vorläufiges Programm

Sonntag, 24. September:	Anreise
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	ab 19.00 Uhr: Zwangloser Begrüßungsabend
Montag, 25. September:	9.00 Uhr: Begrüßungen
	9.30 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt: „Soziobiologie, Sozioendokrinologie, Stress"
	14.00 Uhr: Posterdemonstration
	15.00 Uhr: Kurzvorträge
	16.00 Uhr: Mitgliederversammlung
Dienstag, 26. September:	9.00 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt: „Biologie und Schutz der Fledermäuse"
	14.00 Uhr: Posterdemonstration
	15.00 Uhr: Kurzvorträge
	19.00 Uhr: Geselliger Abend
Mittwoch, 27. September:	9.00 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt: „Biologie und Schutz der Meeressäugetiere"
	14.00 Uhr: Posterdemonstration
	15.00 Uhr: Kurzvorträge
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Donnerstag, 28. September:	Wissenschaftliche Exkursion

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Alle Interessenten, Mitglieder und Nichtmitglieder, sind zu dieser Jahrestagung herzlich nach Groningen eingeladen. Kongreßsprachen werden Deutsch und Englisch sein. Das Programm mit der Vortragsfolge wird den Mitgliedern – auf Anforderung auch Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt. Sollten Sie eine persönliche Einladung benötigen, so wenden Sie sich bitte direkt an den 1. Vorsitzenden der Deutschen Gesellschaft für Säugetierkunde, Prof. Dr. H. Erkert, Zoologisches Institut, Morgenstelle 28, D-72076 Tübingen (Tel. +49-(0)70 71/2 97 29 58; Fax +49-(0)70 71/29 46 34).

Wir bitten um die Anmeldung von Kurzvorträgen (15 min + 5 min Diskussion) und Posterdemonstrationen zu den genannten Themenschwerpunkten und zu weiteren Fachgebieten der Säugetierkunde.

Bitte melden Sie Ihre Beiträge möglichst frühzeitig, spätestens jedoch bis zum 30. April (Ausschlußfrist) beim Geschäftsführer der DGS, Prof. Dr. R. Schröpfer, Fachbereich Biologie/Chemie: Ethologie, D-49069 Osnabrück (Tel. +49-(0)5 41/9 69-28 48, Fax: +49-(0)5 41/9 69-28 62, e-mail: schroepfer@biologie.uni-osnabrueck.de) 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 angenommenen Kurzfassungen werden wieder in einem Sonderheft der Zeitschrift für Säugetierkunde publiziert. Sie sind nach folgendem 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). Aus arbeitsökonomischen Gründen bitten wir dringend darum, zusätzlich zum ausgedruckten Abstract möglichst noch eine Fassung auf Diskette (3.5″, IBM-kompatibler DOS-PC) in Form eines Word-Dokuments, Word Perfect- oder ASCII-Files mitzuschicken. Bitte formatieren Sie diesen File nicht! Die Maße für die Poster werden im Rundbrief 2/2000 der DGS bekanntgegeben.

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Buchbesprechung

Thewissen, J. G. M. (ed.) (1998): **The Emergence of Whales. Evolutionary Patterns in the Origin of Cetacea**. In: Advances in Vertebrate Paleobiology. New York, London: Plenum Press. Hardcover, 477 pp., numerous illustrations and tables. US $ 115.–, British £ 74.75. ISBN 0-306-45853-5

In his preface the editor mentions that research "in whale origins is now in an explosive phase, with a cascade of discoveries adding to our understanding of the evolutionary pattern and a suite of new techniques being applied to address new questions. The objective of this volume is to provide a snapshot of this explosion". The reader can only acknowledge with admiration that much more than just a snapshot is presented in the 16 chapters of this book, which are authored by 24 contributors.

The first two chapters present paleontological overviews, introducing fossil species from the early, middle (Williams), and late Eocene (Uhen). In the following chapter the phylogenetic affinities of cetaceans, as published in previous studies, are depicted in a large number of phylogenetic trees (Gatesy). In addition, phylogentic studies of DNA nucleotide position suggest Cetacea to be nested within the Artiodactyla and they support a sister-group relationship between Cetacea and Hippopotamidae. The "relative absurdity" (Gatesy) of the molecular results as compared with contradicting morphological characters, cannot yet be resolved, but it is a characteristic asset of this remarkable book that discrepancies are clearly addressed and not avoided! In the fourth chapter, which is based on molecular studies, Milinkovitch et al. consider Cetaceans as "highly derived artiodactyls".

Returning to the more "classical" paleontological studies, O'Leary produces evidence of a Mesonychia plus Cetacea clade. As a result of morphological studies dealing with cranial blood vessels, Geisler and Luo come to the conclusion that the monophyletic order Artiodactyla "does not include Cetacea". After chapters dealing with fossil cetaceans from the middle Eocene of India (Bajpai and Thewissen) and with the postcranial osteology of the middle Eocene genus *Georgiacetus* from North America (Hulbert), the following chapter, authored by Luo, discusses homology and transformation of ectotympanic structures in Cetacea. In a fascinating section by Fish biomechanical properties of the origin of cetacean flukes are presented. The evolutionary sequence by which flukes arose will remain speculative until impressions of flukes early in their evolution are found. Buchholtz informs the reader that it is highly probable that undulatory movements changed from the feet to the terminal fluke, which is coincident with dorsoventrally compressed posterior tail vertebra.

The twelfth chapter, authored by Madar, deals with highly variable structural adaptations of long bones in Archaeocetes. The variability in thickness of the cortex and the "trabecular infill" outline a progressively increasing dependence on aquatic habitats. In the following stimulating chapter Pabst et al. present the well-based hypothesis that features of the cetacean reproductive tract are paedomorphic, i. e., that they represent arrested embryonic characters that are retained and specialized in the adult. The following parameters are considered as paedomorphies: intra-abdominal testes, vestiges of the pelvic girdle, plexus of the spermatic and ovarian arteries, and duplicated Venae cavae.

Investigations of oxygen and carbon isotope composition in teeth and bone of Cetacea (Roe et al.) allowed to study terrestrial to marine transition, especially of early cetaceans. After a rapid transition the first fully marine cetaceans appeared in the middle Eocene. This change of habitat is coincident with changes in osmoregulatory physiology and in the types of diet. The palaeobiological perspectives of the origin of whales is dicussed by Gingerich under consideration of the following parameters: body size, trophic specialisation, specialisations of the middle ear, hydrodynamic streamlining, and hindlimb reduction, as well as encephalisation. The author hypothesizes that trophic dental changes represent the first step in transition from land to sea, auditory changes happening next, and locomotor adaptations to a fully aquatic lifestyle followed.

In a final chapter, Thewissen discusses the „evolutionary turmoil during the invasion of oceans" as an important aspect of cetacean origin and sums up the findings presented in this remarkable book. He considers cetacean origins as one of the best documented examples of major morphological change in the fossil record. The reviewer is deeply impressed by the wealth of information on evolutionary patterns and the multitude of viewpoints from which the emergence of whales is presented, discussed, and interpreted. Certainly, this publication is not only informative reading for cetologists, but for mammalogists in general!

P. Langer, Gießen

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ZEITSCHRIFT FÜR
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Zur Habitatwahl der Zwillingsarten *Sorex araneus* und *S. coronatus* (Insectivora, Soricidae) in Nordwest-Deutschland

Von H. Meinig

Institut für Verhaltensphysiologie, Universität Bielefeld, Bielefeld

Eingang des Ms. 26. 01. 1999
Annahme des Ms. 30. 11. 1999

Abstract

Habitat choice of the sibling species Sorex araneus and S. coronatus (Insectivora, Soricidae) in northwestern Germany

The spatial distribution of the sibling species *Sorex araneus* and *S. coronatus* was investigated by collecting 210 animals using pitfall traps. The study site (NSG Fürstenkuhle, Northrhine-Westphalia) was situated in the northern part of the distribution area shared by the two species. For taxon determination qualitative as well as quantitative characters of the skull were used. The species showed constant differences according to preferred habitat types. *S. araneus* occurred in all age-classes during the entire hypergeic period of activity in areas characterized by a high degree of soil humidity. *S. coronatus* occurred more irregularly in these areas. Young animals searching for unoccupied territories and older non-resident animals were overrepresented in the catches. At nearby locations, where dryer conditions dominate, *S. coronatus* was observed at higher consistency. These findings were compared to those from different landscapes, including flat and hilly areas.

The small scale distribution of *S. araneus* and *S. coronatus* is dependent on the same factors found to be influential in both Switzerland and the south of Germany. In northern Germany the spatial separation of the two species is less obvious because the variations in altitudes of the landscape coupled with different climates are less than in the south. Depending on weather conditions, the same area may be occupied by one species during one year and by the other species during the following year. The distribution of the two species in general can be characterized as parapatric in the geographical area studied.

Key words: *Sorex araneus, S. coronatus*, ecology, morphology, spatial separation

Einleitung

Im südlichen gemeinsamen Verbreitungsgebiet der Zwillingsarten *Sorex araneus* und *S. coronatus* liegt eine klare parapatrische Verbreitung vor (z. B. Hausser 1978; Searle 1984; Hausser et al. 1985; Brünner und Neet 1991). Nur wenige Kontaktzonen wurden bisher festgestellt (Meylan 1964; López-Fuster et al. 1985; Neet 1989; Neet und Hausser 1990). Im nördlichen gemeinsamen Areal ist dagegen ihre ökologische Einnischung weiterhin unklar. Während Meinig (1991) eine relativ klare Trennung im Bergischen Land und an einigen weiteren Mittelgebirgsschwellen (Teutoburger Wald, Wiehengebirge, Rhön) beobachtete, berichten Olert (1973), Loch (1977), Hutterer und Vierhaus (1984), Mys et al. (1985), Handwerk (1987), Kulzer et al. (1993) und Berger et al. (1992) von sympatrischen Vorkommen, bei denen z. T. beide Arten an den gleichen Fallenstandorten nachgewiesen wurden.

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Einigkeit scheint darin zu bestehen, daß *S. araneus* eine größere Toleranz gegenüber hoher Bodenfeuchte aufweist und kontinentaler geprägte Mikroklimate bevorzugt als *S. coronatus* (Brünner und Neet 1991; Meinig 1991; Neet und Hausser 1990; Turni und Schönherr 1994). Durch welche Faktoren das Vorkommen der einen oder anderen Art im nordwestdeutschen Raum bestimmt wird, bleibt weitgehend unklar.

Bei der Bearbeitung von Kleinsäugermaterial aus Bodenfallen aus dem Naturschutzgebiet (NSG) Fürstenkuhle (NRW; Meinig 1995a, b, 1999) wurden beide Arten festgestellt, allerdings mit Vorkommensschwerpunkten in unterschiedlichen Habitattypen. Durch eine Analyse dieses Materials und unter Einbeziehung anderer Untersuchungen soll versucht werden, die Faktoren zu ermitteln, die das Vorkommen und die ökologische Einnischung der beiden Zwillingsarten in diesem Teil ihres gemeinsamen Verbreitungsgebietes bestimmen.

Material und Methode

Untersuchungsgebiet

Das NSG Fürstenkuhle liegt im Naturraum „Westmünsterland" (Meisel 1961) (Kreis Borken, NRW; Meßtischblatt 25 000 4008/3). Das Kerngebiet bildet ein 27 ha großer Hochmoorrest mit hoher Bodenfeuchte, der seit 1942 bzw. 1965 unter Schutz steht. 1988 wurde das Schutzgebiet auf 88 ha erweitert (Glandt et al. 1990). Zuschlagsflächen waren vor allen Dingen abgetorfte und drainierte landwirtschaftliche Nutzflächen.

Das Westmünsterland weist ein atlantisch geprägtes Klima mit milden Wintern und mäßig warmen Sommern auf. Der jährliche Niederschlag liegt zwischen 700 und 800 mm mit einem Maximum im Sommer. Die mittlere jährliche Temperaturamplitude liegt bei 16 °C, die Mitteltemperatur des kältesten Monats (Januar) liegt knapp über dem Gefrierpunkt (Kürten 1977; Müller-Temme 1986).

Material

Durch das Biologische Institut Metelen wurden 1984 und 1985 Untersuchungen zur terrestrischen Ökologie des Moorfrosches (*Rana arvalis*) im NSG Fürstenkuhle durchgeführt (Büchs 1987a, b; Hartung 1991). Hierzu wurde 1984 ein Laichgewässer mit einem ca. 220 m langen Amphibienzaun umgeben, an dem 35 Bodenfallen gestellt wurden. 1985 wurden zusätzlich zu den Fanggefäßen am Laichgewässer noch 10 „geflügelte Landfallen" (Hartung und Glandt 1988) auf dem Moorkörper installiert. Die Fallen wurden von Anfang März bis Anfang Dezember gesetzt, Kleinsäugerbeifänge liegen aus den Monaten März bis Oktober vor (Meinig 1995a). Fallenkontrollen wurden während der Hauptwanderungsphasen des Moorfrosches von März bis Mai und von September bis November täglich durchgeführt, außerhalb dieser Zeit in 3–4 tägigem Abstand. Das tot in den Fallen vorgefundene Kleinsäugermaterial wurde in Alkohol, nach Monaten getrennt, aufbewahrt.

Zusätzlich wurden 1988 und 1989 auf landwirtschaftlichen Extensivierungsflächen östlich des Moorkörpers Untersuchungen zur Carabidenfauna mit Barberfallen durchgeführt (Schäfer et al. 1995). Als Fangflüssigkeit diente eine 4–5%ige Formollösung. 1988 wurden 45 Fallen vom 13. 05. bis 10. 10. auf 6 Maisäckern unterschiedlicher Nutzungsintensität, Maisackerbrachen und einem Moorstandort betrieben (Meinig 1995b). 1989 wurde die Untersuchung auf Grünlandstandorten unterschiedlicher Nutzung und Nutzungsintensität mit je 12 Fallen auf 8 Flächen (160 Fallen) vom 5. 04. bis 4. 11. durchgeführt. Fallenleerungen erfolgten alle 10 Tage, angefallenes Kleinsäugermaterial wurde getrennt nach Fallenstandorten (Meinig 1999) mit Datumsangabe in 70%igen Alkohol überführt.

Während der Witterungsverlauf 1988 Niederschläge im Rahmen des langjährigen Mittels erbrachte, war das Jahr 1989 ausgesprochen niederschlagsarm und erbrachte fast 100 mm weniger Regen. Dies führte zu einem Absinken des Grundwasserspiegels, zu beobachten an der verringerten Wasserführung von Bächen und Gräben. Die Jahresmitteltemperatur lag um 1,3 °C über dem langjährigen Mittel. Die Auswirkungen von Trockenheit und erhöhter Temperatur führten dazu, daß der zweite Grasschnitt im September auf den Untersuchungsflächen nicht durchgeführt werden konnte.

Von dem in Alkohol fixierten Material wurden Hinterfuß- und Schwanzlänge gemessen, und soweit möglich, Reproduktionszustand und Geschlecht bestimmt. Die Schädel wurden mit einem Kaltwaschmittel mazeriert (Meinig und Verwiebe 1993). Insgesamt liegen aus den 4 Untersuchungsjahren 210 Individuen der Zwillingsarten vor. Es handelt sich um 118 *S. araneus* und 92 *S. coronatus*, von 57 Individuen konnten auch Bälge konserviert werden.

Determination

Die Bestimmung erfolgte zunächst nach qualitativen Merkmalen am Unterkiefer (v. Bülow 1989). Nachfolgend wurden die Tiere nach der von Turni und Müller (1996) entwickelten Diskriminanzfunktion nachbestimmt. Die Messungen am Unterkiefer (Meßstrecken AH und AB) erfolgten mit einer digitalen Schieblehre (Mitutoyo digimatic) mit einer Genauigkeit von 0,01 mm. Es wurde ausschließlich die linke Mandibel vermessen. Die Meßstrecken am Oberkiefer wurden unter einem Binokular mit Meßeinrichtung (Zeiss GSZ) ermittelt, Meßstrecke FV bei 32facher, Meßstrecke PB bei 16facher Vergrößerung (zur Lage der Meßstrecken siehe Turni und Müller 1996).

Bei drei Tieren war der Schädel, wahrscheinlich durch Fraß anderer mitgefangener Kleinsäuger, soweit zerstört, daß nicht mehr sämtliche Meßstrecken am Oberkiefer genommen werden konnten, hier wurde ausschließlich auf die Strecken AH und AB zurückgegriffen, in diesen Fällen jedoch bei beiden Mandibelseiten.

Altersbestimmung

Die relative Altersbestimmung erfolgte nach zwei Verfahren. In Anlehnung an Conaway (1952) wurde die Länge des Incisivus im Unterkiefer sowie die Höhe von M_1 bei 32facher Vergrößerung gemessen, um metrisch erfaßbare, abnutzungsbedingte Größenreduzierungen zur Altersbestimmung heranzuziehen. Auch hier wurde ausschließlich die linke Mandibel betrachtet. Als zweites Verfahren wurde auf die auf Abnutzungsstadien des gesamten Gebisses beruhende Methode von Spitzenberger (1978) zurückgegriffen, die eine Einteilung von Altersklassen ermöglicht. Die einzelnen Altersklassen bedeuten: 1 – völlig unabgenutzt; 2 – Abnutzungsspuren an M^3; 3 – Hypoconid des M_3 von außen betrachtet flach und ohne rotes Pigment, M^3 weist nur noch an 2 schmalen Stellen Spuren der roten Pigmentierung auf; 4 – M^3 ganz ohne rotes Pigment, vorderer Lobus des I^1 so hoch wie hinterer; 5 – M^3 und M^2 ohne rotes Pigment, M_3 bis zu den Wurzeln abgekaut, I_1 ganz oder fast ohne rotes Pigment.

Ergebnisse

Determination

16 (7,6%) der 210 zur Verfügung stehenden Tiere wurden nach der Methode von v. Bülow (1989) fehlbestimmt. 12mal wurde *S. coronatus* als *S. araneus* bestimmt, 4mal *S. araneus* als *S. coronatus*. Auffällig war, daß es sich bei den Fehlbestimmungen zum größten Teil nicht um Tiere handelte, bei denen die Diskriminanzfunktion nahe 0 lag, d. h. deren Artzuordnung nach Turni und Müller (1996) unter Einbeziehung von Unter- und Oberkiefer eindeutig war. Den Ergebnissen nach dem Verfahren von Turni und Müller (1996) wurde Vorrang gegeben.

Im Verhältniss zu den Ergebnissen von Turni und Müller (1996) für Baden-Württemberg sind die Arten in Westfalen durch die neue Diskrimminanzfunktion weniger gut differenziert (Abb. 1). Es liegen mehrere Tiere im Bereich des trennenden 0-Punktes. Auch Turni und Müller (1996) weisen auf Größenunterschiede in Abhängigkeit vom Herkunftsort des Materials hin (vgl. auch v. Knorre 1998), halten diese aber für so gering, daß eine Anpassung der Diskriminanzfunktion nicht notwendig erscheint.

Alter

Bei der Beurteilung des Alters nach Conaway (1952) ergab sich bei einigen Tieren die Schwierigkeit, daß I_1 teilweise beidseitig abgebrochen war. Die Zahnlänge entsprach nicht dem ansonsten jungen Gesamteindruck des Gebisses. Die Länge von I_1 wurde daher

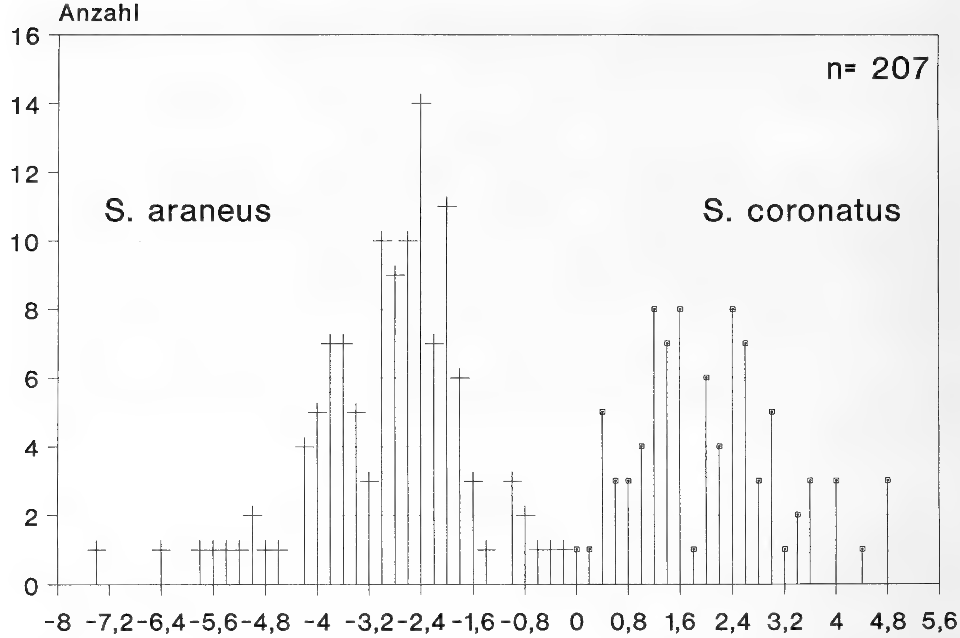

Abb. 1. Verteilung der Arten *S. araneus* und *S. coronatus* aus dem NSG Fürstenkuhle nach der auf Meßstrecken am Ober- und Unterkiefer beruhenden Diskriminanzfunktion von Turni und Müller (1996). Im Verhältnis zu Material aus Süddeutschland waren die beiden Zwillingsarten in Norddeutschland weniger gut getrennt.

nicht weiter in die Betrachtung einbezogen. Die Höhe von M_1 zur Altersabschätzung stellte sich ebenfalls als problematisch dar, da *S. araneus* gegenüber *S. coronatus* durchschnittlich größere Zähne aufweist. Dies läßt sich aus der Gegenüberstellung der Zahnhöhen mit den jeweiligen Altersklassen nach Spitzenberger (1978) ableiten (Abb. 2). Damit setzt sich die Tendenz, daß *S. araneus* in Westfalen durchschnittlich größer ist als *S. coronatus* (Hutterer und Vierhaus 1984) auch in den Zahndimensionen fort (Olert 1973). Auch dieses Maß wurde daher nicht weiter in die Abschätzung des Alters miteinbezogen. Ebenfalls gegen diese Methode spricht, daß die individuelle Variabilität oder eine etwaige Geschlechtsabhängkeit der Zahnmaße methodisch bedingt unberücksichtigt bleibt.

Bei der Altersklasseneinteilung nach Spitzenberger (1978) ergab sich das Problem, daß eine eindeutige Differenzierung zwischen den Altersklassen 1 und 2 nicht immer möglich war, da Tiere auftraten, bei denen eine Kieferhälfte keine Abnutzungsspuren aufwies, diese aber auf der anderen eindeutig zu erkennen waren. Diese Tiere wurden der Altersklasse 2 zugerechnet.

Die Waldspitzmaus zeigte in den Fängen des Jahres 1984 eine größere Kontinuität als die Schabrackenspitzmaus (Tab. 1). In den drei Monaten mit den höchsten Fangzahlen (Juni – August) waren Tiere der Altersklasse 1 bis 4 vertreten, eine Ausnahme stellte der Juli dar, in dem keine *S. araneus* aus der Altersklasse 3 gefangen wurde. Die Schabrackenspitzmaus dagegen war jeweils nur mit wenigen Einzelindividuen vertreten.

Ein ähnliches Bild vermitteln die Fänge des Jahres 1985. *S. araneus* war mehr oder weniger kontinuierlich mit allen 4 Altersklassen in den Fängen von Mai bis Oktober vertreten. Ausnahmen sind Juli, August, September und Oktober, in denen einzelne Altersklassen ausfielen. *S. coronatus* war nur mit Tieren der Altersklassen 1 und 2 vertreten.

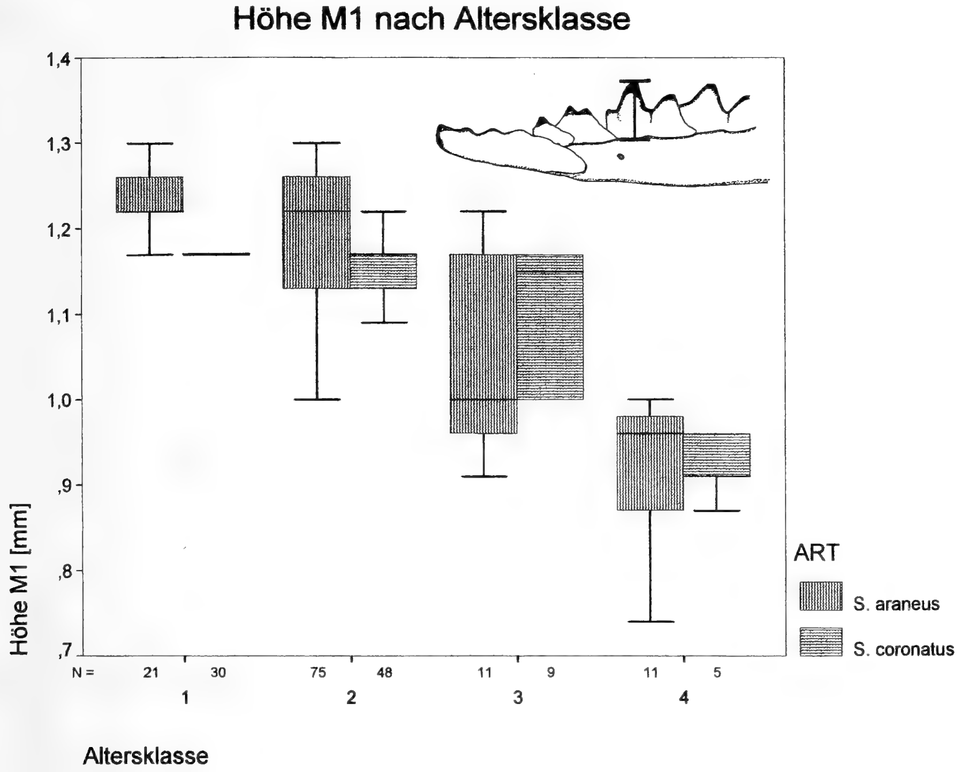

Abb. 2. Box-and-Whisker-Plot der Größe von M_1 bei *Sorex araneus* und *S. coronatus* in den unterschiedenen Altersklassen (AK) 1–4. (*S. araneus* AK 1: n = 21, AK 2: n = 73, AK 3: n = 13, AK 4: n = 11; *S. coronatus* AK 1: n = 30, AK 2: n = 49, AK 3: n = 8, AK 4: n = 5). Ein * bezeichnet Extremwerte, die mehr als das 1,5fache des Interquartilbereichs außerhalb der Box liegen. Bedingt durch unterschiedliche Zahnmaße von *S. araneus* und *S. coronatus* konnte die metrisch erfaßbare Zahnabnutzung im interspezifischen Vergleich nicht zur Altersabschätzung herangezogen werden.

Lediglich ein Tier der Altersklasse 3 wurde im Juni gefangen. Die Altersklasse 4 kam bei der Schabrackenspitzmaus in den Monaten mit den höchsten Fangergebnissen überhaupt nicht vor. Der Zuwachs von Fängen der Altersklassen 1 und 2 bei der Schabrackenspitzmaus erreicht nicht die gleiche Höhe in den Monaten Juni und Juli wie bei der Waldspitzmaus.

In den Fängen von den landwirtschaftlichen Nutzflächen aus dem Jahr 1988 zeigte *S. coronatus* eine größere Kontinuität, doch fiel diese nicht so deutlich aus, wie dies für 1984 und 1985 bei den Fängen vom Moor für die Waldspitzmaus der Fall war.

Zahlenverhältnisse der Fänge

Die Anteile von *S. araneus* und *S. coronatus* auf dem Moor und den landwirtschaftlichen Nutzflächen unterschieden sich erheblich: aus den Fallen im Bereich des Moores (1984, 1985) liegen 98 *S. araneus* und 27 *S. coronatus* vor (Verhältnis 3,6 : 1), aus den landwirtschaftlichen Nutzflächen (1988, 1989) 20 *S. araneus* und 65 *S. coronatus* (Verhältnis 1 : 3,3). Die Unterschiede in den Fangfrequenzen der beiden Arten sind in den einzelnen Jahren hochsignifikant (1984: 36 *S. a.*, 9 *S. c.*, $p = 5{,}7 \times 10^{-5}$; 1985: 62 *S. a.*, 18 *S. c.*,

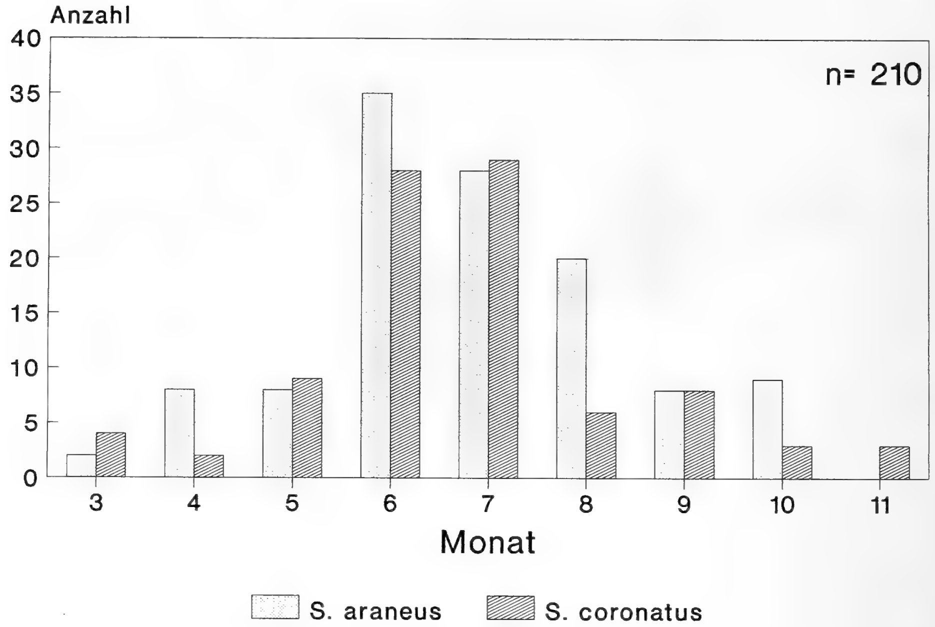

Abb. 3. Verteilung von *S. araneus* und *S. coronatus* auf die Monate in den Fängen aller Probeflächen und Jahre. Die Zwillingsarten zeigten nach dem vorliegenden Material eine weitgehend gleiche Populationsentwicklung und Oberflächenaktivität.

$p = 8{,}6 \times 10^{-7}$; 1988: 19 *S. a.*, 41 *S. c.*, $p = 4{,}5 \times 10^{-3}$; 1989: 1 *S. a.*, 24 *S. c.*, $p = 4{,}2 \times 10^{-6}$, Chi^2-Test). Ein überwiegen von *S. araneus* auf Hochmoorstandorten wurde bereits von Handwerk (1987) im belgischen Teil des Hohen Venns festgestellt.

Hinzuweisen ist auf die Verteilung der Fänge auf zwei Flächen des Jahres 1988. Während auf dem frischen Standort 14 Schabrackenspitzmäuse und nur eine Waldspitzmaus gefangen wurden, wurden auf der staunassen Fläche je 6 Individuen beider Arten gefangen (Meinig 1995 b). Die Fläche grenzt direkt an den Hochmoorrest.

Diskussion

Die artliche Zusammensetzung von Kleinsäugerzönosen entspricht bestimmten, z. T. konkurrenzbedingten Gesetzmäßigkeiten (Schröpfer 1990). Zwischen den Zwillingsarten *S. araneus* und *S. coronatus* bestehen keine oder nur geringe Größenunterschiede (Hutchinson-Indices, vgl. Schröpfer 1990). Diese können nicht dazu herangezogen werden unterschiedliche Nahrungsnischen für die beiden Arten zu vermuten, durch die eine Koexistenz möglich würde. Untersuchungen zum Nahrungsspektrum der beiden Arten im gemeinsamen Vorkommensgebiet liegen bisher kaum vor, deutliche Unterschiede lassen sich aber nicht erkennen (Braun und Kischnick 1987). Die beiden Formen stehen in Konkurrenz (Neet und Hausser 1990). Daneben spielen andere Faktoren wie Nahrungsverfügbarkeit (Pucek et al. 1993), Bodenbeschaffenheit (Bock 1988; Weidling und Stubbe 1998) oder Isolation (Meinig 1998 a) eine wichtige Rolle in der qualitativen und quantitativen Ausprägung einer Kleinsäugergemeinschaft. Weitere Faktoren, die für die Zusammensetzung des Fanges auf einer Fläche verantwortlich sind, ist die Emigration von selbstständig gewordenen Jungtieren auf der Suche nach eigenen Revieren und auch

Tab. 1. Verteilung der Altersklassen AK 1–4 von *S. araneus* (*ara.*) und *S. coronateus* (*cor.*). Auf den Moorstandorten (1984 und 1985) war *S. araneus* kontinuierlicher als *S. coronateus* mit allen 4 differenzierten Altersklassen vertreten. Umgekehrte Verhältnisse waren in den Fängen von an das Moor angegrenzten landwirtschaftlichen Nutzflächen (1988 und 1989) zu beobachten.

Jahr	Art	AK				AK				AK				AK				AK				AK				AK				AK				AK			
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
1984	*ara*	–	–	–	–	–	2	–	–	–	–	–	–	6	8	3	1	1	5	–	1	1	6	1	1	–	–	–	–	–	–	–	–	–	–	–	–
n = 45	*cor*	–	–	2	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	1	–	1	–	1	–	–	–	–	–	–	–	–	–	1	–	–
1985	*ara*	–	2	–	–	–	4	2	–	2	2	2	1	2	11	1	2	1	10	1	–	1	2	2	–	–	3	1	1	2	5	–	2	–	–	–	–
n = 80	*cor*	–	–	1	1	–	–	–	–	–	5	–	–	3	–	1	–	2	–	–	–	–	1	–	–	–	2	–	–	1	1	–	–	–	–	–	–
1988	*ara*	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	2	6	–	–	3	3	–	–	–	3	–	–	–	–	–	–	–	–	–	–
n = 60	*cor*	–	–	–	–	–	–	–	–	2	–	–	–	4	6	–	–	7	12	–	2	–	1	–	1	–	4	2	–	–	–	–	–	–	–	–	–
1989	*ara*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
n = 25	*cor*	–	–	–	–	–	1	1	–	-	2	–	–	5	6	–	–	3	2	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	1	1	–
Monat		März				April				Mai				Juni				Juli				August				September				Oktober				November			

das Umherstreunen älterer Tiere, die aus ihrem Revier durch ein jüngeres und/oder stärkeres Individuum verdrängt wurden.

Männliche reproduktive Tiere sind auf der Suche nach Fortpflanzungspartnern wanderfreudig. Weibliche Tiere aus dem Vorjahr besetzen dagegen stabile Reviere, teilweise verlassen sie diese jedoch, nachdem ihre Jungen selbstständig geworden sind (Angaben für *S. araneus* nach Ivanter et al. 1994). Auch durch das Fangen selbst können sich Verschiebungen in Individuenzahl und Artenzusammensetzung ergeben. Durch Fang frei gewordene Reviere können durch eine andere, die gleiche oder eine ähnliche Nische besetzende Art, okkupiert werden (vgl. Neet und Hausser 1990). Die Artenzusammensetzung einer Kleinsäugerzönose ist also nicht starr, sondern von vielen Faktoren abhängig und kann daher jahresbedingt oder saisonabhängig in gewissen Grenzen schwanken. Zur Beurteilung, ob eine ökologische Trennung der beiden konkurrierenden Arten vorliegt, ist zu berücksichtigen, daß lineare Strukturen wie Bachtäler (Ökotone, vgl. Schröpfer 1990) als Migrationswege von den Tieren genutzt werden.

Fänge aus dem Spätsommer und Herbst (Berger et al. 1992) können häufig ebenfalls kein klares Bild vermitteln. Vogel (1972) stellte für *S. araneus* eine durchschnittliche Wurfzahl von drei Würfen mit je 5,9 Jungen / Wurf fest. Zum Sommerende hin sind die Populationsdichten ausgesprochen hoch und folglich entsteht eine große Konkurrenz um neu zu besetzende Winterreviere.

Dies führt zu einer erhöhten Migration und nachfolgend großen Mortalität unter den Tieren, die kein Revier besetzen und verteidigen können (Angaben für *Sorex vagrans* und *S. obscurus* aus Hawes 1977). Untersuchungen zur ökologischen Trennung von Zwillingsarten müssen daher in Vorkommensschwerpunkten erfolgen, und in einer Jahreszeit, in der Reproduktion stattfindet und in der die territorialen Grenzen als relativ stabil angenommen werden können.

Neet und Hausser (1990) wiesen in ihrem Untersuchungsgebiet eine eng verzahnte, aber sich gegenseitig ausschließende Mikrohabitatbindung der beiden Formen nach, wobei *S. araneus* in den feuchteren Bereichen auftrat. Hausser (1978) fand isolierte Populationen von *S. araneus* inmitten von durch *S. coronatus* dominierten Bereichen. Für beide Fälle finden sich auch im Norden des gemeinsamen Verbreitungsgebietes Beispiele. Die erste Möglichkeit war im Bereich des NSG Fürstenkuhle festzustellen. Der zweite Fall war im Neandertal (Kr. Mettmann, Nordrhein-Westfalen) zu beobachten. Bei einer Langzeituntersuchung mittels Bodenfallen konnten im Tal der Düssel im Jahr 1996 kleinräumige, von der Bodenfeuchte abhängige, Schwerpunktvorkommen der beiden Arten beobachtet werden (Meinig unveröff.). Im Bereich der Mittelgebirgsschwelle des Bergischen Landes dominiert die Schabrackenspitzmaus deutlich, nur in wenigen inselhaften Populationen tritt die Waldspitzmaus auf (Meinig 1991).

Brünner und Neet (1991) fingen in der Oberrheinebene (Baden-Württemberg) *S. araneus*, an den bewaldeten Schwarzwaldhängen *S. coronatus* und schließlich auf den Schwarzwaldkuppen wieder *S. araneus*. Ähnliche parapatrische Verteilungen sind auch in Regionen anderer Mittelgebirgsschwellen nachweisbar. In der Fliedeaue (Osthessen) dominiert die Waldspitzmaus gegenüber der Schabrackenspitzmaus in den Gewöllen der Schleiereule (*Tyto alba*). Während *S. araneus* auf vielen Probeflächen nachgewiesen werden konnte, gelangen von *S. coronatus* nur wenige Fänge in einem Buchenwald in Hanglage (Meinig 1998 b). In Pieper's (1978) Material aus der gleichen Region aus Gewöllen des Waldkauzes (*Strix aluco*) überwiegt *S. coronatus*.

Im niederschlagsarmen Jahr 1989 gingen die Bestandsdichten (Anzahl Fänge / Anzahl Fangnächte × 100) im NSG Fürstenkuhle aller Kleinsäugerarten gegenüber dem Jahr 1988 von 3,6 auf 0,31 zurück. Für Wald- und Schabrackenspitzmaus war eine Abnahme von 0,89 auf 0,12 zu verzeichnen. *S. araneus* war in stärkerem Maße betroffen als *S. coronatus*. Dies stimmt mit den Beobachtungen anderer Autoren (z. B. Brünner und Neet 1991; Handwerk 1987; Hutterer und Vierhaus 1984; Kulzer et al. 1993; Meinig 1991; Neet und Hausser 1990) überein, die für *S. araneus* eine größere Toleranz gegenüber hoher Bodenfeuchte angeben. Das bedeutet andererseits, daß *S. coronatus* in weniger feuchten Habitaten Standortvorteile gegenüber *S. araneus* besitzt.

Aus dem vorliegenden Datenmaterial läßt sich ableiten, daß die Besetzung eines Habitates im hier betrachteten atlantisch geprägten Klima des nordwestdeutschen Raumes durch eine der beiden Zwillingsarten nicht starr sein muß, sondern vom Witterungsverlauf des jeweiligen Jahres abhängen kann. Die prinzipiellen Faktoren für die räumliche Separation von *S. araneus* und *S. coronatus* entsprechen auch im norddeutschen Raum denen, die aus dem Süden des gemeinsamen Verbreitungsgebietes beschrieben wurden. Die Verhältnisse können ebenfalls als parapatrisch bezeichnet werden. Wie Neet und Hausser (1990) vermuteten, sind die Übergänge zwischen den bevorzugten Mikrohabitaten aber in ebenen Landschaften nicht so abrupt wie in der Schweiz mit einem starken Oberflächenrelief.

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Zusammenfassung

Anhand von Fängen aus Bodenfallen (Amphibienlandfallen und Barberfallen) aus dem Naturschutzgebiet Fürstenkuhle (Nordrhein-Westfalen) wird die ökologische Trennung der Zwillingsarten *Sorex araneus* und *S. coronatus* im nördlichen Teil des gemeinsamen Verbreitungsgebietes untersucht. Zur Determination wurden sowohl qualitative als auch quantitative Merkmalskomplexe des Schädels herangezogen.

Die Arten zeigten in den Bereichen ihrer jeweiligen Vorkommensschwerpunkte eine unterschiedliche Kontinuität in den Fängen. Während *S. araneus* auf Flächen mit einer hohen Bodenfeuchte während der gesamten hypergäischen Aktivitätsperiode mit allen 4 unterschiedenen Altersklassen auftrat, war das Vorkommen von *S. coronatus* auf diesen Flächen diskontinuierlicher. Auf angrenzenden trockeneren Flächen waren entgegengesetzte Verhältnisse mit einer höheren Kontinuität von *S. coronatus* zu beobachten. Die Ergebnisse werden mit Befunden aus den Bereichen verschiedener Mittelgebirgsschwellen diskutiert.

Die ökologische Separation von *S. araneus* und *S. coronatus* entspricht der, wie sie auch in der Schweiz und im süddeutschen Raum festgestellt wurde. In Norddeutschland ist die ökologische Trennung bedingt durch andere topographische Verhältnisse weniger deutlich. Die Verteilung der Zwillingsarten kann auch im betrachteten geographischen Raum als parapatrisch bezeichnet werden.

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Does protection from hunting favour genetic uniformity in the red fox?

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Abstract

Allozymes and mtDNA sequences were used to assess genetic variability in six hunted and three non-hunted populations of red foxes *Vulpes vulpes* in Central Europe and the Mediterranean area. Allozyme variability was very low (P = 0.0– 4.4; He = 0.0–0.006) and significantly smaller in protected populations than in hunted ones (P = 8.9–15.6; He = 0.010–0.044). As a trend, this result was confirmed by the distribution of mtDNA variation. Differences of genetic variability were independent from sample size. Most likely, foxes evolved under predation by larger carnivores, which probably have primed the turnover of territorial reproducers. In absence of predation, hunting could superficially mimic such an effect and favour a greater genetic variability and, thus, a better viability in the red fox. This may suggest an explanation to the failure of intensive hunting campaigns as a measure to reduce strongly the population size of red foxes.

Key words: *Vulpes vulpes*, genetic variability, hunting, predation

Introduction

The social organisation of the red fox *Vulpes vulpes* (L., 1758) includes territorial individuals, who are resident and thus responsible for reproduction, as well as itinerant individuals, who are subordinate and often subadult, who may reproduce only when they replace a territorial fox (Macdonald 1980 a, 1987). In a fox population genetic variability is most likely dependent on effective population size (Ne), on frequency of replacement events in territories by itinerant individuals, and on the relatedness of the replacing individual to the group. Replacement rate should increase in populations with a high mortality rate in the adult age class, induced by predation or hunting. Several proximate evolutionary determinants may also have an effect on reproduction of red fox populations, thus presumably on their genetic structure. These include effects of mortality rate on the proportion of reproducing vixens and on litter size, as well as dispersal "sinks" (e. g. Harris and Smith 1987; Zimen 1984; Artois 1989, for a review).

Allozymes and DNA sequences are useful markers to study population genetics in mammals. Statistical indices inferred from allele frequencies at protein loci and the distribution of different mitochondrial DNA haplotypes can be used to quantify the extent of genetic variability and differentiation of natural populations. Estimates of genetic diver-

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sity can be correlated with several parameters (ecology, climate, vegetation, population density, life cycle and style), which may influence the level of variability (Nevo et al. 1984), thus providing useful suggestions for management (Moritz 1994). The organisation of mating systems (Apollonio and Hartl 1993) and other factors, e. g., replacement rate of territorial individuals where they are the only reproducers, may also influence genetic variation. In this study we examine the relationships between hunting and protection from hunting with genetic variability in red fox populations.

Material and methods

Standard allozyme and DNA analyses have been carried out on samples of liver tissue removed from foxes freshly killed by hunters in the course of occasional sampling/targeted control operations (i. e. rabies monitoring and livestock protection) and regular hunting (Tab. 1) from selected sites in Central Europe and the Mediterranean range (Fig. 1). Sampling in protected areas was limited because of ethical and legal constraints on the collection of specimens, although all sampled populations of red foxes were abundant. All samples came from adult (> 1 year old) individuals to decrease the probability of close relatedness between them. To our knowledge, no bottleneck has occurred in these populations in the last few centuries. Liver samples were preserved at –80 °C prior to analyses and used to perform an electrophoretic screening of 45 presumptive loci (Grillitsch et al. 1992; Hartl and Höger 1986). A subset of the same samples was used to extract DNA. The 5′-end of the mitochondrial Cytochrome *b* gene (Cyt *b*: 375 bp) was PCR-amplified and sequenced according to the procedure outlined in Simon et al. (1991). A detailed analysis of several statistical parameters derived from allele frequencies and from DNA sequences was obtained with the computer programs BIOSYS-1 (Swofford and Selander 1989), REAP (McElroy et al. 1992) and MEGA (Kumar et al. 1993) and was presented in Frati et al. (1998).

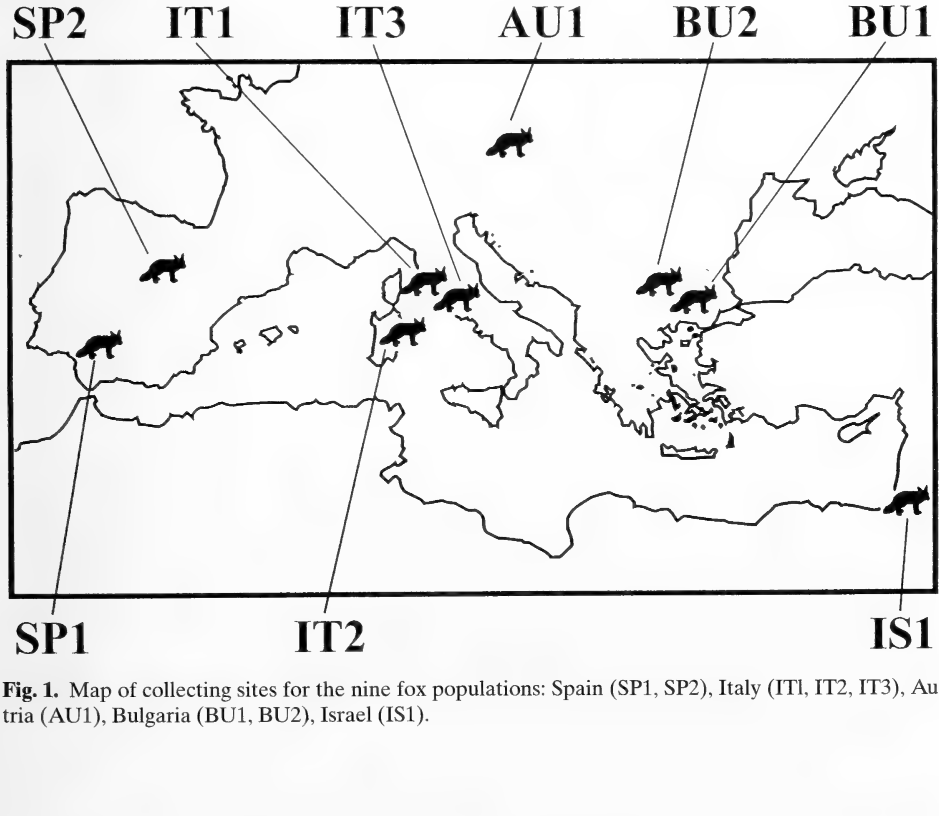

Fig. 1. Map of collecting sites for the nine fox populations: Spain (SP1, SP2), Italy (ITl, IT2, IT3), Austria (AU1), Bulgaria (BU1, BU2), Israel (IS1).

The nucleotide sequences reported in this study have been deposited in the EMBL, GenBank and DDBJ Nucleotide Sequence Databases under accession numbers Z80957-Z80984 and Z80987-Z80997 (cf. FRATI et al. 1998).

Results and discussion

Several indices of genetic variability, inferred from both allozymes and mtDNA, are shown in table 1. Red foxes in non-hunted populations showed a significantly lower level of allozyme variability than those in hunted populations (Mann-Whitney U-test, two-tailed: $U = 0.0$; $n_1 = 3$; $n_2 = 6$; $p < 0.05$, in both the proportion of polymorphic loci and heterozygosity; Tab. 1). Our results might also be a consequence of sample sizes, e. g., only a small number of family groups may have been sampled in the unhunted sites. In fact, there was a significant correlation between sample size and allozyme variability ($r = 0.68$, $df = 7$, $p < 0.05$). We reduced all sample sizes to three specimens, i. e., the smallest sample (IT3), randomly chosen within each population, to avoid partly such a correlation. In spite of this reduction (repeated three times, independently), hunted populations remained much more variable than non-hunted ones at the same level of significance and parameters as above (Tab. 1).

A relationship between hunting and the increase of genetic variability appeared to be confirmed by the two indices inferred from Cyt *b* sequence data (Tab. 1), except for the IT3 population, which showed a higher level of variability than that observed with allozymes. Sequence divergence between haplotypes ranged from 0 to 2.67% and it was maximum among specimens of the AU1 population.

Our data suggest that genetic variability in unhunted fox populations is almost absent, independently from sample size, and it is significantly lower than that in hunted populations where heterozygosity and proportion of polymorphic loci are within the range of those found amongst other wild canids (HAMILTON and KENNEDY 1986; KENNEDY et al. 1991; LORENZINI and FICO 1995). Differences in polymorphism are found not only at the population level, but also at the individual level (Tab. 1, Ho). This should rule out the possibility that a lower variability in non-hunted populations is due to sampling of related individuals.

Variability of fox behaviour and ecology is influenced by habitat structure and richness (e. g. ARTOIS 1989; LUCHERINI and LOVARI 1996; MACDONALD 1980 a). This includes aspects of the reproductive system and of spatial organisation (territory size, dispersal patterns), which in turn may influence genetic structure. The most likely factor underlying an unusually low genetic variability in a population is the local scarcity of assortative mating (CROW and KIMURA 1970). Non-territorial foxes occur in non-hunted populations (e. g. CAVALLINI and LOVARI 1994; LOVARI et al. 1994; LUCHERINI et al. 1995), but apparently they fail to reproduce. Therefore, the nomadic fraction of a fox population may not contribute to reproduction, unless territories become vacant. This effect of protection is perplexing as natural, unhunted populations should be able to maintain enough genetic variability through ecological and behavioural mechanisms.

Polygynous mating systems decrease genetic variability among ungulates, because only a few males contribute to reproduction (APOLLONIO and HARTL 1993). If foxes were polygynous, i. e. one male would reproduce with several females, this could favour the loss of genetic variability. Up to six vixens are known to share their territory with one dog fox, especially at the comparatively high density found in protected areas, with no predators, but normally only the alpha female has cubs (MACDONALD 1979; SCHANTZ 1981; ZABEL and TAGGART 1989). Therefore, little or no difference in allozyme variability can be expected between polygynous and monogamous fox populations.

There may be another explanation to the low level of genetic variability in protected fox populations. The general rule amongst canids is that "larger species dominate – or

Table 1. Estimates of genetic variability in nine populations of red foxes. Abbreviations as in fig. 1. (Compiled from Frati et al. 1998). ss: sample size, P: Percentage of polymorphic loci (99% criterion); He: Expected heterozygosity according to the Hardy-Weinberg equilibrium, Ho: Observed heterozygosity.

Sampling areas				Allozymes								mtDNA		
		complete data set				resamplings with 3 specimens								
						1		2		3				
	Hunted	ss	P	He	Ho	P	He	P	He	P	He	ss	haplotype diversity	nucleotide diversity
Doñana Natl. Park, Sevilla prov. (SP1)	NO	10	4.4	0.006	0.007	2.2	0.007	0	0.000	0	0.000	5	0.000	0.000
Maremma Reg. Park, Grosseto prov. (IT3)	NO	3	0	0.000	0.000	0	0.000	0	0.000	0	0.000	3	0.667 ± 0.314	0.733
Grofit (IS1)	NO	4	0	0.000	0.000	0	0.000	0	0.000	0	0.000	3	0.000	0.000
Valladolid province (SP2)	YES	9	8.9	0.010	0.010	6.7	0.022	4.4	0.015	2.2	0.007	3	0.667 ± 0.314	0.533
Siena province (IT1)	YES	42	15.6	0.025	0.025	4.4	0.021	4.4	0.019	13.3	0.055	9	0.694 ± 0.147	0.236
Sardinia region (IT2)	YES	19	11.1	0.044	0.026	4.4	0.024	8.9	0.043	8.9	0.039	5	0.800 ± 0.164	0.380
Tullner Feld, Lower Austria (AU1)	YES	8	11.1	0.033	0.025	6.7	0.027	4.4	0.024	2.2	0.016	6	0.933 ± 0.122	1.427
Vitocha (BU1)	YES	17	13.3	0.036	0.021	8.9	0.030	8.9	0.039	4.4	0.019	2	1.000 ± 0.500	0.800
Rila (BU2)	YES	6	8.9	0.031	0.028	8.9	0.043	8.9	0.038	8.9	0.039	3	0.667 ± 0.314	0.733

even kill – smaller ones" (Macdonald 1992: 90). This has been reported for, e. g., wolves and coyotes (Carbyn 1982; Fuller and Keith 1981), coyotes and red foxes (Dekker 1983; Major and Sherburne 1987; Voigt and Earle 1983; but see also Gese et al. 1996), red and arctic foxes (Bailey 1992; Frafjord et al. 1989; Hersteinsson and Macdonald 1992; Rudzinski et al. 1982), coyotes and kit foxes (Ralls and White 1995; White et al. 1994). Most likely, if the red fox evolved under the pressure of a community of larger predators such as other canids as well as felids, e. g., cougar and leopard (Cavallini 1996), this may have strongly influenced the development of its great biological flexibility and resilience (Nowak 1991). The only larger canid in southern Europe is the wolf, which is known to feed on foxes on occasion (Matteucci 1992; Meriggi et al. 1991). Presently, predation pressure by the wolf on foxes is likely to be small in most of Europe, as the wolf is an endangered species while the red fox is one of the most successful mammals in terms of numbers and range width. The Iberian lynx *Lynx pardinus* occurs in one (SP1) of the protected areas of our sample, but it is rare and unlikely to prey on red foxes because of its small size (Rau et al. 1985). No wolves – or any other larger predator – have occurred in our other protected sampling areas for at least a few decades. The lack of natural predators may result in relatively stagnant fox populations, where the same individual could successfully defend a territory for several years. This may prevent a frequent turnover of reproducers over several years, eventually leading to a decrease of genetic variability. In polygynous groups of red foxes, vixens are closely related, often mothers (the alpha female) and daughters (Macdonald 1979; Schantz 1981). If the alpha female dies, one of the "helpers" will replace her as reproducer (Macdonald 1987). Thus, some inbreeding can be expected. The occurrence of protected areas, devoid of larger predators, is a very recent event in fox evolution. No equally effective, alternative process to predation may have yet been developed in red foxes to favour genetic variability.

Hunting may increase genetic variability in fox populations by partly mimicking the effects of natural predation with which foxes have probably evolved. A high genetic variability in a population is believed to enhance its viability (Allendorf and Leary 1986; Lacy 1997, for a review). If our hypothesis is correct, this may suggest one important reason why persecution campaigns or intensive hunting have never succeeded to eradicate foxes from large areas, e. g., for rabies control in Europe (Macdonald 1980 b, for a review). In this connection, the ecological adaptability of a generalist species, such as the red fox, should also not be underestimated.

On the other hand, hunting alone is unlikely to be a valid replacement for natural predation. Long-lasting hunting practices can alter the genetic structure of mammalian populations, often acting in an anti-Darwinian sense (Hartl et al. 1991; Hartl et al. 1995; Ryman et al. 1981; Scribner et al. 1985), thus being poor substitutes of natural predation. We wish to stress that our results need confirmation from larger samples and from observational data of territory turnover in areas where a community of predators of foxes does and does not occur. If hunting is in principle an acceptable activity, there is no reason not to admit it for red foxes. Conversely, our data must not be used to justify intensive hunting or persecution campaigns, which are quite a different, controversial issue on biological and ethical grounds, beyond the scope of this paper.

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Zusammenfassung

Trägt die jagdliche Schonung zur genetischen Einförmigkeit beim Rotfuchs bei?

Mittels Allozymelektrophorese und mtDNA-Sequenzierungen wurde die genetische Variabilität von sechs bejagten und drei nicht bejagten Populationen des Rotfuchses *Vulpes vulpes* in Mitteleuropa und in mediterranen Gebieten untersucht. Die genetische Variabilität war deutlich geringer in den nicht bejagten (P = 0,0–4,4; He = 0,0–0,006) als in den bejagten (P = 8,9–15,6; He = 0,010–0,044) Populationen. Die mtDNA (Cyt *b*)-Sequenzen zeigten denselben Trend. Diese Ergebnisse werden wie folgt interpretiert: Wahrscheinlich entwickelte sich der Fuchs im Laufe seiner Stammesgeschichte unter dem Druck von größeren Predatoren, die im territorialen Fortpflanzungsgefüge einer Fuchspopulation eine gewisse Durchmischung bewirkten. In Abwesenheit dieser Räuber wurde derselbe Effekt möglicherweise durch die Jagd hervorgerufen und so eine größere genetische Variation und damit Überlebensfähigkeit bewahrt. Dies mag eine Ursache dafür sein, daß intensiver Jagddruck bisher nicht zu einer bedeutenden Reduktion von Fuchsbeständen geführt hat.

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Morphometric and chromosomal variation in populations of *Oryzomys albigularis* (Muridae: Sigmodontinae) from Venezuela: multivariate aspects

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Abstract

The composite nature of the species *Oryzomys albigularis* Tomes, 1860 has long been recognized from the karyological heterogeneity of diploid and fundamental numbers, with at least two sets of populations in the eastern and northern Andes with 2n = 66 and 2n = 80, respectively. The aim of this study was to test for differences among populations within the species using cranial morphometrics. Populations for the multivariate analyses were defined according to differences in autosomal arm numbers within a single modal diploid number from six locations in two mountain systems of Venezuela, in northern South America. Principal component and canonical variate analyses clearly discriminated among the karyomorphs, the variation at the interorbital, palatal, and incisive foramen regions being the most informative. These traits explained most of the total variance, after adjusting for size effects. We found no evidence for congruence between the patterns of morphometric variation and geographical distance among karyomorphs, but similarity patterns among samples resulted in congruence when morphometric and karyological data were considered. Since variation of these last two datasets can be considered independent of each other, the observed congruence is suggestive of a phylogenetic structure in the data. Our results are consistent with a composite nature for the species, as most of the observed cranial variation appears to be associated with major karyotypic differences. Given the theoretical relevance of the implied karyotypic changes as a means of reproductive isolation, morphometric evidence is used to support the splitting of the "*albigularis*" form in at least two distinct species.

Key words: *Oryzomys albigularis*, morphometrics, karyosystematics, congruence, composite species

Introduction

A major issue in Rodent systematics has been the instability of the taxonomy of the South American cricetids, or Sigmodontinae. Although there is a moderate level of agreement in the definition of genera and subgenera, this is not so at the specific or subspecific levels (Reig 1986). The genus *Oryzomys* Baird, 1858 exemplifies much of the observed taxonomic confusion, being one of the most diverse genera in the family (Musser and Carleton 1993). Its widespread geographical distribution covers locations in North America, Central America, and northern through southeastern South America (Musser and Carleton 1993). Several authors have recognized the need for more detailed systematic studies within this genus (Honacki et al. 1982; Musser and Carleton 1993).

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Most of the revisions of the species *Oryzomys albigularis* Tomes, 1860 do not agree at the subspecific level. Tate (1932) recognized two subspecies, *albigularis* and *moerex* Thomas, 1914, both from Ecuador, whereas Gyldenstolpe (1932) and Ellerman (1941) included also *maculiventer* Allen, 1899, with the type locality in northern Colombia. Cabrera (1961) included 11 subspecies, while Hershkovitz (1966) used the phallic morphology to include two subspecies previously defined as *O. devius* Bangs, 1902. More recently, Honacki et al. (1982) excluded two subspecies, while Musser and Carleton (1993) listed as synonyms the subspecific names *caracolus* Thomas, 1914, *childi* Thomas, 1895, *maculiventer*, *moerex*, *meridensis* Thomas, 1894, *oconnelli* Allen, 1913, *pectoralis* Allen, 1912, *pirrensis* Goldman, 1913, and *villosus* Allen, 1899. The current *O. albigularis* includes populations from eastern Panama through northern Peru; the holotype is from the Chimborazo Province in Ecuador (Patallanga, 1 509 m, Musser and Carleton 1993).

Gardner and Patton (1976) first recognized the composite nature of the species based on the karyological evidence. They found Andean populations with different diploid numbers (2n = 88 and 66 from Peru, and Colombia and Venezuela, respectively), and they suggested to keep *albigularis* for the 2n = 66 populations. Working with populations from Venezuela, Aguilera et al. (1995) recently found further support for the supraspecific nature of *O. albigularis.* They found differences in the number of autosomal arms or fundamental number (FN) and in the morphology of the sexual pair among several populations from two main mountain systems in the country (Fig. 1). G banding was used to support the status of reproductive isolation between the populations with the extreme FN 90 and 104. Differences in 7 out of 33 chromosome pairs resulted from pericentric inversions. These rearrangements are currently considered as causing hybrid sterility, i. e. postmating reproductive isolation (King 1993). Thus, Aguilera et al. (1995) suggested to keep *O. caracolus* and *O. meridensis* for the populations with FN = 90 and 104, respectively, while a third population with FN = 92 was provisionally assigned to *Oryzomys* sp.

In this study, we use multivariate morphometrics to analyse the cranial variation of the karyomorphs defined by Aguilera et al. (1995). Our aim is to assess the morphological evidence associated to the variation of the "*Oryzomys albigularis* complex", as given by the karyological results. A detailed description of the morphological variants is accomplished through the interpretation of multivariate results.

The joint interpretation of the variation patterns showed by independent data sets from the same populations may reveal important information for inferring the relationships among these populations. We compare karyotype (Aguilera et al. 1995; Gardner and Patton 1976) and morphometric similarity patterns among *O. albigularis* populations to study the extent of congruence between these independent datasets.

Material and methods

Population sample

Samples were assembled to represent karyomorphs, and thus individuals were sorted out by their karyotypes. However, sample size limitations led us to pool several localities for some karyomorphs, whereas some were represented by a single locality. Five samples were defined altogether, comprising several localities in Venezuela (Fig. 1):

Avi: El Ávila National Park, Distrito Federal (6 females, 14 males, and 1 of unknown sex); FN = 90; 1 470 m asl. Approx. 10°33′ N, 66°52′ W.

Mac: Macarao National Park and surroundings, Miranda y Aragua states (1 female, 13 males); FN = 90; 1 845 m asl. Approx. 10°25′ N, 67°17′ W.

HPi: Henri Pittier National Park, Aragua state (28 females, 54 males, and 1 of unknown sex); FN = 90; 1 280 m asl. Approx. 10°21′ N, 67°40′ W.

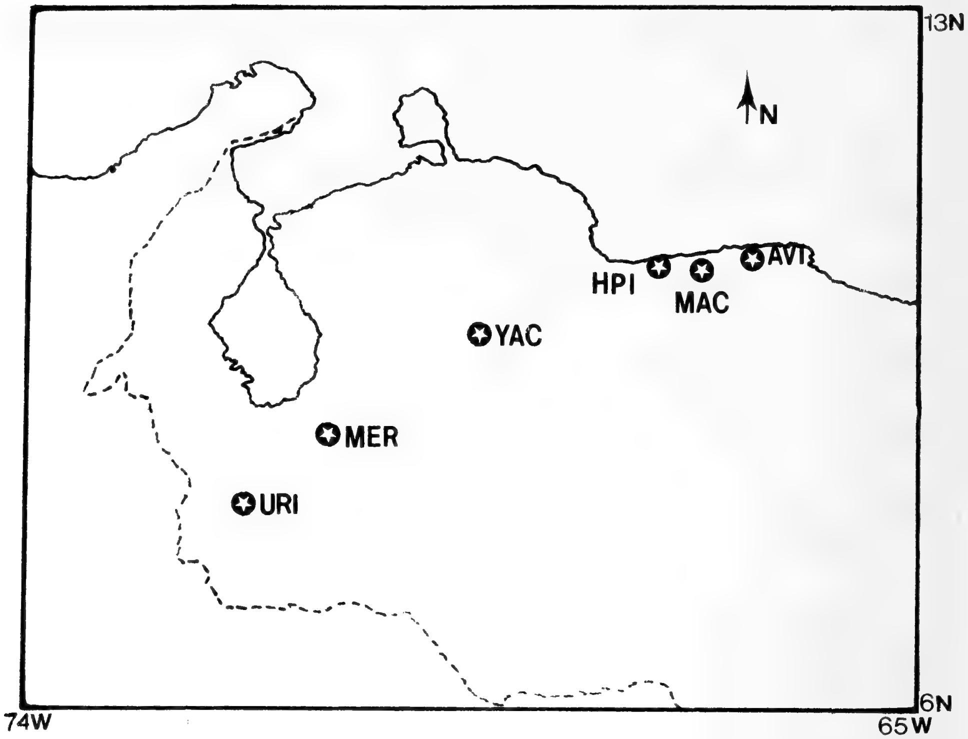

Fig. 1. Map showing the *Oryzomys albigularis* population sample locations in the present study. Morphometric samples: Avi: El Ávila N. P., HPi: Rancho Grande Henri Pittier N. P., Mac: Macarao N. P., Yac: Yacambú N. P., Mer: Monte Zerpa, and Uri: La Trampita. Avi, HPi, and Mac represent karyomorphs with FN = 90, Yac and Mer, karyomorphs with FN = 104, and Uri, the karyomorph with FN = 92. Modified from Aguilera et al. (1995).

Mer: Monte Zerpa, Mérida state, and related localities (5 females, 15 males); FN = 104, X chromosome metacentric; 2 140 m asl. Approx. 9°21′ N, 70°18′ W.

Yac: Yacambú National Park, Lara state (18 females, 33 males); FN = 104, X chromosome acrocentric; 1 645 m asl. Approx. 9°40′ N, 69°37′ W.

Uri: La Trampita, Siberia, sector Uribante, Táchira state (7 females, 6 males); FN = 92; 1 100 m asl. Approx. 7°50′ N, 71°57′ W.

Sex, general body measurements, taxonomic status, and locality were read from the museum labels.

Measurements

Criteria for the selection of multivariate morphometric characters can be found elsewhere (Steppan 1997 a; Voss 1988). These criteria include: homology of landmarks across individuals; uniform bone sampling; preference of measurements on single bones and avoidance of redundancy; and non-coincidence of end landmarks over two or more measurements. We selected 21 cranial and 3 mandible measurements to match those criteria where possible (Tab. 1), but we chose some that might aid comparisons with other studies. An additional consideration was to maximize the sample size, since in a considerable portion of the material several traits were missing. All measurements were taken using a Digimatic caliper Mitutoyo (MTI Corp., Aurora IL, USA) to the next 0.01 mm. In order to reduce the sampling errors due to cranial asymmetries, measurements on symmetric duplicated structures were taken twice on each specimen, and we used the mean in statistical analyses.

Table 1. Description of the measurements taken from the *Oryzomys albigularis* skulls.

Name of variable, Acronym		Description
Total length of skull	TL	From the most anterior portion of nasal to posterior-most portion of occipital
Nasal length	NL	From anterior-most to posterior-most portions of nasals
Nasal-maxillary suture length	NMSL	Limited by both extreme points at the dorsally posterior-most portions of nasals
Least interorbital breadth	LIB	Least distance among the orbits in dorsal surface
Fronto-parietal suture length	FPSL	Dorsal distance of suture among parietal and temporal bones
Maximum breadth of braincase	MB	Greatest width of skull, among temporal bones
Maximum rostral height	MRH	Greatest height of rostrum, among frontal bones and parapterigoid plates
Braincase height	BH	Greatest height of skull, among parietal and basisphenoid bones
Basilar length	BL	From posterior-most edge of incisive alveoli to anterior-most edge of foramen magnum
Upper alveolar length	UAL	Greatest length of the upper molar alveolus
Length of palate bone	PBL	From posterior-most margin of maxillary to posterior-most margin of palate
Breadth of palate bone	PBB	Limited by both lingual alveolar margins
Palatilar length	PL	From posterior edge of incisive alveolus to posterior-most margin of palate
Upper diastema length	UDL	From posterior edge of incisive alveolus to anterior edge of molar alveolus
Premaxillary-maxillary suture length	PMSL	Ventral distance along posterior-most margin of premaxillary
Incisive foramen breadth	IFB	Distance at the middle of both incisive foramina
Incisive foramen length	IFL	From anterior-most to posterior-most margins of incisive foramina
Tympanic bulla length	TBL	Greatest distance along the meatus-bullar tube axis of tympanic bulla
Tympanic bulla breadth	TBB	Greatest distance perpendicular to the meatus-bullar tube axis of tympanic bulla
Incisive-maxillary length	IML	Lateral distance between anterior-most incisive edge of premaxillary and posterior-most margin of capsular projection for upper incisive
Incisive-zygomatic length	IZL	From incisive edge of premaxillary to posterior-most portion of zygomatic arch
Mandible length	ML	Greatest length of mandible, excluding incisive teeth
Mandibular diastema length	MDL	From posterior edge of lower incisive alveolus to anterior edge of lower molar alveolus
Lower alveolar length	LAL	Greatest length of mandible molar alveolus

Age criteria

A common problem when defining age classes is to find an age criterion that applies to all of the samples. Size and weight are poor age indices across several independent populations, because the variation in these parameters may be a result of evolutionary divergence. On the other hand, molar toothwear criteria do not necessarily relate to developmental events (e. g. weaning, sexual maturity). These events are the obvious choices to define age classes independently in populations, but they are usually not available for collection-based surveys.

In order to define the age classes, we devised a method that incorporates developmental and toothwear information. Starting from a sample of 41 individuals that were brought alive from the Yacambú N. P. (Yac) and reared under laboratory conditions (R. MOSCARELLA, unpubl. data), each specimen was labelled as immature or mature, depending upon the developmental stage of its genitalia (vagina open or closed, testes descended or not). A "juvenile" stage was defined when all the individuals were immature, and an "adult" stage when all were mature animals. The intermediate stage was defined as "sub-adult". Sexes were pooled since no differences were detected between them before adulthood. The end points of weight and body length of each stage were recorded, and then used to classify a sample of 51 museum specimens from the same locality whose skulls were available. For each specimen, molar toothwear was observed and related to the corresponding stage. We employed the resulting descriptions as the criteria for classifying the individuals from the remaining populations. The three defined age classes were characterized as follows:

Juveniles: upper M3 unerupted or partially erupted; incipient wear of all molars.

Sub-adults: occlusal surface of upper M3 with intermediate wear. Labial cusps of upper M1 slightly worn. Lingual cusps of upper M1–M2 partially worn.

Adults: upper M3 totally worn. Labial cusps of upper M1 with intermediate to advanced wear. Lingual cusps of upper M1–M2 with intermediate to advanced wear. This class includes senile individuals, which had lost most of their enamel components.

As all toothwear-based age criteria, this method assumes a monotonic wear of the enamel components of the molar teeth, which is also positively correlated with time (Voss et al. 1990). Since the method involves schedules of events related to the development, the homogeneity of these schedules throughout the populations is also assumed.

Sex dimorphism

A population by sex two-way Type I analysis of variance (ANOVA) was performed on each measurement, excluding specimens with unknown sex and those from Macarao N. P., where only one female was available. The significance of interactions was taken as evidence of sexual dimorphism, which led us to perform separate analysis with each sex.

Analysis of geographic variation

Evolutionary divergence and ontogenetic variation are usually taken as the main sources of variation of measurement data between and within populations, respectively. In order to minimize the ontogenetic component of the variation, we used only adult specimens in the morphometric analyses. However, allometric variation may be expected to remain in an adult sample (PATTON and ROGERS 1983). There are several commonly used methods for excluding this effect from the data. In the present study, the preferred method was the shearing of principal components (HUMPRIES et al. 1981; ROHLF and BOOKSTEIN 1987), which is based on an explicit causal model of the covariation among characters.

We used multivariate techniques to evaluate the extent of differentiation among population samples. A covariance matrix was constructed by pooling the log-transformed data from the six samples, and principal components were extracted. Resulting eigenvectors were employed to interpret the patterns of among-sample variation. To study the degree of support of the observed eigenstructure to the hypothesis of differentiation between the karyomorphs, we performed univariate analyses of variance (ANOVA) on the principal component scores. Multiple comparisons among pairs of samples were performed by using GT2 tests at a level of significance of $\alpha = 0.05$ (SOKAL and ROHLF 1995). According to the aims of our study, only those components that showed significant between-sample differences were taken into account for interpretation.

We estimated the standard errors of eigenvalues as the standard deviations of $n = 1\,000$ bootstrap replicates of the log-transformed data (KLINGENBERG 1996). In order to support the interpretation of a principal component, its associated variance must not represent merely measurement error (ANDERSON 1963). Given that this error is supposed to be the same for all measurements, ANDERSON (1963) provided a criterion to test for the equality of the last q_r eigenvalues. We applied this criterion to the principal component analysis results to support the choice of components to be interpreted.

Canonical structure of between-group data was further examined using canonical variate analysis, and a discriminant function was extracted to verify the percentages of correct re-substitution classification of specimens. These analyses were performed based on the initial 24 measurements, and also removing specific ones, which were shown as the dominant sources of between-sample variation by previous analyses. The purpose of these extra analyses was to assess the degree of generalization supported by the data to the observed differentiation of the karyomorphs.

In order to check the adequacy of the least sample sizes employed in the present study (Mac and Uri samples), we compared the re-substitution classification of those specimens with the results of a cross-validation procedure. Unlike re-substitution, the linear discriminant function employed in cross-validation for classifying each specimen is estimated from the data after excluding this individual. Although a slight increase of error rates can be expected, it should not affect overall results if sample sizes are representative of population variability.

Statistical analyses were performed on the Version 6.08 for the PC of the Statistical Analysis System (SAS Institute 1993). Computational tasks were programmed using combinations of procedures IML, CANDISC, DISCRIM, GLM, and others. The program for shearing was based on Rohlf and Bookstein (1987) algorithm.

Results

Sex dimorphism

Analyses of variance showed all measurements to have a highly significant population effect, whereas most characters did not evince a significant sex effect. Only the maximum rostral height and the braincase height showed the sex effect to be marginally significant at a level of $\alpha = 0.05$. The interaction effect resulted significantly only in three measurements (total length, and upper and lower alveolar length), but two of them had P-values above 0.04. These differences were not considered sufficient to separate sexes in multivariate analyses. Sex dimorphism usually is not detected in morphometric studies with sigmodontine rodents (Voss et al. 1990). The differences observed in the present study may reflect a slight body size dimorphism, which has been previously detected in adults of *O. albigularis* raised under laboratory conditions (R. Moscarella, unpubl. data).

Analysis of geographic variation

Univariate statistics calculated for the population samples (Tab. 2) show a roughly consistent pattern of between-measurement variation across the samples. Means and standard deviations are correlated in all cases, but are not correlated to coefficients of variation. It can be noted that measurements with the highest coefficients of variation are located on the interorbital, palatal, and sub-facial regions, whereas upper and lower alveolar length, and neurocranial measurements bear the lowest ones. Facial skull and total length measurements show intermediate values.

Eigenvalues of the total-sample principal component analysis (Tab. 4) demonstrate the first axis to account for 39–44% of the total variance. Ten axes were needed to extract 90% of the total variance. However, the first three axes attain a 69%, whereas the fourth falls to 4%, then decreasing steadily.

Principal components above the first were sheared for removing the common within-sample allometric variation from the total-sample covariance matrix. The first principal component of the pooled within-group covariance matrix (W1) was taken as the best representation of this common latent factor, sometimes regarded as size.

When contrasted with the first principal component of the total-sample covariance matrix (PC1; Tab. 3), the W1 coefficients of measurements situated on localized cranial regions have lower values, whereas measurements on the facial and neural regions and total-length measurements (total skull and basilar length) have consistently higher values. On the other hand, a comparison between the sheared (H2; Tab. 3) and non-sheared (PC2) second principal components shows the former to have lower coefficients for measurements that are often related to allometric variation (e. g. nasal length, maximum rostral height, basilar length, mandibular diastema length). Thus, W1 appears to be a good choice for representing a common size factor.

Table 2. Univariate statistics for the six population samples of *Oryzomys albigularis* analysed in this study. For each sample, first columns are means in mm, second columns are standard deviations, and third columns are coefficients of variation. See Tab. 1 for character acronyms. Avi: El Ávila N. P.; HPi: Rancho Grande, Henri Pittier N. P.; Mac: Macarao N. P.; Mer: Monte Zerpa; Uri: La Trampita; Yac: Yacambú N. P.

Variables	Population Samples																	
	Avi			HPi			Mac			Mer			Uri			Yac		
TL	34.2	1.63	4.77	35.5	1.14	3.21	35.1	1.10	3.14	35	1.37	3.92	35.3	1.15	3.27	34.2	0.86	2.52
NL	13.2	1.04	7.87	13.5	0.70	5.20	13.5	0.45	3.34	13.2	0.69	5.25	13.5	0.82	6.07	12.8	0.56	4.37
NMSL	7.3	0.46	6.24	7.8	0.38	4.93	7.4	0.39	5.25	7.5	0.35	4.72	7.7	0.37	4.85	7.5	0.36	4.82
LIB	4.9	0.25	5.20	5.2	0.27	5.18	5	0.27	5.29	4.7	0.36	7.64	5.2	0.19	3.56	4.8	0.28	5.72
FPSL	6.2	0.51	8.17	6.5	0.48	7.37	6.3	0.40	6.26	5.1	0.44	8.50	6.2	0.34	5.56	5.4	0.38	6.96
MBB	13.6	0.39	2.87	13.9	0.36	2.63	13.9	0.39	2.79	14	0.37	2.66	13.6	0.24	1.72	13.9	0.31	2.24
MRH	8.2	0.52	6.37	8.7	0.36	4.16	8.6	0.23	2.69	8.5	0.40	4.66	8.6	0.45	5.16	8.5	0.27	3.13
BH	10	0.32	3.20	10.49	0.34	3.29	10.26	0.34	3.29	10.39	0.32	3.07	10.46	0.37	3.54	10.30	0.26	2.48
BL	26.2	1.30	4.95	27.2	1.02	3.74	26.7	0.95	3.55	26.9	1.12	4.18	27.3	1.07	3.93	26.4	0.82	3.09
UAL	5.6	0.20	3.54	5.7	0.19	3.28	5.8	0.19	3.24	5.7	0.25	4.43	5.6	0.23	4.10	5.4	0.15	2.81
PBL	6.4	0.39	6.10	6.7	0.39	5.82	6.7	0.34	5.05	7.1	0.37	5.25	6.4	0.30	4.60	6.7	0.34	4.99
PBB	1.9	0.16	8.36	1.9	0.15	7.72	2	0.11	5.26	1.8	0.12	6.40	2	0.14	7.08	1.7	0.14	7.85
PL	14.1	0.69	4.87	14.6	0.53	3.66	14.3	0.59	4.11	14.7	0.78	5.26	14.4	0.49	3.42	14.3	0.51	3.56
UDL	9.2	0.58	6.30	9.5	0.50	5.25	9.4	0.34	3.61	9.4	0.57	6.11	9.5	0.47	5.00	9.1	0.35	3.87
PMSL	5.5	0.41	7.47	5.8	0.27	4.74	5.7	0.51	8.89	5.4	0.22	4.12	5.6	0.27	4.85	5.5	0.24	4.32
IFB	2.5	0.15	5.96	2.4	0.17	7.07	2.5	0.12	4.70	2.3	0.18	7.74	2.6	0.21	8.26	2.3	0.17	7.46
IFL	6.1	0.43	7.11	6.1	0.37	6.09	6	0.50	8.27	5.6	0.35	6.21	6	0.34	5.63	5.4	0.37	6.73
TBL	6.9	0.34	4.91	7.2	0.44	6.11	7	0.38	5.50	7.1	0.29	4.12	7.2	0.25	3.55	7	0.25	3.63
TBB	5	0.18	3.53	5.2	0.18	3.40	5.1	0.17	3.33	5.2	0.18	3.46	5.4	0.13	2.50	5.1	0.16	3.07
IML	6.2	0.60	9.71	6.7	0.48	7.14	6.5	0.42	6.39	6.3	0.38	5.97	6.7	0.42	6.19	6.2	0.29	4.71
IZL	23	1.15	5.02	24	0.92	3.84	23.5	0.88	3.74	23	1.01	4.39	23	0.90	3.93	22.6	0.50	2.22
ML	17.3	0.81	4.67	18	0.72	4.02	17.6	0.63	3.59	17.7	0.54	3.05	18	0.68	3.77	17.7	0.59	3.31
MDL	4.5	0.31	6.90	4.6	0.33	7.11	4.5	0.32	7.23	4.5	0.28	6.29	4.6	0.28	5.98	4.4	0.25	5.57
LAL	5.7	0.18	3.22	5.8	0.20	3.43	5.8	0.23	4.05	5.8	0.23	3.96	5.7	0.24	4.20	5.5	0.19	3.43

The main between-sample differentiation is obtained with the H2 scores by itself (Fig. 3 b), whereas both the first and second non-sheared principal components are required to depict this pattern (Fig. 2), possibly indicating the presence of size-related variation in the non-sheared vectors.

The arrangement of specimens on the ordination plots (Figs. 2, 3 b) displays the formation of two clusters, including the Avi, HPi, Mac, and Uri samples, and the Mer and Yac samples, respectively. While the former includes individuals from three coast cordillera

Table 3. Measurement coefficients of the first principal component of the pooled within-group covariance matrix (W1), first and second principal components (PC1 and PC2, respectively) and first principal component (H2) of the sheared total-sample covariance matrix. See Tab. 1 for character acronyms.

Character	W1	PC1	PC2	H2	Character	W1	PC1	PC2	H2
TL	0.196	0.167	0.117	0.035	PL	0.215	0.144	0.188	0.103
NL	0.265	0.226	0.147	0.038	UDL	0.283	0.218	0.184	0.072
NMSL	0.185	0.186	0.034	–0.042	PMSL	0.244	0.231	0.086	–0.014
LIB	0.082	0.196	–0.256	–0.287	IFB	0.257	0.237	0.003	–0.086
FPSL	0.034	0.367	–0.735	–0.750	IFL	0.276	0.331	–0.069	–0.182
MBB	0.064	0.039	0.053	0.030	TBL	0.158	0.135	0.108	0.039
MRH	0.234	0.182	0.152	0.059	TBB	0.102	0.078	0.106	0.060
BH	0.104	0.076	0.087	0.044	IML	0.345	0.309	0.180	0.034
BL	0.223	0.174	0.151	0.061	IZL	0.216	0.206	0.082	–0.009
UAL	0.073	0.113	–0.006	–0.047	ML	0.193	0.144	0.142	0.065
PBL	0.176	0.063	0.293	0.221	MDL	0.281	0.221	0.184	0.071
PBB	0.213	0.316	–0.133	–0.229	LAL	0.060	0.088	0.003	–0.031

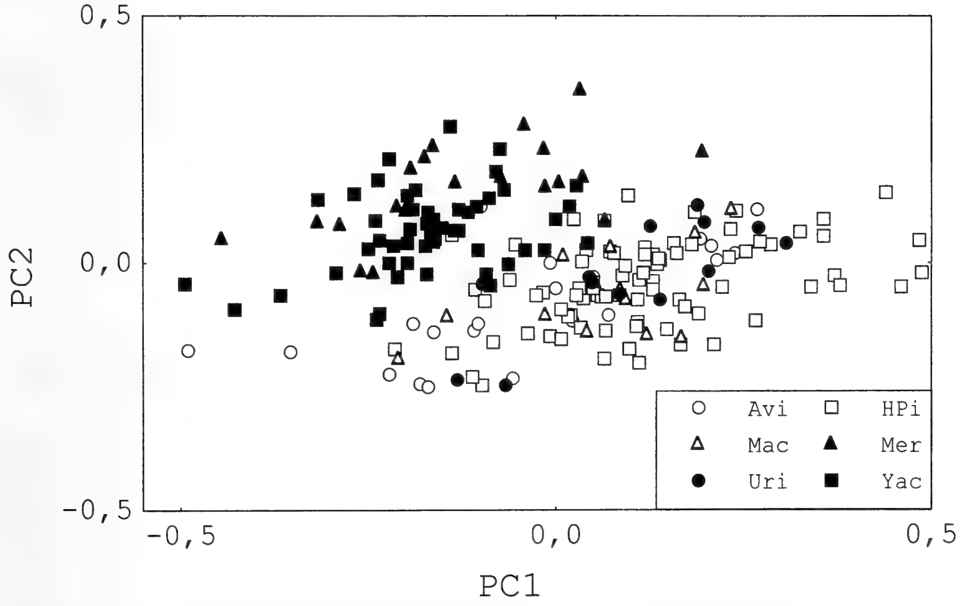

Fig. 2. Scores for the *Oryzomys albigularis* individuals from the six population samples on the first and second principal component of the total covariance matrix. Open marks represent samples from the coastal cordillera, and closed ones from the Andean cordillera.

and one Andean cordillera populations, the latter only incorporates specimens from Andean populations. The respective FNs (Fig. 1) are 90, 90, 90, 92, 104 and 104. Thus, it is evident that some extent of correspondence exists between morphometric variation and karyomorph similarity patterns, irrespective of the geographical location of the samples. The eigenvector coefficients (Tab. 3) of the axes that best represent this pattern demonstrate that contrasts among measurements located on the interorbital, palatal, and incisive foramen regions are the responsible ones for the karyomorph separation. Specimens with FN = 104 seem to have a long and narrow palate bone, whereas the coastal and Uri specimens seem to have wider interorbital bones. There seems to be a slight difference between samples, related to the length of incisive foramen, which covaries positively with the interorbital region, and negatively with the length of the palate bone.

Analyses of variance on the specimen scores resulted in significant between-population mean differences ($\alpha = 0.05$) in 1st through 5th, 7th, 8th, 10th, 11th, and 14th principal components (Tab. 4). Application of the ANDERSON's (1963) criterion to test for the differences of 14th through 24th eigenvalues produced significant results ($X^2 = 473.26$, d. f. = 65); thus the remaining eigenvalues (1st through 13th) are considered relevant for interpretation.

Vectors W1 and H2 were used instead of PC1 and PC2 for projecting the morphometric data, since the latter are probably confounding size and size-independent variation. GT2 test on W1 scores (ANOVA $F = 14.47$, $P < 0.001$) arranged four overlapped groups, with the HPi and Mac samples in the upper extreme, and the Avi and Yac samples in the lower one (Fig. 3 a). This result could be revealing an East-West size gradient along the coastal cordillera populations.

Application of the GT2 test on the H2 scores (ANOVA $F = 87.95$, $P < 0.001$) confirmed the pattern depicted by the plots (Fig. 3 b). Analysis of the scores of principal components above the second, further discriminated the samples initially grouped in two clusters. Sample 95% confidence intervals of third principal component scores seemed to

Table 4. Eigenvalues (and SE) of the first 14 principal components of the total-sample covariance matrix, cumulative variance extracted, and results from the ANOVA on principal component scores to test for population effects. Eigenvalues and their SE are multiplied by 100. Standard errors calculated as bootstrap standard deviations with n = 1 000 replicates.

Principal Component	Eigenvalue	% Cumulative variance
1***	3.533 (0.350)	41.78 (2.49)
2***	1.337 (0.128)	57.59 (1.81)
3***	0.929 (0.089)	68.58 (1.61)
4***	0.417 (0.036)	73.51 (1.38)
5***	0.350 (0.027)	77.65 (1.16)
6	0.285 (0.023)	81.01 (0.96)
7*	0.242 (0.019)	83.87 (0.80)
8***	0.211 (0.015)	86.37 (0.66)
9	0.207 (0.014)	88.81 (0.54)
10**	0.151 (0.011)	90.60 (0.45)
11***	0.139 (0.009)	92.24 (0.37)
12	0.134 (0.008)	93.82 (0.30)
13	0.104 (0.007)	95.06 (0.25)
14**	0.090 (0.006)	96.12 (0.21)
Total variance	8.458 (0.408)	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

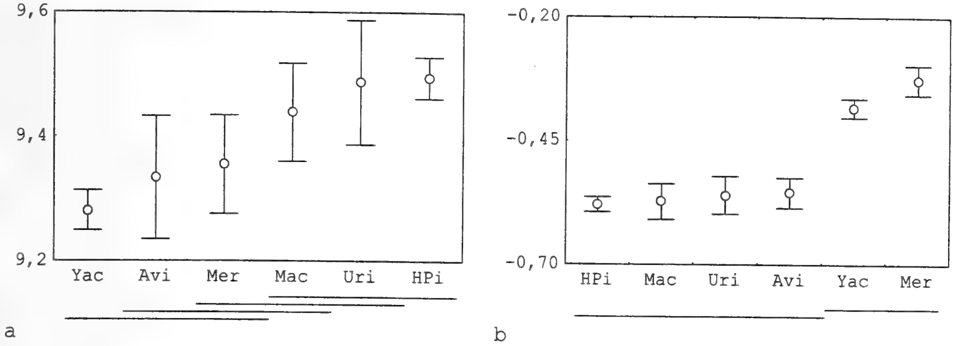

Fig. 3. Sample means and 95% confidence intervals of the scores of *Oryzomys albigularis* log-transformed data projected on the (a) first eigenvector of the pooled within-group covariance matrix, and (b) first eigenvector of the sheared total-sample covariance matrix. Lines under plots represent results of multiple comparison tests (GT2) to test for mean differences among samples.

differentiate the HPi sample from the Mac, Avi, and Uri ones, but the GT2 test did not support these observations. Eigenvector coefficients of the third axis (11% of total variance) contrasted the length of palate bone and interorbital measurements, with the length and breadth of the incisive foramen and breadth of the palate bone. Tests of between-sample differences and observations of the confidence intervals supported the discrimination of the Yac and Mer samples on the eighth axis (2.5% of total variance), due to a contrast between the alveolar, palate, and tympanic bulla lengths. On the other hand, Uri is not separated from the coastal samples until the 11th principal component (1.6% of total variance). The remaining significant principal components showed no further differentiation of the groups of karyomorphs evinced in the second sheared principal component.

Mahalanobis distances among karyomorphs showed the same similarity pattern described by previous analyses (Tab. 5). The coastal cordillera samples yielded the least D values, which were correlated with geographic distance; the Yac and Mer D value was also low. Mahalanobis distances between Uri and remaining samples were intermediate; however, these specimens were closer to coastal samples than to Andean ones. Hotelling T^2 tests significantly differentiated almost every pair of samples. Only the Avi-Mac distance resulted in a non-significant P value at $\alpha = 0.05$. When the significance value was adjusted for 15 non-independent comparisons (Dunn-Šidák $\alpha' = 0.0034$), the HPi-Mac distance was non-significant as well.

Table 5. Mahalanobis distances (above diagonal) among the six population samples of *Oryzomys albigularis*, and F-values of the Hotelling's T^2 statistic for pairwise comparisons of centroids (below diagonal). See text for population acronyms.

Samples	Avi	HPi	Mac	Mer	Uri	Yac
Avi		2.41	2.25	4.92	4.41	4.80
HPi	3.58***		2.06	4.77	3.69	4.40
Mac	1.57	1.87*		4.89	4.20	4.96
Mer	9.11***	13.49***	7.25***		5.37	2.70
Uri	5.74***	5.62***	4.38***	8.36***		4.71
Yac	12.60***	22.51***	9.96***	3.85***	8.45***	

* $P < 0.05$, *** $P < 0.001$.

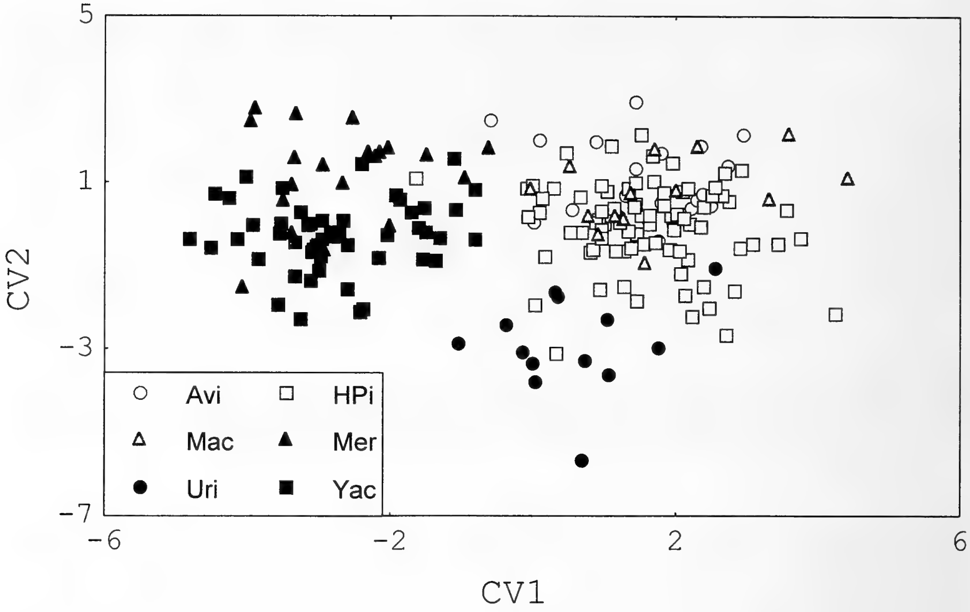

Fig. 4. Scores for *Oryzomys albigularis* individuals from the six population samples on the first two canonical variates computed from 24 morphometric variables.

Canonical variate analysis also resulted in a similar pattern (Fig. 4); the main between-sample separation occurred at the first canonical variate (67.73% of total extracted variance). This analysis discriminated the Uri sample and the three coastal ones at the second canonical axis (14.29% of total variance). The utilization of a linear discriminant function for classifying by re-substitution yielded error rates from 0.077 to 0.357; incorrect a posteriori classifications occurred within the same cluster (coast cordillera or Mer-Yac samples), bearing the Uri sample the least error rate.

As expected, the classification of specimens by a cross-validated discriminant analysis resulted in a slight increase of error rates in almost every sample. However, the overall pattern of results was not altered, and almost every misclassified specimen was assigned to a locality with an identical karyotype. Exceptions to this pattern were the same seen in previous classifications and no exception was found in the Macarao N. P. (Mac) sample, despite bearing the highest increase in error rate (+ 28.57%). The cross-validation of Uribante (Uri) data resulted in the same percentage of correct classification as with re-substitution; the same individual was misclassified in both procedures. This coherence was also evident when different character sets were used to classify the data. The overall patterns observed for the Uri and Mac samples may be used as an indicative of within-sample cohesion, what might be a consequence of representative sample sizes.

Results from principal component and canonical variate analyses show a pattern in which the Uri sample lies closer to the coast than to the remaining Andean ones. Coefficients of total-sample eigenvectors and the canonical structure indicate this pattern to be mainly due to measurements on interorbital bones, palate bone, and incisive foramen. Standardized loadings on the second canonical axis associate the separation of the Uri and coastal samples with a contrast between the incisive foramen, incisive-zygomatic, palate bone lengths, and tympanic bulla breadth, mandible, and incisive-maxillary lengths.

Recalculation of canonical variates and Mahalanobis distances after removing measurements on interorbital, palatal, and incisive foramen regions yielded similar results.

However, the Uri specimens were arranged closer to the remaining Andean than the coastal ones. When only these characters were used to calculate the canonical variates and Mahalanobis distances, a unique sample discrimination was observed in the first axis (83.31% of the total variance), depicting the same pattern that had been observed with the complete set of characters. This result reveals that the similarity of the Uri and coastal cordillera populations could be a consequence of the covariation pattern among the implied six measurements.

Discussion

Previous investigators (Aguilera et al. 1995; Gardner and Patton 1976) have documented the relatively high karyological diversity of northern South America populations of *O. albigularis*. Northernmost Venezuelan populations (the Avi, Mac, and HPi samples herein, FN = 90) have been shown to be more similar to those located at the southern Venezuelan Andes (the Uri sample, FN = 92), and at the southern Colombian Andes (FN = 94; Gardner and Patton 1976), whereas populations from northern Venezuelan Andes (the Yac and Mer samples, FN = 104) resemble those from northern Colombia (FN = 112; Gardner and Patton 1976). These results have been employed to argue that *O. albigularis* is as a supraspecific complex, by considering also that pericentric inversions have played a major role in the differentiation of the karyotypes (Aguilera et al. 1995).

The main objective of the present study was to elucidate the systematic relationships among several karyotypic variants of *O. albigularis* using multivariate skull morphometrics. Although this kind of data may not be suitable for reconstructing phylogenetic relationships (Bookstein 1991), phenotypic differentiation of forms can be expected when evolutionary divergence has caused the gene flow among populations to stop (Lande 1980). The pattern of morphometric variation observed in the present study showed a clear relationship with the karyological and geographical patterns of the analysed populations, in addition to allowing the craniometric characterization of the karyomorphs.

Multivariate ordinations clustered specimens with identical or nearly identical karyotypes. Single factors, such as the first eigenvectors of both total-sample and pooled within-group covariance matrices, produced the best within-karyomorph discrimination of population samples with FN = 90 and 104. This pattern suggests allometry as a major factor in the evolutionary divergence of the closest related forms, perhaps through the intervention of heterochronic processes (Klingenberg 1998). This result allowed us to disregard size as being important for karyomorph distinction, in accordance with the traditional approach, which considers "shape" as a more relevant factor for the study of evolutionary morphometric divergence (Rohlf and Bookstein 1987).

The present analyses give morphological support to the proposal of defining Venezuelan populations of *O. albigularis* as a species complex instead of a single nominal species (Aguilera et al. 1995). Following early classifications (Ellerman 1941; Gyldenstolpe 1932; Tate 1932), the terms *O. meridensis* and *O. caracolus* should be retained for populations from the northern Andean range (i. e. Yac and Mer samples), and from the coast cordillera. For the Uribante (Uri) population, Aguilera et al. (1995) have preferred the provisional denomination of *Oryzomys* sp.

An important finding emerging from our results is the observed coincidence of the patterns of karyomorph similarity when either karyotypic or morphometric data are considered. Discrimination of the three karyomorphs with different FN resulted in two clusters, constituted by coastal cordillera and Uri samples, and Mer and Yac ones, respectively. This pattern was kept almost the same even when a different combination of characters was employed, with the exception of the Uri sample, whose relationship with remaining samples relied on the set of traits employed. Measurements related to interorbital breadth, palatal breadth and length, and incisive foramen dimensions caused the Uri to resemble the coastal samples, whose karyotypes are probably closely related. Removal of those characters bridged morphometric similarity with geographical distance, disregarding karyotype similarity as being important in establishing relationships.

The congruence of patterns derived from independent data sets has been regarded elsewhere as evidence of a common causal factor affecting variation in both sets (THORPE et al. 1991). Since independent portions of organisms are unlikely to diverge in the same way by means of selection after population isolation, phylogeny has been invoked as the most probable common causal factor for the actual patterns (THORPE 1996; THORPE et al. 1991).

A phylogenetic hypothesis for explaining morphometric and karyotypic similarity would involve the Uribante and coastal cordillera populations to be more closely related to each other than to the northern Andean ones. Moreover, if we take into account the GARDNER and PATTON (1976) observations of the karyological similarity among the southern Colombia and coastal cordillera individuals, the Uribante population could be considered as a member of the same clade. The pattern of geographical distances among the populations sampled for the present study does not match with the observed similarity. Thus, acceptance of a phylogenetic hypothesis would require a biogeographic model which explains the actual disjointed distribution of the members of the low FN clade, with the high FN clade in the middle of their range.

Results that these considerations depend on are based on the covariation patterns of a few localized cranial regions. Although a rigorous test of the evolutionary significance of the involved characters is outside the aims of the present study, a thorough inspection of our results can help to assess the validity of a phylogenetic hypothesis. If common history did not cause observed patterns, these would relate to local effects acting independently on current populations (THORPE et al. 1991), such as directional selection and adaptation. On the other hand, absence of selection would be a strong indicator of phylogeny, but its presence would prevent us from distinguishing phylogeny from chance as the main cause of congruence.

The morphological evolution of the palate bone has been recognized as an important aspect within the radiation of the sigmodontines (HERSHKOVITZ 1962). Its variation has been related to the progressive invasion and adaptation to the diverse habitat types that these rodents actually occupy. In spite of being unable to extrapolate these observations to our study, a selective value of the palate bone cannot be excluded as a possible explanation for the observed variation in *O. albigularis*. Nonetheless, the validity of this reasoning depends on the ecological variability associated with these traits. Characters located on the incisive foramen and interorbital regions have not been explicitly related to sigmodontine diversification, but they received attention in early descriptions of "*caracolus*" and "*meridensis*" forms (GYLDENSTOLPE 1932) as diagnostic characters.

The observed high covariation between palate bone dimensions and the interorbital region suggests their morphological integration, possibly due to epigenetic factors acting in these traits as a group (LEAMY et al. 1999; RISKA 1985; WRIGHT 1932). Covariation of palate bone with incisive foramen measurements must be reflecting non-independent variation caused by their proximity. In the case where these regions were evolving as a character complex, an "ecogenetic" explanation could not be ruled out for the observed pattern of variation, based on the convergence or parallelism of the FN = 90 and 92 morphometric trait means for this group of characters. Nevertheless, rejection of a common-cause hypothesis for the observed congruence would imply the acceptance of a high number of chromosomal changes among populations with extreme FN.

A last issue that can be integrated in the interpretation of present results is the extent of variability shown by individual measurements, as given by the coefficients of variation. Those traits associated with the main karyomorph discrimination, with the highest total-sample variances, were also those with the highest coefficients of variation within the samples. This pattern resembles a series of findings discussed several years ago, the so-called "Kluge and Kerfoot (1973) phenomenon", which consists of high positive correlations among within- and between-sample coefficients of variation. Although the methods employed to detect this pattern were criticized (see Rohlf et al. 1983 and references therein), the question concerning its true existence remained to be documented. Although our results do not account for such a correlation, it seems remarkable that shifting of means over populations is most evident in traits whose variances remained consistently high amongst diversification. Explanations given to this sort of pattern tend to involve considerations on selection and developmental constraints, and commonly assume an inverse relationship between the variation of a trait and its effect upon fitness, or the strength of the constraint (Rohlf et al. 1983). This conclusion favors a phylogenetic hypothesis, because of the implicit reduction of the selective value associated with highly variable characters.

Stability of patterns of variation across evolutionary divergence of means has been demonstrated for variances (Lande 1976) and covariances (Lande 1979; Riska 1985; Steppan 1997b). This has led authors to hypothesize a long-term stability of variance-covariance patterns caused by constraints on morphology, despite short-term divergence of developmental paths. This stability is not restricted to whole morphological structures, but has been invoked to explain the evolution of groups of traits controlled by their own constraints (Riska 1985; Wright 1932).

Patterns depicted by our data could be the consequence of a non-selective shift of means, as evinced by their congruence with karyology and the high within-population variance; and selective maintenance of variances and covariances, probably by means of stabilizing selection on several correlated characters. These observations, along with the association with "shape", instead of "size" of the discrimination between karyomorphs, led us to propose phylogeny as the most parsimonious hypothesis to explain the observed pattern of similarity. Testing of this hypothesis and analysis of Colombian specimens will help to clarify the taxonomic confusion within the species, through the understanding of the cladistic arrangement of the karyomorphs and populations.

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Zusammenfassung

Morphometrische und chromosomale Variation von Oryzomys albigularis (Muridae: Sigmodontinae) aus Venezuela: Multivariate Aspekte

Der zusammengesetzte Charakter der Art *Oryzomys albigularis* ist aufgrund der karyologischen Heterogenität im Hinblick auf Chromosomenzahl und FN lange bekannt. Aus den östlichen und den nördlichen Anden wurden zwei Gruppen von Populationen mit 2n = 66 bzw. 2n = 80 beschrieben. Das Ziel der vorliegenden Arbeit war die Abschätzung von Unterschieden zwischen Populationen an Hand von metrischen Schädelmerkmalen. Die für multivariate Analysen verwendeten Populationen wurden auf der Grundlage von Unterschieden in der Zahl autosomaler Chromosomenarme definiert. Hauptkomponentenanalysen und kanonische Varianzanalysen erlaubten eine klare morphologische Unterscheidung zwischen den Karyomorphen. Die meiste Information lieferte dabei die Variation im Interorbitalbereich, im Palatalbereich und im Bereich der Foramina incisivi. Nach einer vorgenommenen Korrektur für Größenunterschiede erklärten diese Merkmale den größten Teil der Gesamtvarianz. Über die einzelnen Gruppen hinweg ergaben sich bemerkenswert ähnliche Varianzen für alle Maße, was auf stabile Muster innerhalb der Gruppen hindeutet. Es wurde kein Hinweis auf eine Kongruenz zwischen den Mustern der morphologischen Variation und dem geographischen Abstand zwischen den Karyomorphen gefunden, aber die Ähnlichkeitsbeziehungen zwischen den Stichproben erwiesen sich für morphologische und chromosomale Merkmale als übereinstimmend. Da die beiden Merkmalsbereiche voneinander unabhängige Information liefern, kann angenommen werden, daß unsere Daten phylogenetische Beziehungen wiedergeben. Unsere Ergebnisse bestätigen den polytypischen Charakter der untersuchten Art, da die meisten morphologischen Unterschiede durchgehend mit den grundlegenden karyologischen Unterschieden zusammenfallen.

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Effects of predation on temporary autumn populations of subadult *Clethrionomys glareolus* in forest clearings

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Abstract

Using netting to exclude both avian and mammalian predators in a field experiment we investigated the effect of predation and predation risk on survival, body weight development and microhabitat preferences of temporary, subadult *Clethrionomys glareolus* populations in two forest clearings during the autumn of 1996. Female bank voles were found to be influenced to a higher degree than males. Female survival was higher on predator-excluded grids compared to predated grids, whereas there was no clear response in males. Females also gained more weight on predator-excluded grids compared to both males on the same grids and females on predated grids. There was no clear treatment effect when mean body weights were compared in each trapping period. However, mean female body weights on predator-excluded grids were significantly higher in November than in September. This was not the case on predated grids.

There was a clear treatment effect on female microhabitat preferences. On predated grids female bank voles were captured at trap stations with more cover than females on net grids. A similar but less clear tendency was seen in males. On both net grids in both September and November female bank voles were trapped at trap stations with less cover than males, whereas the opposite was true for both predated grids in both months.

Key words: *Clethrionomys glareolus*, survival, predation risk, microhabitat preference

Introduction

Since slightly more than the last decade attention in studies of predation on small rodents has been increasingly directed towards the indirect effects on the prey animals. Apart from the more direct effects on survival, recent studies have dealt with effects on activity, reproduction, foraging behaviour, spatial distribution, microhabitat selection, and body weight (Abramsky et al. 1996; Hendrie et al. 1998; Holmes 1991; Jedrzejewska and Jedrzejewski 1990; Jedrzejewski et al. 1993; Koivunen et al. 1998; Koskela et al. 1996; Lagos et al. 1995; Otter 1994; Ylönen and Ronkainen 1994; Yoccoz and Mesnager 1998).

Bank voles (*Clethrionomys glareolus*) have been shown to suppress reproduction in the laboratory in response to odours from small mustelids and in the field in response to actual predation (Ylönen 1989; Heikkilä et al. 1993; Korpimäki et al. 1994; Ylönen and Ronkainen 1994; Mappes and Ylönen 1997). Recently, however, the laboratory results have been questioned (Mappes et al. 1998). In seminatural enclosure experiments intraspecific aggressiveness in the bank voles decreased in response to predation risk (Jedrze-

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JEWSKA and JEDRZEJEWSKI 1990). Bank voles have also been shown to respond to perceived predation risk by decreasing other activities, e. g. foraging activity (JEDRZEJEWSKI et al. 1993; YLÖNEN and RONKAINEN 1994). This decreased foraging activity has been suggested as the cause of the decreased body weights found in predator-exposed bank voles in some laboratory studies (YLÖNEN 1989; YLÖNEN and RONKAINEN 1994; KOSKELA and YLÖNEN 1995). Other studies have found no effects on body weights under laboratory conditions (KOSKELA et al. 1996; MAPPES et al. 1998). In the field a few studies on bank voles also point at a negative effect of predation on body weight (MARTINSSON et al. 1993; YOCCOZ and MESNAGER 1998) but other researchers found no effects (MAPPES et al. 1998).

Accordingly, the influence of predation on body weight in bank voles is still debated while field studies on the issue are scant. Body weight may affect social status, survival, and reproductive output (STENSETH et al. 1977; COLE and BATZLI 1978; IMS 1987; PUCEK et al. 1993; CARLSEN et al. 1999) and therefore we regard the question of the influence of predation on body weight as rather important. The aim of the present short-term field study was to investigate effects of predation on survival, individual body weight, and microhabitat preferences in a population of subadult *Clethrionomys glareolus.*

Material and methods

The field tests were carried out in two large clearings, planted with young beech or oak trees in a forest near (< 40 km) Copenhagen, Denmark. Two sites (A and B) with all together 4 trapping grids were established. Two grids (net grids NA and NB) of 8400 and 6000 m^2 respectivly were covered with nets (mesh size 70 mm, height 2 m and fastened to the ground along the sides) to exclude predators, two grids (predator grids PA and PB) of 8100 and 7000 m^2 respectively were equipped with 4.5 m tall perches and nestboxes for kestrel *Falco tinnunculus* (Linnaeus, 1758) and tawny owl *Strix aluco* (Linnaeus, 1758).

The setup was aimed at research on field voles *Microtus agrestis.* However, 1995 was a beech and oak mast year in Denmark and the following peak year (1996) was characterized by large autumn populations of *Clethrionomys glareolus* in some forest clearings. These populations consisted mainly of subadults and disappeared almost completely during the winter 1996/97. These populations of subadult bank voles were studied with respect to the effects of predation and predation risk on survival, body weight, and microhabitat choice.

We did not obtain data to quantify the presence of predators on the grids. Predator activity estimates were mainly based on observations done during trapping sessions and – as a consequence – very rough. However, sand and snow tracking, faeces collections, and observations of dug out burrows showed that foxes *Vulpes vulpes* (Linnaeus, 1758), cats *Felis silvestris f. catus,* and least weasels *Mustela nivalis* (Linnaeus, 1766) were frequent guests on both predator grids. Occasionally, tracks or faeces from *Martes* sp. were found as well. Least weasels could pass the nets and were captured on all 4 grids, but not more often on the otherwise predator-free net-covered grids. Tawny owls *Strix aluco* (Linnaeus, 1758) and buzzards *Buteo buteo* (Linnaeus, 1758) were frequently observed and occasionally kestrels were seen hunting. On both predator grids the perches were used frequently by raptors and owls but it is not known whether this led to a more intensive predation on these grids.

Ugglan "Special" and Ugglan "Lämmel" multiple live-traps (Grahnab, Hillerstorp, Sweden) were used, one of each type at each trapping station. Traps contained wood chips for bedding and wheat for bait. There was a 10 m spacing between rows as well as between trapping stations in each row. Bank vole data from sites A and B come from trappings conducted for four consecutive nights in September and November 1996. All captured bank voles were toe clipped for individual identification. Body weight, sex, reproductive condition, trap type, and trap location were recorded for each capture. Body weight can vary with e. g. time spent in the trap or with amount of food in the digestive system. The influence of time spent in the trap was reduced by inspecting the traps on all grids at the same time of the day (between 9 and 12 a. m.) assuming that the voles by then would have spent largely the same amount of time in the traps. Furthermore weight measured on the first capture occasion of an individual in each trapping period was used to reduce the influence of weight changes caused by repeated captures within a short time.

Relative individual body weight change between two capture sessions was calculated as the difference in body weights between the two sessions divided by the body weight at the first of the two sessions. That is, for any given interval the individual weight change is calculated using the weights of individuals captured at both ends of this interval.

Return rate is the product of survival and capture probabilities and generally underestimate survival probabilities. Furthermore, differences between groups do not necessarily imply differences in survival probabilities (Lebreton et al. 1993). Despite this shortcoming return rate has the advantage that it can be used with only two trapping sessions.

At each trap station vegetation and litter cover were estimated during February and March 1997. Cover from vegetation or litter was judged at a scale from 1 (no cover) to 5 (full cover). The vast majority of the cover was constituted by perennial grasses, litter, *Epilobium angustifolium*, and *Rubus fruticosus*. The cover score on the 1 to 5 scale was therefore largely similar irrespective of time of the year.

Results

The return rate was 46–75% for both sexes at all grids between September and November (Tab. 1). At both net grids females had higher return rates than the females on the neighbouring predator grids. Males at net grid A had lower return rate than males at predator grid A, whereas males at net grid B had higher return rates than males at predator grid B. None of these differences, however, were significant (Tab. 1).

At both site A and B females on the net grids gained weight between September and November (Tab. 2). At site A males on the net grid and both sexes on the predator grid lost weight. At site B the weight gain of net grid males and both males and females on the predator grid was less than the weight gain of net grid females. None of the differences were significant (Tab. 2). However, the pattern of the individual weight changes was almost identical at the two sites. Individual weight changes of net grid males and predator grid females and males were all similar at each site, and the difference between net grid females and net grid males or between net grid females and predator grid females were very similar (Tab. 2).

We found no significant differences in mean body weights between the sexes on any grids in any month. In September female bank voles on predator grid A had a significantly higher mean body weight than females on net grid A (Tab. 3). Apart from that no significant differences between grids were found. On both net grids, however, the mean body weight of females was significantly higher in November than in September (Tab. 3). Also males on predator grid B weighed significantly more in November than in September. No other significant differences in mean body weights between trapping periods were found. As immigrants (newly marked individuals) in November 1996 constituted only 11–19% of the bank vole populations at sites A and B we consider changes in mean weights mainly a result of individual weight changes.

Females on predator grids were trapped at trap stations with significantly more cover than females on net grids (Tab. 4). Duncan's mutiple range tests shows a clear treatment

Table 1. Return rate of female and male bank voles between September and November 1996 on the two net grids (NA and NB) and two predator grids (PA and PB). Results of chi-square test are shown.

Sex	Site	Net grid	Predator grid	Chi-square	P
Female	A	0.714	0.556	1.06	0.303
	B	0.688	0.481	1.73	0.189
Male	A	0.500	0.750	3.05	0.081
	B	0.667	0.462	2.08	0.149

Table 2. Mean individual weight change/g body weight for bank voles between September and November 1996 on the two net grids (NA and NB) and two predator grids (PA and PB) with 95% confidence intervalls. Results of all effects ANOVA and Duncan's multiple range test are shown.

Site A	All Effects: F = 1.605, P = 0.201			P-values of each pair		
				NA		PA
Grid	Sex	N	Mean individual weight change/g	Females	Males	Females
NA	Females	14	0.060 ± 0.089			
	Males	13	–0.021 ± 0.041	0.118		
PA	Females	9	–0.018 ± 0.085	0.111	0.954	
	Males	14	–0.025 ± 0.069	0.115	0.941	0.902

Site B	All Effects: F = 1.252, P = 0.301			P-values of each pair		
				NB		PB
Grid	Sex	N	Mean individual weight change/g	Females	Males	Females
NB	Females	11	0.149 ± 0.094			
	Males	12	0.057 ± 0.106	0.126		
PB	Females	13	0.049 ± 0.085	0.109	0.891	
	Males	18	0.061 ± 0.063	0.120	0.949	0.852

effect in both September and November where the mean cover index value for female bank vole captures were significantly higher on both net grids compared to any of the predator grids. The males too showed a tendency for captures under denser cover on the predator grids but the pattern is not as obvious as for the females (Tab. 4). The clear pattern in the females compared to the males resulted in females being captured at trap stations with denser cover than males on the predator grids, whereas they were captured at stations with less cover on the net grids (Fig. 1). The difference between the sexes was only significant on predator grid B in September where females captures were under denser cover than male captures. However, the described difference between net and predator grids were consistent on all grids in both trapping periods.

Discussion

In laboratory and semi-natural experiments higher weight losses in voles exposed to predator odours compared to control voles have been frequently found (Ylönen 1989; Ylönen and Ronkainen 1994; Koskela and Ylönen 1995; Mappes and Ylönen 1997; Carlsen et al. 1999) although some researchers did not find any effect of predator odour (Koskela et al. 1996; Mappes et al. 1998).

In the field several studies have found rodent foraging behaviour to be influenced by predation risk (Otter 1994; Abramsky et al. 1997). Common for these field studies is the fact that the rodents did not necessarily reduce foraging activity but rather redistributed it to include a larger proportion of relatively safe areas. However, researchers have suggested that predation does have an effect on body weights in the field. Martinsson et al. (1993) found higher body weights in a bank vole population on a predator-free island compared to a mainland population. Yoccoz and Mesnager (1998) found higher body

Table 3. Mean weights of female and male bank voles on the two net grids (NA and NB) and two predator grids (PA and PB) with 95% confidence intervalls. t-test results for the comparisons between grids at each site and for the comparisons between months for each sex are shown.

Females				Site A		
		September		November	Comparison between months	
	N	Mean weight	N	Mean weight	t	P
Net	23	16.0 ± 1.0	20	17.5 ± 1.2	2.072	0.045
Predator	19	17.5 ± 1.1	21	17.4 ± 1.0	0.136	0.893
t		2.266		0.029		
P		0.029		0.977		
Males				Site A		
		September		November	Comparison between months	
	N	Mean weight	N	Mean weight	t	P
Net	31	16.2 ± 0.6	19	16.7 ± 1.2	0.853	0.398
Predator	19	17.0 ± 1.2	19	16.2 ± 0.8	1.237	0.224
t		1.310		0.836		
P		0.196		0.410		
Females				Site B		
		September		November	Comparison between months	
	N	Mean weight	N	Mean weight	t	P
Net	20	16.7 ± 0.8	12	19.1 ± 1.4	3.427	0.002
Predator	31	17.5 ± 1.0	15	18.3 ± 0.8	1.043	0.303
t		1.211		1.165		
P		0.232		0.255		
Males				Site B		
		September		November	Comparison between months	
	N	Mean weight	N	Mean weight	t	P
Net	23	17.6 ± 0.9	16	18.6 ± 0.9	1.544	0.131
Predator	46	17.0 ± 0.5	21	18.9 ± 1.2	3.361	0.001
t		1.100		0.398		
P		0.275		0.693		

weights in alpine bank voles compared to lowland populations and suggested that lower impact of predation was the cause. We have previously shown negative influence of predation risk on *Microtus agrestis* body weights in the field as well as in the laboratory (CARLSEN et al. 1999).

The present study shows larger individual weight increase in female bank voles in autumn in predator-excluded populations compared to predated populations. Males, on the other hand, did not respond so clearly to predator exclusion. As immigrants only made up a small proportion of the November population the individual weight increases in net grid females influenced mean body weights so that female November weights on net grids were significantly higher than female September weights on these grids. However, we found significant differences in mean body weight between treatments only in one case in September. This stresses that possible effects of predation on body weight in the field may be better shown by comparisons of individual body weight changes and mean weight differences over time than by comparing differences in mean weight between treatments (CARLSEN et al. 1999).

Also regarding survival and microhabitat preferences females responded more clearly to predator exclusion than males. Female survival was higher on both net grids whereas male survival did not show clear treatment effects. This is in accordance with results on *Microtus agrestis* indicating female survival to be more affected by predator exclusion

Table 4. Mean cover index for bank vole captures with 95% confidence intervals. Results of Mann-Whitney U-test for individual comparison are shown. Also Results of Kruskal-Wallis H tests are given. N is the number of voles. Grids are not significantly different from each other share significance terms (ST).

Females Grid	N	Mean cover index value/capture September 1996 H = 46.118, P = 0.0000	ST	U for each pair			P for each pair		
				NA	NB	PA	NA	NB	PA
NA	21	3.03 ± 0.17	c						
NB	64	3.20 ± 0.09	b	448.5			0.010		
PA	14	3.71 ± 0.15	a	23	116		0.000	0.000	
PB	35	3.53 ± 0.12	a	120	566.5	176	0.000	0.000	0.077
Grid	N	Mean cover index value/capture November 1996 H = 41.170, P = 0.0000	ST	U for each pair			P for each pair		
				NA	NB	PA	NA	NB	PA
NA	19	3.08 ± 0.23	c						
NB	20	3.00 ± 0.15	c	154			0.268		
PA	18	3.94 ± 0.19	a	24	12		0.000	0.000	
PB	18	3.39 ± 0.11	b	104	68	42	0.019	0.000	0.000
Males Grid	N	Mean cover index value/capture September 1996 H = 12.583, P = 0.006	ST	U for each pair			P for each pair		
				NA	NB	PA	NA	NB	PA
NA	31	3.10 ± 0.18	c						
NB	64	3.33 ± 0.09	b	754			0.037		
PA	19	3.61 ± 0.26	a	157.5	405.5		0.004	0.016	
PB	58	3.22 ± 0.14	bc	772	1651	339	0.237	0.240	0.007
Grid	N	Mean cover index value/capture November 1996 H = 12.337, P = 0.006	ST	U for each pair			P for each pair		
				NA	NB	PA	NA	NB	PA
NA	19	3.24 ± 0.33	b						
NB	17	3.18 ± 0.13	b	146			0.599		
PA	16	3.69 ± 0.22	a	94.5	44		0.048	0.000	
PB	28	3.29 ± 0.14	b	264	208	108	0.963	0.418	0.003

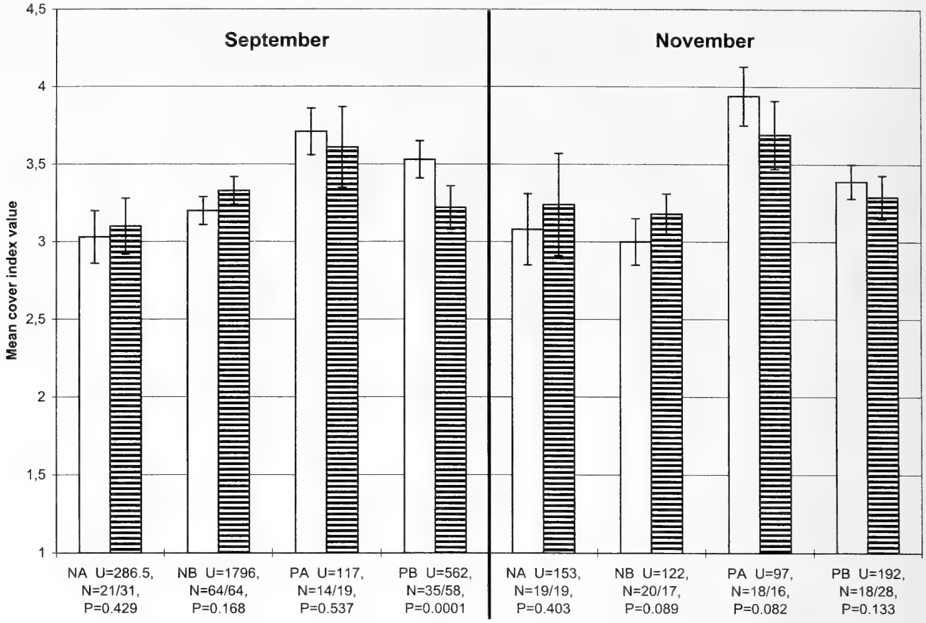

Fig. 1. Mean cover index value for female (white columns) and male (barred columns) bank voles on the two net grids (NA and NB) and two predator grids (PA and PB) in September and November 1996 with 95% confidence intervals. Results of Mann-Whitney U-test are given below the columns.

than male survival both in and outside the breeding season (unpublished data). Female rodents have been found to be more susceptible to mammalian predation at least in the reproductive season (CUSHING 1984; NORRDAHL and KORPIMÄKI 1998) while males are more susceptible to avian predation (BEACHAM 1979; KORPIMÄKI 1985; KOIVUNEN et al. 1996). The present results indicate that female bank voles outside the reproductive season may be under heavier influence of combined mammalian and avian predation than males.

Microhabitat choice have often been found to be influenced by predation. Pikas *Ochotona collaris* did not venture far from protective talus piles despite better food opportunities further away (HOLMES 1991). The herbivorous South American rodent *Octodon degus* used spaces away from shrubs more often when predators were excluded (LAGOS et al. 1995). In bank voles the use of trap sites have been found to be positively correlated with the percent cover of shrubs and tall herbaceous plants (JENSEN 1984; GEUSE et al. 1985; CHETNICKI and MAZURKIEWICZ 1994; MAZURKIEWICZ 1994). The most important function of this shrub layer is suggested to be protection from predators (CHETNICKI and MAZURKIEWICZ 1994; MAZURKIEWICZ 1994). In the present study especially females on net grids respond to the exclusion of predators by using trap sites with significantly less cover than the females on predator grids. Males showed the same tendencies but not as clearly as females. As a result the mean cover index value for females on net grids was consistently smaller than for males, whereas the opposite was true for predator grids. This is in accordance with results on *Microtus agrestis* showing a slightly increased preference for cover on predated grids compared to predator-exclusion grids (unpublished data).

The finding that female survival and female weight changes were influenced to a higher degree by predation than that of males could be a function of heavier predation pressure upon females than upon males also outside the breeding season. Experiments by

JEDRZEJEWSKA (1989), however, showed that the susceptibility of reproductively non-active bank voles to weasel predation did not differ from that of reproductively active females. Outside the breeding season females showed a more consistent clumping tendency than males which had less overlapping home ranges (KARLSSON 1986). This could make them more vulnerable to patch-seeking predators. Furthermore, it might enable the females to clump in patches with a higher degree of cover in response to increased predation risk. The males relative avoidance of each other would make them unable to respond to predation risk by increasing the use of cover to the same degree as females. Irrespective of age, males had larger home ranges than females in October (MAZURKIEWICZ 1971). A larger home range in a heterogeneous environment may also increase the chance of the male being captured at stations with less cover.

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Zusammenfassung

Auswirkungen von Feinddruck auf Herbstpopulationen von subadulten Clethrionomys glareolus in Waldlichtungen

Unter Ausschluß von Prädation durch Vögel und Säuger mit Hilfe von Netzen wurden im Herbst 1996 in einem Freilandexperiment die Auswirkungen von Feinddruck auf Überlebensrate, Körpergewichtsentwicklung und Habitatwahl bei subadulten Rötelmäusen auf zwei Waldlichtungen untersucht. Weibliche Rötelmäuse zeigten dabei stärkere Effekte als männliche. In Abwesenheit von Prädatoren ergab sich gegenüber einer normalen Situation bei Weibchen eine höhere Überlebensrate, bei männlichen jedoch nicht. Weibchen zeigten auch eine stärkere Gewichtszunahme bei Ausschluß von Feinddruck verglichen mit Männchen in entsprechender Situation und gegenüber Weibchen mit Feinddruck. Unterschiede ergaben sich auch in bezug auf bevorzugte Microhabitate, denn weibliche Rötelmäuse wurden bei ausgeschlossenem Feinddruck in größerem Ausmaß in Fallen in offenem Gelände gefangen, unter Feinddruck hingegen stärker in solchen, die in der Vegetation versteckt plaziert waren. Bei Männchen zeigte sich eine ähnliche, allerdings weniger deutliche Tendenz.

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The decline and local extinction of a population of water voles, *Arvicola terrestris*, in southern England

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Abstract

A colony of water voles occupying 1.6 km of the river Windrush (England) is described before it disappeared due to mink predation. Individuals were trapped every month for a week during 19 months. In addition, some individuals were radio-tracked in order to estimate their ranges and movement patterns. The numbers of latrines were counted seasonally and compared with the numbers of captured animals. The population reached a peak in July 1996 when 20 individuals were known to be alive indicating that the population was already very small. The number of individuals caught decreased in winter and new individuals appeared during the next spring although the population crashed in July 1997 due to mink predation. The sex ratio was similar to that reported elsewhere for British populations, but densities were lower than those reported elsewhere. Body size was smaller than previously recorded in the same catchment. Home ranges were significantly smaller in summer than in spring resembling situations of high and low densities respectively. Individuals showed restricted movements and no dispersal event was recorded. Available data seem to suggest that females form linear ranges that, though overlapping other juvenile females, exclude adult females. Males, on the other hand, have linear ranges that overlap several females and males.

Key words: *Arvicola terrestris*, water voles, rodents, home range, population

Introduction

The water vole *Arvicola terrestris*, is a microtine rodent distributed widely in the Palearctic region. In most of their range, water voles are closely associated with aquatic habitats occurring along rivers, brooks, and on the shores of lakes and gravel pits. In the mountainous areas of central Europe and the Pyrenees, water voles show fossorial habits and differ widely in their population characteristics from the aquatic forms. Fossorial water vole populations undergo 5–8 year multi-annual fluctuations reaching very high densities (Saucy 1994) and are considered a pest in parts of their range. On the other hand, aquatic water voles do not show multi-annual cycles and their densities are always lower than those reached by fossorial water voles. Aquatic water voles are larger, darker and polygynous whereas fossorial forms live in monogamous pairs that defend small territories (Pelikan and Holisova 1969; Reichstein 1982; Strachan and Jefferies 1993).

In Britain, the population ecology of water voles has been previously studied by Stoddart (1970) in Scotland, Leuze (1976) in East Anglia, and Woodall (1993) in the Thames region. At the time these studies were carried out, stable populations of water voles occurred in all these study areas. Home ranges were always linear with water voles staying within 1–2 m from the edge of the water. These home ranges, however, differed from those of some populations of water voles in aquatic habitats of continental Europe and the former USSR that show polygonal shapes (Jeppsson 1986, 1990).

In mammals, factors affecting distribution and spatial organisation vary with the sex of individuals. In general, female distribution is dependent on the dispersion of resources whereas males depend on females distribution (Jeppsson 1990; Ostfeld 1990). In Britain, distribution of water voles varies from uniform (Stoddart 1970), to clumped (Woodall 1993), to fragmented (Lawton and Woodroffe 1991) along river banks. Woodall (1993) attributed these differences in distribution to differences in habitat between the study sites. Nevertheless, the difference might be related to the process of decline that British populations of water voles have experienced since the beginning of the century and particularly for the last 30 years (Jefferies et al. 1989). The study by Stoddart (1970) was carried out during the late 60 s, that of Woodall (1993) during the mid 70 s whereas Lawton and Woodroffe (1991)'s was conducted in late 80 s.

For a given population, it is not only dispersion that may be affected during the process of decline. The population structure is likely to change as well. As populations get smaller, the impact of stochastic factors increases and so does the probability of extinction of local populations. Metapopulation dynamics are disrupted and fragmentation increases in a way that any rescue effect is prevented. Water voles in Britain are declining (Strachan and Jefferies 1993), and whilst recent surveys indicate that the number of sites with evidence of their presence has decreased, it is possible that the population size in the remaining sites has also decreased. The gaps between colonies are becoming larger and the probability of migration between colonies lower. This phenomenon is probably due to, but also aggravated by, the presence of American mink, *Mustela vison*, and habitat disturbance (Lawton and Woodroffe 1991; Strachan et al. 1998).

The river Windrush is a tributary of the river Thames flowing from the Cotswolds in Gloucestershire and joining the Thames at Newbridge in Oxfordshire, England. During the summer of 1996, only 8 colonies of water voles were recorded along the c. 100 km of the river. On average, these colonies occupied less than 800 m of continuous riverbank showing the high degree of fragmentation of this population. The bigger of these colonies, as revealed by the length of river showing evidence of water voles, occupied 1.6 km of river and was chosen for this study. No colony was recorded downstream and the nearest neighbouring colony was located 2 km upstream. The aim of this study was to learn more about water vole populations and to compared this declining population with the stable ones previously studied in Britain.

Material and methods

Study area

The study was carried out along a 1.6 km stretch of the river Windrush (Oxfordshire, England) between grid references SP260115 and SP273117 (Fig. 1), approximately 30 km to the west of Oxford City. The river is 8–10 m wide, the flow is slow and the channel generally deep (1.5–2 m). Banks are generally steep (> 45°) and low (up to 1 m from the water surface). Adjacent land consists of semi-improved neutral grassland managed as pasture for sheep. The sward consists mainly of perennial ryegrass *Lolium perenne* and crested dog's-tail *Cynosurus cristatus*. There are some trees along the banks especially alders *Alnus* sp., (most of them dying from Phytophthora infection) and some pollarded willows *salix* sp. The channel contains considerable quantities of stream water-crowfoot *Ranunculus penicillatus*, perfoliate pondweed *Potamogeton perfoliatus*, spiked water-milfoil *Myriophyllum spicatum* and yellow water-lilly *Nuphar lutea*. Wildlife along the stretch included waterfowl (swan *Cygnus olor* mallards *Anas platyrhynchos*, coots *Fulica atra* and moorhen *Gallinula chloropus*), kingfisher *Alcedo athis*, lapwing *Vanellus vanellus*, little grebe *Tachybaptus ruficollis*, brown hare *Lepus capensis*, rabbits

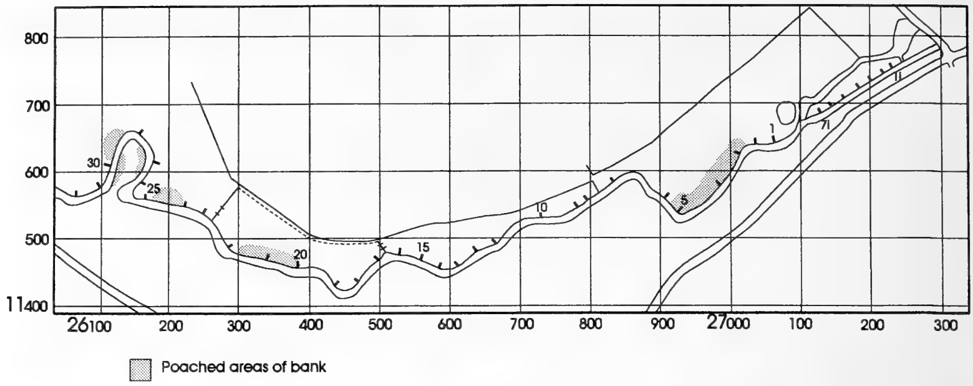

Fig. 1. Study area. The river Windrush near Widford, Oxfordshire, England. Grid references are shown. Every square represents 100 m square. Symbols along the river show trap sites. In total, 1.6 km of river was surveyed.

Oryctolagus cuniculus, bank voles *Clethrionomys glareolus*, field voles *Microtus agrestis*, woodmice *Apodemus sylvaticus* and weasel *Mustela nivalis* among other species. No sign of American mink was observed by the time the study started in May 1996.

Trapping programme

Water voles were live-caught in aluminum traps 33 × 10 × 9 cm (Elliott Ltd.; Victoria, Australia). Traps were baited with apple and placed approximately every 30 m along the river bank. Traps were set in sites where there was evidence of water vole activity (i. e. near burrows, latrines, feeding places, etc.). In some cases, artificial burrows were dug facing the river and traps set in them. Approximately 40 traps were set for a week every month from June 1996 to December 1997. The position of every trap was located on the map and maintained with slight variations for the whole study period. Prebaiting was not implemented as Woodall (1993) found it unnecessary. Traps were checked early in the morning and before sunset. During winter, the traps were covered with hay and other vegetation to protect them against rain and/or frost. Additionally, the number of latrines along the river were counted each season in order to relate this number to the number of animals caught.

Trapped animals were introduced to a gas chamber where they were briefly anaesthetised with inhalant methoxyfluorane (Metofane^{TM}) or halothene (Fluothane^{TM}) and subsequently processed. Each animal was sexed, weighed and standard body measures taken (Total, head-body, ear and hind foot length). A transponder (Trovan^{TM}) carrying an unique identification code was implanted sub-cutaneously in the back of each animal. Some of the animals were equipped with radio-collar transmitters as described below. Handling lasted for a maximum of 5 min and after a few additional minutes the animals, completely recovered, were released at the place of capture.

Radio-tracking programme

Thirteen animals were fitted with radio-collars consisting of 3–4 g TW/4 or TW/5 transmitters (Biotrack; Wareham, UK) and tracked using a Mariner receiver and a three-element Yagi antennae. Fixes were taken every 15 min from a maximum distance of 25–30 m. Batteries lasted for 6 weeks on average but problems with the signal were common throughout the study. Recaptured animals were checked and malfunctioning radios replaced. When there were any signs of abrasion to the neck of the animal, the collar was removed and the individual released. All procedures were done under Home Office project licence PPL 30/00043 and personal licence PIL 30/3873.

Results

The population

In total, 145 captures were made in 4488 trap-nights. Forty five individuals (20 males and 25 females) were caught and tagged. Mean number of captures per individual was 1.6 (1–3) whereas the average efficiency of capture (captures/trap-nights) was 0.04 with a minimum in January 1997 (0) and a maximum in July 1996 (0.16). Captures were not evenly distributed along the stretch (Fig. 2) with some trap sites capturing more individuals with higher frequency. Figure 2 also shows three sectors along which no capture was made. These sectors coincided with areas of river bank poached by cattle or sheep.

The maximum number of latrines was observed in summer 1996. The number declined through winter when no latrines were found. Water vole activity started in spring with an increasing abundance of latrines. However, no signs of water voles were observed from July 1997 onwards. Latrine counts carried out during July 1996 simultaneously to the trapping yielded a total mean frequency of 172.6 latrines (SD = 11.8). This approximates to six latrines per vole and an index of the potential breeding population of water voles as 18 voles/km of occupied river. Interestingly, this figure coincides with that reported by Woodroffe et al. (1990) when studying water voles in Yorkshire, northern England.

Figure 3 shows the abundance of water voles along the study area from June 1996 until November 1997. The highest number of animals was observed during July 1996 but the population crashed a year later. Juveniles (6 individuals) were trapped only in June and July 1996 (Tab. 1). No water voles were trapped, or signs observed, between July and December 1997. No untagged water vole was caught in February and March 1997 but new individuals started to appear from April indicating a potential population recovery. It is important to note that signs of American mink were observed for the first time in May 1997 and a radio collared water vole was found dead inside a willow hollow on

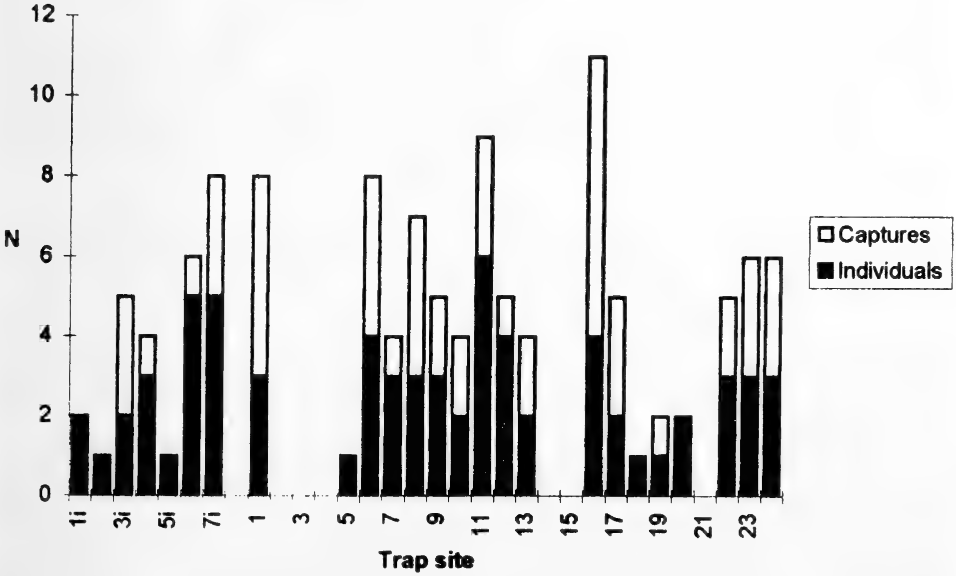

Fig. 2. Number of captures, and individuals caught, in each trap site along the study area. Trap sites with no capture coincide with trampled areas. Location of traps is shown in figure 1.

13th June. A hole was observed in the skull of this animal. In the same place there was another water vole and a coot. The presence of footprints near the site suggest that a mink had made the kills. Two juvenile mink were caught in July 1997; one female trapped around trap-site 24 and a male trapped near trap-site 1 i. A third mink, presumably an adult female, was observed in July and August but it was not trapped.

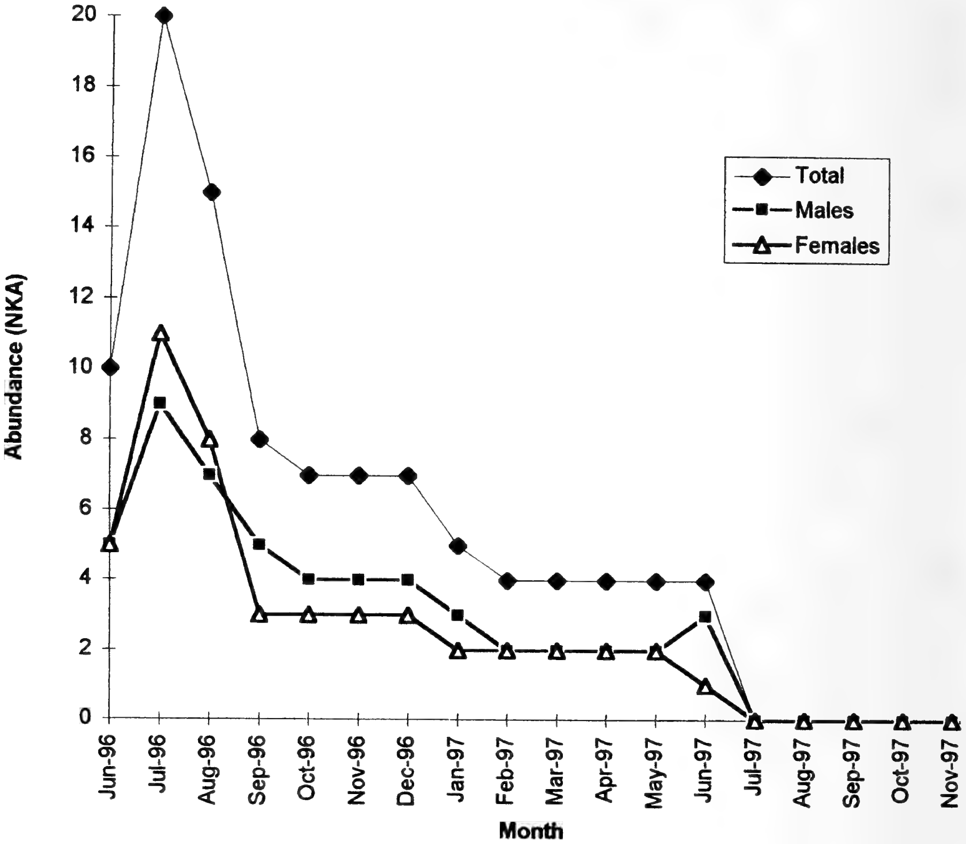

Fig. 3. Abundance of water voles along the study area from June 1996 until November 1997. The population crashed in summer 1997. Additional trapping carried out in Summer 1998 showed no water vole had colonised the area yet. NKA: numbers known alive.

Table 1. Number of individuals caught each season discriminated by age. Only one individual (an adult male) was trapped during winter and it is not shown here. Number of adult males: females shown in brackets.

	Juveniles	Sub-adults	Adults [males : females]	Total
Summer 96	6	7	18 [9 : 9]	31
Autumn 96	0	2	12 [9 : 3]	14
Spring 97	0	0	7 [3 : 4]	7
Summer 97	0	1	3 [2 : 1]	4
Autumn 97	0	0	0	0

The individuals

Comparing standard measures revealed that no significant differences were found between sexes in total length ($t = 0.82$; $df = 41$; $p > 0.05$), head-body length ($t = 0.74$; $df = 38$; $p > 0.05$), and weight ($t = 1.0$; $df = 34$; $p > 0.05$). Both ears and hind feet, however, were significantly longer in males (Tab. 2) Maximum weight recorded were 350 g in a female and 360 g in a male, both caught in June. Although the average weight of adults was slightly lower during autumn, there were no significant differences among seasons ($F_{[1,5]} = 1.15$; $p > 0.05$).

Table 2. Standard measures (mean ± SE) of male (M) and female (F) water voles caught between June 1996 and July 1997 along a 1.6 km stretch of the river Windrush, Oxfordshire, England. TL: total length; HBL: head-body length; EL: ear length; HFL: hind foot length; Wt: weight. From 20 males and 21 females. P-values for t-tests are given.

	TL (mm)	HBL (mm)	EL (mm)	HFL (mm)	Wt (g)
M	302.2 ± 8.8	188.4 ± 4.8	16.9 ± 0.4	34.5 ± 0.4	196.4 ± 15.0
F	292.5 ± 4.1	180.9 ± 7.8	15.2 ± 0.4	32.9 ± 0.4	218.8 ± 17.0
p	0.421	0.491	0.0041	0.0056	0.160

Water vole ranges

Animal recaptures provided an insight into the range of water voles in this declining population. During the summer of 1996, one 257 g adult male used a range of 220 m, which embraced the 100 m range of one female, and within which seven juveniles (four males and three females) were also trapped (we were able to estimate the ranges of three of these young males and none exceeded 30 m). Separated from this cluster of voles by an apparently unoccupied strip of 320 m, a second adult male of 353 g occupied a 200 m strip, within which three juvenile males (mean = 141.6 g) and three females (90, 114, and 188 g respectively) were trapped, along with two mature females (250 and 228 g). A third adult male (232 g) occupied a contiguous range stretching 200 m upstream. Other individuals were trapped only once and therefore no range can be given.

During autumn and winter very few captures were made and most of the individuals trapped were caught only once. In spring one adult male was caught in traps separated by 110 m, and his weight increased from 214 g in August 1996 to 305 g in June 1997. An adult female that had been stayed around one trap for at least nine months between June 1996 and March 1997, was trapped 600 m downstream in April.

Between 34–525 radio fixes were taken on individuals tracked in the summers of 1996 and 1997. In 1996 four females had ranges averaging 62 m, whereas two males had ranges averaging 64.5 m. In spring 1997 (Fig. 4), three females averaged 163.3 m, and two males 550 m. Males roamed as far as 800 m although they tended to stay several days within a range of 20–30 m before changing their centre of activity. One male used a range with two centres of activity each overlapping with a different female and separated by 300 m. Another male undertook an 800 m excursion during one day, to stay two days with a new female before returning to its original range. Similarly, one female travelled 300 m upstream in one day and returned to its original range two days later.

Overall, home ranges were smaller in summer than in spring and all ranges were linear, no vole was ever being found even on top of the bank. In general, juveniles stayed within 30 m of river bank and most of the time in the same place. Male 544, for example, was tracked for three weeks and did not go further than 10 m from the nest. During this

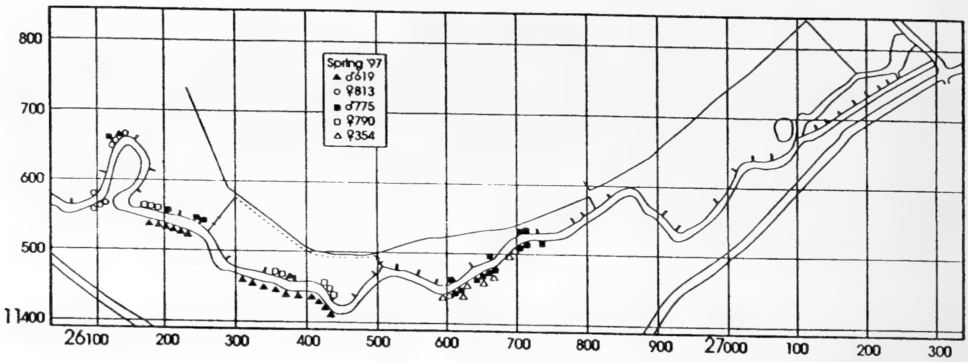

Fig. 4. Ranges of five radio-tracked individuals during spring 1997. Symbols represent locations where 80 % of fixes were recorded.

time its weight increased from 52 g to 98 g. A month later the collar was removed, it was caught 50 m away from the nest weighing 170 g.

No two adult females were ever caught in the same trap during the same trapping period. Males, on the other hand, used longer home ranges and overlapped not only other females' but other males' too. We saw one pair mating and 20 days later they were sharing the same burrow.

Discussion

The density recorded in the study area (maximum density = 1.25 ind/100 m) was lower than densities reported elsewhere. Pelikan and Holisova (1969) reported densities between 4 and 9.3 ind/100 m in a similar habitat in the Czech Republic. In Britain, Leuze (1976) found a maximum of 2.8 ind/100 m of river, and Strachan and Jefferies (1993) estimated overall densities of 4 to 16 ind/100 m for the whole country. A comparison of surveys in the Thames catchment from 1989 and 1995, showed that water voles are disappearing from many sites and it is not a surprise that the density along the sites where they still occur has diminished. Barreto et al. (1998 a) showed that the rate of decline between 1989 and 1995 was higher than during the previous 15 years. This may account for the difference found between the densities reported by Strachan and Jefferies (1993) and that reported in this study.

Despite being small, the population showed an expected maximum size in summer and a minimum size in winter. The capture of new individuals during spring 1997 suggested that the population was starting a new cycle of increase. During that spring, however, a breeding female mink established in the area. Recent studies carried out in the rivers Soar and Amber in Leicestershire and Derbyshire respectively showed that the American mink decimated a water vole population in less than a year (Strachan et al. 1998) from the time it arrived to the area. Home ranges of mink, though wider, are also linear overlapping several water vole ranges (Gerell 1970; Dunstone 1993). Strachan et al. (1998) found that a female breeding mink was likely to produce the worst effects on the water vole population as it hunts intensively around the den in order to feed its kits. The situation is aggravated because mink breeding season starts in February and kits are born in May, and by this time the water vole population is still recovering from the previous winter. The population studied by Strachan et al. (1998) occupied a longer stretch of river, so it took one year for two different breeding mink to eliminate water voles from this stretch. In the case studied here, the population was far smaller, and only one female

Table 3. Body measures of water voles from different areas. HB: head body length; HF: hind foot length. Mean ± SE. Range in brackets.

	Weight (g)	HB (mm)	Tail (mm)	HF (mm)	Source
Oxfordshire	291.5 (225–386)	222 (206–242)	134 (115–146)	34 (32–36)	Boyce (1991)
Oxfordshire	207.6 ± 16.0	184.6 ± 6.3	112.7	33.7 ± 0.4	This study
North Germany	153.6 ± 6.99	157.1 ± 3.40	118.4 ± 2.49	30.9 ± 0.21	Reichstein (1982)
South Germany	147.7 ± 6.28	159.3 ± 2.35	115.9 ± 2.38	30.1 ± 0.17	Reichstein (1982)

mink was enough to patrol the stretch where the whole colony inhabited and eliminate the population in only three months. A visit to the study area in July 1998, showed no water vole had recolonised the river. In fact, the nearest colony inhabited a stretch of river 2 km upstreams separated between each other by the town of Budford where the river banks are mostly reinforced, thus becoming a barrier for water voles. Should these colonies were a metapopulation, it is apparent that it no longer exists as such, as the degree of fragmentation is too high.

British water voles have been reported to be bigger than water voles from the continent (Reichstein 1982) and body measures taken during this study support these data (Tab. 3). However, water voles measured in this study were smaller than those studied by Efford (cit. in Boyce 1991) in Oxfordshire during the mid 80 s (Tab. 3). It is not clear why the average size obtained in this study turned out to be lower than that of water voles from the same area studied more than ten years ago. One possibility is related with a decrease in the quality of the habitats. Krebs (1978) and Boonstra and Krebs (1979) discussed a hypothesis (Chitty hypothesis) according to which extra large individuals appear during the peak phase of the multi-annual cycles observed in microtines. Regardless of the assumptions of these hypothesis, these extra-large animals would increase the average size in the population. Lidicker and Ostfeld (1991) showed later that in the case of California voles (*Microtus californicus*), extra large individuals did indeed appear in the population at high densities although they attributed this phenomenon to conditions for good growth and survival that last long enough for large size to be achieved. There is no evidence in Britain suggesting that water voles experience multi-annual cycles although it is clear that the population size is decreasing. Is it possible that current conditions for growth are not good enough and water voles are not achieving the size they used to achieve ten or more years ago? Water voles have experienced a loss of suitable habitats during the second part of this century (Barreto et al. 1998 a) and it is apparent that across the Thames catchment they have been occupying areas better characterised by the absence of mink than by any especial habitat feature (Barreto et al. 1998 b). Water voles are absent from the lower part of the river Windrush and the available data suggest that this section possesses the best habitats for water voles so it is possible that a decrease in habitat quality or the occupancy of marginal habitats is being reflected in smaller animals. This is an intriguing issue and more data on other populations will be needed to clarify these ideas.

Pooling the results from trapping and those from radio-tracked animals shows that during the summer home ranges were smaller than during spring. Spring defines the beginning of the breeding season and it is characterised by an increase in the number of latrines. An increase in the size of the home range reflects a period of major activity. Similar changes during spring have been observed in other vole species such as *Microtus californicus* (Salvioni and Lidicker 1995), *M. townsendii* (Lambin and Krebs 1991) and *M. oeconomus* (Gliwics 1997).

Regardless of the length, the range of water voles was always linear and no water vole was caught or observed out of the water edge on the bank top. They did not even run or swim along a ditch dug from the river. The situation was similar to that reported by Pelikan and Holisova (1969) in the Czech Republic and Stoddart (1970) in Scotland although different from water voles in Sweden that live in marshes and have polygonal ranges (Jeppsson 1990). During summer the home range of recaptured animals were similar to those reported by Leuze (1976) in high density areas, although radio tracked animals occupied very small ranges with females and males ranges being similar. In spring, the home ranges were longer and similar to those reported in low density areas by Leuze (1976). In the Czech Republic, home ranges were 170 m and 135 m long on average in males and females respectively (Pelikan and Holisova 1969). Over the winter, these authors reported home ranges of 500 m in males and 80 m in females. These figures came from trapping data throughout the winter. Observations from the present study revealed that although the home range of an adult water vole may reach 500 m during the spring, individuals tend to use a short sector of this range during several days and then, they move into a new burrow, stay there for another time, and so on. It is apparent, then, that during the season the individuals shift the centres of activity although staying within a short stretch for several days.

Despite their morphological conservatism, Microtine rodents are extremely variable in their social and spatial organisation (Ostfeld 1990). This variation is not only interspecific but intra-specific. Townsend's voles (*Microtus townsendii*), for example, are territorial and monogamous during the spring but display overlapping ranges and are polygynous during the summer (Lambin and Krebs 1991). Fossorial water voles form monogamous pairs that defend small territories (Saucy 1988) but aquatic water voles seem to be polygynous with the females defending territories and the males overlapping several females (Jeppsson 1986). However, the available data are not yet clear as Jeppsson (1986) reported on females changing territories within the breeding season or living in cluster of possible relative females. Data from Stoddart (1970) and this study seem to support the idea that females form territories within which relatives are allowed to stay, and males overlap several female territories. In the middle part of the stretch, for example, there were 8 individuals within 250–300 m: six were juveniles (3 males and 3 females) and two adult females caught on the extremes of this stretch. Males, on the other hand, used longer home ranges and overlapped not only other females's but other male's too. Nevertheless, the observation of male 775 mating a female and sharing her burrow 20 days later, suggests that some kind of dominance among males is established. Female water voles are poly-oestrus with post-partum oestrus and suspension of oestrus during lactation (Perry 1943). It is therefore advantageous for a male to stay near a pregnant female just before she gives birth. In that way, the male assures a second mating.

Available data on social and spatial organisation of water voles are scarce but the evidence suggests three types of spatial organisation: 1. Small territories defended by a monogamous pair, 2. Territorial females or territorial clusters forming polygonal home ranges and males overlapping several female ranges and 3. Linear ranges with territorial females or clusters of related females and males overlapping several females and younger males to whom they compete for mates. The disappearance of the population studied here did not allow further comparisons between years, so a longer term study and a comparison of different areas will provide the necessary data to clarify this interesting problem.

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Zusammenfassung

Die Abnahme und lokale Extinktion einer Population von Schermäusen (Arvicola terrestris) im südlichen England

Eine Population von Schermäusen, welche 1,6 km des Flusses Windrush in England bewohnte, wird beschrieben, bevor sie durch Mink-Predation eliminiert wurde. Über einen Zeitraum von 19 Monaten wurden monatlich eine Woche lang Individuen eingefangen; außerdem wurden einige Individuen mit Radiosendern versehen, um Information über Wohnareal und Bewegungsmuster zu erhalten. Die Zahl der Latrinen pro Jahreszeit wurde gezählt und mit der Anzahl von gefangenen Individuen verglichen. Die Population erreichte ein Maximum im Juli 1996, als sie 20 lebende Individuen zählte, was beweist, daß sie bereits sehr klein war. Die Zahl der eingefangenen Individuen verringerte sich im Winter und neue Individuen erschienen während des darauffolgenden Frühjahrs, dennoch brach die Population im Juli 1997 infolge Predation durch eine verwilderte Farmnerzfähe zusammen. Das Geschlechterverhältnis war ähnlich jenem für andere in Großbritannien ermittelte Populationen, die Dichte war jedoch geringer. Die Körpergröße war geringer als jene, welche vorher für denselben Flußbereich angegeben war. Die „home ranges" waren deutlich kleiner im Sommer als im Frühjahr, was auf höhere und geringere Dichten schließen läßt. Die Individuen zeigten begrenzte Bewegungsmuster und kein Fall von Dispersion wurde beobachtet. Aus den vorliegenden Daten läßt sich schließen, daß die weiblichen Individuen lineare Reviere besetzen, die sich wohl mit denen junger weiblicher Individuen überschneiden können, nicht aber mit jenen ausgewachsener Weibchen. Die Männchen hingegen besetzen lineare Reviere, die sich mit jenen verschiedener Weibchen und Männchen überschneiden können.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Eudiscopus denticulus (Osgood 1932) in Thailand with notes on its roost (Chiroptera: Vespertilionidae)

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Key words: *Eudiscopus denticulus*, Thailand, size, roosting behaviour, bamboo phytotelmata

The monotypic genus *Eudiscopus* Conisbee, 1953 is endemic in central SE. Asia. *E. denticulus* (Osgood 1932) was described from six specimens collected at Phong Saly, 21°40′N–102°06′E, N. Laos. Two females of this species were recorded by Koopman (1970) from Yetho River (not localised), Pegu Yoma, southern Central Myanmar (Burma), and two males from Song Ma, Son La, 21°20N′–103°55′E, NW. Vietnam, by Cao Van Sung (1976) and Dang Huy Huynh et al. (1994).

On May 1, 1999, the fauna of the internodes of giant bamboo, *Gigantochloa* sp. (Gramineae), was studied in Khlong Lan National Park, ca. 16°13′N–99°17′E, Kamphaeng Phaet (= Phet) Prov., W. Thailand by the junior author. Opening an internode approximately 5.5–6 m above ground, a frog was found and in the internode adjoining below seven bats were discovered. They obviously differed in coloration from the common bamboo-inhabiting flat-headed bats, *Tylonycteris pachypus* (Temminck 1849) and *T. robustula* Thomas, 1915. One individual which had its wings hurt during the sawing operation to open the internode was preserved in alcohol for documentation. The remaining 6 individuals took flight.

Upon examination it proved to be the rare *E. denticulus* (SMF 88495). It possesses all diagnostic characters of previous descriptions, e. g. reddish brown coloration, large pads on hind feet, longish ears, long and broad rounded-tipped tragus, flattened skull with broad rostrum and three lower premolars, the central one intruded from the toothrow (Osgood 1932; Koopman 1970, 1972; Hill 1992); additionally the thumb is relatively short and thick.

The adult female is of the following dimensions in mm: Head and body 43; tail 36; hindfoot s. u. (without pad) 5.15; tibia 16.8; ear 13.5; forearm including carpalia 36.6; 5th finger 48.3.

Skull: Greatest length to incisive alveoli 14.25; condylobasal length to incisive alveoli 13.63; mastoid breadth 7.32; breadth of braincase 6.68; height of braincase 3.74; zygomatic width 9.08; width across upper canines (crowns) 3.66; width across last molars M3/-M3/ 5.96; length of upper toothrow Cs-M3/ (crowns) 5.48; postorbital constriction 3.46; length of mandible to condylus 10.59; length of mandible to proc. angularis 10.57; length of lower toothrow Ci-M/3 (crowns) 5.83. In size this Thai specimen agrees with the series collected at the type locality and being slightly larger than the two specimens from Pegu Yoma (Koopman 1970).

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The mammae are not enlarged, and no embryo is present. Neither spinturnicid mites nor nycteribiid flies were detected.

In Vietnam one *E. denticulus* was collected in a house, a second one in forest (Cao Van Sung 1976). The bamboo containing this species in Khlong Lan N. P. grew in the steep hill range of the Thanon Thongchai Mts. predominantly covered by tropical broad-leaved evergreen forest and partly with submontane broad-leaved evergreen forest.

The bamboo internode in which the present specimens sheltered was ca. 5 m above ground, 57 cm long and 9.2 cm in diameter. The thickness of the bamboo wall was 8 mm. The internode was accessible by a vertical slit of 80 × 8 mm. Below the slit was a smaller hole, which was ca. 1 cm in length. Thus, the entrance was similar to the one shown by Medway and Marshall (1970: plate 2). Almost half of the internode was filled up with water and bat guano (thickness of the guano layer: 10–15 cm). The foul-smelling water and the bat guano layer contained ca. 30 hover fly larvae (Syrphidae, length up to 3 cm), ca. 200 mosquito larvae (Culicidae) and additional unidentified Diptera larvae.

The seven bats stayed in the upper part of the internode close to each other apparently using the adhesive discs on their feet to attach themselves on the wall. This was also observed in a specimen which was placed in a semi-transparent plastic bottle stored on its side. After a while the bat was seen hanging upside down from the upper part of the plastic bottle clinging to the smooth plastic wall by its adhesive discs.

Three vespertilionid genera are characterised by flattened skulls (also found in few petrophilous Molossidae), i. e. the Afrotropical *Mimetillus moloneyi* (Thomas 1891), and the two Oriental genera *Tylonycteris* Peters, 1872 and *Eudiscopus*. Food pads in *Tylonycteris* and *Eudiscopus* are shared with *Glischropus* Dobson, 1875 of the Asian tropics, which roosts inside dead bamboo stalks with oval to elongate holes (Kofron 1994). *Mimetillus* is known to roost under the bark of dead trees (Kingdon 1974), *Tylonycteris* is typically roosting in groups inside bamboo internodes (Medway and Marshall 1970).

Walker (1964) speculated that the adhesive disks on the feet of *E. denticulus* might indicate frond and leaf roosting habits. According to Koopman (1972) the flattened skull suggests that this bat must crawl through narrow crevices and the foot pads suggest it must cling to relatively smooth surfaces. The present record documents that *E. denticulus* shares the habit of roosting inside hollow bamboo stems with *Tylonycteris*, a member of the same tribe Vespertilionini.

Medway and Marshall (1970) suggested that the holes used by *Tylonycteris* to enter bamboo internodes are made by the leaf beetle *Lasochila goryi* and are sometimes modified by woodpeckers. According to our own observations in the same area (Ulu Gombak, W. Malaysia) most entrance holes used by *Tylonycteris* are made by woodpeckers, which hunt larvae of bamboo-inhabiting leaf beetles, long-horned beetles or pyralid moths (see Kovac 1998). The entrance hole used by *Eudiscopus* was not made by *L. goryi* and was untypical of a woodpecker hole. It seems that the hole was made in an early stage of the culm development and subsequently became enlarged during elongation process of the internode.

Bamboo internodes provided with holes fill up with rain water. This peculiar aquatic habitat called bamboo phytotelma harbours a specialized arthropod animal community (Kovac 1998). In old, upright bamboo culms only a few arthropod specimens are found in a single internode. For example, in the internode next to the *Eudiscopus*-internode, which was inhabited by a frog (Rhacophoridae), we only found one semiaquatic bug specimen belonging to a new species of *Lathriovelia* (= *Baptista* sp. in Kovac 1998). Mosquito larvae or other arthropods were lacking. In contrast, the *Eudiscopus*-internode contained more than 200 specimens of Diptera larvae belonging to at least three different families. The Diptera species found in the *Eudiscopus*-internode did not occur in normal bamboo internodes investigated in Khlong Lan (n = 20) or in Ulu Gombak, W. Malaysia (ca. n = 500). This shows, that the eutrophication of the water caused by bat faeces considerably changes the composition of the arthropod community.

The thickness of the guano layer and the occurrence of various larval stages of Diptera indicate that the roost was used more or less regularly. It appears that *E. denticulus* roosts in groups as it is supported by the original collecting of six specimens at Phong Saly. The flat skull is a mere adaptive convergence to its roosting site, as it is in all other flat-headed bat genera, otherwise completely unrelated (MENU 1987). The adhesive foot pads appear to be an adaptation to the smooth bamboo walls, since all three Asian bat genera having foot pads roost in bamboo internodes.

The junior author has examined in recent years ca. 40 internodes in W. Thailand, more than 500 internodes in Ulu Gombak, W. Malaysia and about 40 internodes in Singapore, and about the same amount in Sabah and W. Sumatra. Only in Thailand *E. denticulus* was found once, while in other regions mentioned above it was always one of the *Tylonycteris* sp. Furthermore, the Ulu Gombak region was investigated very intensively by MEDWAY and MARSHALL (1970). They recorded 448 roosting parties of *Tylonycteris* between 1962 and 1968. If bamboo roosting is a regular habit of *E. denticulus*, very probably its occurrence does not extend south into W. Malaysia and beyond.

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Home range size of adult raccoons (*Procyon lotor*) in Germany

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The raccoon (*Procyon lotor* L.) is a Central- and North American carnivore (Kaufmann 1982) and was introduced into Europe 70 years ago (Müller-Using 1959). For the first time home range sizes of raccoons were studied outside the Americas (Hohmann 1998). The study was conducted between December 1992 and April 1996 in the southern Solling forest, a wooded variegated sandstone plateau in Lower Saxony, Germany (51° 41′ N, 9° 32′ E). The terrain is elevated between 100–350 m. The climate is oceanic with mild winters and cool summers. This area consisted of 66% mixed forests with a patchy distribution of different tree species (mainly beech *Fagus sylvatica*, oak *Quercus robur*, and *Q. petrea*, and spruce *Picea abies*). 27% of the area was designated as agricultural fields, 6% as human settlements, and 1% as watersheds (Hohmann 1998).

The forested parts af the study area were mostly fenced to prevent ungulate species (in particular red deer, *Cervus elaphus*) from damaging adjacent agricultural lands.

Between 12 and 27 traps were baited with sardines and plum jam within an area of 3,000 ha. After a baiting period of 29 to 40 days only three to five traps were set simultaneously for several consecutive days. Traps were checked every two to three hours during the night. For ease of checking and to prevent disturbance of the trap sites, radio transmitters were installed at the traps. Upon capture, raccoons were anesthetized with a mixture of ketamin hydrochloride and xylazin (20 mg : 1 mg per kg body weight). The anesthetized raccoons were weighed, sexed, aged (see Grau et al. 1970), marked with a transponder, and finally radiocollared. A collar weighed between 90 g and 155 g (which is 1.8% to 3% of a 5 kg raccoon). Each captured raccoon was released at the capture site.

Seven adult males (older than 24 months, for details see Hohmann 1998) and eight adult females (older than 12 months) were radio-tracked on average once per day and four times per night. To reduce autocorrelation of location data successive fixes were separated by a minimum of 60 min., but otherwise taken on an abitrary sampling regime (Rooney et al. 1998). In total 6 378 fixes were obtained, resulting in a mean of 425 fixes per individual (SD = 284). Of those approximatly 60% were night fixes. Each data set was separated into summer and winter seasons (see Tab. 1). Home ranges were determined by using both a Convex-Polygon (MCP, Mohr 1947) and a Kernel estimator (CWK, Worton 1987).

Each seasonal data set was considered as unbiased by sample size if the size of the home range did not increase over 20 added fixes. Not all individuals were studied for an equal number of seasons. To reduce the excessive influence of those individuals studied for long periods we took the mean of the same seasonal data for these individuals (Harris et al. 1990).

The home range median of adult male home ranges over both seasons was 1 236 ha (MCP) and 680 ha (CWK) respectively, the corresponding value for adult females was

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Table 1. Summer and winter home range of raccoons in the Solling, Germany, 1992–1996. Values in the row "range" refer to single seasonal home ranges. MCP: 100%-Minimum Convex Polygon-estimation; CWK: 95% Core-Weighted-Kernel-estimation, optimal smoothing factor by sixth square root of SD.

	Summer (16.4.–15.10.)				Winter (16.10–15.4)			
	Adult males		Adult females		Adult males		Adult females	
	MCP (ha)	CWK (ha)	MCP (ha)	CWK (ha)	MCP (ha)	CWK (ha)	MCP (ha)	CWK (ha)
Median	1 420	784	543	257	977	622	330	166
Mean	2 099	1 012	677	374	1 400	754	553	273
SD	1 830	719	403	356	1 047	526	547	227
Range	661–5 815	282–2 475	385–1 572	144–1 391	391–6 543	125–3 348	150–1 729	92–724
N	7	7	7	7	6	6	7	7

514 ha (MCP) and 243 ha (CWK) respectively (Tab. 1). Thus, adult males had approximately 2 to 3 times significantly larger home ranges than adult females (Mann-Whitney Rank Sum Test, summer: $p < 0.01$; winter: $p < 0.05$). Although summer home ranges of adult raccoons tended to be 23% to 50% larger than their winter home ranges this difference was not significant (Tab. 1, Mann-Whitney Rank Sum Test, $p > 0.05$).

Apart from one study in the unforested prairies of North America (Fritzell 1978) raccoon home ranges in Germany are the largest measured (Tab. 2). One reason could be that old oak stands, which provide important food sources like acorns, shelter and den sites (Kaufmann 1982; Hohmann 1998) were scattered in small patches of less than 50 ha and made up only 20% of the whole forest. Consequently, there is evidence that raccoons have to roam over larger areas to compensate for an inferior habitat.

Another reason could have been that oak forests in Germany in general are of lower diversity than in northern America (Ellenberg 1982; Sork et al. 1993). Thus, acorn masting events in Germany might be more pulsed and more coordinated than in America (Burschel and Huss 1997; Sork et al. 1993). Thus, the observed raccoons might have to cope with years in which acorns are scarce. They may again have to roam over larger areas to include enough oak forests into their home range to meet their needs.

A third effect could have forced the studied raccoon population to use larger areas: In the last decade the fenced red deer population reached high densities of more than 5 individuals per 100 ha (C. v. Prolius, pers. comm.). The red deer is a powerful browser and can reduce the available understory, and this in turn could have reduced the availability of food sources for raccoons.

It is noteworth that a rough estimation of the raccoon population density in the study area yields 2 to 4 individuals per 100 ha (Hohmann 1998). This estimate is based on a steady increasing recapture rate reaching 4 recaptures per one new capture in the last 19 months of the study. Compared with other studies providing estimates on population densities in forested areas (Endres and Smith 1993; Gehrt 1994; Kaufmann 1982; Seidensticker et al. 1988) this is a fairly low density and again indicates the apparent poor quality of the habitat in the study area.

Apart from the above-mentioned differences in the absolute quantities of the areas used by the raccoons, intrasexual differences were similar to their American counterparts (Gehrt and Fritzell 1997).

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Table 2. Comparison of home ranges sizes of adult raccoons from different study areas in North America and one study area in Germany (this study). Authors considered in this table calculated the home ranges on a monthly time base and tracked the animals over a 24-hour cycle. All authors used radiotelemetry and Minimum-Convex-Polygon estimator (MCP) or a Kernel estimator (KERNEL) for determining home range areas. List arranged according to size of home range.

				Estimator MCP		Estimator KERNEL	
Publication	Location	Habitat	Definition of given values	Home range of adult males (ha)	Home range of adult females (ha)	Home range of adult males (ha)	Home range of adult females (ha)
Fritzell (1978)	North Dacota	rural	mean	2560	806		
this study	Lower Saxony	mostly forest	mean	1776	615	893[1]	324[1]
this study	Lower Saxony	mostly forest	median	1236	514	680[1]	243[1]
Lehman (1984)	Indiana	rural	mean	486	264		
Gehrt and Fritzell (1997)	Texas	partly rural/forested	median	339	79	416[2]	90[2]
Glueck et al. (1988)	Iowa	partly rural/forested	mean	131	79		
Johnson (1970)	Alabama	mostly forest	1 individual	93			
Urban (1970)	Ohio	marshland	mean	88			
Rosatte et al. (1991)	Ontario	urban	mean	42			
Hoffmann and Gottschang (1977)	Ohio	urban	mean	16	4		

[1]: 95%-Core-Weighted-Kernel
[2]: 95%-Adaptive Kernel

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Buchbesprechung

Andersen, R.; Duncan, P.; Linnell, J. D. C. (eds.) (1998): **The European roe deer: The biology of success.** Oslo, Stockholm, Copenhagen, Oxford, Boston: Scandinavian University Press. Hardcover, 376 pp., numerous illust. Norwegian Kr 378,–/DM 86,–/US$ 48,–. ISBN 82-00-37682-6.

This book introduces the reader to a wide range of biological and conservational aspects of the most common European ungulate species. 39 authors from 26 institutions in nine countries have cooperated and produced a volume that is much more than an introduction to a game species. Hunting lore cannot be found in this book at all, but a wealth of information about *Capreolus capreolus.* This cervid extended its range during the course of the last century far into Fennoscandia. A small "population ... in 1850 has extended to cover much of Sweden, Norway and Finland" (Holand et al., this volume).

The contents of the present publication consists of 14 chapters, all of them multi-authored. According to the impression of the reviewer these chapters can be grouped into five sections: In the first one (chapters 1 to 4) a general portrait of *Capreolus capreolus* is presented, followed by an introduction into general morphology and evolution of this successful species and into its glacial and post-glacial distribution. A chapter on its genetics follows, as was revealed by modern investigations on molecular variability, population history and structure.

The second section (chapters 5 and 6) deals with feeding and physiology of digestion and – extraordinarily interesting – with physiological and behavioural adaptations of the species to northern environments. The following four chapters could be grouped under the headline "General and special ecology". Roe deer is discussed as a prey of carnivorous mammals (red fox, wolf, and lynx); the reproductive physiology of *Capreolus capreolus* is dealt with and information on the social organization, as well as on the mating systems (under special consideration of male territoriality) are considered in detail. The section comprising chapters 11 to 13 deals with the early period of roe deer life and discusses life-history parameters, as well as population dynamics of that species. The concluding chapter 14 presents information on the management of *Capreolus capreolus* and on the influence of this species on the environment.

The editors managed to present the different chapters in similar styles. At the end of each chapter the authors give an extensive list of references and the book is concluded by a useful index of 3 1/2 pages. As a whole, this most informative volume on an interesting and successful cervid species is excellent reading for any mammalogist. It has to be considered as a special asset of this book that emphasis is paid to roe deer in northern Europe and not so much to those from the central part of the continent where extensive reviews have been published previously (v. Raesfeld 1965; Strandgaard 1972; Ellenberg, 1978). From this new synthesis the reader can collect a wealth of up-to-date information not only on roe deer, but on general aspects of ecology, population dynamics and ungulate biology, to name just a few.

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Foraging areas and relative density of bats (Chiroptera) in differently human transformed landscapes

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Abstract

This study on the foraging areas of bats was conducted on 64 transects (2 km long) in different habitats and urban zones in central Poland. Relative bat densities in the city (Warsaw) were only slightly lower than in comparable habitats outside the city. The maximum densities of foraging bats were noted in wooded and riparian habitats (in the city respectively 2.0 and 1.0 records/100 m per count; outside of the city – 1.8 and 1.5 records/100 m per count). Open areas were the least frequently visited by foraging bats. Built-up areas outside the city were characterized by higher densities than city built-up areas. The percent of *Eptesicus serotinus* records was highest in the central zone (about 66%) and decreased with the distance from the city centre. The main foraging areas of *Nyctalus noctula* were distributed in riparian habitats of all zones. *Pipistrellus nathusii* and *Myotis* spp. were more frequent in a landscape less transformed by human activity. Tree cover within a foraging site was the most important factor influencing bat density.

Key words: Chiroptera, foraging, habitat use, urbanization, Poland

Introduction

Most European bat species are synanthropic, frequently using human-made structures as roosts. They feed mainly on small invertebrates and therefore seem dependent of natural habitat types, especially rich in vegetation and water (Thomas 1988; Walsh and Mayle 1991). Studies on bat communities inhabiting areas highly transformed by man, namely cities, showed that a relatively low number of species is adapted to live in densely built-up areas (Jones and Jayne 1988; Benzal and Moreno 1989). Urban bat communities compared with non-urban ones are characterized by a lower number of species, decreased species diversity, and a strongly expressed dominance of a single species (Kurta and Teramino 1992). However, there is little data on this subject and the variation of urban bat communities is still poorly known.

Typical urban species in this group of animals, which are absent or scarce in non-urban habitats, were not recorded. Inhabiting a variety of landscapes, bats show plasticity in space use. Up to now few publications have focused on the variability of foraging areas in relation to anthropogenic changes of the environment. It was pointed out that bat densities in a city are lower than in non-urban habitats. A longer period of foraging in the city is an effect of reduced insect abundance (Geggie and Fenton 1985; Furlonger et al. 1987; Kurta and Teramino 1992; Rydell 1992).

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So far there are no data showing the foraging sites and bat densities in a broader urbanization gradient – from the city centre through suburbs to the interior of a large forest. Therefore, the aim of this study was to determine the bats preference to different foraging areas in different landscapes and to conclude in what way it reflects the space use and bat community structure in the city and outside.

Material and methods

The study area covered lowland landscapes from the centre of a large city (Warsaw – about 2 million inhabitants) through its suburbs to the relatively undisturbed coniferous and mixed forest of the Kampinos National Park (Fig. 1). The Vistula river-bed, a few hundred metres wide, determined the northeast border of the study area. We divided the area into 5 urban zones, in the city: central (I) and outskirts (II), and outside of the city: suburbs (III), non-urbanized, close to the city – 15–22 km from the city centre (IV), non-urbanized far from the city – over 22 km from the city centre (V) (Fig. 1, Tab. 1). The central zone was located in densely built-up areas inside a historical centre where only some small areas were covered by residential houses and parks. The outskirts differed by relatively large areas covered by new residential houses (mostly multistorey, less than 30 years old). New low buildings dominated the built-up area of the suburban zone. The percentage of wooded area and arable fields was considerably higher compared to the city. Only villages occurred in non-urbanized zones (the border of 2 zones was arbitrarily determined taking into account the distance from city centre). The landscape was dominated by forests and arable fields.

The study was conducted between 1992–1994. Bats were recorded and counted by using an ultrasound detector (type PETTERSSON D 90 and D 100) along line transects 2 km long. In total 64 transects were surveyed (from 9 to 18 in each zone). We also classified them to 4 habitat types. Each transect represented one habitat type: wooded (forest or park), open area, built-up area, riparian.

Before starting the count we determined the atmospheric condition and selected only warm evenings (min. +15 °C but preferably > 20 °C), with little or no wind and no rain. Each transect was surveyed 3 times a season (in June, July, August). A single count lasted 2 hours starting with the calendar hour of sunset. During that time the transects were walked 3 times (each walk lasted 40 minutes). Bat records were mapped, and the following categories of behaviour were noted: (1) passes, (2) passes with foraging – we heard "feeding buzzes" or saw clear turns and changes in the height of flight, (3) circling with feeding. We also took note of the number of individuals (if we could see or hear many at the same time) and the species (if identified). Frequently it was too dark to observe bats, in some cases we did not know if we had heard the same or another individual (therefore we gave the number of records, not individuals). The next record (even if it was possibly the same individual already recorded) was noted after a break in bat calls of at least one minute. When bats were calling continuously, successive records were noted every two minutes.

During each count a detector was focused on 30–35 kHz, and after detecting a bat, the right frequency was found. The range of frequencies used by bats in the community studied was rather narrow – from 20 to 45 kHz. The species of bats were determined based on the rhythm, intensity and frequency of sounds, compared to records on the cassette (Ahlén 1989). We were able to identify 3 species. Bats of the genus *Myotis* were not distinguished, but taking into account their presence in roosts

Table 1. Number of transects under study in different habitats and zones (total 64).

Habitat type	Zone				
	Central (I)	Outskirts (II)	Outside city		
			Suburban (III)	IV	V
Built-up	6	8	4	4	3
Wooded	4	6	2	5	4
Open	0	2	2	4	3
Riparian	2	2	1	1	1

and results from netting (Kowalski and Lesiński 1995), probably the most common were *Myotis nattereri* and *Myotis daubentonii*, less frequently *Myotis brandtii* or *Myotis mystacinus*. Some records were not classified to species.

We described the intermediate surroundings of the transect within a 60 m wide belt (30 m on either side of the transect). If the habitat was not uniform, the transect was subdivided into sections not shorter than 200 m. We estimated the percentage cover of: trees, shrubs, open areas (crop fields, meadows, pastures, wasteland – if not in the range of tree canopy or shrubs), areas covered with concrete or asphalt, buildings, and waters. Also the number of working street lamps was noted.

Results

Relative density of foraging bats

The number of bat records on transects showed high variability within the urban zones (Fig. 1). Both transects rich and poor in bats occurred at each zone. The highest density of feeding bats was noted in a belt a few km wide along the river. Most bats in the city were recorded in riparian habitats, both in the central zone (2 records/100 m per count) and in the outskirts (1.3 records/100 m per count). Outside of the city the maximum bat densities were noted along the river (IV zone – 1.8 records/100 m per count) and in

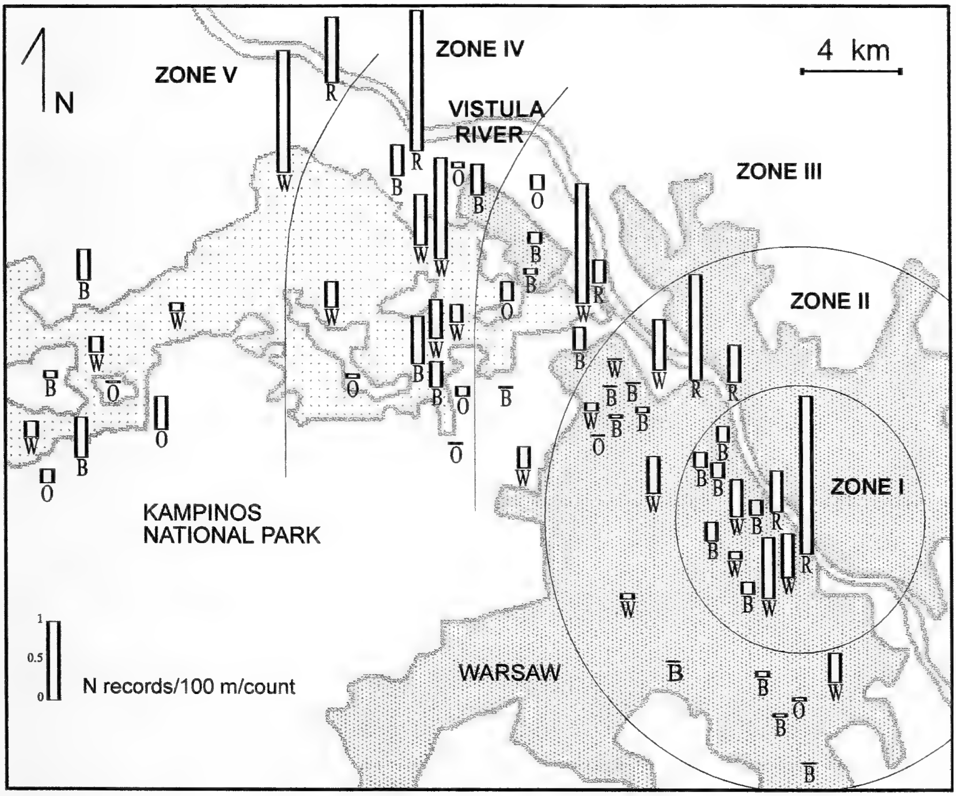

Fig 1. Total relative bat densities on transects within distinguished zones. I – central, II – outskirts, III – suburban, IV – non-urban close to the city, V – non-urban far from the city. Densely built-up area – dark grey, forests – light grey. Habitat type: O – open, B – built-up, W – wooded, R – riparian

wooded habitats: suburban zone III – 1.5 records/100 m per count, zone V – 1.6 records/100 m per count. Built-up areas in the city (especially the outskirts) were characterized by a low number of foraging bats (from 0 to 0.2 records/100 m per count). There were up to 0.5 records/100 m per count in the built-up areas outside of the city. The lowest number of bats was noted in open habitats. At 3 transects in the outskirts of Warsaw, located in open habitats, bats did not appear during all counts. Bats were rarely recorded also in open habitats outside of the city (up to 0.4 records/100 m per count at transects with relatively numerous trees).

Species composition of bats foraging in the city and outside of it

Eptesicus serotinus dominated the bats recorded by detectors in the whole study area. More than 60% of the records in the central zone dealt with this species. For many urban transects it was the only bat species noted. Its contribution in the community decreased with the decreasing level of urbanization. However, *Nyctalus noctula* and *Pipistrellus nathusii* were noted less frequently in the city. *Myotis* species densities were slightly lower in suburban and central zones, and higher further away from the city (Tab. 2).

Table 2. Total and percent of records represented by each species within the diverse zones. n – the sum excluding unidentified bats *Es* – *Eptesicus serotinus*; *Nn* – *Nyctalus noctula, Pn* – *Pipistrellus nathusii*

Zone	n	*Es*	*Nn*	*Pn*	*Myotis*
City					
Central (I)	334	66.5	28.4	1.2	3.9
Outskirts (II)	247	53.0	32.8	2.4	11.8
Outside city					
Suburban (III)	233	46.3	42.1	7.7	3.9
IV	409	46.2	34.2	5.4	14.2
V	222	43.2	29.3	3.2	24.3

Preferred bat foraging areas

The most numerous species, *Eptesicus serotinus* and *Nyctalus noctula* used each habitat type differently, both occurred less frequently in open areas (arable fields or meadows). The foraging of *Eptesicus serotinus* in a city was focused mainly on wooded and riparian habitats. The riparian habitat was rarely visited outside of the city (no more frequently than open areas), but the built-up area was as important as the forests. *Nyctalus noctula* was frequently noted in riparian habitats of all zones (up to 92% of records outside of the city), and rarely in built-up areas. The species frequently used wooded habitats in the city and suburban zone (Tab. 3).

The significant differences between *Eptesicus serotinus* densities in the city and outside of it were obtained in built-up areas and riparian habitats (Tab. 4). Also *Nyctalus noctula* foraged more frequently in riparian habitats located outside of the city than in Warsaw. Taking into consideration all detected species, the differences in preferred habitats outside of the city were noted for open and built-up areas.

The density of bats foraging over open habitats in Warsaw were significantly lower than in wooded and riparian habitats, both for *Eptesicus serotinus*, *Nyctalus noctula*, and all bat species. Regarding outside city zones, *Eptesicus serotinus* mostly foraged in wooded and built-up areas, and *Nyctalus noctula* distinctly preferred riparian habitats (Tab. 4).

For all bat species the least attractive hunting area was located in open habitats. Similar densities were noted in non-urban built-up areas and forests but were higher in a river valley compared to built-up and open areas. The highest density of an urban bat community occurred in parks and along the river (Tab. 4).

Among the 6 habitat characteristics described for the 60 m transect belt, five significantly influenced the density of detected species (Tab. 5). The percentage of shrub cover

Table 3. The use of different habitat types by *Eptesicus serotinus* (*Es*) and *Nyctalus noctula* (*Nn*) in urban zones (% of records per transect). x – no data, N – number of records

Zone	Species	N	Wooded	Built-up	Riparian	Open
City						
Central (I)	*Es*	222	47.1	20.6	32.3	x
	Nn	95	48.9	5.3	45.8	x
Outskirts (II)	*Es*	105	24.0	2.5	72.2	1.4
	Nn	49	17.2	2.2	78.0	2.7
Outside city						
Suburban (III)	*Es*	58	73.5	26.5	0	0
	Nn	41	29.9	6.7	52.2	11.2
IV	*Es*	154	44.1	45.7	6.2	4.0
	Nn	137	2.2	4.5	92.0	1.3
V	*Es*	96	41.4	41.4	6.9	10.3
	Nn	65	4.4	5.8	80.8	9.0

Table 4. Comparison of the relative densities of bats (number of records per 1 km of a transect) in different habitats in the city (central zone + outskirts) and outside the city. Median values (M), lower and upper quartiles (LQ, UQ) are given. Habitat type: O – open, B – built-up, W – wooded, R – riparian. Differences: NS – not significant, * – $p < 0.05$, ** – $p < 0.001$

Species	Habitat type	Non-urban habitats (1)			Urban habitats (2)			Differences 1 v. 2
		M	LQ	UQ	M	LQ	UQ	
Eptesicus serotinus	O	0.8	0	1.5	0.3	0	0.5	NS
	B	4.0	2.0	7.0	1.3	0	3.5	*
	W	5.0	0.8	11.0	8.0	1.0	9.5	NS
	R	1.0	0	1.0	6.5	3.0	13.0	*
Nyctalus noctula	O	1.0	0	1.8	0	0	0.5	NS
	B	1.0	0	3.0	0	0	0.5	*
	W	1.0	0.5	2.3	1.5	0.5	3.5	NS
	R	16.5	8.0	44.0	6.5	4.0	8.0	*
All species	O	2.8	1.0	5.3	0.5	0	1.0	*
	B	9.5	4.0	11.5	2.0	0.5	5.5	*
	W	13.0	6.3	23.3	12.5	2.5	16.5	NS
	R	25.0	10.0	51.0	16.0	13.0	25.0	NS

Differences between habitat types:
E. serotinus – non-urban: OB-*,O/W-*,O/R-NS, B/W-NS, B/R-*,W/R-*;
urban: OB-NS, O/W-*, O/R-*, B/W-NS, B/R-*, W/R-NS
N. noctula – non-urban: OB-NS, O/W-NS, O/R-*, B/W-NS, B/R-* *, W/R-*;
urban: OB-NS, O/W-*, O/R-*, B/W-*, B/R-**, W/R-*
All species – non-urban: OB-*, O/W-*, O/R-*, B/W-NS, B/R-*, W/R-NS;
urban: OB-NS, O/W-*, O/R-*, B/W-*, B/R-**, W/R-NS

Table 5. Correlation coeffcients between number of bat records and habitat characteristics of transects (% cover by different elements of habitat structure or number of elements per 100 m).
NS – not signifcant, * – $p < 0.05$, ** – $p < 0.001$

Habitat characteristics	*Eptesicus serotinus*	*Nyctalus noctula*	*Pipistrellus nathusii*	Total
Trees (%)	0.39*	NS	0.27*	0.51**
Open areas (%)	–0.38*	NS	NS	–0.45**
Waters (%)	NS	0.29*	NS	NS
Buildings (%)	NS	–0.39*	NS	–0.36*
Street lamps (n)	NS	–0.29*	–0.32*	–0.27*

Table 6. Correlation coeffcients between the number of bat passes without foraging or records of foraging bats and the habitat characteristics of transects.
Explanations as in table 4.

Habitat characteristic	*Eptesicus serotinus*		*Nyctalus noctula*	
	passes	foraging cases	passes	foraging cases
Trees %)	0.34*	0.39*	NS	NS
Open areas (%)	–0.34*	–0.40*	NS	NS
Waters (%)	NS	NS	NS	0.37*
Buildings (%)	NS	NS	–0.36*	–0.26*
Street lamps (n)	NS	NS	–0.32*	NS

appeared not to be significant in any case. The area covered by trees was the main factor for bats, especially *Eptesicus serotinus* and *Pipistrellus nathusii* (positively correlated with their densities). An increase in the percent of water showed increased *Nyctalus noctula* density. Working street lamps were not significant for bats or negatively correlated with the density of some species (*Nyctalus noctula* and *Pipistrellus nathusii*).

Separate analysis of passes without foraging and passes with “feeding buzzes” or clear turns (Tab. 6), showed that most of the obtained relationships were similar. Differences were noted in the case of *Nyctalus noctula*. The number of its passes did not correlate with the percentage cover of water. No correlation was found between foraging cases and density of working street lamps.

Discussion

Relatively low differences in bat density of comparable habitats within a city and outside of it indicate that urban habitats are only slightly less attractive for bats than non-urban ones. Many species find a variety of shelters in cities, and the main factor limiting their density seems to be the occurrence of trees and of water as resulted from this study. Vegetation obviously is especially important because potential bat prey is associated with trees or shrubs. Quantitative decreases in urban bat communities (Geggie and Fenton 1985) mostly depend on differences in the vegetation cover.

Eptesicus serotinus dominates the studied community because of its synanthropy and connection with anthropogenic shelters, both in winter and summer (Kowalski and Ruprecht 1984; Stebbings and Griffith 1986). The results of this study showed that feeding individuals of *Eptesicus serotinus* mostly fly near vegetation in parks and forests. Probably its numerous presence depends on the distance from shelters. For example, the riparian habitats were frequently visited in Warsaw (close to built-up areas with many lofts – preferred shelters) and rarely outside of the city. Nevertheless, comparatively long flights between shelters and foraging areas are known, usually up to 2 km (Glas 1980/81; Degn 1983), rarely more (Perez and Ibañez 1991; Catto et al. 1996).

The proportion of smaller species, e. g., *Pipistrellus nathusii* or *Myotis* spp. in the studied community could be higher than observed, because of the lower rate of detection (weaker sounds). However, even taking this into consideration, the dominance of *Eptesicus serotinus* is highly expressed, at least in urban habitats.

Our results confirm the high importance for bats of areas bordering on waters (McAney and Fairley 1988; Walsh and Mayle 1991; Rachwald 1992; de Jong 1994; Vaughan et al. 1997; Gaisler et al. 1998), both in the city and outside of it. Despite a lack of direct evidence, we can assume that in the study area *Nyctalus noctula* regularly flies between daily shelters in forests and foraging areas in the Vistula river valley. Also in Zürich this species frequently hunted on insects near the river (Stutz and Haffner 1985/86). Similar to our study area, cases of *Nyctalus noctula* foraging inside a forest were rather rare in the vicinity of Munich, but usually noted at forest edges and in open areas near a lake, up to 2.5 km from shelters (Kronwitter 1988). The lack of correlation between *Nyctalus noctula* passes without foraging and the percent of waters in the study area, indicates that in many cases these bats fly over nonspecific foraging areas whilst commuting.

Many studies have demonstrated the low importance of open areas for bats (McAnney and Fairley 1988; Gaisler and Kolibac 1992; de Jong 1994, 1995) and this was confirmed in Warsaw and the surrounding area. The lowest bat densities were noted in this habitat type independently from the level of urbanization. It can be explained by the lower abundance of potential prey (de Jong 1995), although not for all species of bats (Ekman and de Jong 1996), and perhaps also by a lack of linear landscape elements, that help bats to commute safely and make easier orientation possible (Limpens and Kapteyn 1991; Speakman 1991; Ekman and de Jong 1996).

Urban built-up areas appeared to be less attractive to bats than non-urban ones, this results from the low volume of vegetation among city buildings and generally lower densities of insects (Geggie and Fenton 1985; Jones and Jayne 1988).

Working street lamps have no distinct importance in bat foraging in the landscapes under study. Even the avoidance of sites with lamps were pointed out which contrasts with some data from western and northern Europe (Rydell 1991). Our study was carried out from June to August, therefore during the period of high insect activity. Working street lamps may be more important for bats in early spring and autumn when insects are less numerous and their local concentrations make foraging easier.

Results for *Eptesicus nilssoni* in Scandinavia also confirm this explanation. Until the first of May almost all individuals foraged near lamps but only 25–50% in June and July (Rydell 1991). Geggie and Fenton (1985) noted that foraging of *Eptesicus fuscus* near lamps occurred in non-urban habitats, and not in the city. Similar patterns were absent in the community under study.

For *Eptesicus serotinus*, feeding mostly on beetles (Robinson and Stebbings 1993), working street lamps are not attractive (those insects are not attracted to lamps). However, the negative correlation between *Nyctalus noctula* or *Pipistrellus nathusii* densities obtained here and the density of working street lamps was rather accidental. Both species are less numerous in urban habitats compared to built-up areas, where street lamps are common.

The results of this study have pointed out that detected bat species show different preferences for foraging areas. The described relationships, however, were not strict and explained rather a low percentage of variability in the observed bat densities. Probably it was because bats are opportunistic in foraging site selection and change habitats in relation to seasonal variation in the abundance of insects. This phenomenon has been shown for *Eptesicus serotinus* in southern England (Catto et al. 1996) and for the north American *Myotis yumanensis* (Brigham et al. 1992). *Eptesicus serotinus* can be identifed as best adapted to live in urban habitats of central Poland. *Nyctalus noctula* clearly penetrates the outskirts of Warsaw. *Pipistrellus nathusii* and some *Myotis* sp. show the highest level of avoidance of urban habitats.

Zusammenfassung

Jagdreviere und relative Dichte von Fledermäusen (Chiroptera) in von Menschen unterschiedlich veränderten Landschaften

Diese Studie über die Jagdreviere von Fledermäusen wurde auf 64 Transekten (je 2 km lang) in verschiedenen Habitaten und urbanen Regionen im zentralen Polen durchgeführt. Diesbezügliche relative Dichten von Fledermäusen in der Stadt (Warschau) waren nur wenig geringer als in vergleichbaren Habitaten außerhalb. Die höchsten Dichten ergaben sich für Baumbestände und Flußufer (in der Stadt: 2,0 und 1,0 Ortungen/100 m pro Zählung; außerhalb: 1,8 und 1,5 Ortungen/100 m pro Zählung). Offenes Gelände wurde von jagenden Fledermäusen am seltensten aufgesucht. Bebaute Regionen außerhalb der Stadt zeigten höhere Dichten als die städtischen. Die relativen Nachweise von *Eptesicus serotinus* waren im Zentrum der Stadt (mit ca. 66%) am höchsten und verringerten sich mit zunehmender Entfernung vom Stadtkern. *Nyctalus noctula* suchte in allen untersuchten Zonen hauptsächlich an Flußufern Nahrung. *Pipistrellus nathusii* und die Arten von *Myotis* waren häufiger in den weniger vom Menschen beeinflußten Landschaften zu finden. Baumbestände in den Jagdrevieren waren der wichtigste beeinflussende Faktor für die Fledermausdichte.

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Sexual segregation, roosting, and social behaviour in a free-ranging colony of Indian false vampires (*Megaderma lyra*)

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Abstract

We investigated roosting structures and social interactions of free-living Indian false vampire bats (*Megaderma lyra*) in a colony of about 60 individuals. False vampires entered the roost between 05.00 h and 05.45 h. Emergence was between 18.00 h and 19.00 h. An analysis of roosting patterns during day time revealed that sexes partially segregated within the roost during the period of pregnancy and lactation, although individual bats differed in compartment fidelity. Our study contradicts previous views reporting that false vampires roost in contact clusters. Our findings show that false vampires roost at a median distance of 9 cm. Occasionally, however, up to five false vampires established body-body-contact, sometimes initiated by 'greetings'. Body-contact was never observed between adult males and in captivity it was restricted to mother and offspring.

Key words: *Megaderma lyra*, Chiroptera, roosting, social behaviour, sexual segregation

Introduction

Echolocation, foraging ecology, and behaviour of bats are fairly well documented (NEUWEILER 1989, 1993). BRADBURY and VEHRENCAMP (1976 b) emphasised that the distribution of food and foraging behaviour may be important for the formation and structure of groups in bats. Nevertheless; knowledge about roosting structure and social interactions among bats is still limited (e. g. BRADBURY 1977; BRADBURY and EMMONS 1974; BRADBURY and VEHRENCAMP 1976 a, b, 1977a, b;. KOZHURINA 1993; LEIPPERT 1991, 1994; PORTER 1979 a, b; O'SHEA 1980; VAUGHAN and VAUGHAN 1986; WICKLER and UHRIG 1969; WILKINSON 1985 a, b, 1986).

Indian false vampire bats (*Megaderma lyra*) are easy to keep in captivity. Hence echolocation and foraging techniques are well known (ADVANI, 1981; FIEDLER 1979; HABERSETZER 1983; MARIMUTHU and NEUWEILER 1987; MARIMUTHU et al. 1995; SCHMIDT 1992). Recently LEIPPERT (1994) discovered elaborated flight manoeuvres accompanied by social vocalisations in captive false vampires, suggesting that social interactions may be important also in this species. However, little is currently known about roosting behaviour and social organisation of free-ranging false vampires and results of previous studies are contradictory. The only study concerned with foraging behaviour of free-ranging false vampires reported merely that individuals share perches with conspecifics and do not forage in exclusive territories (AUDET et al. 1991). False vampires hang in contact clusters (BROSSET 1962) and live in year round multi-male and multi-female groups of several to hundreds of animals (GOPALAKRISHNA and BADWAIK 1989; HABERSETZER 1983) or they segre-

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gate when birth is imminent (Balasingh et al. 1994; Nowak 1991). Mating occurs in November and December and gestation takes almost five months (Gopalakrishna and Badwaik 1989). Data from a captive colony, however, suggest a gestation time of only three months (D. Leippert, pers. obs.).

A previous study done at the same colony as the present study (Balasingh et al. 1994) suggested that males leave the colony during the time females give birth and rear their young. However, Balasingh et al. (1994) did not quantify these results and thus the presence of merely a few males can change this picture of a pure nursery colony. The present study aimed to collect quantitative data on sexual segregation and roosting habits of female and male Indian false vampire bats during the time when females give birth and rear their young. Furthermore, we aimed to study social interactions of this carnivorous bat species inside the day roost.

Material and methods

Field work was conducted during the end of the cool season and the beginning of the dry season between February and end of April, 1995, when females were expected to give birth and rear their young (Balasingh et al. 1994).

Natural roosts of *Megaderma lyra* are caves but this species will also readily exploit man-made structures (Audet et al. 1991; Balasingh et al. 1994; Marimuthu et al. 1995). Cave dwelling false

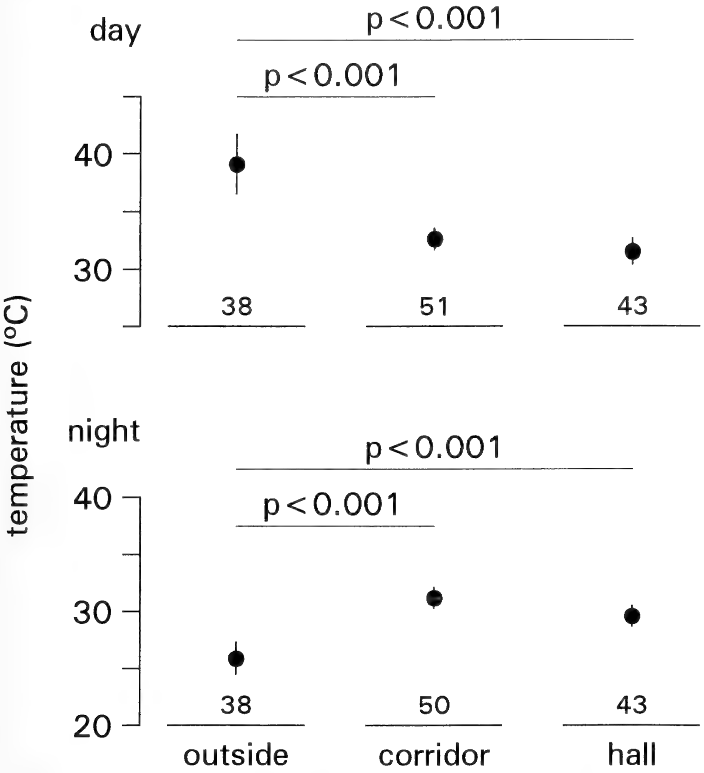

Fig. 1. Mean temperatures during the day and the night. Numbers indicate sample size. Maximum outside temperatures were significantly higher than in the hall (Wilcoxon signed-ranks test, N = 26, z = 4.457) and the corridor (N = 28, z = 4.644). Minimum outside temperatures were significantly lower than in the hall (N = 26, z = –4.514) and the corridor (N = 28, z = –4.671).

vampires are very shy and difficult to observe (Habersetzer 1983), hence we investigated a temple dwelling colony, which readily got used to our presence. The colony of about 60 false vampires roosted in an old Hindu-temple in Krishnapuram, a small village about 15 km south east of Tirunelveli (southern India). The temple consisted of 4 main compartments: the hall, the chimney room, the corridor, and the spire. Similar to a cave the temple significantly buffered outside temperature fluctuations (Fig. 1). The area around the temple was savannah-like with *Prosopis* and *Acacia* scrubs predominating (Audet et al. 1991) and included a lake and banana plantations.

The temple was continuously illuminated with dim red light (nine 15 W bulbs). The red light did not seem to disturb the false vampires, as bats often hung close to the bulbs.

False vampires were caught and tagged in order to allow individual identification. During 22 days one or two mist nets (4 m×2.5 m and 6 m×2.5 m) were strained between bamboo-sticks in the surroundings of the temple. During emergence between 18.45 h and 19.30 h we knelt beside the net and trapped a total of 69 bats (including recaptures of the same individuals), which were removed from the net immediately after capture. Lactating females carrying a pup were released without further handling to avoid injuries of the pup. Other individuals were sexed and weighed to the nearest gram. Forearm length was measured with a pair of vernier callipers to the nearest millimetre. The reproductive state of females (nulliparous, parous, pregnant, non-pregnant, lactating) was determined. We distinguished males with prominent and non-prominent testes.

Seventy percent of caught individuals already had been fitted with a collar and coloured plastic beads during a previous study (Balasingh et al., 1992). The beads, however, were invisible most of the time and only a few bats could regularly be identified from these tags. To enable individual identification we tagged them with wing bands (Museum Alexander-Koenig, Bonn, Germany, size E). The bands were modified using reflecting tape of 6 different colours. The tape was glued to the bands in different colour combinations to allow individual identification of 34 individuals (>50% of the colony). We tagged males on their left and females on their right forearms.

Observations in the day roost were conducted by one or two persons in three different compartments of the temple. We concentrated on periods in the morning and evening, when social activity peaked. Total observation time in the temple comprised 335 hours (4–6 hours per day). Most of the behavioural observations were made in the so-called chimney room. The seclusion of this room allowed us to come very close (ca. 4 m) to the bats without disturbing them. Watching individual behaviour was also possible in the corridor but sometimes obstructed by pillars. Periods of continuous observations lasted on average 2 hours.

Behavioural data were collected using the ad libitum sampling method (Martin and Bateson 1993). Observations were done using binoculars. Occasionally bats were briefly identified with white-light torches. After having spent at least 15 minutes at an observation point we recorded the positions of the bats either on diagrams of roosting compartments in the northern corridor, the hall, and the chimney room or registered the positions of bats in the hall and chimney room with a dictaphone. The latter method was faster and more convenient. The roosting records of the chimney room were used to calculate distances between individuals. For that purpose we covered the bar in the chimney room with yellow strokes in 15 cm intervals.

We assessed whether male and female false vampires segregated by calculating sex ratios in the hall, the northern corridor, and the chimney room using the data of the roosting records. Only individual data of banded bats were considered. To calculate distances between individuals we analysed one diagram or dictaphone record of the chimney room per day. If there were more than one plot/record per day we only considered the first one.

As there was no obvious change in the sex composition of false vampires in different compartments during the observation period we used the cumulative number of banded males and females in 3 compartments of the day roost (chimney room, N = 32 days; hall and northern corridor, N = 22 days each), to calculate the sex ratio in these compartments. We compared the results with expected values calculated from the sex ratio of banded bats. As the first records originated before we completed tagging false vampires, the number of banded males and females increased over time. To take this into consideration when calculating the expected sex ratios at each roosting compartment we counted the total number of banded males and females for every particular day. Then we summed up the number of banded females ($\Sigma\, n_{females}$) and males ($\Sigma\, n_{males}$) for all days on which samples were taken. Thus the expected value for females ($p_{females}$) was:

$$p_{females} = \Sigma\, n_{females} / (\Sigma\, n_{females} + \Sigma\, n_{males})$$

Correspondingly we determined the expected value for males (p_{males}).

To distinguish whether single bats used only one compartment or several compartments for roosting we calculated the proportion of records where an individual was sighted in the chimney room, the hall or the corridor.

Statistical analyses were done with SYSTAT 5.0 (Wilkinson 1990), following the procedures recommended by Conover (1980), Sokal and Rohlf (1996), and Lamprecht (1992). Results were considered significant if $p < 0.05$ (two-tailed). Data are presented as mean ± SD or, when skewed as median/interquartile range.

Results

Morphometrics

17 females (74%) were pregnant, one female was a nulliparous yearling (J. Balasingh, unpubl. data). The mean forearm length was 65.0 ± 1.8 mm in females ($N = 23$) and 65.0 ± 1.8 mm in males ($N = 30$). There was no significant difference between males and females (Mann-Whitney U-test, $U = 382$, n. s.). Body mass of non-pregnant females was 34.3 ± 2.7 g ($N = 6$). Males weighed 33.2 ± 1.8 g ($N = 30$). The difference between males and females was not significant (Mann-Whitney U-test, $U = 120$, n. s.). Forearm length and mass of non-pregnant females and males correlated significantly (Fig. 2; Spearman rank-correlation, $r_s = 0.404$, $N = 36$, $p < 0.01$). 71% percent ($N = 20$) of all tagged males (either collar or band) had prominent testes, whereas 29% ($N = 8$) had non-prominent testes. There was no significant difference in forearm length between males with prominent and males without prominent testes (Mann-Whitney U-test, $U = 55.5$, n. s.).

Inflight and emergence

Between 05.00 h and 05.45 h in the morning (before and during dawn) the false vampires returned from foraging and entered their day roost. Most of the animals roosted in the northern corridor (38/31–46 animals, $N = 22$). 12/10–15 animals ($N = 32$) stayed inside the chimney room and 5/2–8 animals ($N = 29$) mainly roosted in the hall. There was little activity during day time. In the evening activity started from 18.00 h onwards. Emergence started at dusk between 18.45 h and 19.00 h and lasted for 15–30 minutes.

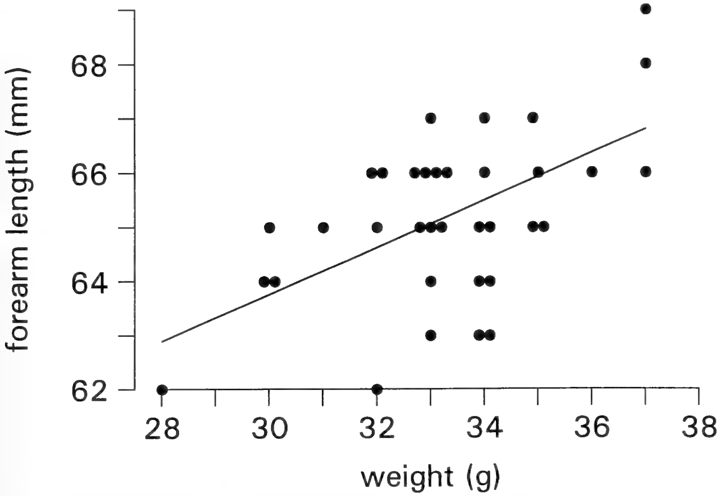

Fig. 2. Forearm length and weight of captured Indian false vampires ($N = 36$) excluding pregnant females and unbanded bats ($y = 0.436x + 50.692$).

Table 1. Median numbers of banded female and male false vampire bats at three roosting places inside the day roost.

part of temple	N	sex	min. no.	1st quartile	median no.	3rd quartile	max. no.
chimney room	32	♀♀	1	2.5	4.5	5.5	7
	32	♂♂	0	0.0	1.0	1.0	2
hall	22	♀♀	0	0.0	0.0	0.0	1
	22	♂♂	0	1.0	1.0	2.0	5
northern corridor	22	♀♀	0	1.0	1.5	2.0	4
	22	♂♂	1	3.0	4.5	5.0	8

Table 2. Total numbers of banded Indian false vampires in several parts of the day roost ($p_{♀♀\mathrm{exp}}$ = expected proportion of females, $p_{♂♂\mathrm{exp}}$ = expected proportion of males).

part of temple	N	no. of ♀♀	no. of ♂♂	$p_{♀♀\mathrm{exp}}$	$p_{♂♂\mathrm{exp}}$	binomial test
chimney room	32	130	22	0.463	0.537	$p < 0.001$
hall	22	1	37	0.466	0.534	$p < 0.001$
northern corridor	22	36	102	0.467	0.533	$p < 0.001$

Sex ratios at different roosting compartments of the day roost

In total 53 individuals were tagged either with collars (BALASINGH et al. 1994) or wing-bands. We recorded 23 females (43.4%) and 30 males (56.6%). The overall sex ratio was not significantly biased (Binomial test, N = 53, x = 23, n. s.).

Males and females tended to segregate in different compartments of the day roost (Tab. 1 and 2). In the chimney room 86% of all banded bats were females. This sex ratio was significantly female-biased (Tab. 2) and all males present were yearlings. In the hall and the northern corridor the sex ratio was significantly male-biased (97% and 74%, Tab. 2).

Compartment fidelity

From 31 identified banded bats 12 were seen in only one compartment 16 in two different compartments, and 3 in all three compartments. A total of 13 individuals was recorded in the chimney room (Fig. 3 a), another 13 in the hall (Fig. 3 b), and 25 individuals in the corridor (Fig. 3 c). Four banded bats were never seen in any roosting compartment. Two false vampires temporarily left the day roost after they had been banded. They spent one day or two weeks in a ruin close to the temple.

Individual spacing

Individuals usually kept a minimum distance to conspecifics. The median value for the distance of individuals was 9/5–14 cm (N = 321, Fig. 4). However, individuals did also establish close physical associations which we termed body-contact. Typically individuals joined each other by touching each other's bellies (N = 84). Belly-to-back (N = 10) or belly-to-wing (N = 2) contacts were also observed. Sometimes one animal embraced the other with its wing-membranes and up to 5 individuals could be involved in body-contact.

Body-contact was initiated in three different ways. Neighbouring false vampires shuffled towards each other, a bat could pass over other individuals to reach the partner,

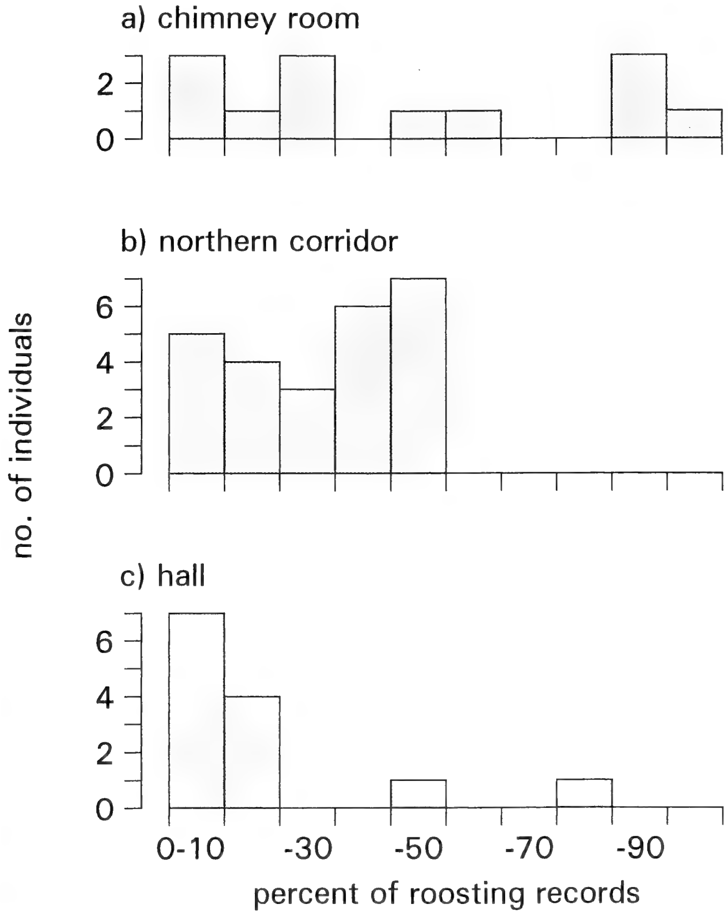

Fig. 3. Numbers of individuals present in proportion of roosting records in a) the chimney room, b) the northern corridor, and c) the hall.

or a false vampire flew to another individual. In 14 out of 49 observations of body-contact initiations a 'greeting ceremony' preceded body-contact. The false vampires sniffed each other and then they mutually rubbed their muzzles before making body-contact. Body-contact with 'greeting' lasted 6/1–8 min (N = 14), whereas body-contact without greeting lasted 2/1–8 min (N = 35). There was no significant difference in body-contact duration with or without 'greeting' (Kolmogorov-Smirnov two-sample test, D = 0.229, p = 0.59).

During body-contact every bat clung to its hanging place with one leg, but often the legs of two bats crossed over. Twice we heard soft purring sounds emitted by body-contact partners. Because these sounds were of low intensity we could not determine whether false vampires always vocalise during this behaviour. False vampires also hung in body-contact and groomed each other (N = 3).

We saw 47 body-contacts where at least one tagged individual was involved, both partners could be identified in 19 cases (Tab. 3). Body-contact occurred between females, between females and males, and between males with non-prominent testes. Body-contacts between males with prominent testes were never observed. Females did not have body-

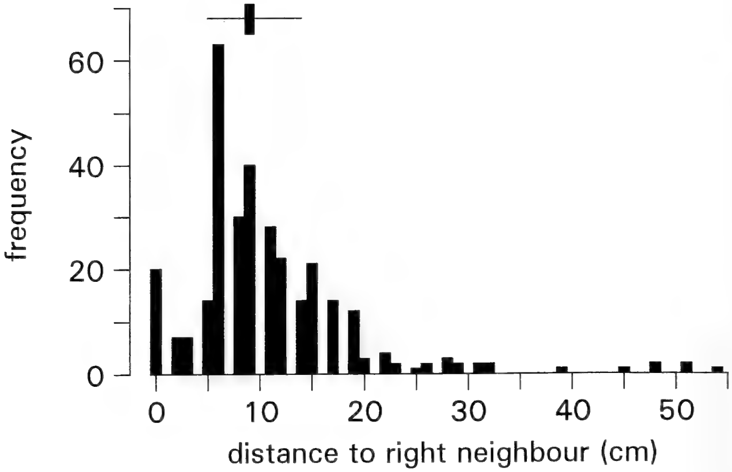

Fig. 4. Distances to the nearest right neighbour (N = 321). The box-plot in the upper left corner indicates median value and interquartile range.

Table 3. Frequency and duration of body-contacts between identified partners. The last two columns show the total number of body-contact in which the respective false vampire was involved including those where only one partner was identified. All males involved had non-prominent testes (bc = body-contact).

1st bat	2nd bat	3rd bat	no. of bc	duration of bc (min)	number of total bc	
					1st bat	2nd bat
♀ 008	♂ 016		4	7, 25, 1, –	9	12
♀ 008	♂ 025		1	0.3	9	1
♀ 008	♂ 741		2	2, 12	9	14
♀ 015	♀ 739	♂ 741	1	4	2	3
♂ 016	♂ 741		3	10, –, –	12	14
♂ 016	♀ 778		1	–	12	1
♀ 020	♀ 017		2	7, 18	8	3
♀ 020	♀ 686		1	12	8	2
♀ 020	♀ 701		1	10	8	3
♀ 028	♂ 741		2	1, 10	2	14
♀ 739	♂ 741		1	15	3	14

contacts more frequently with females than with males (Wilcoxon signed-ranks test, N = 9, z = 0.071, p = 0.94), but in all except three body-contacts (which took place always between the same two males) at least one female was involved.

'Greeting' occurred also without body-contact (N = 13). False vampires responded to individuals which initiated 'greeting' in three different ways: They returned the 'greeting' (N = 9), they ignored the 'greeting' (N = 2) or they made an aggression call (N = 2). When the receiver ignored the 'greeting' or made an aggression call the 'greeting' animal immediately retreated. Individual 'greeting'-data showed that animals of all sex combinations greeted (female-female: N = 3, female-male: N = 3, male-male: N = 3). All males involved in greeting had non-prominent testes.

Discussion

A previous study (GOPALAKRISHNA and BADWAIK 1990) suggested that false vampires avoid light, emerge only when it is completely dark and return to the roost before dusk. We could not confirm these results in our study colony. Most of the false vampires hung in the brightest compartments of the temple: corridor and chimney room. Furthermore the false vampires emerged at dusk and inflight lasted until dawn. In three other temple dwelling colonies we also found the false vampires roosting in rather bright areas of these day roosts.

Individual false vampires did not hang in contact clusters as suggested by BROSSET (1962), but hung at a median distance of 9 cm which allowed them to stretch their forearms or groom themselves without interference. However, they 'clustered' when they got disturbed and had no opportunity to retreat. Hence, it is likely that the animals in this previous study (BROSSET 1962) were not habituated to the presence of observers. Hanging in contact clusters might be disadvantageous: individuals may disturb each other, aggressions may be triggered more easily, and the transfer of ectoparasites may be facilitated. It is unlikely that false vampires face thermo-energetical limitations in a day roost which significantly buffered fluctuation of outside temperatures and provided constant ambient temperatures of more than 30 °C. In a captive colony spacing is common with ambient temperatures of only 25 °C (D. LEIPPERT, unpubl. data). Given these temperatures we consider false vampires unlikely to gain energetic advantages through clustering.

Social behaviour

False vampires regularly engaged in individual body-contacts. This behaviour possibly derives from mother-pup relationships. Pups older than 4 weeks clung to their mothers in such a position (pers. obs.). The same position is known from mother and pup in the yellow-winged bat, *Lavia frons*, that roost on tree branches and where this behaviour seems to be related to thermoregulation (VAUGHAN and VAUGHAN 1987; WICKLER and UHRIG 1969). Grown-up yellow-winged pups hung in close contact with their mothers when the ambient temperature was 22 °C, but they hung separately when the ambient temperature was 28 °C (VAUGHAN and VAUGHAN 1987).

Body-contact in free-living false vampires sometimes was preceded by 'greeting' behaviour and accompanied by purring sounds. In small captive groups body-contact was only observed between mothers and their offspring (D. LEIPPERT, unpubl. data). Our field data were insufficient to test whether body-contact in free-living false vampires is restricted to close relatives or whether individuals choose their partners opportunistically. If body-contact is selective we suggest that it helps to establish and maintain bonds between individuals of a distinct group of close relatives.

Roosting structure

BALASINGH et al. (1994) suggested that males and females inhabit separate roosts during the period of parturition but did not quantify their results. Males and females did not inhabit a separate roost in our study, but there was a partial segregation of sexes within the roost. There was no indication that single males monopolised hanging sites for the establishment of harems. As we only observed the colony during the time when females were either pregnant or lactating, we do not know whether this partial segregation lasts throughout the year.

The majority of identified bats used more than one compartment for roosting. Within the compartments they frequently changed sites. Only 31% of identified individuals roosted in the chimney room in almost every record. In the corridor we only found individuals roosting there in less than 50% of all records. Since the facilities in the corridor did not allow a reliable detection of individuals we may have missed some individuals roosting there more often. This could also be the reason why some banded false vampires were sighted only rarely or not at all. Unlike the chimney room and the corridor the hall was not occupied by bats throughout the day and hence we did not expect to find bats roosting there permanently.

In contrast to our findings cage dwelling false vampires seemed to choose particular sites for roosting (Habersetzer 1983). However, as Habersetzer (1983) did not observe banded individuals he might have observed different individuals using the same sites.

The social organisation of false vampires inside this day roost does not follow simple patterns. There is a partial sexual segregation at least during the breeding period. Individuals keep a minimum distance to conspecifics, but sometimes engage in body-contacts. Currently there is no quantitative evidence that individuals associate with certain other individuals. As some false vampires seemed to form small groups during evening emergence (pers. obs.) tracking such groups into their foraging grounds and investigating their composition and dynamics may help to answer these questions. If groups of false vampires should share foraging territories, links between food abundance and distribution, foraging behaviour, group size, and group composition might be expected, similar to those found in social carnivores (MacDonald 1983).

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Zusammenfassung

Geschlechtertrennung, Schlafplatz- und Sozialverhalten in einer freilebenden Kolonie von Indischen Falschen Vampiren (Megaderma lyra)

Wir untersuchten das Verhalten an Hangplätzen und die sozialen Interaktionen von Indischen Falschen Vampiren (*Megaderma lyra*) im Tagesquartier einer Kolonie von ca. 60 Tieren. Die Falschen Vampire flogen zwischen 5.00 h und 5.45 h in das Tagesquartier ein und verließen es wieder zwischen 18.00 h und 19.00 h. Eine räumliche Analyse der Verteilung von markierten Individuen im Tagesquartier ergab, daß es eine partielle Geschlechtertrennung während des Zeitraums der Trächtigkeit und Jungenaufzucht gab. Dennoch wählten die Individuen nicht immer den gleichen Hangplatz und wechselten auch innerhalb des Tagesquartiers in verschiedene Räume. Unsere Studie widerspricht früheren Ansichten, nach denen Indische Falsche Vampire in engen Kontakttrauben hängen. Wir fanden vielmehr, daß sie auf Lücke hängen und einen mittleren Abstand von 9 cm einhalten. Jedoch kam es hin und wieder vor, daß sich 2 bis 5 Tiere aufsuchten und in engem Körperkontakt zusammenhingen. Diese engen Kontakte wurden manchmal durch eine ‚Begrüßung', die aus gegenseitigem Schnauzenreiben bestand, eingeleitet. Körperkontakte wurden nie zwischen adulten Männchen beobachtet, in Gefangenschaft kamen sie ausschließlich zwischen Mutter und Kind vor.

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A recent collection of bats from Nepal, with notes on *Eptesicus dimissus*

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Abstract

Field work in and near Royal Chitwan National Park, Nepal, conducted during March 1990, resulted in the capture of 143 specimens of bats, including the following species: *Rousettus leschenaulti*, *Cynopterus sphinx*, *Eonycteris spelaea*, *Scotophilus heathi*, *Eptesicus dimissus*, *Pipistrellus javanicus*, *Pipistrellus coromandra*, *Pipistrellus tenuis*, *Nyctalus noctula*, *Hesperoptenus tickelli*, *Miniopterus pusillus*, *Miniopterus schreibersi*, *Murina cyclotis*, and *Kerivoula picta*. Of these, *E. spelaea* and *E. dimissus* are reported for the first time from Nepal, and the presence of *M. pusillus* and *K. picta* is verified and locality records provided. Additional information is provided about the morphology and systematic status of *E. dimissus*, which is currently known only from the holotype.

Key words: *Eptesicus dimissus*, Chiroptera, mammals, systematics, Nepal

Introduction

The bats of Nepal have received surprisingly little attention. In a recent compilation of the chiropteran fauna of the Indian subcontinent, Bates and Harrison (1997) indicated that only 47 species have been recorded from Nepal. Based on their distributions in neighboring areas, however, we suspect that at least 40 additional species might be expected to occur in that country. The aim of this study was to improve knowledge of the bat fauna of the especially poorly known lowlands of southwestern Nepal.

Material and methods

Bats were collected in the Royal Chitwan National Park, Chitwan District, Narayani, Nepal, during March 1990. A small collection was also made in Kathmandu. All collecting was done using mist nets. In total, 143 bats were collected; specimens are deposited in the University of Michigan Museum of Zoology, American Museum of Natural History, and Tribhavan University Natural History Museum in Nepal. All specimens were preserved in formalin and later transferred to alcohol; skulls were removed from some to facilitate identification.

This report provides a brief description of collecting sites and an account of the species collected. Previous published records of each species from Nepal are noted (but only if they refer to actual specimens collected, rather than being summaries of previous work or providing lists of species "antici-

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pated“ for Nepal). Some species clearly exhibit considerable geographic variation, but these patterns are poorly documented. For that reason, we report standard skin and forearm measurements of all bats (TL = total length, T = tail length, HF = hind foot length with claws, E = ear length from notch, TR = length of tragus, FA = forearm length) and cranial measurements for specimens for which cleaned skulls are available (CB = condylobasal length; CC = breadth across canines; MAX = maxillary toothrow length; LPAL = length of palate, measured from the anterior border of the palatines at the midline to the anterior border of the mesopterygoid fossa; BPAL = breadth of palate, the maximum distance between right and left upper molar toothrows measured from the labial sides; ZYGO = breadth across the zygomatic arches; BB = breadth of braincase measured at the widest point). All measurements were taken with calipers and are given as an average expressed in mm. Sample size is also reported.

Results and discussion

Collections were made at the following localities:

(1) Kathmandu 85°19.6′E, 27°43.2′N, elevation 1 340 m (3 March). A net was suspended from a bridge at the mouth of a large sewage tunnel, approximately 3 m high by 5 m wide. The above-ground stream formed by the effluent was lined by a thick growth of small trees and shrubs.

(2) Sauraha, Narayani, 84°29.5′E, 27°34.2′N, elevation 200 m (5–11 March). The Nepal Conservation Research and Training Center consists of a large brick laboratory-office building and 12 wooden buildings in a clearing at the edge of Royal Chitwan National Park. It is surrounded by the town of Sauraha and agricultural fields to the north, deciduous riverine forest south and west and a government elephant camp to the east. The forest is characterized by trees up to 20 m high, a non-continuous canopy, and dense undergrowth. It is transected by many trails made by people, domestic elephants, and wild rhinos. A river, the Dungari Khola, passes 200 meters from the research station. It is approximately 20 m across and appears to average 1–1.5 m in depth. Nets were placed at the edge of a clearing and over trails entering into the clearing (10 net-nights), near buildings in which bats (pipistrelles) were observed to roost (10 net-nights), and over the river (10 net-nights).

(3) Royal Chitwan National Park, Nandon Tal 84°28.7′E, 27°32.1′N (7 March). The forest is fairly open. Sal (*Shorea robusta*) trees are dominant, and in most areas there is a heavy understory of shrubs and grasses. Nets (six total) were placed over a stream, two small ponds, and across forest trails.

(4) Royal Chitwan National Park, Dudora Nala/Park rd 84°27.4′E, 27°33.6′N, 4.3 km SW Sauraha (13–15 March). At this locality, a small, slow stream, the Dudora Khola, crosses Park Road. The stream averages around 5 m wide and 30 cm deep. The surrounding mixed deciduous forest consists of large sal and simal (*Bombax ceiba*) trees, with a mid-story of vellar (*Trewia nudiflora*), *Litsea monopetala*, *Carea aborea*, *Ehretia laeuis*, *Butea monosperma*, and *Bahinia malabarica*. The treetops are covered with vines and epiphytes. Trees overhang the river, creating obvious flyways for bats. Over three nights we placed a total of ten nets across the stream and five in nearby forest.

(5) Royal Chitwan National Park, Tamar Tal NS 84°20.3′E, 27°31.9′N, approx. 13 km E Sauraha on Park Rd (16 March). Bats were captured over and near a large, shallow lake, approximately 1 km long and 1–200 m across. The lake is surrounded by grassland on one side and sal forest on the other. We placed three nets extending from shore towards middle of lake, one net in the surrounding sal forest, three nets in an old clearing, and one along a nearby small stream.

(6) Royal Chitwan National Park, Tiger Tops, Dhangari Khola 84°11.5′E, 27°32.2′N, approximately 33 km west of Sauraha (17–18 March). Tiger Tops is located along the Reu River, approximately 5 km east of its junction with the Narayani River, at the base of

rugged hills that are a part of the Siwalik Range. The forests, which are dominated by large sal trees (30–65 cm dbh), are taller and more diverse than those near Sauraha. Epiphytes and lianas are abundant and the understory is dense. The Dhangari Khola is a small tributary of the Rapti. It runs over rocks and sands through a moderately deep ravine (sides up to 30 m high). In the area we netted, the stream averaged 3 m across or less. Over two nights we placed fourteen nets over the stream and ravine, plus two additional nets across the Rapti River near its junction with Dhangari Khola.

(7) Royal Chitwan National Park, Simal Ghol Tal 84°28.6′E, 27°33.9′N, 2.5 km SW Sauraha (20–21 March). Simal Ghol is a small, shallow lake lying in grassland but adjacent to a small area of riverine forest. Over two nights we set two nets over the lake, 13 over forest trails or at the edge of the forest, and one over a small stream.

(8) Royal Chitwan National Park, Bardhaha Khola 84°28.2′E, 27°30.8′N, 3 km SW Bwanipur Chauki (22–23 March). This locality, which is dominated by sal forest, is in the Churia range of the Siwalik hills, around 500 m elevation. Many trees are very large, exceeding 30 m height. The forest floor is very open, with a sparse understory of grasses and shrubs. The large trees are scattered and the canopy is not continuous. Nets were set across the bed of a river, the Bhardhaha Khola, in an area where it is around 70 m across. The banks are low, no more than a few meters above the bed. The flow was reduced to a trickle at the time of our visit. We set three nets over the river bed and three in surrounding forest. On 23 March we moved upstream approximately 1 km to the point where the Bardhaha Khola is joined by another river, the Aap Khola. We set four nets along each stream and one at the confluence. Here, both stream beds are 10–20 m in breadth with banks ranging up to 30 m in height.

(9) Royal Chitwan National Park 84°28.1′E, 27°33.7′N, 3.8 km SW Sauraha (24 March). Seven nets were set across trails through riverrine forest and one across a road.

The following species of bats were collected:

Pteropodidae

Rousettus leschenaulti (Desmarest, 1820): (1 female; locality 6). This species has previously been listed for Nepal by Scully (1887), Fry (1925), Frick (1969), Mitchell (1978), and Mitchell and Punzo (1976). Our specimen entered a mist net set over a small stream in a forested ravine at about 9:30 pm. TL = 119, T = 11, HF = 20, E = 20, FA = 71.4.

Cynopterus sphinx (Vahl, 1797): (7 males, 12 females; localities 2, 3, 4). *Cynopterus sphinx* has been reported in Nepal by Frick (1969), Mitchell (1978), Mitchell and Punzo (1976), Johnson et al. (1980), and Bates and Harrison (1997). This common species was captured near banana plants adjacent to houses, in dense riparian vegetation, over trails through forest, and over a stream. On March 17, 16 individuals entered a net set approximately 3 m above the ground (we released seven); late arrivers appeared to be attracted by the distress calls of other *Cynopterus* as we removed them from the net. External measurements (n = 19): TL = 107.2, T = 7.9, HF = 14.4, E = 22.2, FA = 67.1. Cranial measurements (n = 6): CB = 29.2, CC = 6.5, MAX = 10.1, LPAL = 13.8, BPAL = 9.0, ZYGO = 18.9, BB = 13.0.

Eonycteris spelaea (Dobson, 1871): (2 males; localities 2 and 6). This is a new record for Nepal, although the species has been found in adjacent areas of India. One specimen was captured among banana plants near houses; the other, in a net set along a stream through a ravine. External measurements (n = 2): TL = 123.0, T = 10.5, HF = 18.0, E = 21.0, FA = 72.4. Cranial measurements (n = 1): CB = 32.2, CC = 7.8, MAX = 11.2, LPAL = 15.2, BPAL = 8.8, ZYGO = 24.3, BB = 14.6.

Vespertilionidae

Scotophilus heathi (Horsfield, 1831): (5 males, 7 females; localities 2, 3, 4, 6, 8). *Scotophilus* has been reported from Nepal by Frick (1969), Agrawal and Chakraborty (1971), Mitchell (1978, 1980), Mitchell and Punzo (1976), Johnson et al. (1980), and Bates and Harrison (1997). We found this species to be common. Most captures were over water (rivers, streams, and ponds). *Scotophilus* were often the first bats caught in the evening. Females appear to be distinctively larger than males. External measurements (n = 5 males, 6 females): TL = 143.6, T = 54.7, HF = 13.1, E = 17.4, TR = 11.1, FA = 60.6. Cranial measurements (n = 4): CB = 20.2, CC = 7.3, MAX = 7.7, LPAL = 7.4, BPAL = 9.5, ZYGO = 15.3, BB = 10.1.

Eptesicus dimissus (Thomas, 1916): (4 males, 4 females; localities 4 and 6). External measurements (n = 7): TL = 100.0, T = 36.7, HF = 8.9, E = 14.4, TR = 6.7, FA = 39.7. Cranial measurements (n = 2): CB = 15.4, CC = 5.9, MAX = 5.9, LPAL = 6.4, BPAL = 7.9, ZYGO = 12.5, BB = 8.1.

Most recent authorities report this species as *Eptesicus "demissus"*, which appears to be a misspelling. *Eptesicus dimissus* is known only from the type specimen, collected in Thailand. Lekagul and McNeely (1977) include a photograph of the cranium of the holotype, which is broken, and a description of the skin. Our identification of this species is based on that photograph and the description of Thomas (1916). Because this species is so poorly known, we include here drawings of cranium, teeth, and baculum (Fig. 1), and a brief description of the pelage and wing morphology.

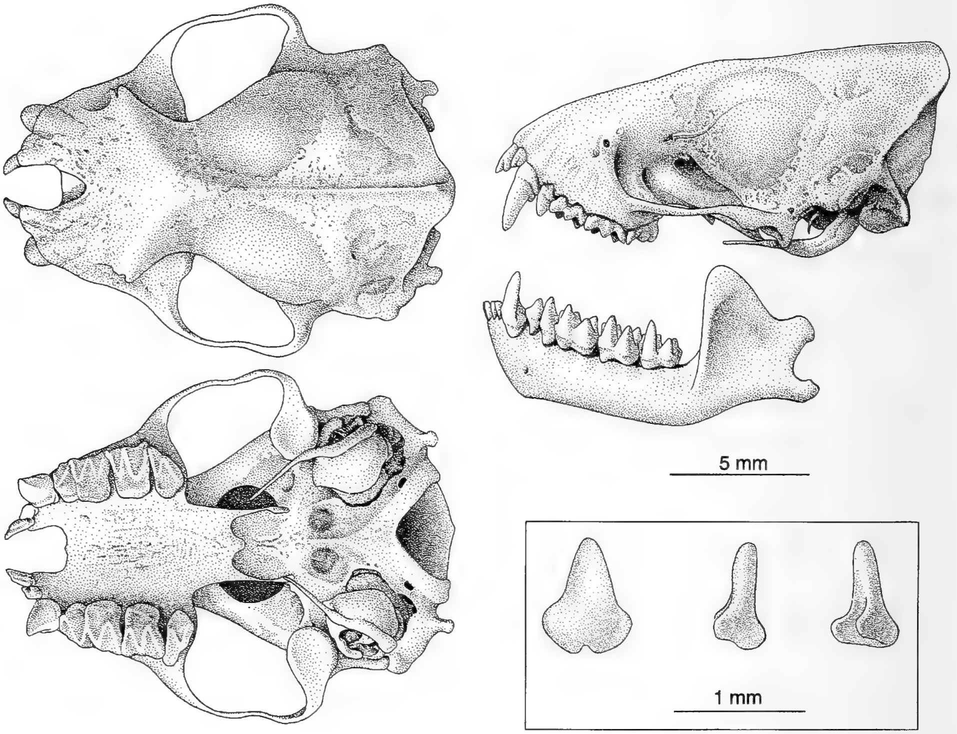

Fig. 1. *Eptesicus dimissus* Dorsal, lateral, and ventral views of cranium; dorsal, lateral, and oblique views of baculum (distal end at top). The cranium illustrated is from UMMZ 172218, a female collected at Royal Chitwan National Park, Dudora Nala/Park rd 84°27.4′E, 27°33.6′N, 4.3 km SW Sauraha on 15 March 1990 by P. Myers and J. D. L. Smith. The baculum is from UMMZ 172219, a male collected at Royal Chitwan National Park, Tiger Tops, Dhangari Khola 84°11.5′E, 27°32.2′N, approximately 33 km west of Sauraha, on March 17 1990 by P. Myers and J. D. L. Smith.

Externally, our specimens of *E. dimissus* have short, sparse pelage that is chestnut-brown dorsally and pale brown ventrally. Individual hairs on the dorsum have pale bases and brown tips, while ventral hairs are uniform pale brown in color. Ears are short and rounded, naked on the posterior surface and sparsely furry on the anterior. The anterior border of the pinna is slightly convex, while the posterior edge is nearly straight. The tragus is short and rounded, with a distinctly convex anterior margin and strongly concave posterior. The posterior margin of the tragus, and the basal part of the anterior edge of the pinna, both appear to be slightly thickened. The muzzle is exceptionally broad. The skin over the forehead is loose, and in most specimens it forms a distinctive fold running from ear to ear.

All patagial membranes appear to be nearly hairless. The wing membranes join the legs at the level of the middle of the metatarsals. The metacarpal of the third digit averages 38.6 mm in length, while the first phalanx of the same digit averages 15.3 mm ($n = 7$). The calcar has a well-developed keel. In all of our specimens, the tail extends 1–3 mm beyond the edge of the uropatagium.

The baculum is slightly less than 1 mm in length, 0.67 mm in breadth, and roughly triangular in dorsal view. The proximal end is notched while the distal end is bluntly rounded.

Compared to *Eptesicus fuscus* (Beauvois, 1796), *E. dimissus* has a relatively short and broad cranium. The rostral region is especially short. Strong sagittal and lambdoidal crests are present, and the braincase is moderately inflated. Zygomatic arches flare sharply laterally from their anterior roots. The dorsal profile of the rostrum and cranium is almost flat. The palate is moderately domed, as in *fuscus*. The basisphenoid pits are large, deep, and well defined. The glenoid fossa for the articulation of upper and lower jaws appears to be especially broad and strong compared to its condition in *fuscus*. Well-developed paroccipital processes are present.

The second upper incisor of *E. dimissus* is bifid and scarcely extends beyond the cingulum of the canine. I^3 is about 2/3 the length of I^2. The upper canines are notably long, extending more than twice the length of the adjacent premolar (P^4). The canine has a pronounced cingulum and a trace of a secondary cusp. P^4 is relatively narrow compared to its condition in *E. fuscus*.

The lower jaw of *E. dimissus* is short and broad relative to that of *E. fuscus*, and its angular process is stouter.

Eptesicus pachyotis (Dobson, 1871) is another poorly known species from the Indomalaysian region that may be closely related to *E. dimissus* (Corbet and Hill 1992). Based on the original and a subsequent description by Dobson (1871, 1876), plus photographs of the skull and dentition in Lekagul and McNeely (1977), our specimens resemble *pachyotis* in their flat and broad muzzle, fold of skin over the forehead, and shape of ear and tragus. They also show some thickening of the anterior edge of the ear and tragus (but probably not to the extreme described for *pachyotis*). The Nepali specimens clearly differ from *pachyotis,* however, in several respects. The basisphenoid pits of *E. pachyotis* are shallow, while those of these specimens are pronounced. *Eptesicus pachyotis* has a relatively large P^4 compared to the canine, in contrast to the condition in our specimens. (The basisphenoid pits and relative size of P^4 and canine for both species are clearly shown in photographs of the holotypes in Lekagul and McNeely 1977.) The wing membranes of *pachyotis* join the legs at the level of the base of the toes; in our specimens (and in the type of *dimissus*, Thomas 1916), they join in the middle of the metatarsals.

Pipistrellus javanicus (Gray, 1838): (8 males, 25 females; localities 2, 4, 5, 6, 7). Nepali specimens of this species are often reported under the name *Pipistrellus babu* Thomas, 1915 (Hinton and Fry 1923; Frick 1969; Mitchell 1978; Mitchell and Punzo 1976; Kock 1996). Bates and Harrison (1997) also list localities in Nepal. This species was common around houses (locality 2), where it tended to be captured earlier than other pipistrelles. It was also sometimes abundant over water; over 50 individuals were captured at locality 4.

The identification of this and the other pipistrelles reported below is controversial. We identify this species as *javanicus* based on its relatively large size, broad interorbital region (3.6–3.9 mm), bicuspid I^2, relatively large I^1, P^2 intruded from toothrow, canine with a posterior cusp, relatively strongly domed palate, and nearly straight baculum ca. 7 mm in length. External measurements (n = 33): TL = 88.8, T = 33.6, HF = 7.0, E = 12.4, TR = 6.6, FA = 34.0. Cranial measurements (n = 9): CB = 13.1, CC = 4.6, MAX = 5.0, LPAL = 4.8, BPAL = 6.0, ZYGO = 9.1, BB = 6.7.

Pipistrellus coromandra (Gray, 1838): (13 males, 11 females; localities 4, 5, 6, 7, 8). This species was reported for Nepal by Hinton and Fry (1923), Frick (1969), Mitchell (1978), and Bates and Harrison (1997). Unlike the other pipistrelles reported here, this species was not seen near houses; most individuals were captured over streams. This species is intermediate in size among the three pipistrelles we collected. It has a bicuspid I^2, relatively large I^1, P^2 intruded from toothrow, and canine with a posterior cusp. Compared to *javanicus*, these specimens have only a moderately broad supraorbital region (3.2–3.5 mm), a rostrum that is slightly less flattened dorsally, a less strongly domed palate, and a shorter baculum (ca. 6 mm). The distal end of the baculum is not strongly deflected. External measurements (n = 24): TL = 81.9, T = 31.7, HF = 6.5, E = 12.0, TR = 6.1, FA = 30.8. Cranial measurements (n = 13): CB = 12.0, CC = 4.2, MAX = 4.4, LPAL = 4.4, BPAL = 5.4, ZYGO = 7.9, BB = 6.4.

Pipistrellus tenuis (Temminck, 1840): (11 males, 10 females; localities 2, 4, 5, 6, 7). Hinton and Fry (1923), Frick (1969) and Mitchell (1978, 1980) list this species for Nepal (as *Pipistrellus mimus* Wroughton, 1899). It was a common inhabitant of the buildings at locality 2, where it roosted under roofs made of galvanized metal sheets. Several specimens were also captured over streams, ponds, and forest trails. These specimens stand out due to their very small size. Like members of the other two species, they have a bicuspid I^2, relatively large I^1, and P^2 intruded from toothrow. Their interorbital region is relatively narrow (3.1–3.3 mm), their rostrum is not flattened dorsally, and their palate is weakly domed. External measurements (n = 21): TL = 72.4, T = 28.6, HF = 5.4, E = 9.8, TR = 5.4, FA = 27.8. Cranial measurements (n = 6): CB = 10.4, CC = 3.5, MAX = 3.7, LPAL = 3.5, BPAL = 4.8, ZYGO = 7.1, BB = 6.0.

Nyctalus noctula (Schreber, 1774): (2 males; localities 3 and 7). *Nyctalus noctula* was listed as occurring in Nepal by Frick (1969) and Bates and Harrison (1997). Both individuals were captured several hours after dark in nets set over small ponds. External measurements (n = 2): TL = 132.0, T = 48.5, HF = 11.5, E = 18.0, TR = 10.5, FA = 53.1. Cranial measurements (n = 1): CB = 18.2, CC = 7.1, MAX = 6.9, LPAL = 6.1, BPAL = 8.8, ZYGO = 13.0, BB = 9.4.

Hesperoptenus tickelli (Blyth, 1851): (2 males, 4 females; localities 3, 4, 5, 6). Frick (1969) and Mitchell (1978, 1980) noted the presence of this species in Nepal. These bats entered nets set over a ravine (3 individuals), a stream (1 individual), a pond (1 individual), and extending from forest edge into grassland (1 individual). External measurements (n = 5): TL = 133.8, T = 50.2, HF = 12.0, E = 18.8, TR = 10.0, FA = 58.1. Cranial measurements (n = 1): CB = 19.2, CC = 6.9, MAX = 7.7, LPAL = 9.1, BPAL = 9.8, ZYGO = 14.4, BB = 9.5.

Miniopterus pusillus Dobson, 1876: (1 male, 1 female; locality 6). Maeda (1982) reported this species in Nepal; however, this record has been questioned by Corbett and Hill (1992). We captured this species in nets spanning a ravine. External measurements (n = 2): TL = 100.5, T = 43.0, HF = 9.0, E = 11.0, TR = 6.5, FA = 41.6. Cranial measurements (n = 1): CB = 13.5, CC = 4.0, MAX = 5.2, LPAL = 5.8, BPAL = 5.4, ZYGO = 8.0, BB = 7.3.

Miniopterus schreibersi (Kuhl, 1817): (6 males, 5 females; locality 1). The occurrence of this species in Nepal has been noted by Scully (1887), Frick (1969), Mitchell (1978), Kock (1996), and Bates and Harrison (1997). Our specimens were captured as they exited a large sewer tunnel (approximately 3 m×5 m at the entrance) in Kathmandu. External measurements (n = 11): TL = 117.8, T = 52.2, HF = 11.2, E = 11.8, TR = 7.0, FA = 48.43. Cranial measurements (n = 2): CB = 15.4, CC = 4.9, MAX = 6.2, LPAL = 6.3, BPAL = 6.8, ZYGO = 9.0, BB = 8.2.

Murina cyclotis Dobson, 1872: (1 female; locality 9). This species was listed as occurring in Nepal by Frick (1969) and Bates and Harrison (1997). Our single specimen was caught in a net set across a road through dense riverine forest; it entered the net at around 7:30 pm. This individual is slightly larger in several cranial dimensions than the series reported by Bates and Harrison (1997), but its color and the relative sizes of the talonids and trigonids of the lower molars suggest that it should be assigned to this species. External measurements (n = 1): TL = 83, T = 31, HF = 8, E = 17, TR = 9, FA = 33.8. Cranial measurements (n = 1): CB = 15.6, CC = 4.2, MAX = 5.7, LPAL = 8.1, BPAL = 5.8, ZYGO = 10.0, BB = 7.8.

Kerivoula picta (Pallas, 1767): (1 female; locality 6). *Kerivoula picta* was listed as occurring in Nepal by Frick (1969) but without citation of records. Our specimen was captured at around 9 PM in a net set over a stream running through a steep-sided ravine. External measurements (n = 1): TL = 86, T = 37, HF = 7, E = 14, TR = 11, FA = 35.2.

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Zusammenfassung

Eine neue Sammlung von Fledermäusen aus Nepal mit Bemerkungen über Eptesicus dimissus

Freilandstudien an 9 Lokalitäten im und nahe des Royal Chitwan National Park in Nepal, die im März 1990 durchgeführt wurden, ergaben eine Sammlung von 143 Exemplaren von Fledermäusen folgender 14 Arten: *Rousettus leschenaulti*, *Cynopterus sphinx*, *Eonycteris spelaea*, *Scotophilus heathi*, *Eptesicus dimissus*, *Pipistrellus javanicus*, *Pipistrellus coromandra*, *Pipistrellus tenuis*, *Nyctalus noctula*, *Hesperoptenus tickelli*, *Miniopterus pusillus*, *Miniopterus schreibersi*, *Murina cyclotis*, *Kerivoula picta*.

Von diesen Arten konnten *E. spelaea* und *E. dimissus* erstmalig für Nepal nachgewiesen und ferner das unsichere Vorkommen von *M. pusillus* und *K. picta* bestätigt werden. Den knapp gekennzeichneten Fangorten werden die Arten zugeordnet und einige mittlere Körper- und Schädelmaße werden angegeben. Zusätzlich wird etwas detaillierter über morphologische Besonderheiten und systematische Stellung von *E. dimissus* informiert, da diese Art bislang nur vom Holotyp aus Thailand bekannt war.

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Geographic variation in *Aethomys chrysophilus* (Rodentia: Muridae) from southern Africa

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Abstract

Patterns of intraspecific variation in *Aethomys chrysophilus* De Winton, 1897 from southern Africa suggest the recognition of two subspecies: *A. c. chrysophilus* De Winton, 1897 and *A. c. imago* Thomas, 1927, which differ both in cranial size and shape. The morphological discontinuity of the proposed subspecies broadly coincides with an altitudinal limit of either below or above 500 m above sea level in the eastern part of southern Africa.

Key words: *Aethomys chrysophilus*, cranial morphometrics, geographic variation, southern Africa

Introduction

The species conventionally regarded as the red veld rat, *Aethomys chrysophilus* De Winton, 1897 is widely distributed in southern Africa (Meester et al. 1986; Skinner and Smithers 1990; Musser and Carleton 1993). However, the species is apparently composed of two electrophoretically distinct cytotypes (2n = 44 and 2n = 50) that also differ in gross sperm and bacular morphology (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker et al. 1988; Breed et al. 1988). The absence of hybrids in areas of sympatry has been suggestive of reproductive isolation between the two chromosomal races (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986). This led to a recent systematic revision of the genus in southern Africa based on morphometric analysis as well as qualitative cranial morphology (Chimimba 1997, 1998; Chimimba et al. 1999).

The morphometric analysis of cytogenetically known and other specimens of *A. chrysophilus* (sensu lato), revealed two sympatric, widely distributed, morphologically similar species referred to the nominate species, *A. chrysophilus* De Winton, 1897 (2n = 50) and a newly recognized *A. ineptus* Thomas and Wroughton, 1908 (2n = 44) (Chimimba 1997, 1998; Chimimba et al. 1999). This is concordant with observations on qualitative cranial morphology (Chimimba 1997; Chimimba et al. 1999) and the earlier investigations involving cytogenetics, protein electrophoresis, and gross sperm and bacular morphology (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker et al. 1988; Breed et al. 1988).

Additional analyses involving type material led to two previously described forms, *acticola* Thomas and Wroughton, 1908, and *imago* Thomas, 1927, to be assigned to *A. chry-*

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sophilus as junior synonyms (Chimimba 1997; Chimimba et al. 1999). Nevertheless, the nature and extent of geographic variation within the currently recognized *A. chrysophilus* from southern Africa remains virtually unknown, and only a few other southern African rodents have been subjected to a rigorous analysis of intraspecific variation (see Chimimba et al. 1998). The present study therefore, represents the first attempt to evaluate both morphometric and morphological patterns of intraspecific variation in *A. chrysophilus* from southern Africa over a more extensive geographical range than has previously been considered for the species.

Material and methods

The analysis of geographic variation in *A. chrysophilus* is based on a subset of data that formed part of the revision of the genus in southern Africa (Chimimba 1997; Chimimba et al. 1999) in which the homogeneity of the sample as representative of a single, widely distributed species was confirmed. This included 365 specimens from 161 localities, which provided an adequate geographical coverage of the species in southern Africa (Fig. 4). Since the data matrix was too large for simultaneous specimen-level analyses, geographically contiguous localities were pooled into 31 operational taxonomic units (OTUs; Sneath and Sokal 1973) (Fig. 4; Chimimba 1997; Chimimba et al. 1999) with reference to phytogeographical zones (Acocks 1988) and vegetation maps (Keay 1959).

Specimens examined are in the American Museum of Natural History, New York (AMNH), The Natural History Museum, London (BMNH), Durban Natural Science Museum, Durban (DM), Kaffrarian Museum, King William's Town (KM), McGregor Museum, Kimberley (MMKM), National Museum, Bloemfontein (NMB), National Museum of Natural History, Washington D. C. (USNM), Natural History Museum of Zimbabwe, Bulawayo (NHMZ), and the Transvaal Museum, Pretoria (TM). Type material examined is listed in the section on taxonomy, while a list of all other specimens examined and a gazetteer are provided in Chimimba (1997).

Eleven cranial measurements were recorded using a pair of Mitutoyo digital callipers and DataQ (D. L. Schultz pers. comm.) for direct data input into Quattro (Borland International 1987). These variables, defined by Chimimba and Dippenaar (1994, 1995) and Chimimba (1997) and selected on the basis of a procedure developed by Taylor (1990), Taylor and Meester (1993), Chimimba and Dippenaar (1995) and Chimimba (1997), are: greatest length of skull, greatest length of frontals, length of nasals to zygomatic arch, greatest width of bulla, foramen magnum height, length of M^1, width of M^2, length of angular process to mandibular condyle, length of mandibular foramen to condyle, length of I_1 to M_3, and width of M_2.

The data set also included four descriptive cranial (breadth of braincase, interorbital breadth, greatest length of bulla, and greatest height of skull), and four external measurements (length of head and body, length of tail, length of hindfoot, and length of ear) recorded from specimen labels. None of these variables were included in multivariate analyses (Chimimba and Dippenaar 1995; Chimimba 1997).

To reduce the effect of age variation, character recording and analyses were based on adult specimens of toothwear classes IV, V, and VI (Chimimba and Dippenaar 1994; Chimimba 1997). The absence of sexual dimorphism in the genus (Chimimba and Dippenaar 1994; Chimimba 1997, Chimimba et al. 1998) resulted in the pooling of sexes.

Multivariate analyses

Multivariate analysis included unweighted pair-group arithmetic average (UPGMA) cluster analysis, principal components analysis (PCA), and minimally connected networks (MST) of the 31 OTU means based on standardized variables (Sneath and Sokal 1973). UPGMA cluster analysis and MST were performed on both average taxonomic distances and product-moment correlation coefficients among OTUs, whereas PCA was computed from product-moment correlation coefficients among characters (Sneath and Sokal 1973). Although sample means were used, the observed major patterns of variation were verified by analyses of specimens (including holotypes) from the entire distributional range of *A. chrysophilus* in southern Africa.

The phenetic groupings obtained were further examined using pairwise canonical variates (discriminant) analysis (CVA; Sneath and Sokal 1973) and multivariate analysis of variance (MANOVA;

Willig et al. 1986; Willig and Owen 1987) based on two groupings of data: 1) all specimens within delineated phena; and 2) specimens from a zone of parapatry of the delineated phena. Diagnostic CVA was used to classify specimens excluded from the analyses.

Univariate analyses

Univariate analysis included Model I analysis of variance (ANOVA; Sokal and Rohlf 1981) of the 31 OTUs. Where significant differences were detected, maximally non-significant subsets were derived by the *a posteriori* sum of squares simultaneous test procedure (SS-STP; Gabriel and Sokal 1969; Sokal and Rohlf 1981) using ranked means (Power 1970).

All statistical procedures were accomplished using algorithms in BIOΣTAT I and II version 2.0 (Pimentel and Smith 1986 a, b), UNIVAR (Power 1970) and NTSYS-pc version 1.01 (Rohlf 1986).

Qualitative morphological variation

After having delineated phena morphometrically, representative specimens (n = 204) of each phenon (including holotypes) from the entire subregion were re-examined for qualitative morphological variation in for example, molar cusp pattern and structures in the basicranial region of the skull. This included the comparison of pelage colouration in natural light using colour standards in Oyama et al. (1967).

Intraspecific nomenclature

The intraspecific nomenclature of the delineated phena was resolved by separate analyses that included the holotypes of *A. chrysophilus* and its two junior synonyms, *acticola* and *imago* (Chimimba 1997; Chimimba et al. 1999).

Results

Multivariate assesment

A distance phenogram showed two discrete geographical clusters, designated A and B (Fig. 1a) which broadly coincide with an altitudinal limit in the eastern part of southern Africa (Clark 1967; Fig. 2). With the exception of OTUs 12, 17, and 26 (indicated by arrows), cluster A comprises OTUs from above 500 m above sea level, whereas cluster B consists of OTUs from below 500 m above sea level.

A correlation phenogram showed similar discrete geographical clusters (A and B; Fig. 1b), but the phenetic relationships were more evident than those shown by the distance phenogram. Except for OTU 12, the other two OTUs (17 and 26) that were of uncertain placement in the distance phenogram fell within a geographically meaningful, altitude-related assemblage of OTUs in the correlation phenogram.

The cluster analysis-derived phena were subsequently used as reference groupings to demarcate clusters in PCA scatterplots. This included the superimposition of MSTs based on both distance and correlation coefficients. There was evidence of two size- and shape-related groups within both the distance (Fig. 3 a) and correlation phenogram-based (Fig. 3 b) PCA scatterplots, which are consistent with the corresponding cluster analyses (Figs. 1 a and 1 b).

Apart from OTU 12, both distance- and correlation-based MSTs connected OTUs 17 and 26, which were of uncertain placement in the distance phenogram, to their geographically meaningful, altitude-related cluster of OTUs in multivariate space. The first component, which accounts for 46.4% of the variance and also has most eigenvector loadings of similar sign (negative) and relative magnitude, shows that overall size accounts for the greatest portion of the variance (Tab. 1). The second component, which is dominated by

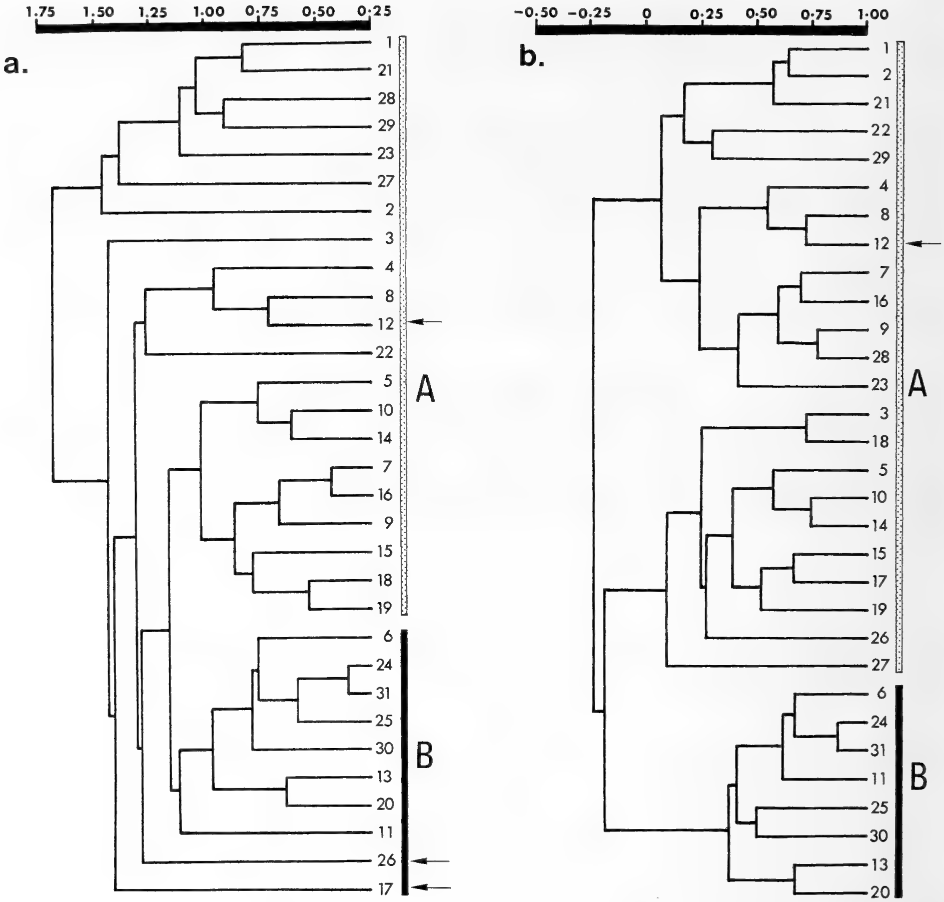

Fig. 1. Distance (a) and correlation (b) phenograms from UPGMA cluster analyses of pooled samples (OTUs) of *Aethomys chrysophilus* from southern Africa. OTUs correspond to those in Fig. 4, while arrows indicate OTUs of uncertain placement. Cophenetic correlation coefficients = 0.66 and 0.69, respectively.

greatest width of bulla and foramen magnum height (positive eigenvector loadings), and width of M^2 (negative loading), accounts for 14.9% of the variance (Tab. 1). These results indicate that cranial shape configuration of the bulla, foramen magnum region, and maxillary dental characteristics are also intraspecifically important in *A. chrysophilus* from southern Africa. The phenetic affiliation of specimens excluded from all multivariate analyses because of small sample sizes were verified by additional distance- and correlation-based UPGMA cluster analysis and MST, and PCA.

A geographical summary of these results (Fig. 4) suggests two cranially distinct, size- and shape-related phena which broadly coincides with an altitudinal limit of either below or above 500 m above sea level in the eastern part of southern Africa. OTU 12 is tentatively referred to the OTU assemblage from below 500 m above see level since the majority of OTUs clustered with their geographically meaningful groupings of OTUs.

Pairwise CVAs based on two groupings of data were broadly similar. Results presented are those based on specimens from zones of parapatry of the two delineated phe-

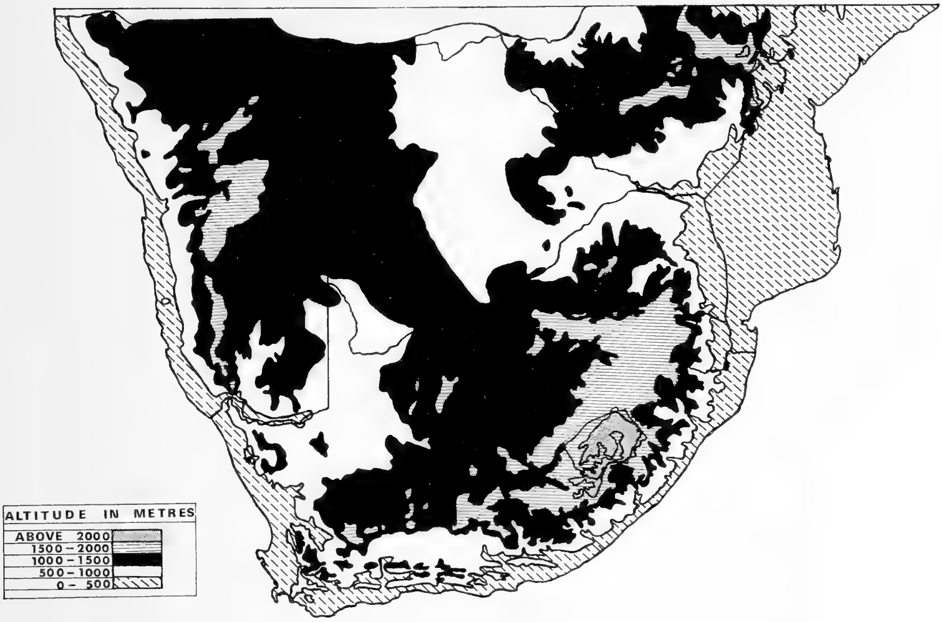

Fig. 2. Topographic map of southern Africa (after Clark 1967).

na. Despite overlaps in discriminant score ranges, pairwise CVA of the two delineated phena produced a 74% correct *a posteriori* classification (n = 365). A MANOVA indicated significant differences between group centroids (F = 6.90; $P < 0.001$: group centroid of OTUs from above 500 m above see level = –0.80; score range: –3.01 – 1.42; OTUs from below 500 m above see level: centroid = 0.52; range = –1.96 – 2.63).

Univariate assessment

Model I ANOVA of the 31 OTUs revealed statistically significant differences ($P < 0.05$) in 14 of the 15 measurements examined. The order of ranked means revealed three contrasting patterns as illustrated by selected measurements (Tab. 2).

The first pattern involved four measurements with F-values ranging from 3.22 to 5.44. As is evident in greatest width of bulla (Tab. 2 a), there is a trend in the order of ranked means for larger values to be associated with low-altitude OTUs and lower values with high-altitude OTUs. The uniqueness of high- and low-altitude OTUs was also evident in all multivariate analyses (Figs. 1 and 3).

The second pattern involved width of M^2 (F-value = 2.04; Tab. 2 b), in which a trend opposite to that in greatest width of bulla (Tab. 2 a) was revealed. There was a tendency for lower values to be associated with low-altitude OTUs and larger values with high-altitude OTUs. These two assemblages are also consistent with the two major patterns revealed by all multivariate analyses (Figs. 1 and 3).

Variation involving nine measurements with F-values ranging from 1.68–5.62, was not meaningful geographically. This is exemplified by breadth of braincase and greatest height of skull (Tabs. 2 c and 2 d). A similar pattern was also evident in foramen magnum height, the measurement with the lowest, and the only statistically non-significant F-value (F-value = 1.45; $P > 0.05$) among the 15 measurements examined.

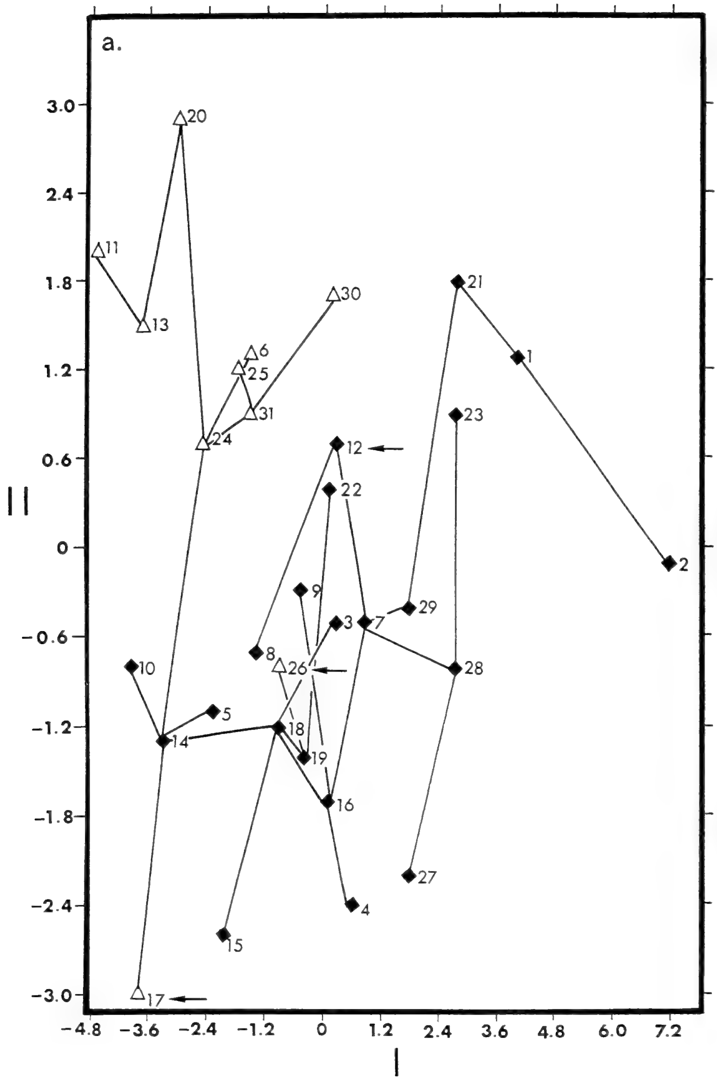

Fig. 3 a.

Taxonomic status of delineated phena

The phenetic difference between the two delineated phena and their association with an altitudinal limit of either below or above 500 m above sea level in the eastern part of southern Africa, provides support for their recognition as distinct subspecies. To further resolve the intraspecific nomenclature, the phenetic affiliations of holotypes of *A. chrysophilus* and the two described forms, *acticola* and *imago* (Chimimba 1997; Chimimba et al. 1999), were verified by UPGMA cluster analyses, PCA, MST and CVA.

All holotypes phenetically associated with their geographically meaningful assemblages of OTUs (Fig. 4). As is convention, the earliest described taxa within OTU assemblages were considered senior synonyms of the two delineated phena. Consequently, the

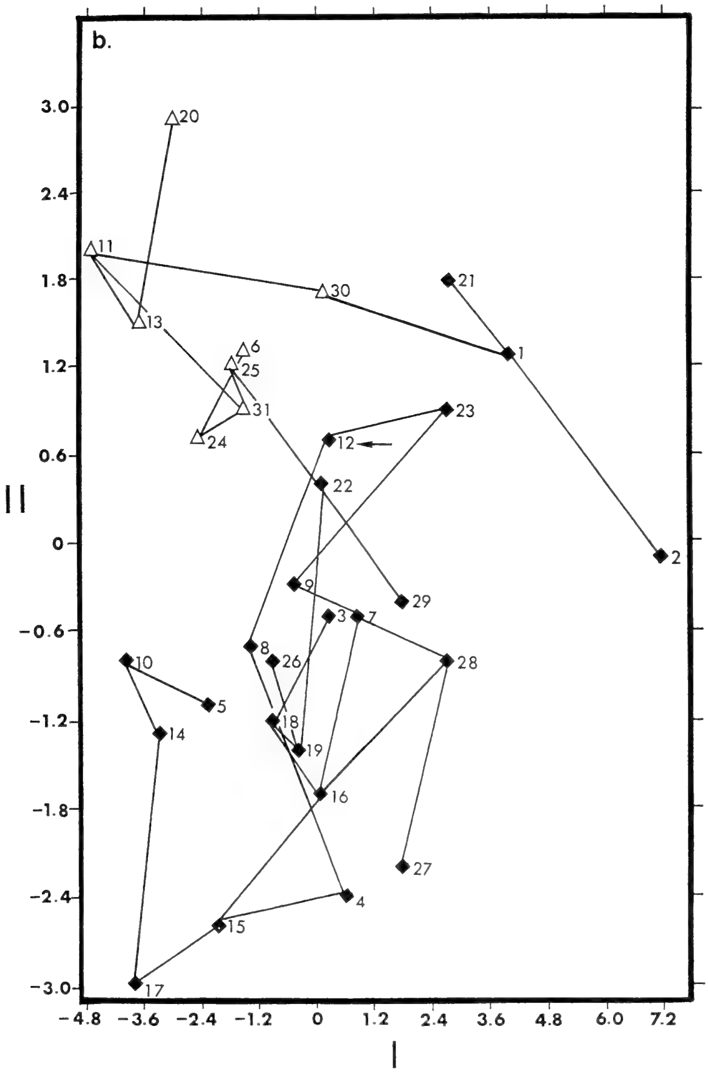

Fig. 3 b.

Fig. 3. Components I and II from a principal components analysis of *Aethomys chrysophilus* from southern Africa. A minimum spanning tree is superimposed. Symbols indicate OTUs from major clusters A (solid diamonds) and B (open triangles) delineated by (a) distance (Fig. 1 a) and (b) correlation (Fig. 1 b) phenograms. Arrows indicate OTUs of uncertain placement. OTUs correspond to those in Fig. 4.

nominate subspecies, *chrysophilus* De Winton, 1897, is assigned to low-altitude OTUs from the eastern part of southern Africa, with *acticola* Thomas and Wroughton, 1908, as a junior synonym. *Aethomys chrysophilus* was described from Mazoe in eastern Zimbabwe (De Winton 1897), which falls within the low-altitude assemblage of OTUs. High-altitude OTUs are allocated to *A. c. imago* Thomas, 1927.

Table 1. Loadings of variables on components I and II from a principal components analysis of pooled samples (OTUs) of *Aethomys chrysophilus* from Southern Africa. The percent variance contributions appear in brackets. Measurements are defined in CHIMIMBA and DIPPENAAR (1994,1995) and CHIMIMBA (1997).

Variable	Principal components	
	I	II
Greatest length of skull	–0.423 (91.11)	–0.032 (0.16)
Greatest length of frontals	–0.314 (50.16)	–0.063 (0.65)
Length of nasals to zygomatic arch	–0.426 (92.44)	–0.013 (0.03)
Greatest width of bulla	0.158 (12.79)	0.548 (49.34)
Foramen magnum height	0.040 (0.83)	0.421 (29.13)
Length of M^1	–0.269 (37.01)	0.025 (0.11)
Width of M^2	–0.108 (6.00)	–0.606 (60.45)
Length of angular process to mandibular condyle	–0.394 (79.18)	0.124 (2.53)
Length of mandibular foramen to condyle	–0.294 (44.23)	–0.186 (5.67)
Length of I_1 to M_3	–0.369 (69.34)	0.227 (8.48)
Width of M_2	–0.230 (27.06)	–0.218 (7.79)
% Trace	46.4%	14.9%

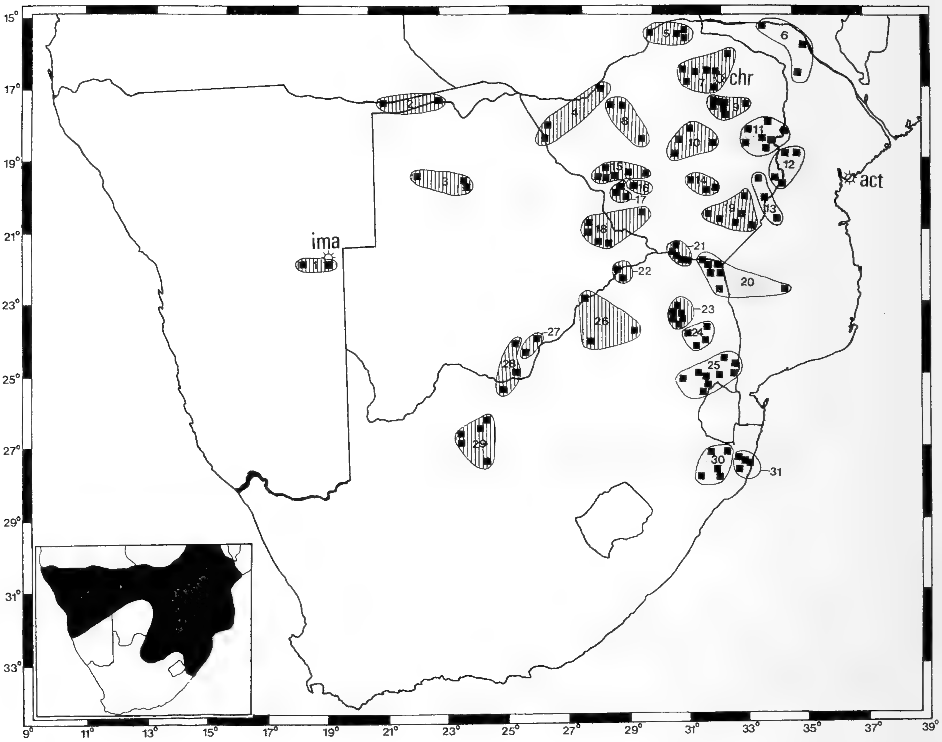

Fig. 4. Collecting localities and pooled samples (OTUs) of *Aethomys chrysophilus* from southern Africa and a geographical representation of delineated phena based on collation of UPGMA clustering, minimum spanning trees and principal components analysis results, and the tentative placement of OTU 12 into a geographically meaningful assemblage of OTUs. Samples represent phenetic assemblages that coincide with localities from the eastern (shaded) part of southern Africa, below 500 metres above sea level, and western (horizontal lines) part of this region (cf. CLARK 1967; Fig. 2). Abbreviations represent type localities of *A. chrysophilus* (chr) and its two described subspecies in southern Africa, *acticola* (act) and *imago* (ima). Insert represents the distribution of the species in southern Africa.

Table 2. Results of sum of squares simultaneous test procedure (SS-STP) of selected cranial measurements of pooled samples (OTUs) of *Aethomys chrysophilus* from Southern Africa. Non-significant subsets ($P > 0.05$) are indicated by vertical lines to the right of each array of means. OTUs correspond to those in Fig. 4. Measurements are defined in CHIMIMBA and DIPPENAAR (1994, 1995) and CHIMIMBA (1997).

(a)

Locality code	Sample size	Standard deviation	Arithmetic mean	Non-significant subsets							
Greatest width of bulla											
($F = 4.28$; $P < 0.05$)											
20	22	0.11	5.8	│							
25	11	0.27	5.7	│	│						
12	7	0.09	5.7	│	│	│					
6	4	0.25	5.7	│	│	│	│				
21	6	0.27	5.7	│	│	│	│	│			
22	10	0.14	5.7	│	│	│	│	│	│		
13	6	0.19	5.7	│	│	│	│	│	│		
11	15	0.16	5.6	│	│	│	│	│	│		
31	8	0.12	5.6	│	│	│	│	│	│	│	
24	11	0.19	5.6	│	│	│	│	│	│	│	
26	4	0.20	5.6	│	│	│	│	│	│	│	│
30	7	0.18	5.6	│	│	│	│	│	│	│	│
3	4	0.32	5.6	│	│	│	│	│	│	│	│
9	9	0.17	5.6	│	│	│	│	│	│	│	│
29	6	0.32	5.6	│	│	│	│	│	│	│	│
10	10	0.24	5.6	│	│	│	│	│	│	│	│
19	11	0.16	5.5	│	│	│	│	│	│	│	│
18	13	0.20	5.5	│	│	│	│	│	│	│	│
14	46	0.22	5.5		│	│	│	│	│	│	│
23	5	0.21	5.5		│	│	│	│	│	│	│
7	29	0.23	5.5		│	│	│	│	│	│	│
16	12	0.16	5.5		│	│	│	│	│	│	│
5	6	0.35	5.4		│	│	│	│	│	│	│
15	23	0.18	5.4			│	│	│	│	│	│
17	9	0.17	5.4				│	│	│	│	│
28	5	0.07	5.4					│	│	│	│
1	5	0.11	5.4						│	│	│
2	8	0.20	5.3							│	│
27	6	0.14	5.3							│	│
8	4	0.30	5.3							│	│
4	4	0.08	5.3								│

(b)

Locality code	Sample size	Standard deviation	Arithmetic mean	Non-significant subsets		
Width of M^2						
($F = 2.04$; $P < 0.05$)						
15	23	0.08	2.0	│		
16	12	0.07	2.0	│	│	
17	9	0.08	2.0	│	│	│
9	9	0.08	2.0	│	│	│
4	4	0.13	2.0	│	│	│
5	6	0.05	2.0	│	│	│
11	15	0.06	2.0	│	│	│
18	13	0.06	2.0	│	│	│
7	29	0.07	2.0	│	│	│
14	46	0.07	2.0	│	│	│
3	4	0.06	2.0	│	│	│
8	4	0.06	2.0	│	│	│
19	11	0.07	2.0	│	│	│
28	5	0.02	2.0	│	│	│
10	10	0.05	2.0	│	│	│
29	6	0.07	1.9	│	│	│
27	6	0.05	1.9	│	│	│
25	11	0.06	1.9	│	│	│
6	4	0.04	1.9	│	│	│
22	10	0.06	1.9	│	│	│
23	5	0.05	1.9	│	│	│
13	6	0.05	1.9	│	│	│
31	8	0.03	1.9	│	│	│
20	22	0.03	1.9	│	│	│
24	11	0.05	1.9	│	│	│
21	6	0.06	1.9	│	│	│
30	7	0.03	1.9	│	│	│
1	5	0.05	1.9		│	│
12	7	0.06	1.9		│	│
26	4	0.02	1.9		│	│
2	8	0.05	1.9			│

Diagnostic morphological and morphometric characters

Variation in qualitative morphological and pelage colouration was not geographically meaningful. Both within and among the two delineated phena, upper parts ranged from brown (7.5 YR 4/3) to dark brown (7.5 YR 3/4), sprinkled with brownish black (7.5 YR 3/1) to very dark brown (7.5 YR 2/3) hairs; cheek, sides and thighs from light grey (7.5 YR 8/2) to light brown-grey (7.5 YR 7/2); underparts and feet from light yellow-orange (7.5 YR 8/4) to orange (7.5 YR 6/8); the few scattered hairs on ears from yellow-orange

Table 2. Continued

(c)

Breadth of braincase

(F = 4.93; P < 0.05)

Locality code	Sample size	Standard deviation	Arithmetic mean	Non-significant subsets					
11	15	0.61	15.5	|					
13	6	0.37	15.3	|	|				
14	46	0.44	15.2	|	|				
6	4	0.33	15.1	|	|	|			
15	23	0.40	15.1	|	|	|			
8	4	0.60	15.1	|	|	|			
24	11	0.62	15.0	|	|	|			
4	4	0.38	15.0	|	|	|	|		
17	9	0.41	15.0	|	|	|	|	|	
10	10	0.49	15.0	|	|	|	|	|	
18	13	0.55	15.0	|	|	|	|	|	
9	9	0.39	15.0	|	|	|	|	|	
5	6	0.76	14.9	|	|	|	|	|	
7	29	0.39	14.9	|	|	|	|	|	
12	7	0.35	14.9	|	|	|	|	|	|
3	4	0.56	14.8	|	|	|	|	|	|
22	10	0.42	14.8	|	|	|	|	|	|
20	22	0.34	14.8	|	|	|	|	|	|
16	12	0.54	14.8	|	|	|	|	|	|
30	7	0.38	14.8	|	|	|	|	|	|
26	4	0.53	14.8	|	|	|	|	|	|
25	11	0.46	14.7		|	|	|	|	|
19	11	0.43	14.7		|	|	|	|	|
21	6	0.37	14.6		|	|	|	|	|
28	5	0.20	14.6		|	|	|	|	|
31	8	0.25	14.5			|	|	|	|
27	6	0.34	14.4			|	|	|	|
1	5	0.38	14.3			|	|	|	|
29	6	0.29	14.2				|	|	|
2	8	0.40	14.2					|	|
23	5	0.29	14.1						|

(d)

Greatest height of skull

(F = 1.68; P < 0.05)

Locality code	Sample size	Standard deviation	Arithmetic mean	Non-significant subsets		
8	4	0.29	11.9	|		
11	15	0.25	11.8	|	|	
3	4	0.40	11.8	|	|	|
10	10	0.42	11.7	|	|	|
5	6	0.61	11.7	|	|	|
6	4	0.17	11.7	|	|	|
4	4	0.27	11.7	|	|	|
15	23	0.27	11.7	|	|	|
16	12	0.37	11.6	|	|	|
9	9	0.43	11.6	|	|	|
31	8	0.26	11.6	|	|	|
7	29	0.31	11.6	|	|	|
13	6	0.25	11.5	|	|	|
24	11	0.33	11.5	|	|	|
25	11	0.41	11.5	|	|	|
17	9	0.27	11.5	|	|	|
28	5	0.25	11.5	|	|	|
20	22	0.30	11.5	|	|	|
14	46	0.32	11.5	|	|	|
29	6	0.48	11.4	|	|	|
23	5	0.22	11.4	|	|	|
18	13	0.30	11.4	|	|	|
27	6	0.27	11.4	|	|	|
12	7	0.38	11.4	|	|	|
30	7	0.36	11.4	|	|	|
2	8	0.39	11.4	|	|	|
19	11	0.39	11.4	|	|	|
21	6	0.35	11.4		|	|
26	4	0.11	11.4		|	|
22	10	0.25	11.4			|
1	5	0.30	11.3			|

(7.5 YR 7/8) to orange (7.5 YR 6/8); the bicoloured basal half of tail from brown (7.5 YR 4/6) to dark brown (7.5 YR 3/4) above and orange (7.5 YR 6/8) to bright brown (7.5 YR 5/8) below, and the unicoloured terminal portion from yellow-orange (7.5 YR 7/8) to orange (7.5 YR 6/8). This suggests that intraspecific variation in qualitative morphology and pelage colour within *A. chrysophilus* from southern Africa is either subtle or does not form part the delineated patterns of cranial and dental morphological variation.

As an additional aid to subspecies identification, a search was made for simple ratios from standard statistics of the 11 basic cranial, four descriptive cranial and four external measurements examined (Tab. 3). Cranial ratios, using all specimens from the subregion, were computed for characters with high negative (width of M^2) and positive (greatest width of bulla and foramen magnum height) loadings in the shape-related axes II of PCA

Table 3. Standard statistics of external and cranial measurements in millimetres of subspecies of *Aethomys chrysophilus* from southern Africa: *A. c. chrysophilus* and *A. c. imago*. $\overline{X}$ = arithmetic mean; SD = standard deviation; n = sample size; CV = coefficient of variation; Range = observed range of variation. External measurements were obtained from specimen labels. Measurements are defined in CHIMIMBA and DIPPENAAR (1994, 1995) and CHIMIMBA (1997).

Variable	*A. c. chrysophilus*					*A. c. imago*				
	$\overline{X}$	SD	n	CV	Range	$\overline{X}$	SD	n	CV	Range
Length of head and body	143.5	10.85	47	7.57	125.0–169.0	143.1	10.01	79	7.00	120.0–165.0
Length of tail	167.7	10.64	47	6.34	144.0–185.0	160.5	12.93	79	8.06	135.0–190.0
Length of hind foot	29.7	2.47	47	8.32	21.0–35.0	29.0	2.19	79	7.54	20.0–33.0
Length of ear	20.9	1.65	47	7.94	16.0–25.0	20.4	1.94	79	9.53	15.0–27.0
Greatest length of skull	36.6	1.36	91	3.71	33.7–39.8	36.3	1.40	235	3.87	32.1–40.6
Greatest length of frontals	11.4	0.39	91	3.42	10.0–12.1	11.2	0.53	235	4.72	9.6–12.1
Length of nasals to zygomatic arch	25.6	1.02	91	3.98	23.5–28.1	25.2	1.09	235	4.32	21.8–27.7
Breadth of braincase	15.0	0.52	91	3.46	14.0–16.5	14.9	0.52	235	3.48	13.6–16.1
Interorbital breadth	5.2	0.24	91	4.66	4.7–6.0	5.1	0.25	235	4.94	4.5–5.9
Greatest length of bulla	7.7	0.23	91	3.02	7.0–8.5	7.5	0.31	235	4.13	6.7–8.6
Greatest width of bulla	5.7	0.18	91	3.09	5.2–6.3	5.5	0.22	235	4.04	4.8–6.2
Greatest height of skull	11.6	0.33	91	2.86	10.7–12.2	11.5	0.35	235	3.01	10.4–12.7
Foramen magnum height	4.9	0.22	91	4.46	4.4–5.4	4.8	0.25	235	5.15	4.1–5.5
Length of M^1	2.9	0.11	91	3.96	2.6–3.4	2.9	0.16	235	5.65	2.5–3.4
Length of M^2	1.9	0.05	91	2.57	1.8–2.1	2.0	0.07	235	3.53	1.8–2.2
Length of angular process to mandibular condyle	7.6	0.33	91	4.38	6.4–8.7	7.4	0.44	235	5.97	7.0–8.4
Length of mandibular foramen to condyle	5.6	0.30	91	5.34	5.0–6.4	5.5	0.38	235	6.88	4.4–6.6
Length of I_1 to M_3	10.6	0.37	91	3.50	9.7–11.9	10.4	0.36	235	3.52	9.0–11.3
Width of M_2	1.8	0.05	91	2.97	1.7–2.0	1.8	0.07	235	3.63	1.7–2.1

(Tab. 1). Greatest length of skull, one of the two highly negative size-related character on PC Axis I was also included, but all combinations, including external ratios were not informative.

Discussion

The present study represents the first analysis of intraspecific variation in *A. chrysophilus* from southern Africa over a more extensive geographical coverage than has previously been considered for the species. Morphometric analysis revealed the presence of two major assemblages of OTUs within *A. chrysophilus* from southern Africa.

A taxonomic interpretation of the detected variation suggests that *A. chrysophilus* in southern Africa is polytypic and can be separated into two subspecies: *A. c. chrysophilus* De Winton, 1897 and *A. c. imago* Thomas, 1927. These results presented a classical intraspecific taxonomic problem of having to decide whether the two delineated phena were sufficiently different to justify the recognition of subspecies (Mayr and Ashlock 1991).

In this study, however, one of the prerequisites considered for recognizing the two subspecies within *A. chrysophilus* from southern Africa was the pattern of variation which was both size- and shape-related. More importantly, the phenetic discontinuity broadly coincides with an altitudinal limit (Clark 1967) of either below or above 500 m above sea level in the eastern part of southern Africa. The subspecies *A. c. chrysophilus* occurs below 500 m above sea level in the eastern part of southern Africa, whereas *A. c. imago* occurs outside this region. It is possible that the altitudinal limit in geographical distribution may act as a potential barrier to gene flow. Subspecies as units of evolution are expected to be represented by transitional zones that coincide with partial or complete, present or past, geographical or ecological barriers (Endler 1977; Barton and Hewitt 1985).

Of additional importance is that the recognition of subspecies was supported by a variety of both size- and shape-related morphometric characters, which also showed no evidence of clinal variation. The identification key below, however, is based only on geographical distributions because the characters were so subtle to be useful for practical diagnostic purposes.

An examination of pelage colouration in *A. chrysophilus* showed considerable and geographically discordant variation. This was also evident in *A. namaquensis*, *A. ineptus*, and *A. granti* from southern Africa (Chimimba 1997; Chimimba et al. 1998, 1999), and may be interpreted as an adaptive response to local climatic conditions. In Botswana, Smithers (1971) considered specimens of *A. chrysophilus* (sensu lato) with pure white or nearly pure white underparts to occur on the fringes of the Kalahari but refrained from recognizing subspecies. These pelage colour forms were not discernible in the present study.

Key to subspecies of *Aethomys chrysophilus* from southern Africa

1. Restricted to the eastern part of southern Africa, below 500 m above sea level (Figs. 2 and 4) .... *A. c. chrysophilus*
2. Occurring outside the above region .... *A. c. imago*

Taxonomy

Aethomys chrysophilus chrysophilus (De Winton, 1897)

Mus chrysophilus De Winton, 1897: Proc. Zool. Soc. Lond. 1896: 801.

Mus chrysophilus acticola Thomas and Wroughton, 1908: Proc. Zool. Soc. Lond. 1908: 547.

Holotype: BM 95.11.3.23 (original No. 54); adult female; Mazoe, Mashonaland, eastern Zimbabwe (17°31′S, 30°58′E). Both the holotype of *A. c. chrysophilus* and that of its junior synonym, *A. c. acticola* (BM 7.6.2.59; male; Beira, Mozambique: 19°50′S, 34°55′E) were examined.

Distribution: Occurring in the eastern part of southern Africa, below 500 m above sea level, including Mozambique, eastern Zimbabwe, eastern Northern Province, eastern Mpumalanga and eastern KwaZulu-Natal (Figs. 2 and 4).

Diagnosis: Medium-sized (observed range: length of head and body: 125–169 mm; greatest length of skull: 33.7–39.8 mm); dorsal and ventral colour clearly demarcated; upper parts brown (7.5 YR 4/3), sprinkled with brownish black (7.5 YR 3/1) hairs; cheek, sides, and thighs light grey (7.5 YR 8/2); underparts and feet light yellow-orange (7.5 YR 8/4); ears naked apart from a few scattered yellow-orange (7.5 YR 7/8) hairs; apart from a few short adpressed hairs that increase in number and length towards the tip, tail almost naked and more coarsely scaled; shiny, mica-like scales present; basal half bicoloured, brown (7.5 YR 4/6) above and orange (7.5 YR 6/8) below; terminal portion unicoloured yellow orange (7.5 YR 7/8).

Etymology: A combination of two Latin words, *chrysos* = gold and *philos* = having affinity for, to denote the golden dorsal surface.

Aethomys chrysophilus imago Thomas, 1927

Aethomys chrysophilus imago Thomas, 1927: Proc. Zool. Soc. Lond. 1927: 387.

Holotype: BM 26.12.7.220 (original No. 1832); adult male; Stampriet, eastern Gobabis, east-central Namibia (22°29′S, 19°32′E), was examined.

Distribution: Occurring widely in southern Africa above 500 m above sea level, from northern and central Namibia, northern and eastern Botswana to western Zimbabwe, western Northern Province and the northern sector of the Northern Cape Province around Kuruman (Figs. 2 and 4).

Diagnosis: Medium-sized (observed range: length of head and body: 120–165 mm; greatest length of skull: 32.1–40.6 mm); dorsal and ventral colour clearly demarcated; upper parts yellowish brown (10 YR 5/6), sprinkled with dark brown (10 YR 3/4); underparts, thighs light grey (10 YR 8/1); ears naked apart from a few scattered bright yellowish brown (10 YR 6/8) hairs; basal half of tail bicoloured, brown (10 YR 4/4) above and bright yellowish brown (10 YR 7/6) below; terminal portion unicoloured dark brown (10 YR 3/3).

Etymology: The subspecies name is probably derived from a Latin root, imago meaning "image, copy, likeness, similarity", perhaps reflecting its resemblance to the nominate subspecies.

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Zusammenfassung

Geographische Variation von Aethomys chrysophilus (Rodentia: Muridae) aus dem südlichen Afrika

Muster intraspezifischer Variation bei *Aethomys chrysophilus* De Winton, 1897, aus dem südlichen Afrika legen die Unterscheidung zweier Unterarten nahe: *A. c. chrysophilus* De Winton, 1897 und *A. c. imago* Thomas, 1927. Diese zwei Unterarten unterscheiden sich sowohl in Cranium-Größe als auch Form. Die morphologische Diskontinuität der vorgeschlagenen Unterarten deckt sich weitgehend mit einer Höhengrenze von über oder unter 500 m NN im östlichen Teil des südlichen Afrika.

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Influence of the subterranean herbivorous rodent *Ctenomys talarum* on vegetation and soil

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Abstract

The influence of the subterranean herbivorous rodent *Ctenomys talarum* (tuco-tuco) on vegetation and soil was evaluated in a coastal grassland. Plant species composition, dry plant biomass, soil pH, moisture, and nutrient content (N, P, Na, K, Mg, and Ca) were compared between areas with and without the influence of tuco-tucos. *C. talarum* apparently does not affect either plant species diversity or plant species richness, but modifies plant species composition at sites contiguous to burrows, where forbs occur more frequently than at sites without burrows. Abundance of most common grass and forb species, soil nutrient content, pH, and moisture were modified by *C. talarum*. Nitrogen, phosphorous, sodium, potassium, and magnesium had higher concentrations in areas with *C. talarum*, whereas calcium showed the converse. Soil pH and percent moisture were lower in areas with burrows of *C. talarum*.

Key words: *Ctenomys talarum*, coastal grasslands, herbivores, soil disturbance

Introduction

Subterranean rodents of the genus *Ctenomys* (tuco-tucos) occur broadly in South America. They are distributed throughout Argentina, southern Brazil, and areas of Bolivia, Chile, Paraguay, Perú, and Uruguay (Woods 1984). All species are strictly herbivorous that excavate and inhabit extensive burrow systems and deposit the tailings as mounds on the soil surface or in abandoned tunnels.

Ctenomys talarum is a long-lived herbivore that inhabits a secure, permanently sealed burrow system. Although most of its activities are restricted to its tunnel system, it makes brief surface excursions for collecting plant material. Diet analysis showed that individuals consume almost all plant species available in the field. However, they strongly prefer some species. Contrary to the prevalent consumption of roots reported for other fossorial rodents, *Ctenomys* species eat mainly above-ground plant parts (Comparatore et al. 1995).

This species has a social system with individual territoriality; both sexes and all ages (except preweaned young that occupy their mother's burrow system) are sedentary and maintain exclusive territories (Busch et al. 1989). Individuals maintain and expand extensive tunnel systems, resulting in the deposition of soil mounds on the surface.

Subterranean rodents may have important effects on vegetation and soil due principally to both burrowing and feeding activities, which may strongly modify the structure

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and dynamics of many ecosystems (ANDERSEN and MACMAHON 1981; CONTRERAS and GUTIÉRREZ 1991; HUNTLY and INOUYE 1988; REICHMAN et al. 1982). Burrowing activities exert a major impact on soil structure and nutrient availability, affecting both succession and abundance of plants (ANDERSEN 1987; INOUYE et al. 1987; TILMAN 1983).

Mounds of fossorial rodents may cover 5–15% of the soil surface (TURNER et al. 1983), burying existing vegetation. However, mounds also can serve as important germination sites (PLATT 1975; SCHAAL and LEVERICH 1982), creating open spaces for colonizer species that are competitively inferior in undisturbed sites. Repeated soil disturbance may be necessary for the maintenance of some plant communities (WHITE 1979). Although plant community complexity may be similar on and off animal-generated soil disturbanees, the species composition of the community may not be (PLATT 1975). Over the long term, mining and translocation of soil can modify topography, creating large-scale patterns of Mima mounds, one of the most remarkable effects of animal activity on landscape formation (COX and SCHEFFER 1991; MIELKE 1977).

Effects of subterranean rodents on vegetation are difficult to assess experimentally, presumably because manipulating the presence of these animals is logistically much more difficult than performing manipulative experiments with above-ground species. Where manipulative experimentation is not achievable, one way to overcome this shortcoming is to conduct mensurative experiments (sensu HURLBERT 1984) having an appropriate sampling design.

The present study aims to quantify the impact of tuco-tucos on vegetation by comparing plant diversity and biomass in areas with and without burrows of *Ctenomys talarum*. In addition, the present study reports about the influence of tuco-tucos on soil nutrient characteristics, as well as on the extent of burrowing-related disturbances as compared to undisturbed areas.

Material and methods

Field work was conducted at Mar Chiquita (37°41′S, 57°23′W), 40 km north of Mar del Plata, Buenos Aires Province, Argentina. The area is a natural coastal grassland described by CABRERA (1941). Sampling was performed at the end of the growing season (December 1994), when plant productivity is greatest, thus enhancing the chance of detecting the effects of tuco-tucos on soil and vegetation characteristics.

To evaluate the impact of *Ctenomys talarum* on vegetation and soil, ten 10- by 10- m plots were established in areas where fresh mounds of tuco-tuco were found. In addition, ten equally sized control plots were established in areas where *C. talarum* activity was not observed. No obvious differences in vegetation and topography were apparent between these areas, other than the presence or absence of burrows of *Ctenomys.*

In each control plot, 5 vegetation samples were taken by assigning random X-Y coordinates, hereafter referred to as CONTROL samples. In plots where activity of tuco-tucos was observed, we first identified all fresh mounds within a plot, and the burrow system associated to each mound was probed with a thin rod to locate branches over which samples could be taken. When a sample was taken, the underlying burrow was obvious so it was possible to verify that the sample actually was taken over a burrow. A total of 12 active burrow systems was identified. Three vegetation samples, ≅ 50 cm apart, were then taken directly above each burrow system (BURROW samples). Plant abundance and species composition in these samples were considered to illustrate the direct impact exerted by tuco-tucos on vegetation. Three additional samples (INTER-BURROW samples) were taken ≅ 1 m adjacent to each BURROW sample.

In addition, 5 vegetation samples (as determined by randomly chosen X-Y coordinates) also were taken in each tuco-tuco plot (RANDOM samples). At the time they were taken, RANDOM and INTER-BURROW samples clearly were not over old burrow systems. Comparisons between RANDOM and INTER-BURROW samples were intended to assess if tuco-tuco forage in the most productive areas.

Vegetation was sampled with vertical cores, 20 cm in diameter and 30 cm deep, which is the depth at which tuco-tucos are active. Samples included above- and below-ground vegetation and they were sieved to exclude most sand around plant roots, placed in plastic bags, labeled and transported to the lab. Plant fragments from each sample were identified to the species level, then separated into above- and below-ground fractions. Above-ground standing plant fractions were further classified into live and dead material. Unidentified roots and litter were also sepeated. All portions of a sample were bagged individually and oven-dried for 48 h at 60 °C, and then weighed to the nearest centigram.

Numbers and measurements (length, width, and height) of fresh mounds (1–2 days old) were recorded, and the surface area covered by the mounds in each plot was calculated as the area of an ellipse with the major axis equal to mound length and the minor axis equal to mound width. Volumes of mounds were calculated assuming that they had the shape of elliptical cones. These records would allow estimation of the average daily rate of excavation per ha, as well as the impact of tuco-tucos on vegetation by plant burial.

In areas where activities of tuco-tucos were observed, soil samples of approximately 200 ml were taken directly over each mound, whereas five randomly selected samples were taken in plots without tuco-tucos. Moisture, pH, N, Ca, Mg, Na, K, and P contents of the soil were determined. Nitrogen was determined by Kjeldahl, extractable P was determined colorimetrically, and Ca, Mg, Na, and K were determined by atomic absorption spectrophotometry.

Differences in mean dry biomass (g/sample) and Shannon-Wiener diversity index among groups of vegetation samples were statistically assessed by Kruskal-Wallis tests and Tukey-type multiple comparisons. Nutrient content of soil samples from plots with and without tuco-tucos was compared by Mann-Whitney U tests (Zar 1984).

Similarity in plant species composition between sample categories with and without tuco-tucos (RANDOM, INTER-BURROW, BURROW, and CONTROL, respectively) was measured with Margalef's similarity index ($M_{ij} = \frac{a(a+b+c+d)}{(a+b)(a+c)}$; Digby and Kempton 1987), where a is the number of species common to both sample categories, b is the number of species present in sample category i but not present in sample category j, c is the number of species present in sample category j but not present in sample category i, and d is the number of species not present either in sample category i or in sample category j. This index measures similarity taking into account both joint occurrences and absences of species and lies between 0 and s/a, where s is the total number of species present in both sample categories.

The significance of observed similarity between sample categories was assessed by generating distributions of the similarity index in a computer, assigning randomly plant species to each sample with a probability equal to that species' frequency of occurrence in all samples. The presence or absence of each plant species in randomly generated samples was recorded for each sample category and Margalef's similarity index between sample categories was computed 5 000 times. Three distributions of the similarity index were thus generated: one for the similarity index between sample categories both with 50 samples (CONTROL vs. RANDOM), one for sample categories with 50 and 36 samples each (CONTROL vs. INTER-BURROW and BURROW, and RANDOM vs. INTER-BURROW and BURROW), and the other for sample categories both with 36 samples (INTER-BURROW vs. BURROW). If the observed values of similarity between sample categories were lower than the 5 percentile of the corresponding distribution these sample categories were considered significantly dissimilar at $\alpha = 0.05$. These procedures were programmed in Visual Basic for Excel® 5.0 (Microsoft Corp., Redmond, WA).

Results

A total of 20 plant species (5 grasses; 15 forbs) was recorded in all samples taken during this study. Grasses constituted 85% and forbs 15% in dry weight of all sampled vegetation. The grasses *Panicum racemosum*, *Poa lanuginosa*, *Androtrichum trigynum* and the forbs *Baccharis genistifolia*, *Hydrocotyle bonariensis*, *Margyricarpus pinnatus* and *Solidago chilensis* were the most abundant plant species (Tab. 1).

There were no significant differences in plant species diversity (Kruskal-Wallis statistic = 0.848, P = 0.83) and plant species richness (Kruskal-Wallis statistic = 1.700, P = 0.64)

Table 1. Occurence (% frequency) and abundance (g/sample) of plant species in areas with and without influence of tuco-tucos. tr indicates abundances less than 0.01 g/sample.

	Without Tuco-tucos		With Tuco-tucos	
	g/sample	% Freq.	g/sample	% Freq.
Grasses				
Androtrichum trigynum	1.96	28.00	4.42	50.82
Distichlis scoparia	–	–	tr	1.64
Oenothera mollissima	0.01	6.00	0.01	4.10
Panicum racemosum	10.23	100.00	5.21	83.61
Poa lanuginosa	1.26	92.00	4.89	92.62
Forbs				
Achyrocline satureioides	0.04	4.00	–	–
Adesmia incana	0.05	4.00	tr	0.82
Ambrosia tenuifolia	0.04	10.00	0.03	8.20
Baccharis genistifolia	–	–	0.71	12.30
Conyza blakei	–	–	0.15	3.28
Daucus pusillus	–	–	0.01	1.64
Gamochaeta sp	tr	8.00	tr	1.64
Hydrocotyle bonariensis	0.16	24.00	0.66	44.26
Margyricarpus pinnatus	2.64	42.00	0.26	13.93
Medicago lupulina	0.15	14.00	0.08	12.30
Medicago minima	tr	2.00	tr	2,46
Melilotus officinalis	0.01	4.00	0.09	7.38
Polygala cyparissias	0.01	2.00	–	–
Solidago chilensis	0.11	22.00	0.25	31.97
Tessaria absinthioides	–	–	tr	0.82

Table 2. Comparisons of species richness (S), species diversity (H′), and dry biomass of herbaceous vegetation in absolute values (g/sample), in areas with and without burrows of *Ctenomys talarum*. H′ values for one-way nonparametric ANOVAs (Kruskal-Wallis test). $^*P < 0.05$. $^{**}P < 0.01$. Shared lowercase letters among sites with and without tuco-tucos within vegetation components indicate statistically indistinguishable values at $P = 0.05$ for nonparametric Tukey-type muliple comparisons.

	Without Tuco-tucos	With Tuco-tucos				
	CONTROL	RANDOM	INTER-BURROW	BURROW	Kruskal-Wallis statistic	
Number of samples	50	50	36	36		
Species diversity (H′)	1.22	1.50	1.60	1.53	0.84	NS
Species richness (S)	15	15	15	14	1.70	NS
Total Biomass	26.60 ± 16.04 a	33.69 ± 16.09 bc	35.84 ± 21.2 ab	35.20 ± 19.6 ab	8.62	*
Live	18.97 ± 12.97	16.53 ± 8.93	20.34 ± 12.61	17.94 ± 10.64	1.85	NS
Dead	7.64 ± 7.38 a	17.16 ± 10.48 b	15.50 ± 11.97 b	17.26 ± 11.79 b	29.98	**
Above ground	7.19 ± 5.84	5.58 ± 4.84	8.87 ± 7.29	7.37 ± 6.82	7.00	NS
Live	4.00 ± 4.57 ab	2.73 ± 2.82 a	5.32 ± 4.82 bc	3.41 ± 2.69 ab	10.75	*
Dead	3.19 ± 3.30	2.85 ± 3.64	3.55 ± 4.51	3.96 ± 5.97	3.38	NS
Underground	14.97 ± 9.79	13.8 ± 7.4	15.02 ± 10.58	14.53 ± 9.73	0.27	NS
Litter	4.44 ± 6.22 a	14.31 ± 11.09 b	11.89 ± 12.82 b	13.25 ± 12.44 b	24.48	**
Unidentified roots	5.49 ± 6.18	4.43 ± 3.26	4.5 ± 7.37	5.25 ± 6.29	3.04	NS

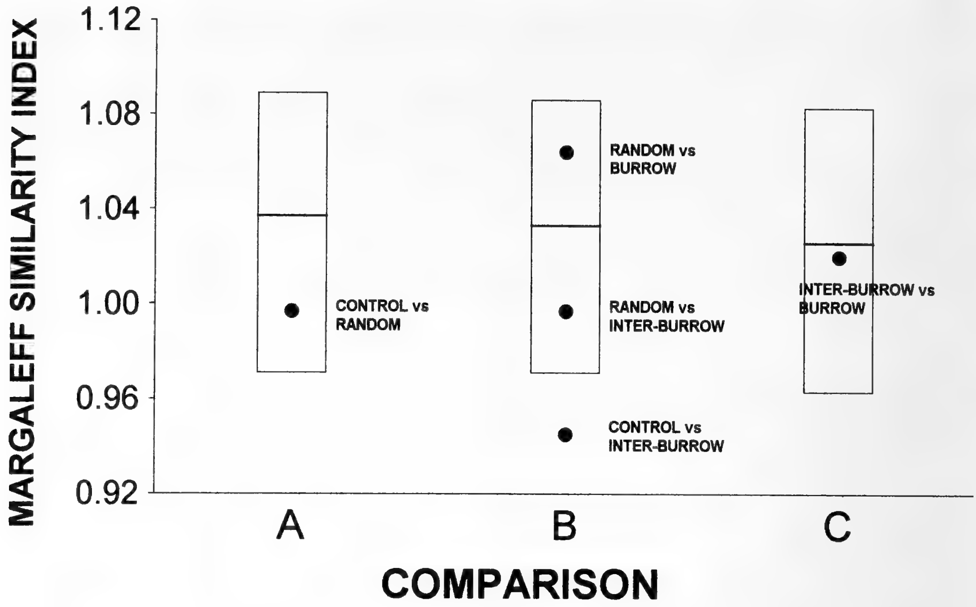

Fig. 1. Margalef's similarity index for plant species composition between sample categories with (BURROW, INTER-BURROW, RANDOM) and without burrows (CONTROL) of tuco-tucos. Top horizontal lines of boxes represent upper 2.5 percentiles of the index null distribution. The center and lower horizontal lines represent the median and the lower 2.5 percentile, respectively. A) Comparison of observed similarity indices between sample categories with 50 vegetation samples against the null distribution; B) between sample categories with 50 and 36 vegetation samples; and C) between sample categories both with 36 vegetation samples. Number of samples used to generate null distributions in each comparison was equal to that actually taken in the field.

between areas with and without tuco-tucos (Tab. 2). Although these indices suggest an overall similarity in plant community structure between areas, the composition of plant species differed substantially, principally owing to differences in the occurrence of forb species. *Baccharis genistifolia*, *Conyza blakei*, *Daucus pusillus*, *Tessaria absinthiodes* (forbs), and *Distichlis scoparia* (a grass) occurred only in samples from plots with tuco-tucos while *Achyrocline satureioides* and *Polygala cyparissias* (forbs) were recorded only in samples from sites without tuco-tucos. Differences in plant species composition were most marked between CONTROL samples and INTER-BURROW samples (Margalef's similarity index 0.945, $P = 0.012$); the remaining comparisons did not show significant differences (Fig. 1).

Several significant differences in plant biomass between areas with and without tuco-tucos were observed (Tab. 2). Comparisons among CONTROL, RANDOM, and INTER-BURROW samples indicated that tuco-tucos did not forage in areas with significantly more plant biomass. Litter was significantly higher in areas with tuco-tucos, resulting in increased total plant biomass and total dead material as compared to samples from areas without tuco-tucos. Above-ground live material was highest in INTER-BURROW samples, which differed significantly from RANDOM samples.

Abundances of total grasses and forbs did not differ between areas with and without tuco-tucos. Although individual species of each group differed significantly between areas (Kruskal-Wallis test, $P < 0.05$), some showed opposing directions in abundance, yielding no consistent pattern of change between areas.

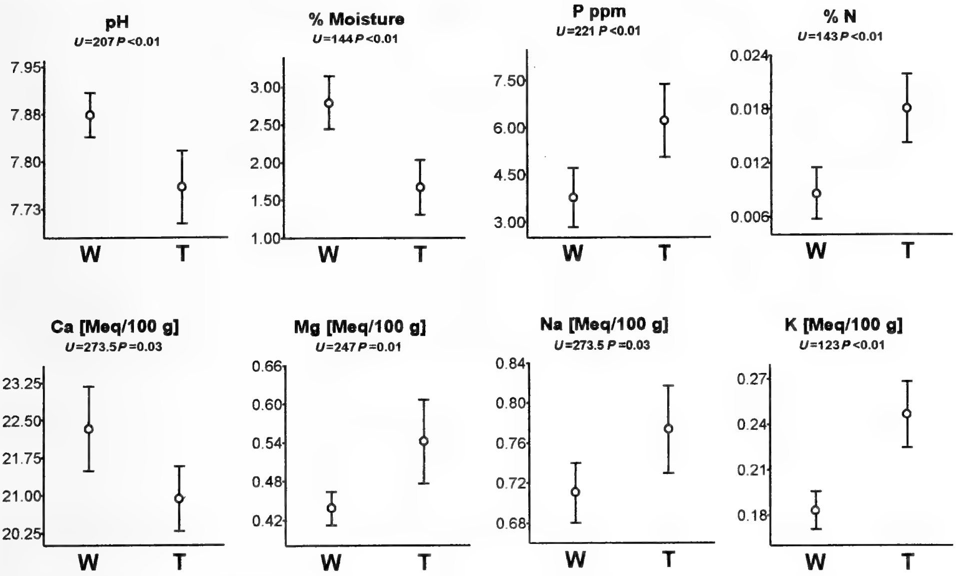

Fig. 2. Comparisons of mean (± 1.96 SE) pH, % moisture and soil nutrient concentrations in soil samples from sites with (T) and without (W) burrows of *Ctenomys talarum*.

The two most frequent grasses in the study area, *Panicum racemosum* and *Poa lanuginosa*, clearly illustrates this situation. *Poa lanuginosa* was more abundant where tuco-tucos occurred, whereas *Panicum racemosum* was more abundant in areas without burrows of tuco-tucos.

The most abundant forb in the area, *Margyricarpus pinnatus*, was considerably less abundant where tuco-tucos occurred. Conversely, *Baccharis genistifolia* and *Hydrocotyle bonariensis*, showed increased biomass in areas with tuco-tucos.

In areas where activities of tuco-tucos were observed 23 fresh mounds were measured, giving an estimate of mound coverage of 43.5 m^2/ha of soil surface. If we assume that this is the initial influence of mounds, they could have reduced the above-ground plant biomass in the field only by as much as 0.43%. Taking into account that mean burrow length and mean tunnel diameter for *Ctenomys talarum* are 14 m and 0.08 m, respectively (Antinuchi and Busch 1992), the total area covered by underlying burrows is 737 m^2/ha (7.4% of total area). Volume of excavated soil per ha was 4.7 m^3/ha; estimated from mean burrow volume (0.07 m^3) and mean animal density (approx. 65 ind/ha; Busch et al. 1989). Thirty percent (1.4 m^3/ha) of excavated soil remained as mounds on the ground surface. Multiplying mound soil volume by soil density (2,750 kg/m^3) gives us 3,824 kg/ha of soil deposited in mounds in 15 days (the span of the sampling period), which represents an excavation rate of 91,785 kg/ha/yr.

Soil nutrient concentration differed between areas with and without tuco-tucos (Fig. 2). Phosphorous (P), Nitrogen (N), Magnesium (Mg), Sodium (Na), and Potassium (K) had significantly higher concentrations in areas with tuco-tucos than in areas without tuco-tucos, whereas Calcium (Ca) showed the converse. Both soil pH and moisture content were significantly lower where tuco-tucos occurred.

Discussion

Our results show that tuco-tucos exert substantial effects on vegetation and soil. In reference to the effects of tuco-tucos on vegetation, they reduce the abundance of the most prevalent species of grasses and forbs, thereby increasing the occurrence of typically less common species from both plant groups. The differential occurrence of forb species, mainly in inter-burrow areas (INTER-BURROW samples), suggests that a slightly distinct plant community is maintained by the activities of tuco-tucos.

Zenuto and Busch (1995) found that the impact of *Ctenomys australis* on a dune grassland was to increase the abundance of early colonizers such as *Panicum racemosum* and *Hydrocotyle bonariensis*. Effects of *C. talarum* documented here differ with regard to *P. racemosum*, possibly due to differences in the successional stage of plant communities at both study sites. The plant community studied here represents a later successional stage than that impacted by *C. australis*.

Studies of North American pocket gophers (Geomyidae) have consistently concluded that burrows and mounds of these animals generate a notable reduction in overlying vegetation, enhancing plant biomass directly adjacent to the distubance (Reichman et al. 1993). Our results show that changes in plant species composition are most marked in areas adjacent to the disturbance produced by mounds and burrows of *Ctenomys talarum*, yet plant biomass in these areas did not differ from that in areas directly over burrows or from that in areas without burrows.

Generally, forbs would suffer greater impact from a fossorial herbivore than grasses because of the differences in root configuration (Reichman and Smith 1985). However, most of the difference in plant species composition noted above was made by forb species, which occurred most frequently adjacent to disturbed areas. Vegetation adjacent to the burrow could be stimulated by altering local soil-water relations, or by being freed from competition by the depletion of vegetation directly over the burrows (Reichman and Smith 1985). Rather than increasing the growth of grass species, the disturbance generated by mounds and burrows of *C. talarum* apparently promoted a replacement by forbs. The loss of roots in burrows and the burying of vegetation by mounds produce small-scale gaps in the grassland. Hence, physical disruption of the soil by digging activities, breaks up stable aggregates of soil particles, thus increasing mineralization rates. Thus, the combined effects of reduced competition for resources and increased mineralization rates (along with water runoff from mounds, decomposition under mounds, and urine and fecal deposits within burrows) may be responsible for stimulating plant biomass and changing plant species composition directly adjacent to the disturbances. In addition, roots of grasses have an intricate configuration that, under certain soil conditions, may prevent settlement of forb propagules, therefore monopolizing the local grassland. If burrow construction causes the removal of roots of grasses, forb species would have a higher probability of settlement in areas with increased nutrient content adjacent to the burrows.

We found no evidence that *Ctenomys talarum* choose to forage in portions of the field that contain more plant material than unused areas, unlike what was generally found in pocket gophers (Reichman and Smith 1985).

In reference to the effects of burrowing mammals on soils, the most obvious one is illustrated by the deposition of soil on the surface that results in mound formation that bury existing vegetation. The magnitude of this primary effect of subterranean rodents varies greatly; from 8% (Grant et al. 1980) to 28% (Reichman and Jarvis 1989) of surface area covered by mounds. Our estimate of 0.43% suggests that the effect of *C. talarum* is relatively low. However, the highest effect reported by Reichman and Jarvis (1989) for three species of Bathyergids contains miscalculations, that resulted from equating one ha. to 1,000 m^2 instead of 10,000 m^2. The correct estimate for this study is 2.8% of surface area covered by mounds (2.4% for *Bathyergus suillus*, 0.28% for *Geory-*

chus capensis, and 0.12% for *Cryptomys hottentotus*), which now comes closer to the estimate for *C. talarum*.

The rate of soil excavation for different species of subterranean rodents varies by as much as two orders of magnitude from 0.8 ton/ha/yr (MIELKE 1977) to 105 ton/ha/yr (COX 1990; MILLER 1957). The excavation rate for *C. talarum* at Mar Chiquita (91.78 ton/ha/yr) ranks in the upper 28% of 12 reports (BUECHENER 1942; COX 1990; COX et al. 1995; ELLISON 1946; GRANT et al. 1980; MIELKE 1977; MILLER 1957; RICHENS 1966; SPENCER et al. 1985). It seems to be very unlikely that the above rate of mound formation, estimated for such a short period, applies uniformly throughout the year. Nevertheless, in our calculation we did not consider backfilling of tunnels, which for some pocket gophers may involve 86% of excavated soil (ANDERSEN 1988, 1990). Hence, the estimation of the excavation rate for *C. talarum* can be considered rather conservative.

Tuco-tucos provide an example of the importance of non-consumptive behaviour in altering ecosystem structure. Most obviously, the physical structure of the soil as well as the structure of the above-ground plant community are modified, but the nutrient status of the soil also may be affected, as reported by GRANT et al. (1980) for pocket gophers. Formation of new mounds by tuco-tucos increased the levels of P, Na, K, and Mg. Nitrogen also increased significantly in areas with tuco-tucos. On the other hand, Ca, pH, and moisture content of soil were higher in undisturbed areas.

Soil moisture may be affected by tunnel construction by tuco-tucos, since burrowing changes soil characteristics, e. g. by creating spaces in the soil matrix, decreasing soil moisture content by aeration that promotes evaporation. However, in areas characterized by harder soils, holes in the surface makes it easier for the water to penetrate the ground during dry seasons, which counteracts losses by evaporation and run-off.

Like other burrowing mammals, tuco-tucos may alter the habitat near burrows either indirectly by moving, mixing, and bringing soil to the surface from lower horizons, or directly by feeding, by burying vegetation, or by deposition of feces and urine in the vicinity of burrow systems, thus creating patches of high nutrient availability. Furthermore, the relative increase of nutrients in tuco-tucos mounds may also occur because of the presence of a litter layer next to the mounds. This layer is important in holding nutrients near the surface, serving as a nutrient trap. Hence, movements of chemical subtances from deeper to upper soil layers may add to the nutrients already present in surface soil to yield a higher total nutrient content near tuco-tucos mounds. This additive effect of nutrients in combination with the distribution of litter may enhance the area on the perimeter of mounds as microsites for plant germination and growth. On the other hand, the presence of an acidic litter layer off the mounds may be responsible for the lower soil pH recorded in these areas.

Differences in Na concentration between areas with and without tuco-tucos may be explained by the influence of the marine breeze on the study area, which was located a few hundred meters from the sea-shore. Greater quantities of Na found in soils with tuco-tucos mounds may be thus related to their external morphology, since their dome-shaped surface would increase the deposition of Na through salt spray from the sea.

Several studies have examined the effects of burrowing organisms on nutrient availability and have reported increased levels of cations in the surface soil as a result of soil moving activities. Nevertheless, the specific cations affected have not always been the same. For pocket gophers, mound soil frequently differs from that of surrounding undisturbed soil in the levels of various soil nutrients, including N, P, K, Na, Ca, which may be significantly higher (ABATUROV 1972; ANDERSEN and MACMAHON 1985; GRANT and MC BRYER 1981; HOLE 1981; KOIDE et al. 1987; LAYCOCK and RICHARDSON 1975; MIELKE 1977; ZINNEL 1988) or lower (HUNTLY and INOUYE 1988; INOUYE et al. 1987; KOIDE et al. 1987; MC DONOUGH 1974; SPENCER et al. 1985) in comparison with undisturbed soil. For other burrowing mammals, soil near burrows did not differ from mound soil (CONTRERAS et al. 1993; Swihart 1991). The inconsistency of these results may be due primarily to regional differences in soil types.

Our evidence suggests that the influence of tuco-tucos is certainly not trivial, and that at high densities such as those found in Magdalena, Argentina, (Pearson et al. 1968) where density of tuco-tucos reaches 203 individuals/ha, these animals may have a profound impact on vegetation and soil.

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Zusammenfassung

Einfluß des unterirdischen herbivoren Nagers Ctenomys talarum auf Vegetation und Boden

Der Einfluß des unterirdisch lebenden und herbivoren Nagers *Ctenomys talarum* (Tuco-Tuco) auf die Vegetation und den Boden wurde auf einer Küstenwiese in Argentinien untersucht. Das Artenspektrum der Pflanzen, das Trockengewicht der Pflanzenbiomasse, Boden-pH, Feuchtigkeit und Nährstoffgehalt des Bodens (N, P, Na, K, Mg und Ca) wurden dazu zwischen Gebieten mit und ohne Besiedlung durch Tuco-Tucos verglichen. Offensichtlich beeinflußt die Besiedlung weder die Artendiversität noch den Artenreichtum der Pflanzengesellschaft. Dagegen ändert sich die Artenzusammensetzung, da in der Umgebung der Baue ein höherer Anteil krautiger Pflanzen festgestellt wurde als an Stellen ohne Baue. Ebenso wurden die Abundanzen der häufigsten Gräser und Kräuter, der Nährstoffgehalt, sowie Boden-pH und Feuchtigkeit durch die Aktivität von *C. talarum* beeinflußt. Die Stickstoff-, Phosphor-, Natrium-, Kalium- und Magnesiumgehalte lagen in Gebieten mit Tuco-Tuco-Besiedlung höher, während der Kalziumgehalt erniedrigt war. Boden-pH und relative Feuchtigkeit waren in Gebieten mit Bauen geringer.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

On the pupping season of grey seals (*Halichoerus grypus*) off Amrum, Northern Germany

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Key words: *Halichoerus grypus*, pupping season, Wadden Sea

The grey seal *Halichoerus grypus* (Fabricius, 1791) is distributed along several coasts of the North Atlantic and adjacent seas (Bonner 1981; Anderson 1992). Within this range, the species shows a highly variable timing of reproduction, as compared to other phocids. Grey seals breed from September to March, with distinct seasons in the three commonly recognized sub-stocks of the West Atlantic, East Atlantic, and the Baltic (King 1983; Anderson 1992). Geographic variation is further evident within the East Atlantic stock, particularly around Great Britain (Bonner 1981; Anderson 1992), and along the Norwegian coast (Wiig 1986). Originally, geographic patterns of reproductive timing were simply related to population structure (Davies 1957; Hewer 1974; Summers 1978). However, various other explanations have been suggested (Harrison 1963; Coulson 1981; Boyd 1991).

In the North Sea, the largest aggregation of grey seals is found on the Farne Islands (Fig. 1, King 1983), where pupping occurs mainly from late October to mid December (Coulson and Hickling 1964). A number of smaller breeding colonies has arisen in recent decades on the British east coast and in the Wadden Sea, one of which is situated on the shoal Jungnamensand (54°40′ N, 8°15′ E) off the German island of Amrum (Fig. 1). Although these colonies are commonly assumed to descend from the prolific Farne Islands stock (Harwood and Wyile 1987; 't Hart et al. 1988; Vogel and Koch 1992), there is evidence that in some colonies breeding is considerably later than on the Farnes (Bonner 1981; Vedder et al. 1992; Vogel and Koch 1992). To make this phenomenon more distinct, we analysed reports of grey seal birth dates from the breeding site off Amrum.

Pupping on Jungnamensand was monitored over 10 seasons from autumn 1988 to spring 1998. Sightings of pups were made by volunteers on boat trips, for the most part by the crew of a customs patrol boat routinely passing the site. With some exceptions, surveys took place at least weekly. The proportion of missed pups is thus believed to be small, although an occasional pup may have been lost through flooding of the rookery during storms.

Approximate – sometimes even exact – birth dates were derived from morphological clues (e. g. Davies 1949; Radford et al. 1978). The latter also allowed for easy discrimination of pups of different ages, since numbers per season are usually small. However, as survey intensity was not constant and experience of observers limited, the precision of the assumed birth dates varied, with ranges of uncertainty between 1 and 10 days (mean = 3.7).

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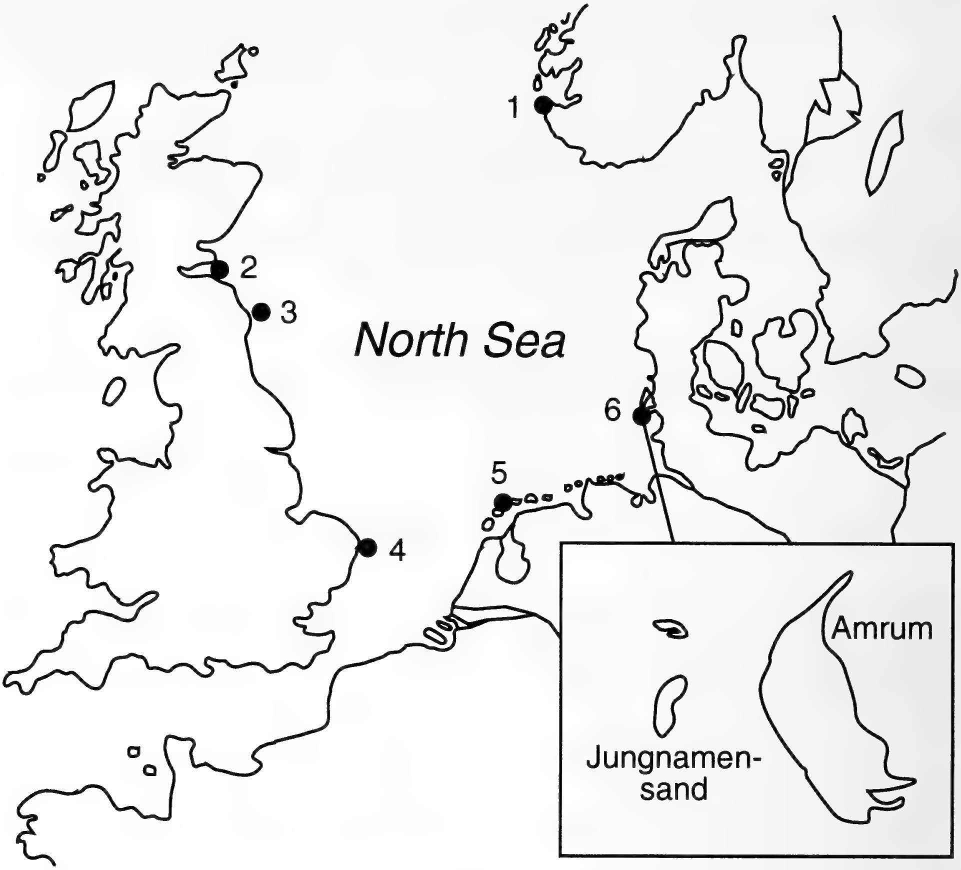

Fig. 1. Location of the study area and other grey seal breeding sites mentioned in the text; 1 = Kjør (S-Norway), 2 = Isle of May, 3 = Farne Islands, 4 = Scroby Sands, 5 = Vlieland (The Netherlands), 6 = Amrum (N-Germany).

A total of 78 pups was recorded, with the number per season varying between 3 and 11 (Tab. 1). The entire range of birth dates was from mid October to late February, i. e. about four months. However, these extreme values occurred only in the season of 1997/98, whereas in 9 of the 10 seasons, pupping did not start prior to mid November, and in 7 seasons ceased by late December or earlier (Tab. 1). In order to avoid bias in parametric analyses through extreme values (which might represent different populations in the statistical and/or biological sense), the joint distribution was truncated at the 2.5- and 97.5-percentiles. In the remaining 74 birth dates, ranging from mid November to mid January (Tab. 1), the average date did not vary significantly between seasons (ANOVA, df = 9, F = 0.815, p = 0.604). Therefore, the peak pupping date was calculated from the pooled data. The latter were not normally distributed (Lilliefors test, n = 74, p = 0.005), which could be attributed to positive skewness (S = 0.724). A log-normal distribution was therefore suggested, the parameters of which were determined by log (x – k) transformation of the data, and fitting k (the origin) to give a minimum departure from normality. With k = 27 October, as found by an iterative least squares procedure, the data conformed remarkably well to a log-normal distribution (Lilliefors test, n = 74, p = 0.516). The corresponding median birth date was 5 December, whereas the mode, i. e. the peak

Table 1. Numbers of grey seal pups born off Amrun, Northern Germany, from autumn 1988 to spring 1998, by pupping season and decade. Figures within the two dotted lines represent the central 95%-mass of the pooled birth dates, from which the peak pupping date (1 December) was calculated.

Pupping season	Month/(Decade)															Σ
	Oct			Nov			Dec			Jan			Feb			
	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	(1)	(2)	(3)	
88/89					1	1	4	1	2							9
89/90							1	2								3
90/91					2		3	1	1							7
91/92					1	3	1		1							6
92/93					1	3		2	1	1	1	1				10
93/94					2	3	1		1							7
94/95						3		1		1						5
95/96						4	6		1							11
96/97						2	5	4								11
97/98		2				2	2	2							1	9
Σ		2			7	21	23	13	7	2	1	1			1	78

pupping date, was 1 December. The central 68%-mass of the probability distribution of births (corresponding to the area between the mean date +sd and –sd on the log scale) occurred from 24 November to 19 December (25 days).

Close genetic relationships and a similiar timing of reproduction among grey seals in the North Sea might be expected. However, with peak pupping in early December, seals off Amrum give birth 3–4 weeks later than on the Farnes (Coulson and Hickling 1964) and on the Isle of May (Caudron 1998). Pupping in a colony in the Dutch Wadden Sea, near the island of Vlieland, is even later, with a peak in early January (Vedder et al. 1992) or, more recently, in late December (P. Reijnders, pers. comm.). Similarly, grey seals at Scroby Sands off the Norfolk coast give birth in late December or early January (Bonner 1981). Thus, pupping in the southwestern North Sea occurs 7–8 weeks later than on the Farnes, while off Amrum it is intermediate. It is interesting in this regard that there is also a north-south gradient in the time of pupping along the west and north coast of Great Britain, but in the opposite direction, i. e. ranging from September in Cornwall until November in northern Scotland (Coulson 1981; King 1983; Anderson 1992). Only in southern Norway, grey seals appear to have a similar birth season as of Amrum (Wiig 1986).

Factors that regulate – and thus may cause geographic variation in – the annual cycle of the grey seal seem to be poorly understood, although having received much attention by scientists. In fact, neither the relevance of genetic differences between sub-stocks (cf. Davies 1957; Hewer 1974), nor the concept of photoperiodical regulation (Harrison 1963), have yet been generally accepted. Coulson (1981) rather suggested response of seals to ambient sea-temperature as the mechanism of – and source of variation in – reproductive timing. Boyd (1991) instead proposed a proximate relation of the time of breeding to seasonal food abundance, which is equivalent to an indirect influence of temperature.

However, none of these ideas seem to help explaining why grey seals off Amrum and Vlieland give birth significantly later than those on the Farne Islands. Some researchers related this phenomenon to a presumably high proportion of primiparous females in the former two sites (Vedder et al. 1992; Caudron 1998; P. Reijnders, pers. comm.). Considering this to be a characteristic of recently founded colonies, they expect a shift towards earlier pupping with rising proportion of multiparous females (cf. Vedder et al. 1992), which would gradually lead to a similar birth season as on the Farnes. However, no such trend is evident from our data. Further, the idea does not appear to be compatible with the virtually well-defined, unimodal pupping season found in the present study.

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Substitution of the deciduous premolar in *Chaetomys subspinosus* (Olfers, 1818) (Hystricognathi, Rodentia) and its taxonomic implications

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Key words: *Chaetomys subspinosus*, Hystricognathi, deciduous forest, premolars, taxonomy

The bristle-spined porcupine, *Chaetomys subspinosus* (Olfers, 1818), is a New World hystricognath rodent endemic to the Brazilian Atlantic rainforest, whose geographical distribution ranges from northern Rio de Janeiro State up to Sergipe State (SANTOS, et al. 1987). The taxonomic position of the monotypical genus *Chaetomys* has been very controversial, having been considered either as a member of the Erethizontidae (e. g.: THOMAS 1897; ELLERMAN 1940; LANDRY 1957) or of the Echimyidae (e. g.: MILLER and GIDLEY 1918; PATTERSON and WOOD 1982).

In his general work with the taxonomy of hystricognath rodents, WOODS (1993) lists *Chaetomys* in the family Echimyidae, as suggested by PATTERSON and WOOD (1982) due to the supposed retention of the deciduous premolars (dP4), an echimyid-derived character. This placement of *Chaetomys* within the Echimyidae was strongly contested by MARTIN (1994), who pointed out that *C. subspinosus* lacks the rectangular plate-like interprismatic matrix in the portio interna of the incisor Schmelzmuster (multiserial-right angular incisor enamel microstructure). This character has been considered a key synapomorphy of Octodontoidea, the superfamily, which includes the family Echimyidae. Furthermore, MARTIN (1994) stated, in contrast to PATTERSON and WOOD (1982), that the posterior carotid foramen is in fact present in *Chaetomys*, a condition shared with the erethizontids but not with the echimyids. MARTIN (1994) could not however, find any evidence against the retention of the deciduous premolar in *Chaetomys.*

While examining a sample of 12 specimens of *C. subspinosus* housed at the Museu Nacional, Rio de Janeiro, Brazil, the present author found one specimen (MN 11464) whose successional premolars (P4) could be seen erupting when the deciduous premolars (dP4) were removed (Fig. 1). This condition was found in both the lower and the upper molar series. The dP4 were only slightly more worn than the first molars and were similar in size and crown morphology to the P4. Almost all cranial sutures in this specimen were obliterated and all molar teeth already worn, which indicate the maturity of the specimen (VOSS and ANGERMANN 1997).

None of the other available specimens were found to be in a similar state of tooth replacement (however, in two of these, MN 11202 and MN 11461, it was not possible to remove any of the premolars for observation). Likewise, a premolar clearly less worn than the first molar in a complete molar series, which also would be evidence for premolar substitution, was not present in any of the specimens. This raises the question whether the observed substitution of the dP4 commonly takes place in *Chaetomys*, or whether the observed erupting premolar is an anomalous individual condition.

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Fig. 1. Anterior portion of upper molar series of the specimen MN 11464 showing the left successional premolar (P4) after the removal of the deciduous tooth.

In order to investigate this question, the sample was divided into two separate groups, depending on whether the specimens seemed to be younger or older than the specimen displaying the erupting P4 (MN 11464). The features used for this relative age characterization were the wear of the molar teeth and the closure of cranial sutures (Voss and Angermann 1997). It could be assumed that all premolars in the group of younger specimens would be a dP4, while those in the group of older specimens would be a P4. Thus, any character that could be used to distinguish between a dP4 and a P4 should be consistently different in these two groups.

Eight specimens (MN 9680, MN 11202, MN 11459, MN 11460, MN 11461, MN 11462, MN 50682, and MN 50683) were considered to be younger than the specimen with erupting P4 (MN 11464). Only three specimens (MN 11465, MN 34503, MN 46250) were considered to be older. The morphology of the anterior roots of the upper premolar was consistently different in the specimens of the two groups. The specimens of the younger group presented the two anterior roots of the upper premolars to be divergent and well separated, similar to the anterior roots of the upper dP4 of MN 11464 (Fig. 2 a). In contrast, in all specimens of the older group, the two anterior roots were nearly parallel and fused proximally (Fig. 2 b). Following these results it can be concluded that this character can be used to distinguish the dP4 from the P4, a finding that supports the supposition, that the substitution of dP4 generally occurs in *Chaetomys*. The substitution of the dP4 in *Chaetomys* corroborates the exclusion of the genus from the family Echimyidae as proposed by Martin (1994). This, however, does not add information about its taxonomic affinities, since the substitution of dP4 is considered a plesiomorphic feature for the Hystricognathi.

Martin (1994) has also pointed out that the presence of a posterior carotid foramen and the small enamel thickness of the incisor, with its primitive Schmelzmuster, should be regarded as primitive traits for the Hystricognathi, and hence should not be used as an indication to place *Chaetomys* in the family Erethizontidae. However, in a more recent publication, Bryant and McKenna (1995) suggested that the presence of an internal car-

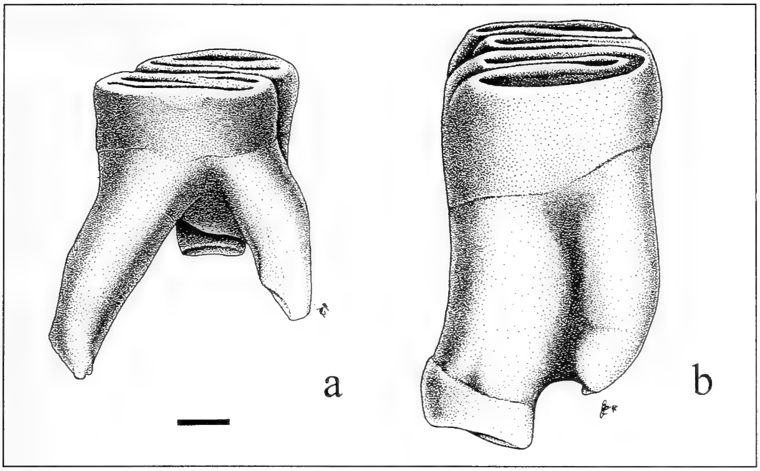

Fig. 2. Anterior roots of the upper premolars of *Chaetomys subspinosus.* a) divergent and well-separated anterior roots of a left upper deciduous premolar (MN 11464); b) proximally fused parallel anterior roots of a left upper premolar of an older adult (MN 34503), supposedly a successional premolar. Scale bar = 1 mm

otid artery, although a primitive condition for rodents, emerges as a synapomorphy of the Erethizontidae within the Hystricognathi, for which the absence of an internal carotid artery is the primitive condition. Hence, the presence of the posterior carotid foramen in *Chaetomys* should actually be reinterpreted as evidence for its association with the Erethizontidae.

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Buchbesprechungen

YAOWALAK CHAIMANEE (1998): **Plio-Pleistocene rodents of Thailand**. Thai Studies in Biodiversity, **3**, 1–303 (BIOTEC, National Science and Technology Development Agency, Rama VI Road, Bangkok 10400, Fax 02 6448106). Softcover, $ 20. ISBN 974-7577-80-1.

SE-Asia is a crucial area for murine and sciurid radiations. Both groups predominate in extant rodent faunas of Thailand (around 92% of all rodent species) and they alone are subject of this book on late Pliocene and Pleistocene rodent associations from there. The paper includes 30 murine and 11 sciurid species, coming from 20 fossil sites (fissure fills and caves). Taxonomy and the assessment of phylogenetic relationships are essentially based on dental occlusal morphology; more general chapters are dedicated to paleobiogeography, paleoecology, and biochronology. Changes in species composition through time suggest increasing humidity and decreasing seasonality from the latest Tertiary on, probably correlating with the uplift of the Tibetan Plateau. Most of the fossil taxa are referred to extant species which are still living in Thailand and adjacent countries; the genus *Rattus* exhibited a distinct radiation during the Plio/Pleistocene.

The book is recommended to all being interested in rodent evolution in SE-Asia and beyond.

G. STORCH, Frankfurt am Main

CHRONOPOULOS, D.: **Die Rückkehr der Gorillas.** Friedrichshafen: Verlag Robert Gessler (1999). Gebunden, 463 pp, 102 schwarz-weiß Fotos, 2 Karten. DM 59.–. ISBN 3-86136-042-X

Die Autorin beschreibt im vorliegenden Buch ihrer Beobachtungen und Erlebnisse als Leiterin eines kongolesischen Camps zur Auswilderung junger Gorillas. Sie schildert detailliert die sich entwickelnden Persönlichkeitsstrukturen der Gorillas und ihre Beziehungen zueinander und zu den Betreuern. Das natürliche Verhalten wild lebender Gorillas ist nicht Inhalt dieses Buches, ebenso wenig wie eine wissenschaftliche Verhaltensprotokollierung.

Der Leser wird vielmehr durch sensibel beobachtete, spannend erzählte und zu einem Gesamtbild verknüpfte Episoden in das Fühlen und Denken der Gorillas eingeführt. Dies kann nur so gelingen, wie die einfühlsame Autorin es folgerichtig versucht: sie skizziert die Charaktere, schildert deren Verhalten und fügt ihre Interpretationen der Gefühle und Motivationen der Akteure hinzu. Diese Interpretationen rechtfertigen die ausführliche Schilderung des Verhaltens der Tiere, sie sind gewissermaßen das wissenschaftliche Ergebnis eines letztlich gescheiterten Projektes. Denn wer verstehen will, was in der Evolution des Menschen und der Menschenaffen wirklich geschehen ist, der muß sich mit der Vielschichtigkeit der Persönlichkeit der Menschenaffen auseinandersetzen, nicht nur mit den intellektuellen Leistungen, die sich in wissenschaftlichen Versuchen offenbaren, oder mit den im Freiland beobachtbaren Sozialstrukturen. Eben das gelingt hier hervorragend und gibt dem Gorilla die Chance, seinen zweifelhaften Ruf als dümmlicher Verwandter des gefeierten Schimpansen endlich abzulegen. Freilich bergen die Notwendigkeit der Verhaltensinterpretation durch die Autorin und die gelungene Erzählweise auch die große Gefahr einer subjektiven Fehleinschätzung zu erliegen, die der Leser kaum erkennen könnte. Die einzige Möglichkeit einer Objektivierung liegt im Vergleich möglichst vieler Interpretationen verschiedener Autoren – wozu Leser und vor allem Autoren ausdrücklich aufgefordert sind.

Ein zweiter, deprimierender Aspekt des Buches ist die ausführliche Beschreibung all jener Hindernisse bis hin zum Bürgerkrieg, die jeder sinnvollen Aufbauarbeit in Afrika entgegenstehen. Die Autorin entlarvt bissig auch die menschlichen Verhaltensmuster auf dem schwarzen Kontinent und macht deutlich, wie wenig sinnvoll naiv-gutgläubige Naturschutzprojekte unter den gegebenen Bedingungen sind. Das Scheitern des Projekts war somit vorbestimmt – die grausame Konsequenz, mit der es dann eintritt, ist trotzdem schockierend.

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Kurzes Fazit: spannende und lehrreiche Unterhaltung, die zum Nachdenken anregt und einen noch lange nach der Lektüre beschäftigt. Je mehr Menschen sich mit dem Naturschutz und mit den Menschenaffen beschäftigen, desto größer wird ihre Lobby – und werden vielleicht auch ihre Chancen.

K.-P. Valerius, Giessen

Röckel, D. (1999): **Die abenteuerliche Geschichte des letzten Wolfs im Odenwald und Letzte Wölfe in Deutschlands Regionen.** Heidelberg: Verlag der Rhein-Neckar-Zeitung. Geb. 127 pp., zahlreiche s/w und farbige Abb. und Karten. DM 34,90. ISBN 3-929295-53-9.

In diesem außerordentlich interessanten Buch werden nach einer Einführung zunächst die Charakteristika von *Canis lupus* und seine Lebensweise kurz geschildert, anschließend wird anhand von Beispielen aus deutschen Regionen die vorurteilsbeladene Beziehung des Mitteleuropäers zum Wolf, dem „mörderischen Untier“, „blutgierigen Feind“, „Räuber“, „frechen Übeltäter“, dargestellt und der völlig anderen und positiven Sichtweise der nordamerikanischen Indianer und Eskimos gegenübergestellt („Pfadfinder“, „Lehrer“). Das folgende Kapitel beschäftigt sich mit Deutschlands letzten Wölfen und beschreibt zunächst Einrichtungen, wie Wolfsangeln oder Luderplätze, mit deren Hilfe der Art der Garaus gemacht werden sollte. Im Gebiet der heutigen Bundesrepublik Deutschland dauerte die Periode der Ausrottung der letzten Wölfe etwa 70 Jahre: In den Bayerischen Alpen, im Rheinland, Münsterland, Siegerland und Hohenzollern wurden in den dreißiger Jahren des 19. Jahrhunderts die letzen Wölfe erlegt, im Saarland hingegen erst 1900 und in der Oberlausitz gar erst 1904! Bereits im 18. Jahrhundert war die Auslöschung der Wolfspopulationen in Mitteleuropa weit fortgeschritten, und es handelte sich bei allen oben erwähnten Individuen um zugewanderte und einzeln oder in kleinen Gruppen streifende Tiere.

Den letzten Wolf im Odenwald ereilte am 12. 3. 1866 sein Schicksal. Anhand einer Fülle zeitgenössischer Quellen und Abbildungen werden die letzten Lebensmonate dieses Tieres geschildert, welches wohl ein Mitglied einer kleinen Gruppe war, deren übrige Angehörige spurlos verschwanden. Zahlreiche Karten demonstrieren, wo und wann im Grenzgebiet von Baden, Hessen, Bayern und Württemberg Wölfe beobachtet werden konnten oder Wild- oder Haustiere von ihnen gerissen wurden.

Die vorliegende bemerkenswerte Studie wird abgeschlossen durch ein umfangreiches Literaturverzeichnis, eine Liste der Ortschaften, in deren Bereich der letzte Odenwaldwolf beobachtet wurde oder Schaden angerichtet hat, sowie durch eine graphische Darstellung von 30 Regionen in Deutschland, sowie dem Zeitpunkt, zu dem dort zum letzten Mal Wölfe erlegt wurden. Das Buch beeindruckt nicht nur durch die Fülle der gebotenen Informationen, sondern auch durch seine schöne Gestaltung durch J.-P. Saltin.

Nach der Lektüre des vorliegenden Bandes fragt sich der säugetierkundlich interessierte Leser, warum so selten zoologisch bedeutende Vorgänge, wie die lokale Ausrottung einer Tierart, in klarer, anschaulicher und packender Weise beschrieben werden. Für die Geschichte des letzten Wolfs im Odenwald allerdings hat der Autor Dieter Röckel diese Aufgabe mit Bravour bewältigt!

P. Langer, Gießen

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Über die Annahme von Ms. zur Veröffentlichung wird gemäß Geschäftsordnung der Deutschen Gesellschaft für Säugetierkunde entschieden. Der Eingang von Ms. wird sofort bestätigt, und nach Erhalt der Gutachten werden die Autoren über die Entscheidung umgehend informiert.

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Thyroptera discifera (Chiroptera: Thyropteridae): A new record for Costa Rica and observations on echolocation

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Abstract

We report the first record of the disk-winged bat *Thyroptera discifera* (Chiroptera: Thyropteridae) found in Costa Rica and present observations on morphology and echolocation behavior of this poorly known species. Diet analysis showed the presence of Lepidoptera scales and spider fragments in the bat's feces. Echolocation calls showed very low intensity and consisted of several frequency-modulated harmonics. Behavior and echolocation calls, together with data from fecal samples, suggest a gleaning insectivore lifestyle for the species.

Key words: *Thyroptera discifera*, Thyropteridae, Costa Rica, echolocation, spider

Introduction

The bat family Thyropteridae, disk-winged bats, is endemic to the neotropics. The characteristic suction caps at the base of thumbs and ankles are an adaptation to their roosting habits, and permit the animals to cling to smooth surfaces of plant leaves during the day (Schliemann 1971). Three species currently are recognized, all in the genus *Thyroptera*. *Thyroptera tricolor* Spix, 1823 is the most widely distributed species and ranges from Veracruz to Brazil (Wilson and Findley 1977; Reid 1997), *T. lavali* Pine, 1993 was recently described from the Amazon basin of northeastern Peru (but see also Czaplewski 1996), and *T. discifera* (Lichtenstein and Peters, 1855) is found mainly in South America, except for two records from Nicaragua and Panama (Wilson 1978; Reid 1997). The sympatric occurrence of *T. tricolor* and *T. discifera* in Costa Rica was suggested by Rodríguez (1993), however, R. M. Timm (pers. comm.) examined the specimen previously considered *T. discifera* in the Museo de Zoología, Universidad de Costa Rica (UCR-1548) and considered it to be a juvenile *Thyroptera tricolor* (Timm and LaVal 1998). In the present study, we report on a new specimen of *T. discifera* recently collected in Costa Rica.

Material and methods

A single adult *Thyroptera discifera* was caught in the lowest shelf of a mistnet set over a trail at 23.00 h on 21 April 1998 at the La Selva Biological Station on the Atlantic slope of Costa Rica, Heredia Province. The capture location lies in a ca. 40-year-old secondary forest in an abandoned cacao plantation in the vicinity of primary rainforest and ca. 80 m distant from the Puerto Viejo river. Morphological measurements were taken following Handley (1988). Fecal pellets were collected and

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preserved in 70% ethanol. The wing proportions, aspect ratio index (ARI) and wing tip index (WTI) were calculated following Findley et al. (1972) with the following formulas:

$$\mathrm{ARI} = \frac{(\mathrm{FA}+\mathrm{F3})}{\mathrm{F5}}; \quad \mathrm{WTI} = \frac{\mathrm{F3}}{\mathrm{FA}}$$

FA: length of forearm (mm), F3: length of third finger (mm), F5: length of fifth finger (mm)

Echolocation calls were recorded with a storage bat detector (Petterson D980) from the flying bat in a large flight cage (8 m×4 m×4 m) with walls of plastic mesh. Calls were reduced in speed to one tenth of original speed and stored on a tape recorder (Sony WM-D6C). Sound analysis was performed using SASLab Pro software Ver. 3.2 (Avisoft Co., Berlin, Germany).

Results

Capture location and observations

Although we previously found *Thyroptera tricolor* roosting during the day within the rolled new leaves of *Heliconia* spp. at La Selva, this animal (Fig. 1) was the first mistnet-capture of the genus for more than 2 years of frequent mistnetting at the station. The lack of distinctly white underparts and a uropatagium sparsely covered with long hairs alerted us initially that the individual was not the commonly seen *T. tricolor*; therefore the animal was collected. The authors' identification of the animal as *T. discifera* was later confirmed by R. K. LaVal, Monteverde and R. M. Timm, University of Kansas (pers. comm.). Our specimen, which is deposited in the Museo de Zoología, Universidad de Costa Rica, represents the first record of *T. discifera* in Costa Rica.

While in a cloth bag the bat was constantly moving; however, it calmed down considerably when we put it in a glass tube where it could attach to the walls with its suction disks. The animal was able to fly in a slow, highly maneuverable flight pattern, within a small cage (1 m×1 m×1 m).

Description

The specimen is an adult male with well-developed testis (testis size 4×3 mm). The fur is pale brown and rather long and woolly in appearance, especially at the posterior dorsum. The ventral fur is only slightly lighter in color than the dorsal and, in contrast to *T. tricolor*, not yellow or white. Suction cups on the base of the thumbs are slightly oval (major and minor diameters 3.5 and 2.5 mm, respectively); suction cups on the hind feet are smaller and round (diameter 2 mm). The dorsal side of the uropatagium is sparsely covered with long hairs. The tail extends 2 mm past the uropatagium. The calcar has one distinct proximal cartilaginous projection and more distally a minute second one which is less than one fourth of the size of the first projection. Length of the tibia is 15 mm, and forearm length is 31.1 mm. Length of 5th finger is 40 mm and of 3rd finger is 52 mm. Based on these data the Aspect Ratio Index of the animal was 2.08 and the Wing Tip Index was 1.67. Body mass at time of capture was 3.1 g. Total length is 65 mm, tail vertebrae 28 mm, ear 13.5 mm, and hindfoot 6.0 mm.

Diet

We obtained four fecal pellets from the animal, each containing scales from small Lepidoptera. We also found fragments of two different sized chelicerae and combed tarsal claws, indicating that the animal had been feeding on several spiders before capture.

Fig. 1. New World disk-winged bat *Thyroptera discifera* caught at La Selva, Costa Rica, in April 1998. Note sparse, long hairs at uropatagium.

Social calls and echolocation behavior

The animal frequently emitted audible sounds when disturbed. These sounds consisted of one or two "chip" notes, which closely resembled sounds made by glass frogs *(Centrolenella* sp.). The sounds were whistling, clear tones that did not sound metallic or harsh.

Echolocation calls were very low in intensity and could only be heard while the bat was flying towards the observer and was within 2–3 m of the bat detector's microphone. The sonagram (Fig. 2) shows broad-banded frequency modulated calls with single calls consisting of the fundamental frequency plus two upper harmonics (H1, H2, H3). Amplitude peaks of the harmonics were ca. 50, 100, and 150 kHz, respectively (Fig. 3). Average duration of calls was 0.90 ms (SD ± 0.23 ms, n = 52). Calls were emitted in series of 3–19 calls with an average of 6.2 calls per series (SD ± 3.4, n = 70). The intervals between calls within a series were remarkably constant ($\bar{x} = 10.7 \pm 1.7$ ms, n = 138).

Fig. 2. Sonagram of echolocation calls from *Thyroptera discifera*. The short FM sweeps consist of the fundamental frequency (H1) and two harmonics (H2, H3). (Sequence was edited: call intervals have been shortened.)

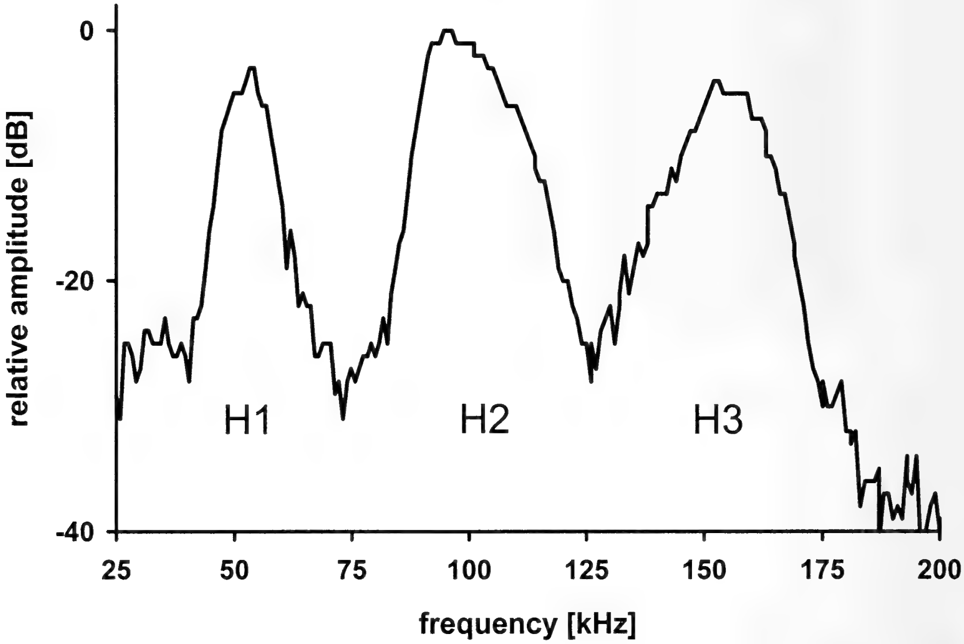

Fig. 3. Average power spectrogram from echolocation calls from *Thyroptera discifera* (n = 9 calls) showing three harmonics (H1, H2, H3).

Discussion

Assuming that the echolocation behavior of the animal was not too greatly affected by the situation of the bat flying in the large flight cage, the call structure closely resembled that from "whispering bats", e. g. phyllostomids, and gleaning insectivorous species, e. g.

the vespertilionid genus *Plecotus*. Wing beat and emission of echolocation pulses are generally synchronized in bats (HEBLICH 1986; SCHNITZLER 1971). Wingbeat frequencies in bats range between 8 and 15 beats per second (NEUWEILER 1993) or ca. 125 to 66 msec per wingbeat cycle. The intervals between calls of *T. discifera* were much shorter (10.7 ms), indicating that the animal emitted not only one but several calls per wingbeat, which is known from gleaning bats (ARITA and FENTON 1997).

The information concerning diet obtained for the animal is consistent with data from the literature for the genus (WHITAKER and FINDLEY 1980) in so far that Lepidoptera are consumed. The presence of spider fragments indicates that the animal used the maneuverable flight we observed in the small flight cage for collecting arthropods from the vegetation. Spider fragments were recently also found in feces of *T. discifera* from the Amazon (RODRIGUEZ-HERRERA et al. 1999) and of *T. tricolor* from Costa Rica (DECHMANN pers. comm.).

Compared with other insectivorous bats from La Selva (HELLER and VOLLETH 1995) *T. discifera* has both a low ARI and WTI. These wing proportions indicate good maneuverability in flight (FINDLEY et al. 1972), which is mandatory for an animal gleaning insects from the vegetation. Our observations on the animal's capability to fly within the restricted space of the 1 m^3 flightcage support these theoretical considerations.

The low intensity echolocation calls of the New World disk-winged bat *Thyroptera discifera* are in sharp contrast to the loud calls observed for the Old World sucker-footed bats (Fam. Myzopodidae) of the genus *Myzopoda* (GÖPFERT and WASSERTHAL 1995). Although both families share distinct morphological adaptations that enable them to roost clinging to leaf surfaces, their echolocation characteristics are very different, indicating a different diet and/or foraging behavior.

In conclusion our observations on wing morphology and flight behavior and the analysis of echolocation calls and diet suggest that *Thyroptera discifera* hunt in highly cluttered habitats and are capable of gleaning behavior. The slow and maneuverable flight might be responsible, at least in part, for the lack of mistnet captures within the genus.

Acknowledgements

R. K. LAVAL (Monteverde, Costa Rica) and R. M. TIMM (University of Kansas) kindly helped with the identification of the specimen. Our thanks to J. GUEVARA SEQUEIRA (MINAE) for assisting in legal requirements. D. CORDES identified the spider fragments from the fecal sample. F. MATT, M. HOLDERIED, K.-G. HELLER, and O. v. HELVERSEN (University of Erlangen) provided helpful advice on echolocation analysis and valuable comments on the manuscript. Financial support was provided by the DFG (Wa 158/4-4).

Zusammenfassung

Thyroptera discifera (Chiroptera: Thyropteridae): Ein neuer Nachweis für Costa Rica und Beobachtungen zur Echoortung

Wir berichten vom ersten Fund der seltenen neotropischen Haftscheibenfledermaus *Thyroptera discifera* (Chiroptera: Thyropteridae) in Costa Rica und stellen Beobachtungen zu Morphologie und Echoortungsverhalten der Art vor. Im Kot fanden sich Fragmente von Schmetterlingen und von Spinnen. Die Echoortungsrufe waren extrem kurze und leise frequenzmodulierte Laute mit mehreren harmonischen Obertönen. Verhaltensbeobachtungen und Charakteristika der Echoortungslaute sowie die Ergebnisse der Nahrungsanalyse deuten daraufhin, daß *T. discifera* die Fähigkeit zum Ablesen ihrer Beute von Blättern („gleaning") besitzt.

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On some bats (Chiroptera) from southern Cambodia with a preliminary checklist

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Abstract

A small number of bats obtained from Cambodia comprises two species new to the fauna of this country: *Megaderma lyra* and *Rhinolophus malayanus*. The occurrence of *Rousettus amplexicaudatus*, previously only generally known from Cambodia, is confirmed.

Taphozous melanopogon, *Hipposideros armiger*, and *Tadarida* (*Chaerephon*) *plicata* previously recorded for Cambodia are confirmed and their distribution in this country is detailed. A critical checklist of Cambodian Chiroptera recorded until present admits 30 species of seven families: Pteropodidae (10 species), Emballonuridae (3 species), Megadermatidae (2 species), Rhinolophidae (4 species), Hipposideridae (3 species), Vespertilionidae (7 species), and Molossidae (1 species). Six species recorded for Cambodia are rejected, because their collecting localities are not within the country, or their identity is doubtful: *Pteropus vampyrus, P. giganteus, Cynopterus horsfieldi, Rhinolophus rouxii, Hipposideros bicolor*, and *Pipistrellus macropus.*

Key words: Chiroptera, Cambodia, records, checklist

Introduction

The aim of this study is to contribute the knowledge of the bat fauna of Cambodia, one of the least explored countries. Specimens collected from caves of the coastal region of Cambodia's Kampot Province, investigated by the German Cambodia Expedition 1995/96 (Anonymous 1996; Laumanns 1996), augmented by a few bats occasionally found by interested collectors were donated to the collections of the Senckenberg Museum, Frankfurt a. M. The identification of these bat remains is presented and discussed. To evaluate the relative significance of these records, a checklist of the bats of Cambodia has been compiled from published data. This list is critically commented.

Material and methods

Several bat skulls were collected from two interconnected caves, Roung Dei Ho and Roung Thom Ken, of Phnom [Mount] Slaptaon. Additionally, few mummified carcasses collected by B. and G. Albrecht were received from Dr. K. Dobat.

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Results

Rousettus a. amplexicaudatus (Geoffroy, 1810)

Material: Caves at Phnom Loang, coastal region ca 20 km N Kampot, Kampot Prov., 14. III. 1998, SMF 89112 (female subad. skull, skeleton), G. Albrecht leg.

Measurements: Forearm 80.3, tibia 36.1; 35.0; 3rd metacarpal 51.2; 3rd digit 1st phalanx 34.3; 3rd digit 2nd phalanx 42.0; 4th metacarpal 49.7; 4th digit 1st phalanx 26.7; 4th digit 2nd phalanx 25.0; 5th metacarpal 48.5; 5th digit 1st phalanx 25.5; 5th digit 2nd phalanx 25.4. Skull: greatest length 36.2; occipito-canine length 34.4; condylobasal length 35.0; condylo-canine length 33.0; zygomatic width 21.5; crown length of upper tooth row C1/-M2/ 13.1; length of lower M/3 1.5.

Comparative material: Thailand: Khao Soi Dao Ai, 12°58′ N–101°48′ E, Pong Nam Ron, Distr., Chanthaburi Prov., SMF 83965 (skull). Kho Kran Yai, 12°43′ N–100°48′ E, Sattahip Distr., Chonburi Prov., SMF 83956–63 (8 skulls).

Rousettus l. leschenaultii (Desmarest, 1820): S-Thailand: Tha Yang Distr., 12°55′ N–99°54′ E, 17 km S of Phetchaburi, Phet Buri Prov., SMF 63166 (skull). Bang Saphan Noi, ca.11°05′ N–99°30′ E, Bang Saphan, Prachuap Khiri Khan Prov., 84022–35 (14 skulls). Thale Noi, 07°47′ N–100°07′ E, Khuan Khanun, Patthalung Prov., SMF 65993 (skull). Kho Khob, 07°24′ N–100°21′ E, Sathing Phra, Songkhla Prov., SMF 84175–6 (2 skulls). West Malaysia, Selangor: Dark Cave, Batu Caves at Kuala Lumpur, SMF 87983–5, 87989, 88041–2, 88408, 88639–40 (9 skulls).

This fruit bat was mentioned for Cambodia by Dobson (1878 b) and has apparently never been recorded again. Skull und tooth dimensions of the present specimen agree with the data found by Rookmaaker and Bergmans (1981) to be discriminating between *R. amplexicaudatus* and *R. leschenaultii* in areas of sympatry. The occurrence of this fruit bat in Cambodia is thus confirmed for the first time by a precise locality.

Taphozous (Taphozous) melanopogon Temminck, 1841

Material: Roung [Cave] Dei Ho and Roung Thom Ken, 10°36′55′ N–104°14′55′ E, Phnom Slaptaon, 10 km E Kampot, Kampot Prov., I. 1996, SMF 83623 (skull), M. Laumanns leg.

Comparative material: Thailand: Khao Wang Kot, Thai Mai Distr., 13°00′ N–101°13′ E, Chantaburi Prov., SMF 75420-1, 75424 (3 skulls). Ta Khli, 15°16′ N–100°21′ E, 30 km E Chainat, Nakhon Sawan Prov., SMF 53173–91 (19 skulls). Nan, 18°47′ N–100°47′ E, Nan Prov., SMF 53162–5 (4 skulls). Myanmar: Pagan, 21°12′ N–94°54′ E, Nyaung-Oo Township, Mandalay Division, SMF 71195 (1 skull). India: Madurai-Kamaraj, Tamil Nadu, SMF 46333–4 (2 skulls).

Taphozous (*T.*) *longimanus* Hardwicke, 1825: Thailand: Chainat, Chainat Prov., SMF 52645, 52648–9 (3 skulls). Bangladesh: St. Martin's Id., 20°37′ N–92°19′ E, Bay of Bengal, SMF 60133 (skull).

Taphozous (*T.*) *theobaldi* Dobson, 1872: Thailand, Lop Buri Prov.: Bullapha Cave, Wat Khao Thambon, 15.13. N–101.18. E, Chai Badan Distr., SMF 63101–3 (3 skulls). Khao Tha Kra, Muang Distr., SMF 87461–4 (4 skulls).

The single skull possesses all characters of this genus and species, being distinctly smaller than that of *T. theobaldi* (see Hill 1992). Additionally, the distance between lower margin of anterior orbita and upper toothrow is narrow, 1.55–1.57 mm (broad in *T. longimanus*, 1.90 mm), and the basisphenoid triangularly rounded anteriorly (broadly rounded in *T. longimanus*). *T. melanopogon* is widespread in S. and SE. Asia (Hill 1992) and although reported for Cambodia it was not listed, but mapped as present throughout the country by Hill (1992). There is no indication that the specimens recorded by Klein (see checklist below) and those from his collection identified by Hill and Thonglongya

(1972) as *T. l. longimanus* were the same sample. The present material is insufficient for subspecies allocation.

Megaderma lyra sinensis (Andersen and Wroughton, 1907)

Material: Roung [Cave] Dei Ho and Roung Thom Ken,10°36′55″ N–104°14′55″ E, Phnom Slaptaon, 10 km E Kampot, Kampot Prov., I. 1996, SMF 83624–5 (2 skulls), M. Laumanns leg.

Measurements: Skull length from occiput to front of canines 29.2, 30.2; skull length from condyles to front of canines 26.0, 27.6; length of upper toothrow along crowns 11.6, 12.2.

Comparative material: *M. lyra lyra* Geoffroy, 1810: India: Madras, SMF 25472 (skull). Near Madurai, Tamil Nadu, SMF 59572, 86452 (2 skulls). Bangladesh: Dacca, Bangl. Agr. Res. Inst. BARI-VPS uncatalogued (skull). *M. lyra sinensis*: Thailand: Rong Kwang, 18°23′ N–100°19′ E, Phrae Prov., SMF 53277 (skull). Ban Tham Tap Tao, 19°42′ N–99°07′ E, Fang Distr., Chiang Mai Prov., SMF 53278 (skull). Tham Khi Nok Wildlife Sanctuary, Huai Kha Kang Distr., Uthai Thani Prov., SMF 83793–4 (2 skulls).

M. spasma (Linnaeus, 1758): Thailand: Prui Station, 12°32′ N–102°10′ E, 14 km E Chanthaburi, Chanthaburi Prov., SMF 53280 (skull). Nam Tok Ton Nga Chang Station, 6°50′ N–100°30′ E, Hat Yai Distr., Songkhla Prov., SMF 66102–3 (2 skulls). Nam Lod Phun Cave, ca. 12°38′ N–102°15′ E; Phu Wiang Mts., Khoen Kaen Prov., SMF 69572 (skull).

By their skull dimensions the specimens from Phnom Slaptaon represent *M. lyra*, a clearly larger species than *M. spasma*. Dimensions of the Cambodian specimens are larger than those of the nominate subspecies of India and agree with the definition of *M. l. sinensis* by Andersen and Wroughton (1907), and with skull measurements given for this subspecies by Shamel (1942), Sinha (1977), Hill (1992), Csorba and Topál (1994), and specimens from Thailand identified as *M. l. sinensis*,

This species is recorded and mapped by Hill (1992) for most of Thailand, in parts of Laos and Vietnam, i. e. only W and N of Cambodia, respectively. Apparently no previous record for Cambodia has been published.

Rhinolophus malayanus Bonhote, 1903

Material: Roung [Cave] Dei Ho and Roung Thom Ken, 10°36′55″ N–104°14′55″ E, Phnom Slaptaon, 10 km E Kampot, Kampot Prov., I. 1966, SMF 83627 (1 incomplete skull), M. Laumanns leg.

Measurements: Length from occiput to front of canines ca. 17.3; width across nasal swellings 5.0; least interorbital width 2.2; zygomatic width 8.9; crown length of upper tooth row C-M3/ 6.9; width across crowns of M3/ 6.7.

Comparative material: Thailand: Doi [Mt.] Pha Hom Pok, 20°08′ N–99°10′ E, Fang Distr., Chiang Mai Prov., SMF 66159 (skull). Doi Ang Khang, 19°53′ N–99°04′ E, Fang Distr., Chiang Mai Prov., SMF 66013–24 (12 skulls). Wat Suphan Kuha, Nongle, Chai Badan Distr., 15°13′ N–101°18′ E, Lop Buri Prov., SMF 63033–4 (2 skulls).

Rh. borneensis (Peters, 1861): Borneo, Sarawak: SE Kuching, SMF 52053 (skull). Sabah: Danum Valley, 04°50′ N–117°30′ E, Taurau Division, SMF 83404 (skull). Gomantong Caves, 05°31′ N–118°04′ E, Sandakan Division, SMF 83703 (skull). Tabin Wildlife Reserve, 05°05′ N–118°40′ E, Tawan Division, SMF 83704 (skull).

Rh. sedulus Andersen, 1905: Malaysia, Selangor: Bukit Lagong, Selangor, SMF 50509 (skull). Ulu Gombak, Selangor, SMF 69279–80, 87479 (3 skulls). Borneo, Sabah: Tabin Wildlife Reserve, 05°05′ N–118°40′ E, Tawan Division, SMF 83708 skull.

The single skull identifed as *Rh. malayanus* agrees in its dimensions, its steep anterior profile of the rostrum and its shape of the rostral inflations not extending laterally with specimens from Thailand (as listed above). It differs from two related species of horseshoe bats similar in skull size to *Rh. malayanus* by the posterior emargination of the palatinum. This emargination is wider between the mesopterygoids than in *Rh. borneensis* (recorded for Cambodia by Hill and Thonglongya 1972), but is narrower than in *Rh. sedulus* (nearest known occurrence in West Malaysia; Hill 1992). Apparently *Rh. malayanus*, known from Thailand, Laos, and Vietnam (Hill 1992), is an addition to the bat fauna of Cambodia.

***Hipposideros armiger* (Hodgson, 1835)**

Material: Roung [Cave] Dei Ho and Roung Thom Ken, 10°36′55″ N–104°14′55″ E, Phnom Slaptaon, 10 km E Kampot, Kampot Prov., I. 1996, SMF 83628–30 (3 subad. skulls), M. Laumanns leg.

Measurements (ranges): Occipito-canine (to front of alveoles) length of skull 27.0–27.8 (n = 2); condylo-canine (alveolar) length 24.2–25.1 (n = 2); basilar length of skull 18.3–19.8 (n = 3); mastoid breadth 13.8–14.6 (n = 3); zygomatic breadth 16.1–17.3 (n = 3); palate length 4.6–5.3 (n = 3); upper toothrow C-M3/ at crowns 13.1.

Comparative material: Thailand (all Fang Distr., Chiang Mai Prov.): 17 km NW Fang, 19°55′ N–99°15′ E, SMF 65828, –30, –32–35 (4 ad., 2 subad. skulls). Doi Ang Khang, 19°53′ N–99°04′ E, SMF 65816–18, –20–26 (1 ad., 9 subad. skulls). Ban Yang, 19°50′ N–99°08′ E, SMF 65843–4, –46–54 (7 ad., 4 subad. skulls).

H. turpis pendlebury Chasen 1936: Thailand: Klung Ching, Ta Sala Distr., Nakhon Si Thammarat Prov., SMF 83777, 84093 (2 skulls). Kkao Nor Chuchi Wildlife Sanctuary, Khlong Thom Distr., ca. 08°05′N–99°20′ E, Krabi Prov., SMF 88499–500 (2 skulls).

The present skulls from Phnom Slaptaon are of a species of the *H. armiger*-group, characterised by the rostral chambers dorsally uninflated (consequently the rostrum having a characteristically flat profile), and by the roof of the narial canal separated from the roof of the mesopterygoid fossa by a step-like discontinuity (Hill 1963). By virtue of the few skull dimensions measurable and by the size of upper molars they are obviously larger than *H. turpis pendlebury*, but are smaller than of most SE. Asian *H. armiger*, including *H. a. debilis* Andersen, 1916, described as a slightly smaller taxon (but synonymized by Hill 1963). In adult *H. armiger* from Thailand the occipito-canine length (to alveoles of C1/) attains 29.3–31.7 and the zygomatic breadth 17.4–18.3, clearly larger than the Phnom Slaptaon specimens.

However, by direct comparison with series of *H. armiger*, these skulls from Phnom Slaptaon were found to agree in size with subadult female individuals (as listed above). Despite the sutures of the skulls being fused, the cristae sagittalia are only weakly developed and the upper PM4/ have their cingula not yet fully emerged from their alveoles, i. e. the tooth is not yet in its ultimate position. This developmental stage results in overall smaller skull measurements. Apparently, skull growth continues despite sutures being fused. A comparative modus of growth has been found in central European *Eptesicus serotinus* (Schreber, 1774) concerning a supposedly small-sized sibling species (Kock and Bogdanowicz 1998).

H. armiger, known from Cambodia (see checklist below), is mapped by Hill (1992) to occur throughout the country although it is not listed. This species seems to be rare in Cambodia, as only one or two specimens were found by Klein (1971, 1972).

Tadarida (Chaerephon) plicata (Buchanan, 1800)

Material: Phnom Penh, V. 1998, SMF 89110–11 (1 male juv. mummy, 1 female juv. skull from discarded mummy), B. Albrecht leg.

Measurements (of juv. female): Tail 35; forearm 42.9; tibia 14.3; 3rd metacarpal 38.5; 4th metacarpal 35.7; 5th metacarpal 23.0.

Comparative material: Central Thailand, Lop Buri Prov.: Wat Khao Thambon, Chai Badan Distr., ca. 15°10′ N–101°18′ E, SMF 63108–24 (17 alcohol). Ban Mi, 19 km W of Khok Samrong, ca. 15°05′ N–100°45′ E, SMF 52572–3, 52575–80, 52582–86 (13 skulls). Indonesia: Lingsar, Lombok Is., SMF 74538 (skull). Bangladesh: Jalchatra Mission, 24°38′ N–90°04′ E, Madhupur Jungle, Tangail Distr., SMF 59122 (skull). India: Anamalai Hill, 20 km NE Madurai, Tamil Nadu, SMF 63712–31 (20 skulls).

Two mummies, found hanging on the outside wall of a house, did not differ in essential taxonomic characters from numerous specimens of *T. plicata* from distant parts of the species' range. However, the immaturity of the specimen does not permit subspecific allocation.

This species is an excellent example for the fragmentary knowledge of the Cambodian bat fauna. Although fleas, *Lagaropsylla putilla*, characteristic parasites of Molossidae, were known from the temples of Angkor Wat, Siem Reap, in the north of the country (Smit 1958), *T. plicata*, the only molossid bat at this locality was only formally recorded for Cambodia by Yoshiyuki (1966), Klein (1969 b, 1971), and Hill and Thonglongya (1972). In Cambodia, *T. plicata* is not less common than in other regions of its vast distribution. A large group (n = 43) was found living under the roof of a house (Klein 1971), another colony comprised ca. 200 individuals (Klein 1971), and thousands of cave roosting *T. plicata* were mentioned by Klein 1969 c, 1971).

Checklist of the bats of Cambodia

Species rejected for inclusion in the bat fauna of Cambodia are listed in square brackets in the present checklist. Their identification appears to be doubtful, or their collecting localities are incorrectly considered as being in Cambodian territory (due to change of boundary delimitation), or their mapped occurrence in this country is not documented by known reference specimens.

Pteropodidae (10 species):

Pteropus hypomelanus Temminck, 1853: "Cambodia" (Gray 1861: sub *P. edwardsii* Geoffrroy 1828 = Dobson 1880: sub *hypomelanus*). The occurrence of this species in Cambodia needs verification in view of its predeliction for roosting only on islands in SE. Asia. Sight records by Matveev (1999), mistakingly thought to be *Pt. lylei*, are reported for Cambodia without indicating a locality.

[*P. vampyrus* (Linnaeus, 1758): Recorded from Phu Quoc Ild., Cochin China, Vietnam by Thomas (1929: sub *P. v. malaccensis* Andersen 1908), but listed for Cambodia by Osgood (1932). Hill (1992) mapped the distribution to include Cambodia, but did not list it].

P. lylei Andersen, 1908: Probably in the region of Phnom-Penh (Matveev 1999).

[*P. giganteus* (Brünnich, 1782): Prek Kadam, Phnom Penh region; Prek Prakong, Phom Penh region (Klein 1970); Prek Phnau, Phnom Penh region (Klein 1972). This fruit bat is not known E of Myanmar and these records from Cambodia must represent instead one of the three species listed above, possibly the large *P. vampyrus*].

Rousettus leschenaultii (Desmarest, 1820): ? Angkor Wat (Rookmaaker and Bergmans 1981: only tentatively identified). Accordingly, the species is listed for Cambodia by Hill (1992) with a question mark only, although the mapped distribution (map 28) includes this country.

R. a. amplexicaudatus (Geoffroy, 1810): "Cambodia" (Dobson 1878 b, 1880; Andersen 1912; Hill 1975; Bergmans and Hill 1980; Rookmaaker and Bergmans 1981). Phnom Loang caves, 20 km N Kampot, Kampot Prov. (this study).

Cynopterus sphinx (Vahl, 1798): Siem-Reap (Thomas 1929; Osgood 1932). Barong, Phnom Penh region (Klein 1969 a: sub *C. brachyotis angulatus* Miller 1898). Angkor Wat

(Klein 1969 b: sub *C. brachyotis angulatus*). Chrui Chang War, W-bank Mekong River, NE Phnom Penh (Klein 1970, 1971, 1972: sub *C. b. angulatus*). Prek Tasek, 8 km NW Phnom Penh (Klein 1970: sub *C. b. angulatus*; Hill and Thonglongya 1972: sub *C. sphinx angulatus* n. stat.). Arey Ksatr, E-bank Mekong River, NE Phnom Penh; Tuol Kork, Phom Penh region; Angkor Forest, Siem Reap (Klein 1970: sub *C. b. angulatus*). 2 km SE Demrey Phong (Paradiso 1971: sub *C. s. angulatus*). Kean Khleang, Phnom Penh region; Prek Phnau, Phnom Penh region; Prek Phot, Phnom Penh region; Kantuot, Phnom Penh region; Angkor Forests, Siem Reap region; Prapéang Chan, Kompong Chhnang region; Kompong Som, Sihanoukville region, S-coast: Poport Village Forest; Bokor Mts., Mapot Prov. (Klein 1972: sub *C. brachyotis angulatus*). Phnom Penh region and/or islands in the Gulf of Thailand (Matveev 1999: sub *C. sphinx*).

Note : A specimen from Sipora Ild. examined by Paradiso (1971) is erroneously listed for Cambodia; Sipora Ild. is in the Mentawi Archipelago off W-Sumatra.

The correct identity of most of the above records of *C. brachyotis angulatus* should be verified. The subspecific epithet might have been used rather conventionally. See remarks below.

C. brachyotis (Müller, 1838): Mainland Cambodia was mapped for the range of this species, but not listed by Hill (1992), before it was collected on unspecified islands in the Gulf of Thailand (Matveev 1999). However, it seems likely that several of the above records of *C. brachyotis angulatus* may pertain to this species.

Cynopterus horsfieldii Gray, 1843: Taingkor, Kompong Thom region (Klein 1970). This species is not known nearer to Cambodia than in W-Thailand and W-Malaysia (Hill 1992). The record listed might have been a misidentified *C. sphinx*, which would be in support of the suspected identity of *C. brachyotis angulatus* listed above as *C. sphinx*.

Megaerops ecaudatus (Temminck, 1837): Poport Village Forest (Klein 1971). Cambodia is neither mapped as part of this species' range nor listed by Hill (1992). The identity of this record needs verification with regard to *M. niphanae* Yenbutra and Felten, 1982, not distinguished at the time of Klein's (1971) record.

Eonycteris spelaea (Dobson, 1871): "Cambodia" (Blanford 1891; Flower 1900).

[*Macroglossus sobrinus* Andersen, 1911: Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

Macroglossus minimus (Geoffroy, 1810): Stung Chral Forest, Kompong Sela, SW Pompong Pseu (Klein 1971, 1972). Cambodia is mapped as part of the species' range by Hill (1992), although not listed.

Emballonuridae (3 species):

Taphozous (*T.*) *melanopogon* Temminck, 1841: "Cambodia" (Pousargues 1904). Angkor Wat, Siem Reap (Klein 1969 b, 1971: sub *T. m. bicolor* Temminck, 1841). Bayon, Siem Reap (Klein 1970, 1971: sub *T. m. bicolor*). Preah Khan Temple, Siem Reap (Klein 1970, 1971, 1972: sub *T. m. bicolor*). Phnom Penh region and/or islands in the Gulf of Thailand (Matveev 1999). Phnom Slaptaon caves, E of Kampot (this study).

T. (*T.*) *longimanus* Hardwicke, 1825: Prek Phnau; Phnom Penh; Phnom Penh Nord km 7; Taingkor, Kompong Thom region (Klein 1970: sub *T. l. longimanus*). "Cambodia" (Hill and Thonglongya 1972: sub *T. l. longimanus*). Takeo (Hurka 1997).

T. (*Saccolaimus*) *saccolaimus* Temminck, 1838: Phnom-Penh and/or islands in Gulf of Thailand (Matveev 1999).

Megadermatidae (2 species):

Megaderma spasma (Linnaeus, 1758): "Cambodia" (Pousargues 1904; Andersen 1918: sub *M. s. minus* n. subsp.). Arey Ksatr, E-bank Mekong River, NE Phnom Penh; Trapeang Chan (Klein 1971). Koh Rong Ild. (Matveev 1999: vidit).

M. lyra Geoffroy, 1810: Phnom Slaptaon caves, E of Kampot (this study: sub *sinensis* (Andersen and Wroughton 1907)).

Rhinolophidae (4 species):

Rhinolophus shameli Tate, 1943: Bayon Temple, Siem Reap (Klein 1969 b: sub *Rh. coelophyllus* Peters, 1867). Preah Khan Temple, Siem Reap (Klein 1969 b, 1970, 1972: sub *Rh. coelophyllus*; Hill and Thonglongya 1972: sub *Rh. shameli*). Angkor temples, Siem Reap (Klein 1971: sub *Rh. coelophyllus*).

Rh. acuminatus Peters, 1871: Preah Khan, Siem Reap (Hill and Thonglongya 1972).

[*Rh. pusillus* Temminck, 1834: Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

Rh. borneensis (Peters, 1861): Preah Khan, Siem Reap (Hill and Thonglongya 1972).

Rh. malayanus Bonhote, 1903: Phnom Slaptaon caves, E of Kampot (this study). NW-Cambodia is mapped as part of the species' range by Hill (1992).

[*Rh. affinis* Horsfield, 1823: Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

[*Rh. rouxii* Temminck, 1835: Bayon Temple, Siem Reap (Klein 1969 b). Preah Khan Temple, Siem Reap (Klein 1969 b, 1970, 1972: sub *Rh. r. rouxi*). Angkor Wat, Siem Reap (Klein 1971: sub *Rh. r. rouxi*). Trapeang Chan, Kompong Chhnang Prov. Klein 1972: sub *Rh. r. rouxi*). The records are highly probable misidentifications, as this species ranges not nearer to Cambodia than N-Laos and N-Vietnam, and is listed for S-China, N-Vietnam, and Myanmar by Hill 1992].

Hipposideridae (3 species):

[*Hipposideros bicolor* (Temminck 1834): Phu Quoc Id. [presently Vietnam] (Pousargues 1904: sub *bicolor* var. *fulvus* Gray 1838). Possibly misidentified *H. pomona* Andersen 1918, which is the only smaller species mapped for Cambodia by Hill 1992 and recorded from Laos and Vietnam].

H. pomona Andersen, 1918: Preah Khan Temple, Siem Reap (Klein 1970, 1972: sub *H. bicolor sinensis* Andersen, 1918). Angkor temples, Siem Reap (Klein 1971: sub *H. bicolor sinensis*),

H. larvatus (Horsfield, 1823): "Cambodia" (Pousargues 1904). Bayon Temple and Preah Khan Temple, Siem Reap (Klein 1969 b: sub *H. l. grandis* G. M. Allen, 1936). Angkor temples, Siem Reap (Klein 1971: sub *H. l. grandis*). Phnom-Penh region and/or islands in Gulf of Thailand (Matveev 1999).

H. armiger (Hodgson, 1835): Preah Khan Temple, Siem Reap (Klein 1970, 1972: sub *H. a. armiger*). Angkor temples, Siem Reap (Klein 1971: sub *H. a. armiger*). Phnom Slaptaon caves, E of Kampot (this study). *H. armiger* is not listed for Cambodia by Hill (1992).

[*H. diadema* (Geoffroy, 1813): Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

Vespertilionidae (7 species):

Myotis rosseti (Oey, 1951): "Cambodia" (Oey 1951: sub *Glischropus rosseti* n. sp.; Godawa-Stormark 1998: sub *M. rosseti*). Prek Phnau, 6 km NE Phnom Penh (Hill 1969: sub *Pipistrellus rosseti* n. stat. = Klein 1970: sub *P. rosseti*). Arey Ksatr, E-bank Mekong River, NE Phnom Penh (Klein 1970: sub *P. rosseti*).

M. (*Selysius*) *muricola* (Gray, 1846): Phnom-Penh region and/or on islands in Gulf of Thailand (Matveev 1999).

M. (*Leuconoe*) *hasselti* (Temminck, 1849): Prek Phnau, 6 km NW Phnom Penh (Klein 1970; Hill and Thonglongya 1972: sub *M. h. continentis* Shamel, 1942). Phnom-Penh region and/or islands in Gulf of Thailand (Matveev 1999).

[*Pipistrellus javanicus* (Gray, 1838): Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

P. tenuis (Temminck, 1840): "Cambodia" (Dobson 1878 a: sub *Vesperugo abramus* (Temminck, 1840); Flower 1900: sub *V. abramus* = Thomas 1928: sub *P. coromandra tramatus* n. subsp. = Hill 1992: sub *P. tenuis*).

[*Pipistrellus macropus*: Angkor temples, Siem Reap (Klein 1971). This taxon is unidentifiable: The name *Vespertilio macropus* Dobson, 1872, for an Asiatic bat, is antedated by *V. macropus* Gould, 1854 (= *Myotis adversus macropus*) of Australia. *V. macropus* of Dobson is synonymous with *Myotis longipes* (Dobson, 1873), occurring only far west in Pakistan and Afghanistan. If *P. macropus* is considered as a misspelling of *Vesperugo micropus* Peters, 1872, it would indicate a bat related to *P. coromandra* (Gray, 1838), known from N-Thailand; see Hill (1992)].

Scotophilus kuhlii Leach, 1821: School-farm Prek Leap near Phnom Phen (Ferris and Usinger 1953: sub *S. temmincki castaneus* Gray, 1838). Prek Phnau, Phnom Penh region; Phnom Chiso, Takeo region (Klein 1969 a: sub *S. temmincki* (Horsfield, 1824)). Prek Phnau, Phnom Penh region; Prek Takong, Phnom Penh region; Tonlé Bati, Takeo region; Ang Sdock, Takeo region (Klein 1970: sub *S. kuhlii gairdneri* Kloss, 1917). Chrui Chang War, Phnom Penh region (Klein 1970, 1972: sub *S. kuhlii gairdneri*).

[*S. heathi* Horsfield, 1831: Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

[*Tylonycteris pachypus* (Temminck, 1840): Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

[*T. robustula* Thomas, 1915: Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

[*Miniopterus schreibersii* (Kuhl, 1817): Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

[*Murina cyclotis* Dobson, 1872: Cambodia is mapped as part of this species' range, but not listed by Hill (1992); no other reference known].

Kerivoula hardwickii (Horsfield, 1824): "Cambodia" (Miller 1906: sub *depressa* n. sp.). Not listed by Hill (1992), but Cambodia mapped as range of this species.

Kerivoula papillosa Temminck, 1840: "Cambodia" (Dobson 1878 a: sub *K. hardwickii* (Horsfield 1824) = Pousargues 1904: sub *K. hardwickei* = Thomas 1916: sub *K. papillosa*).

Molossidae (1 species):

Tadarida (*Chaerephon*) *plicata* (Buchanan, 1800): Angkor Wat (Yoshiyuki 1966; Klein 1969 b, 1970; Hill and Thonglongya 1972). Cave Phnom (Mt.) Samrap Reach, Battambang Prov. (Klein 1969 c, 1970: sub *T. p. plicata*). Phnom Penh (Klein 1970: sub *T. p. plicata*; this study). Siem Reap; Tonlé Bati, Takéo Prov. (Klein 1970: sub *T. p. plicata*). Phnom-Penh region and/or islands in Gulf of Thailand (Matveev 1999).

Discussion

Two of six species recently collected in Cambodia were not definitely or previously known from Cambodia. The bat fauna of Cambodia is so insufficiently documented that a preliminary checklist presently comprises only 30 species, all pertaining to more common and widely distributed Oriental bats. Six species indicated for Cambodia are rejected, either because the localities recorded are outside the Cambodian territory or because the species identification appears highly doubtful. This short list of actually known bats merely indicates a nearly complete lack of field investigations. Presently the biogeographical relations of the Cambodian bat fauna cannot be assessed by the few data available.

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Zusammenfassung

Einige Fledermäuse (Chiroptera) aus dem südlichen Kambodscha mit einer vorläufigen Artenliste

Eine kleine Aufsammlung von Fledermäusen enthält zwei Arten, die neu für Kambodscha sind: *Megaderma lyra* und *Rhinolophus malayanus. Rousettus amplexicaudatus*, bisher nur generell für Kambodscha bekannt, wird bestätigt. Das bekannte Vorkommen von *Taphozous melanopogon*, *Hipposideros armiger* wird von weiteren Fundplätzen dokumentiert, und das von *Tadarida* (*Ch.*) *plicata* bestätigt. Eine kritische vorläufige Liste der für Kambodscha bekannten Fledertiere umfaßt bisher nur 30 Arten. Die Liste führt sechs Arten auf, die für Kambodscha verzeichnet wurden, deren Fundorte aber außerhalb der Landesgrenzen liegen oder deren Identität zweifelhaft ist: *Pteropus vampyrus*, *P. giganteus*, *Cynopterus horsfieldi*, *Rhinolophus rouxii*, *Hipposideros bicolor* und *Pipistrellus macropus*.

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Home range size and spatial organization of Swift fox *Vulpes velox* (Say, 1823) in southeastern Wyoming

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Abstract

We investigated home-range size and spatial arrangement of swift fox *Vulpes velox* (Say, 1823) between September 1996 and March 1997 in a sagebrush-grassland habitat in southeastern Wyoming. Home-ranges ($\bar{x} \pm SE$, $n = 10$) averaged 11.7 ± 1.3 and 7.7 ± 1.1 km^2 using the 95% adaptive kernel method and the 100% minimum convex polygon, respectively. Although the ranges of males seemed about 25% larger compared with females, the difference was not significant. Core areas (50% utilization distribution) consisted of 1 or 2 polygons and averaged $19.0 \pm 2.6\%$ of the total home-range area. Home-range overlap of paired foxes (95% adaptive kernel: $59.6 \pm 7.9\%$; $n = 8$ combinations) was significantly greater than range overlap of unpaired animals (95% adaptive kernel: $9.9 \pm 2.8\%$; $n = 18$ combinations). Paired foxes shared more than 70% of their dens. 75% of the dens were located within an individual's core area. Our results suggested that swift foxes were monogamous.

Key words: *Vulpes velox*, home-range, spatial organization

Introduction

Foxes, which include the smallest canids, are extremely variable in their social structure, which ranges from solitary through monogamous to cooperative (Sandell 1989). However, most of the fox species investigated to date generally fit the pattern predicted by Moehlman (1986, 1989), and confirmed by Hersteinsson and Macdonald (1982): they are usually monogamous, but tend toward polygyny more than larger canids.

The recently declining swift fox *Vulpes velox* (Say, 1823) inhabiting the prairies of the Great Plains belongs to the smallest North American canids. Nocturnal swift foxes appear to be monogamous (Seton 1927), but some polygamy may take place (Kilgore 1969). However, data supporting this are lacking (Egoscue 1979; Scott-Brown et al. 1987). Polygamous units throughout the year have been often reported in the closely related and more investigated kit fox *Vulpes macrotis* (Merriam, 1888) (Egoscue 1956, 1962, 1975; Morrell 1972). Thus, similar findings for the swift fox could be expected.

Because the social structure is largely reflected by the spatial relationships between neighboring foxes, exploration of home-range overlap along with home-range size in different sexes may help to evaluate the social system in free-ranging foxes (Geffen and Macdonald 1992; Zoellick and Smith 1992). Therefore, we focused our efforts on studying the swift fox's space use patterns. Our objective was to determine the size and spatial organization of home-ranges in the sagebrush-grassland habitat of southeastern Wyoming during the dispersal, breeding, and gestation period of the swift fox.

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Material and methods

The 280-km^2 study area near Medicine Bow, Wyoming, (42° N, 106° W) is primarily used for cattle grazing. The site is a sagebrush-grassland community 2,070 m above sea level with low annual precipitation (< 300 mm). The topography is flat to mildly undulating with numerous dry lakebeds. With some exceptions (fencelines, secondary dirt roads etc.), there is little human development in the area.

Foxes were captured in March 1996, radio-collared with 45-g transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) and released. Our trapping effort was designed to trap all the foxes living in the study area, and thus traps were equally spread all over the place. All captured animals were > 1 year of age. Between September 1996 and March 1997, 10 swift foxes were relocated on a weekly basis. Owing to the swift fox's nocturnal activity patterns, we attempted to obtain one location for each collared fox for each night we were in the field for that week. Dens were located during the day between successive nights. We used a Telonics TR-2 Receiver (Telonics, Mesa, Arizona, USA) and a combination of truck roof-mounted dipole antenna and a hand-held, two-element H-antenna to estimate locations using triangulation.

Consecutive observations of the same fox were separated by > 12 hs to avoid autocorrelation (Swihart and Slade 1985; White and Garrott 1990). Radio-locations including 95% error ellipses were calculated using the maximum likelihood technique (Lenth 1981) in program LOCATE II, version 1.3 (Pacer, Truro, Nova Scotia, Canada). The observer's position was determined by a Global Positioning System (GPS) Magellan 1000 (Magellan Systems Corporation, San Dimas, California, USA). To provide a reasonable home-range estimate, we excluded locations with > 3.0 km^2 error ellipse from the analysis. We also excluded inactive locations (i. e. resting in a den) to avoid undue influence on measures of range utilization (White et al. 1996). The 95% error ellipse of selected radio-locations averaged 0.39 ± 0.05 km^2 (n = 203). We finally analyzed range use of 6 males and 4 females (including 4 pairs) using 225 locations (22.5 ± 2.3, range 19–26 locations/fox).

We computed the median center of activity (Mohr and Stumpf 1966) for each fox. Home-ranges were estimated using the adaptive kernel model (Worton 1989) in the program CALHOME (Kie et al. 1996). We calculated the 50% and 95% utilization distribution (UD) as point percentage contours using least-squares cross-validation to choose the optimum kernel bandwidth (smoothing parameter). Den locations were plotted on a map to examine their distribution with distributions of core areas (50% UD). We also calculated home-ranges using the 100% minimum convex polygon, MCP (Mohr 1947), to obtain camparability with data which were already published. Home-range size between sexes was compared by the independent t-test using the pooled variance estimate method (Brosius 1988).

The number of locations needed to obtain asymptotic home-range estimates (area-observation curve) was evaluated for each individual fox (Gautestad and Mysterud 1995). To determine this, we plotted home range size vs. decreasing number of locations removing 2 and 4 randomly chosen observations from the total number of locations, and then we evaluated the magnitude of changes in such an altered home-range size (Harris et al. 1990).

Foxes were considered paired (mates) if they frequently and concurrently shared a den (Egoscue 1975). Locations from mates were pooled to calculate the total home-range of fox pairs. We classified foxes with adjacent home-ranges (neighbors) as paired male-female combination (paired M-F) or unpaired male-female (unpaired M-F) , female-female (F-F), or male-male (M-M) combination.

Overlap of home-ranges and core areas between foxes was evaluated with the Mann-Whitney U-test for unpaired combinations (independent samples) and by the Wilcoxon test for paired foxes (related samples). We examined whether use within overlapping areas differed from use within non-overlapping proportions of home-ranges by comparing the frequency of locations in the overlap areas with an expected frequency (Chi^2-test). The expected frequency was based on the proportion of the home-range in the overlap area.

Standard deviations were given with means ($\bar{x} \pm SD$) unless stated otherwise. Statistical significance was set at $P < 0.05$.

Results

Number of locations/fox needed to obtain asymptotic home range estimates averaged 16.0 and 17.1 for the adaptive kernel (n = 8) and MCP model (n = 10) respectively (range 11 to 20). Using the 95% adaptive kernel model, home ranges reached on average 98.8 ± 13.8% and 103.7 ± 17.4% of their original size with the substraction of the n – 4

Table 1. Estimates of home-range size (km^2) using minimum convex polygon (100% MCP; MOHR 1947) and adaptive kernel estimator (95% with 50%; WORTON 1989) for swift fox at Medicine Bow, Wyoming, 1996–1997.

		MCP			adaptive kernel					
		100%				95%				50%
	n	$\bar{x}$	SD	range	$\bar{x}$	SD	range	$\bar{x}$	SD	range
F	4	6.3	2.2	3.5– 8.7	9.8	2.6	6.5–12.0	1.6	0.8	1.0–2.7
M	6	8.7	4.0	5.5–15.9	13.0	4.7	7.9–19.4	2.6	0.9	1.8–4.0
All	10	7.7	3.5	3.5–15.9	11.7	4.1	6.5–19.4	2.2	1.0	1.0–4.0

and n – 2 random radio-locations, respectively (where n equals the total number of locations a fox was sampled). The MCP produced even a smoother asymptote: 92.4 ± 6.0% (n – 4) and 97.4 ± 5.0% (n – 2).

Home-ranges of males were larger compared to the females (Tab. 1), but the difference was not significant (95% UD: t-test; t = -1.2, 8 df, P = 0.257; 50% UD: t-test, t = -1.9, 8 df, P = 0.107). Core areas contained 19.0 ± 8.3% of total home-range area. We identified an average of 1.5 ± 0.5 core area polygons per home-range with no differences between sexes (t-test, t = 1.3, 8 df, P = –0.242). Total area of home-ranges of 4 fox pairs averaged 15.98 ± 2.49 km^2 (95%, adaptive kernel) and 13.72 ± 4.64 km^2 (MCP).

Nearly all home-ranges bordered or overlapped those of their neighbors (Fig. 1). Home-ranges of mates (n = 8) overlapped an average of 59.6 ± 22.4% (95% adaptive kernel) whereas core areas overlapped by 37.9 ± 20.7%. In both, we did not detect a difference if measuring ranges of females overlapped by males or vice versa (Wilcoxon test), a) home-range: Z = –1.1, P = 0.273, b) core area: Z = –1.5, P = 0.144). Home-ranges of 4 adjacent females overlapped 5.3 ± 1.4%. Home-ranges of 6 adjacent males overlapped on average 9.6 ± 15.0%, but 4 males had no home-range overlap at all. Thus, overlap between F-F and M-M combination did not differ significantly (Mann-Whitney U-test: Z = –0.9, P = 0.379). Shared area of 8 adjacent, unpaired M-F combinations averaged 12.5 ± 13.0% with no difference between sexes (Mann-Whitney U-test: Z = –0.1, P = 0.885). In summary, home-range overlap combined for all possible combinations of adjacent foxes averaged 9.9 ± 12.0% between those classified as unpaired (4 F-F + 6 M-M + 8 M-F; n = 18). This was significantly less than the overlap between mates (Mann-Whitney U-test: Z = –4.0, P = 0.0001). Core areas of unpaired foxes did not overlap.

We measured utilization intensity in shared areas comparing the observed number of locations with the expected number of locations. In 14 of 20 comparisons, the number of locations within areas of range overlap did not differ from expected. However, in 3 of 7 comparisons, females overlapping the ranges of other females or males overlapping females other than their mates, used the shared areas less than expected. Conversely, we located a fox in the area shared with its mate more than expected (males: 2 of 4 comparisons; females: 1 of 3 comparisons). We examined overlapping core area use between paired foxes in 8 cases. Seven of the 8 cases indicated use was as expected. In 1 case a use by a male was less than expected.

Nine foxes were located in as many as 6 different dens. We found that 75.1 ± 27.2% (n = 24) of dens belonging to an individual fox were located within its core area. The distance between the median center of activity of 9 individual foxes and their den sites averaged 824 ± 491 m (n = 34). Paired foxes (n = 3) shared most dens (males: 70.3 ± 26.3%, females: 81.9 ± 18.8%). Total common core areas of the 4 fox pairs contained 84.6 ± 10.8% of their shared dens. Female swift foxes were located in approximately 60% of cases in a den with their mate (range 42–85%; n = 3).

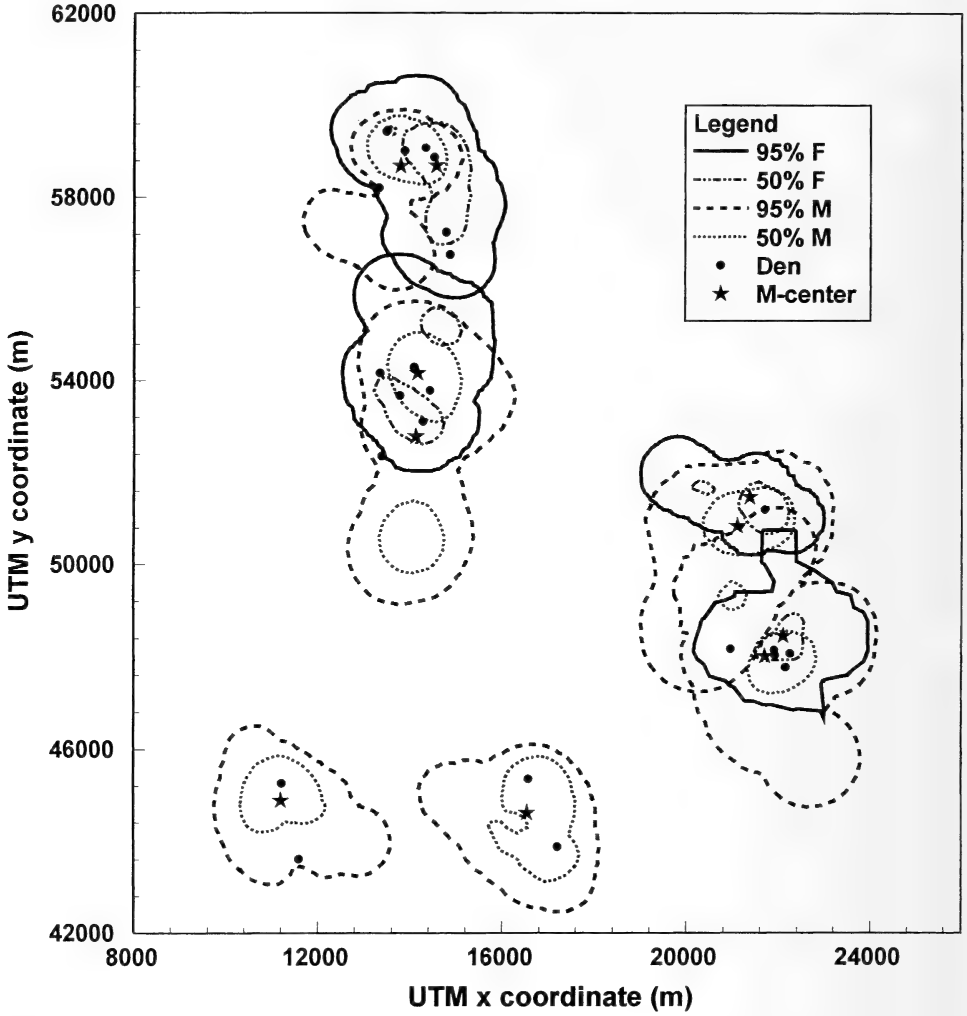

Fig. 1. The spatial organization of home-ranges [95% utilization distribution (UD)] and core areas (50% UD) of 10 radio-collared swift foxes at Medicine Bow, Wyoming, 1996–1997. Home-ranges were plotted using the adaptive kernel method. Note also the distribution of median center of activity and den sites.

Discussion

Size of home-range scales with body size in carnivores (GITTLEMAN and HARVEY 1982; LINDSTEDT et al. 1986). Although male swift foxes are slightly heavier than females (KILGORE 1969), we found no effect of sexes on sizes of home-ranges or core areas. Home-ranges during the dispersal, breeding, and gestation period (September–March) in our study area were considerably smaller than estimates of home-range sizes (11.2–32.3 km^2) elsewhere in swift fox's geographic range (SHARPS and WHITCHER 1984; HINES and CASE 1991). Related kit foxes were reported having home-ranges from 1.4–11.6 km^2 (MORRELL 1972; DANEKE et al. 1984; O'NEAL et al. 1987; ZOELLICK and SMITH 1992; WHITE and

RALLS 1993; CORREA 1996). Small ranges of the swift fox we documented in Wyoming may not have been influenced by the relatively low number of individual's relocations, since we proved based on the area-observatian curve that the given number of relocations (19–26 per fox) adequately estimated the home-range size. However, the home-ranges may have been larger had we included the summer months.

Given the parental investment hypothesis stated by MOEHLMAN (1986), small North American foxes should more likely be polygynous than larger canids. Thus, appreciable home-range overlap among adjacent foxes may be predicted. Overlapping swift fox ranges were not measured, yet. However, the kit fox has been observed having overlapping home-ranges between 56–83% in paired individuals, and up to 25% in non-paired individuals (DANEKE et al. 1984; ZOELLICK and SMITH 1992; WHITE and RALLS 1993; CORREA 1996). Core areas (50% harmonic mean isopleths) were used by kit foxes exclusively (WHITE and RALLS 1993) or overlapped by 59% only between family members (CORREA 1996).

Overlap of home-ranges in our study was extensive between individuals classified as mated pairs, but was low outside of this category, a relationship contrary to the hypothesized polygyny. Because the home-range of a given male overlapped extensively with only one female, opportunities for multiple matings by males may have been limited. Consequently, nocturnal activity centers of paired individuals were close together and mates tend to use overlap area slightly more than expected by its proportion. We found some overlap of home-ranges between unpaired individuals, but those foxes seemed to visit their overlap areas less than expected. Moreover, the lack of core area overlap between unpaired foxes may indicate that a portion of the home-range at den sites was used exclusively. Our sample of 10 foxes was clearly limited to allow overall conclusions, but the results were consistent with a social organization in which mated pairs occupy areas that overlap little with those of adjacent pairs.

Extensive overlap of home-range between pair members, no intersexual difference in size of home-range, and slight physical dimorphism were defined by GEFFEN and MACDONALD (1992) as indicators of monogamy in canids. Hence, our results suggested that swift foxes were monogamous without tending toward polygyny as expected relating to body mass and behavioral trends in canids (MOEHLMAN 1986, 1989). However, some evidence for polygamous units in swift fox has been supported by the fact, that overlap of unpaired M-F combinations was greater than overlap of F-F, and M-M combinations possibly indicating mutual attraction of unpaired foxes.

Spatial organization between neighboring foxes can only be a meaningful reflection of the social system, if all animals in the neighborhood have been tracked. However, little overlap between unpaired foxes in this study may also be influenced by some undetected foxes which may not have been captured. Even if the spatial relationships between neighboring foxes largely reflected their social structure, exploration of home-range overlap and home-range size were not sufficient criteria to confirm their mating system per se. Evaluation of social structure in the swift fox had have required direct observations of social interactions to rule out all social arrangements. Social organization of carnivores can vary with another ecological factors such as availability and dispersion of resources, habitat type and quality, population density, and season (MACDONALD 1983). Despite of some potentionally valuable information about space use by swift foxes, the results of our study are of limited scope to provide inference to larger populations.

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Zusammenfassung

Aktionsraumgröße und Raumorganisation beim Swiftfuchs (Vulpes velox Say, 1823) im südöstlichen Wyoming

Die Aktionsraumgröße und Raumorganisation beim Swiftfuchs wurden zwischen September 1996 und März 1997 untersucht, um mit Hilfe von Radiotelemetrie die soziale Struktur in einer kleinen Population in der Prärie des südöstlichen Wyoming zu beschreiben. Die durchschnittliche Aktionsraumgröße anhand der 95% adaptiven Kernel Methode betrug 11.7 ± 1.3 km^2 (x ± SE, n = 10). Streifgebiete der Männchen waren um ca. 25% grösser als die der Weibchen, allerdings war dieser Unterschied nicht signifikant. Gebiete mit der Nutzungsverteilung von 50% (Kerngebiet) hatten an der Gesamtgröße des Aktionsraums einen Anteil von 19.0 ± 2.6% und setzten sich aus 1 oder 2 Polygonen zusammen. Die Überlappung der Streifgebiete war bei den verpaarten Individuen mit 59.6 ± 7.9% (n = 8 Kombinationen) signifikant größer als die Überlappung der Aktionsräume unverpaarter Füchse (9.9 ± 2.8%; n = 18 Kombinationen). Verpaarte Füchse teilten sich mehr als 70% ihrer Baue, wobei sich 75% der Baue im Kerngebiet der jeweiligen Tiere befand. Die beobachteteten Füchse verhielten sich monogam.

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A new species of grass mouse, genus *Akodon* (Muridae: Sigmodontinae), from Mendoza Province, Argentina

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Abstract

Examination of a collection of specimens of *Akodon* from central Argentina resulted in the recognition of a new species. This species inhabits lower elevations in Mendoza Province, Argentina, in a zone that has undergone great habitat conversion due to agricultural development. Descriptions of cranial, dental, and external morphology are presented. The new species, which is tentatively assigned to the "*varius* group" of *Akodon*, is compared with another member of the group, *Akodon molinae*, which also occurs in the region.

Key words: *Akodon*, Argentina, morphology, systematics, taxonomy

Introduction

In 1995–1996, while examining specimens in the Colección Mastozoológica, Instituto Argentino de Investigaciónes de las Zonas Aridas (IADIZA-CM) in Mendoza, Argentina, J. K. Braun encountered a series of *Akodon* that was not assignable to any known species. Although the tags identified some of the specimens as *A. varius* Thomas, 1902, the tray holding the specimens and the box containing the skulls were labeled as *A. minoprioi*. This name was not found in any published work listing synonymies (e. g., Cabrera 1961; Musser and Carleton 1993). Upon further investigation, it was noted that a series of *Akodon* from the locality where the specimens in question were collected were reported in a study published by Contreras and Rosi (1980 a) on the community ecology of small mammals. They identified the *Akodon* they studied as *Akodon varius neocenus* (Cabrera, 1961). Later, in 1981, Contreras and Rosi presented a study at the Primeras Jornadas de Ciencias Naturales del Litoral in Santa Fe, Argentina, proposing the recognition of a new species of *Akodon* (*Akodon minoprioi*) from Mendoza Province.

The abstract of the study presented at the above meeting in 1981 offers no information regarding a morphological or karyological description of this taxon, and little information about its distribution. A more detailed systematic description was never published. It is likely that many of the specimens used in their study are the same specimens upon which our description is based. This comment is offered for those individuals who may be familiar with the name, *A. minoprioi*, which was used by Contreras for a species that was not formally described (Galliari et al. 1996).

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Herein we present a systematic study, using cranial, dental, and external morphology, of the original series of specimens and other specimens that have been collected from the region. A comparison is made with another species of *Akodon*, *A. molinae*, that is known to inhabit the general region and that is possibly closely related to the new species.

Material and methods

External, cranial, and dental measurements were recorded from 74 specimens in question and from 5 specimens of *Akodon molinae* Contreras, 1968. External measurements (in mm) recorded from the labels were: total length; length of head and body; length of tail; length of hind foot; length of ear; weight (in g).

Cranial and dental measurements were taken with dial calipers to the nearest 0.05 mm. We followed the measurements presented by Myers (1989), with the exception of incisive angle, which was not measured, and we have added width of bullae. Measurements are: length of skull: distance from the posterior border of the supraoccipitals to the tip of the nasals; condyloincisive length: distance from the posterior margin of the occipital condyles to the anteriormost projection of the incisors; length of incisive foramina: distance between the anteriormost and posteriormost projections of the incisive foramina; length of maxillary toothrow: distance from the anterior margin of the alveolus of M1 and the posterior margin of the alveolus of M3; palatal bridge: distance from the anteriormost point on the posterior margin of the palate to the posterior margins of the incisive foramina; length of diastema: distance between the posterolateral margin of the incisive alveolus and the anteromedial margin of the alveolus of M1; zygomatic breadth: greatest distance across the zygomatic arches, perpendicular to the longitudinal axis of the cranium; interorbital breadth: least distance across the frontal bones; mastoid breadth: greatest width across the mastoids; breadth of incisive foramina: greatest distance between the labial margins of the paired incisive foramina perpendicular to the longitudinal axis of the cranium; breadth across molars: the greatest width from the labial side of one upper molar toothrow to the labial side of the other toothrow; width of zygomatic plate: width dorsal to the insertion of the zygomata on the skull, parallel to the longitudinal axis of the skull; length of nasals: greatest length of the nasal bones from the posteriormost projection of the frontal suture to the tip; breadth 1 of rostrum: greatest width of the rostrum across the nasolacrimal capsules; breadth 2 of rostrum: greatest width of the rostrum measured at the top of the arc formed by the roots of the incisors as they pass posteriorly, visible as a raised curve along the rostral walls; breadth of braincase: greatest distance across the braincase, typically on the squamosals; width of bullae: from the medial edge to the lateral edge of the ectotympanic part of the auditory bullae.

Standard names of colors (Ridgway 1912) were used as the reference for the descriptions. Terminology for dentition follows Reig (1977). The relative age of each specimen was based on tooth wear and the five age classes proposed by Myers (1989) were used. Age class 1: teeth unworn; edges of M3 sharp; in many individuals M3 newly or incompletely erupted. Age class 2: slight wear on all teeth, but major cusps distinct; posteroloph on M3 still distinguishable but surface of rest of tooth flat or concave. Age class 3: moderate wear on all teeth; posteroloph on M3 obliterated. Age class 4: major cusps still distinct, but all minor lophs obliterated. Age class 5: surface of teeth entirely flat or concave.

Specimens were examined from the following museums (acronyms given in parentheses): Colección Mastozoológica, Instituto Argentino de Investigaciones de Zonas Aridas, Mendoza, Argentina (IADIZA-CM); Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (OMNH); field numbers of specimens from Argentina in the Sam Noble Oklahoma Museum of Natural History and not yet cataloged are designated Arg. Lists of the specimens examined including locality, catalog number, sex, and type of preparation are given in the specimens examined of the species description. The following specimens (skins and skeletons) of *Akodon molinae* were examined: Argentina: Mendoza Province: 8 km W La Botija, Pampa de las Salinas, 36°14′ S, 66°40′ W, el. 1,400 ft., 5 (5 males, Arg 3210, 3211, 3212, 3213, 3236).

StatView (SAS Institute, Inc. 1998) was used to generate the basic statistics. Although individuals in all age classes were examined, only those in age classes 2–5 were used in data analyses.

Results

Akodon oenos, n. sp.

Holotype: Adult female; skin, skull, partial skeleton; IADIZA-CM 611; collected 31 September 1980 by M. I. Rosi.

Type locality: Argentina: Mendoza Province: Departamento La Valle, La Pega (32°48′ S, 68°40′ W).

Distribution: Known only from central Mendoza Province, Argentina (Fig. 1). Elevation varies from about 600 to about 1200 m.

Etymology: The specific name, *oenos*, which is Greek for wine, is given because this species of *Akodon* is known only from the desert scrub habitat at middle elevations in Mendoza Province. This habitat has been extensively converted for agricultural purposes and the major crop is grapes. Mendoza is known for its wine, and thus it is likely that much of the habitat of *Akodon oenos*, the wine mouse, has been given up to produce the excellent wines of Argentina.

Diagnosis: *Akodon oenos* can be distinguished from other members of the "varius group" of *Akodon* by the following combination of characters: dorsal coloration reddish brown; ventral coloration like the dorsum but with orangish cast; eye ring absent to obsolete; white chin and/or throat absent; size medium for the group; total length < 192 mm ($\bar{x} = 169$ mm); length of tail < 82 ($\bar{x} = 68$ mm); ears small, < 16 mm; means of measurements smaller for most characters; maxillary toothrow relatively large for size, < 5.05 mm ($\bar{x} = 4.75$ mm).

Description and comparison: External and cranial measurements of the holotype and other individuals are given in table 1. Features of the cranium and dentition are presented in figures 2 and 3. Comparisons made with *A. molinae* are presented in parentheses.

Akodon oenos tentatively is included in the "*varius*" group of *Akodon* as delineated by Myers (1989). Clarification of the relationships with the members of this group and with other species of *Akodon* awaits further information.

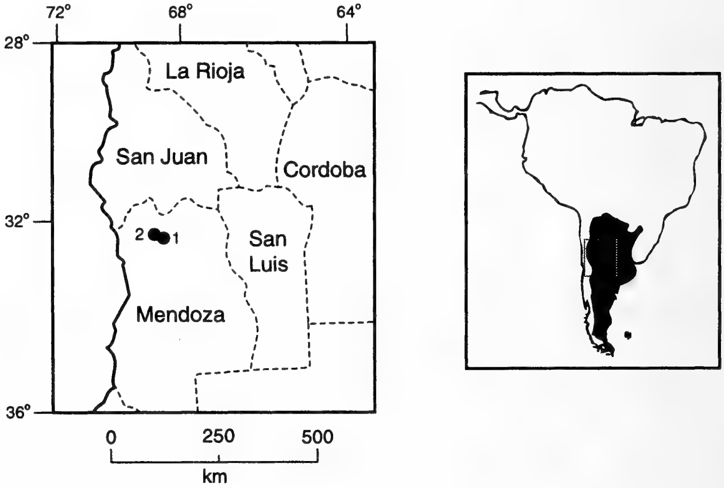

Fig. 1. Map of the provinces of west-central Argentina, including Mendoza Province. Provincial borders are shown as broken lines. The specimen localities are those presented in the text and are as follows: 1) Departamento Guaymallen, La Pega and Departamento Lavalle, La Pega; 2) Departamento Las Heras, 2 km S de Villavicencio Ruta 32.

Table 1. Measurements (in mm) and weight (in g) for *Akodon* (age classes 2–5 only). Means, standard deviations (±), sample sizes ( ), and minimum – maximum are given for each measurement.

Character	*Akodon oenos* Holoype, IADIZA-CM 611, adult female	*Akodon oenos*	*Akodon molinae*
Total length	170	169 ± 12, (62) 140–192	168 ± 14, (5) 151–188
Length of head and body	101	101 ± 7, (63) 80–114	100 ± 7, (5) 91–108
Length of tail	69	68 ± 6, (62) 55–82	68 ± 8, (5) 60–80
Length of hind foot	23	23 ± 1, (62) 20–25	23 ± 1.7, (5) 21–25
Length of ear	13.5	14 ± 1, (62) 11–16	18 ± 1, (5) 16–19
Weight	23.5	24.8 ± 6.3, (63) 11.5–39.7	27.2 ± 2.5, (5) 23.5–30.0
Length of skull	25.9	26.1 ± 0.78, (61) 23.2–27.5	26.6 ± 0.76, (5) 25.4–27.2
Condyloincisive length	24.4	24.5 ± 0.85, (61) 21.2–26.3	25.0 ± 0.88, (5) 23.7–25.8
Length of incisive foramina	5.3	5.8 ± 0.37, (60) 4.8–6.5	5.7 ± 0.15, (5) 5.5–5.9
Length of maxillary toothrow	4.9	4.8 ± 0.19, (61) 4.1–5.1	4.8 ± 0.04, (5) 4.8–4.9
Palatal bridge	3.6	3.3 ± 0.20, (60) 2.8–3.8	4.0 ± 0.31, (5) 3.5–4.3
Length of diastema	6.9	6.7 ± 0.35, (61) 5.4–7.4	6.9 ± 0.47, (5) 6.3–7.5
Zygomatic breadth		13.7 ± 0.45, (53) 12.3–14.7	14.0 ± 0.45, (5) 13.3–14.5
Interorbital breadth	4.6	4.6 ± 0.15, (61) 4.3–5.2	4.7 ± 0.16, (5) 4.6–5.0
Mastoid breadth	11.6	11.6 ± 0.25, (61) 11.0–12.1	11.7 ± 0.31, (5) 11.2–12.0
Breadth of incisive foramina	1.8	1.85 ± 0.13, (58) 1.60–2.25	1.83 ± 0.04, (5) 1.80–1.90
Breadth across molars	5.3	5.2 ± 0.23, (61) 4.5–5.8	5.4 ± 0.25, (5) 5.2–5.7
Width of zygomatic plate	2.5	2.8 ± 0.20, (61) 2.4–3.2	3.1 ± 0.19, (5) 2.9–3.4
Length of nasals	8.8	8.9 ± 0.53, (61) 6.4–9.9	9.3 ± 0.34, (5) 8.9–9.6
Breadth 1 of rostrum	4.7	4.7 ± 0.18, (61) 4.1–5.1	5.0 ± 0.33, (5) 4.6–5.3
Breadth 2 of rostrum	3.9	4.0 ± 0.15, (61) 3.6–4.3	4.2 ± 0.23, (5) 4.0–4.5
Breadth of braincase	12.1	11.9 ± 0.20, (61) 11.5–12.3	12.2 ± 0.28, (5) 11.8–12.6
Width of bullae	2.9	2.8 ± 0.15, (61) 2.3–3.0	3.8 ± 0.14, (5) 3.7–4.0

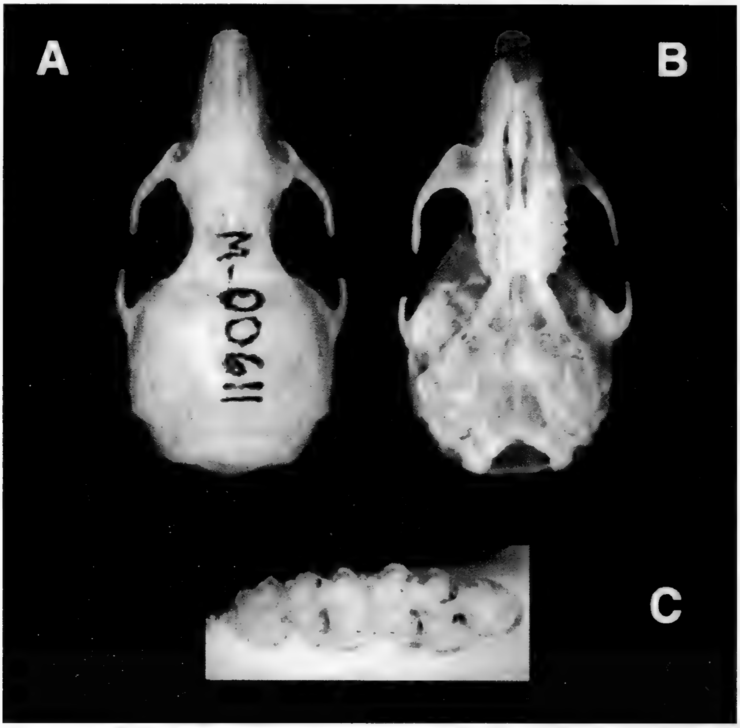

Fig. 2. Dorsal (A) and ventral (B) views of cranium, and view of upper right molar toothrow (C) of *Akodon oenos* (IADIZA-CM 611).

Overall dorsal coloration is deep reddish brown, i. e., a mix of Snuff Brown and Saccardo's Umber (brownish gray with conspicuous gray and yellow "ticking"). Hairs average about 15 mm long on the midrump region. Hairs are white basally for about 1 mm, followed by a Blackish Mouse Gray (light gray) band of about 8 mm that is very dark for the distal 3–4 mm, a 2 mm or so band of Clay, and ending with a 1 mm dark tip. Dark guard hairs are numerous and long, projecting about 5 mm beyond the fur on the rump. The sides and the flanks are similar to the dorsum, although slightly lighter due to the decrease in the number of dark guard hairs. In the midventral region the hairs are Blackish Mouse Gray for about 75% of their length; the tips Clay or Pinkish Buff (whitish). The overall coloration of the venter has an orangish cast (whitish wash). Clay-tipped hairs (whitish) also are concentrated in the perianal region. Hairs of the throat are similar to those of the chest. The chin is without a distinctive white patch; although some whitish hairs may be present, they are not readily apparent (a white chin and sometimes a white throat are present).

The ears are small – 11–16 mm, short, and rounded (large, 16–19 mm); the inner surfaces are well furred. The hairs are grayish basally with Clay tips (tips are not Clay colored). Pre- or postauricular patches are absent. Pale hairs surround the eyes; however, the eye ring is inconspicuous (eye ring present and well developed).

The tail is moderately haired with hairs extending over 3–4 scales. It is moderately bicolored, Fuscous or blackish brown (brownish) above and Drab below. The number of scales, measured at the base of the tail, ranges from 18 to 20 per cm. Fore- and hindfeet are covered with Drab hairs that have pale brownish bases. The hairs surround the claws but do not extend beyond the tips.

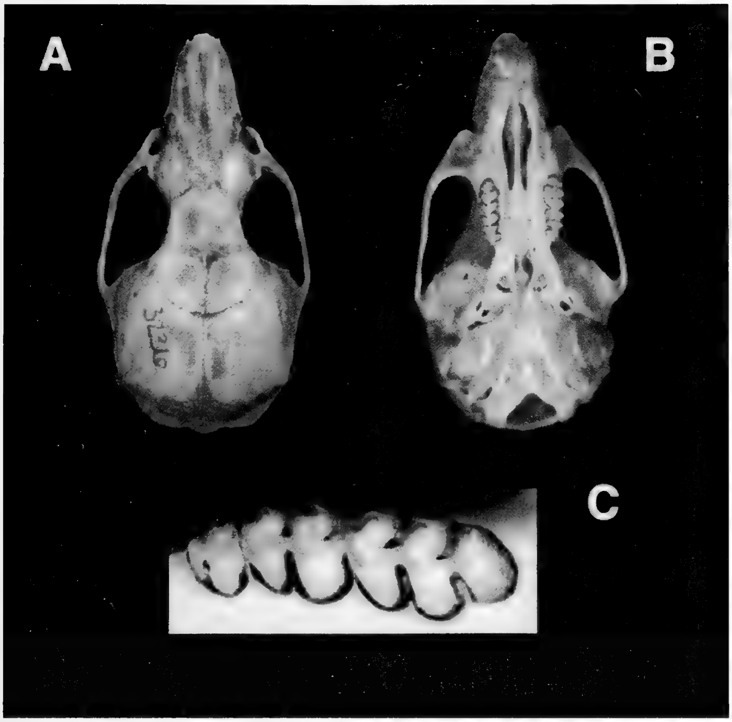

Fig. 3. Dorsal (A) and ventral (B) views of cranium, and view of upper right molar toothrow (C) of *Akodon molinae* (Arg 3236).

The skull is similar to other species of *Akodon*. It is medium to large in size and somewhat heavily built. The gnathic process is slightly developed. The posterior ends of the nasals are blunt and extend just slightly beyond the frontopremaxillary suture. The zygomatic arches are moderately slender, slightly converging anteriorly, and only slightly expanded laterally. The zygomatic notches are moderate in width and depth (wider and deeper). Lacrimals are small. The interorbital region is narrow, rounded (hourglass shaped, although it is often slightly divergent posteriorly in individuals of older age classes); beading and ledges are absent. The frontal sinuses are not conspicuously swollen. The frontoparietal suture is a smooth crescent (generally), although in some individuals a slight angle is formed where the parietals meet at the midline. The braincase is rounded. Temporal and mastoid ridges usually are present but weakly developed. The interparietal is narrow anteroposteriorly (wider) and generally laterally expanded but not extending the breadth of the skull.

The zygomatic plate is of moderate width (wider), the anterior surface is generally flat and oriented vertically to projecting slightly forward. The rostrum, when viewed in profile, is bowed downward. An alisphenoid strut is present. The subsquamosal and postglenoid foramina are about equal in size and are separated by a strap-like hamular process.

The incisive foramina extend posteriorly to the level of the protocone of M1. The palate has grooves of shallow to moderate depth. The posterior palatal foramina are slightly enlarged and are located about even with M2. Located posteriorly and medially to the posterior palatine foramina and about even with the protocone of M3 is a second pair of foramina. Palatal bridge is short (long); mean palatal bridge is 3.32 mm (4.03 mm). The mesopterygoid fossa is simple, tending toward a lyre shape, and extends anteriorly to the posterior root of M3. A pair of posterolateral palatal pits is located to each side of the mesopterygoid fossa posterior to the anteriormost part of the fossa. Anteriorly, the pterygoid fossa are about equal in width to the mesopterygoid fossa; the sides are rather straight, posteriorly divergent, and become wider posteriorly. The paraoccipital processes are small. The tympanic bullae are small and not inflated, mean width of bullae is 2.79 mm (Tab. 1) (bullae are larger and more inflated, mean width of bullae is 3.77 mm; Tab. 1); the eustachian tubes are short and broad. The stapedial spines are present but not well developed.

The mandible is typical for the genus. The rami are slender. Capsular projections, which generally are present as a ridge, lie below the sigmoid notches. The condyloid processes extend well beyond the coronoid process. Masseteric ridges are present but small.

The dentition is of a pattern typical for the genus. Incisors are orthodont (opisthodont). Toothrows are parallel. Molars are moderately hypsodont, but crested in young individuals. Procingulum of M1 with an anteromedian flexus that becomes less obvious to obsolete with age. The major cusps are about equal in size and are arranged somewhat diagonally in relation to each other. Parastyle, anteroloph, mesoloph, and mesostyle are present. A posteroloph is absent to obsolete. The major cusps of M2 are similar to those of M1. A cingulum (= anterolabial conule) is present as are the mesoloph and mesostyle. The M3 is small, about one-half the length of M2. When worn it appears more "C" shaped than "8" shaped and in old adults is in the form of an oval.

In m1, the cusps are about equal in size and are arranged diagonally. An anteromedian flexid, protostylid and loph, ectostylid (if present, tiny), mesostylid, mesolophid (present or absent), and posterolophid are present. Major cusps of m2 as in m1. The anterolabial conulid is present, but becomes obsolete in older individuals. The ectolophid is tiny to obsolete. The posterolophid is present, moderately developed, but is absent to obsolete in older individuals. In m3 the protoconid, metaconid, and hypoconid are present and well developed; the entoconid is present but small. Posterolophid is absent.

Habitat and ecology: The habitat of *A. oenos* includes the lower elevation halophytic desert scrub at the base of the Andean and pre-Andean ranges in central Mendoza Province (Fig. 4). It is among the most xeric parts of Mendoza Province, with rainfall of only

Fig. 4. Habitat of *Akodon oenos* from the type locality, La Pega, Mendoza Province, Argentina. Photo by R. A. Ojeda.

100 mm per year. Soils are very fine with many salts. Major plants include several species of saltbush (*Atriplex lampa*, *A. flavescens*, *A. argentina*) and the halophytic shrub *Suaeda divaricata*. Other desert shrubs such as creosote bush (*Larrea divaricata*), *Bougainvillea espinosa*, *Plectrocarpa tetracantha* and *Prosopis strombulifera* also are found in the area (Contreras and Rosi 1980 a).

Other rodent species known to occur with the species at La Pega include *Calomys musculinus* (Thomas, 1913), *Akodon molinae* Contreras, 1968, *Graomys griseoflavus* (Waterhouse, 1837) (not *Phyllotis darwini*, as reported by Contreras and Rosi 1980 a), *Oryzomys* (= *Oligoryzomys*) *flavescens* (Waterhouse, 1837), *Mus musculus* Linnaeus, 1758, *Rattus rattus* (Linnaeus, 1758), and *Microcavia australis* (I. Geoffroy and d'Orbigny, 1833) (Contreras and Rosi 1980 a, b, c). The community ecology of the small mammals of La Pega, including *A. oenos*, was studied by Contreras and Rosi (1980 a). *A. oenos* was found to have a population density that was projected to be 21 animals/ha, with a biomass of 461 g/ha (although only 8 animals were captured). The home range of a single individual was less than 300 m^2.

At La Pega, males had abdominal testes or were subscrotal in August and September with testis size (in mm) ranging from 7×5 to 11×7. Males with scrotal testes were captured in February, October, and December, and had sizes (in mm) ranging from 12×7 to 13×9. A young male was collected in February with a testes size (in mm) of 7×4.

Females at La Pega were not reproductively active (vagina closed) in August and September (early spring). Pregnant females were captured in October and December. The number of embryos ranged from 3 to 5.

Referred specimens (74 specimens; all skin and skull, except when noted): Argentina. Mendoza Province: Departamento Guaymallen, La Pega, 51 (26 males, IADIZA-CM 10, 42, 53, 78, 79, 81, 85, 89, 513, 514, 516, 535, 543, 574, 584, 614, 653, 666, 670, 672, 677, 697, 720, 721, 723, 728; 25 females, IADIZA-CM 29, 80, 149, 380, 398, 506, 512, 519, 538, 582, 583, 597, 599, 633, 634, 637, 639, 642, 645, 655, 669, 678, 704, 722, 724). Departamento Las Heras, 2 km S de Villavicencio Ruta 32, 2 (2 males, IADIZA-CM 3447, 3448 skin). Departamento Lavalle, La Pega, 21 (11 males, IADIZA-CM 33, 47, 617, 770, 771, 772, 777, 784, 785, 787, 778; 9 females, IADIZA-CM 379, 392, 395, 396, 399, 401, 609, 611 holotype, 622; 1 sex unknown, IADIZA-CM 397).

Discussion

In the last decade we have been engaged in a systematic survey of the mammals of Argentina, especially northwestern Argentina. Argentina has long been of interest to mammalogists, and some would argue that the mammals of the country are well known. However, as our explorations have progressed, we have continued to find taxa that are new to science (both at the generic and specific level; e. g., Braun and Mares 1995; Mares and Braun 1996). In northwestern Argentina, especially, we have found that the geographic pattern of isolated mountain ranges, enclosed basins, and isolated rivers are ideal habitats for discovering new taxa. Nevertheless, we are regularly surprised by the appearance of new taxa in lowland areas, or in habitats near major metropolitan centers.

Mendoza Province is situated in westernmost Argentina in the central part of the country. It is one of the major agricultural regions in the country, and its principal product is wine. Recent studies in Mendoza have resulted in the rediscovery of populations of the rare and unusual octodontid, *Tympanoctomys barrerae* (Lawrence, 1941), (Ojeda et al. 1989, 1996; Torres-Mura et al. 1989; Mares et al. 1997), and new species of mammals (e. g., *Ctenomys validus* Contreras, Roig, and Suzarte, 1977, Contreras et al. 1977; *Abrocoma* n. sp., J. K. Braun and M. A. Mares pers. comm.).

Akodon oenos occurs in disturbed areas that are surrounded by agricultural zones. In addition to supporting cultivated fields, the habitats also are heavily grazed by cattle. Collectors doing survey research often neglect these areas, expecting only to find the "weedy" species that frequent such habitats over a broad region (e. g., *Oligoryzomys longicaudatus* (Bennett, 1832), *Calomys musculinus* (Thomas, 1913), *Graomys griseoflavus* (Waterhouse, 1837). Yet our research has shown that undescribed species frequently can exist in areas that one would expect to have been well studied by scientists, or that might appear too affected by humans and their livestock to harbor unknown species. While it is true that we have discovered many new species in remote regions, it is also true that several new species have been found within very short distances of cities (e. g., *Akodon aliquantulus* Díaz, Barquez, Braun, and Mares, 1999; DÍAZ et al. 1999, discovered within 20 km of the City of Tucumán). *A. oenos* is known only from a very limited area near the type locality, but the halophytic desert scrub habitat with sandy soils is continuing to be reduced as agricultural and grazing lands expand. The status of the species is unknown.

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Zusammenfassung

Eine neue Art der Grasmaus, Gattung Akodon (Muridae: Sigmodontinae) aus der Provinz Mendoza, Argentinien

Systematische Untersuchungen einer Sammlung von *Akodon* Exemplaren aus Mittel-Argentinien führte zur Entdeckung einer neuen Art. Diese Art bewohnt die unteren Höhenlagen in der Mendoza Provinz in Argentinien, eine Region die auf Grund von landwirtschaftlicher Erschliessung große Lebensraumveränderungen erfahren hat. Schädel-, Zahn- und äußere Morphologie werden in Beschreibungen dargestellt. *Akodon oenos* n. sp., welche provisorisch der "*varius*-Gruppe" zugeordnet ist, wird mit *Akodon molinae*, einer anderen Art der Gruppe, die in der selben Region vorkommt, verglichen.

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Intraspecific craniometric variation in a chromosome hybrid zone of *Ctenomys minutus* (Rodentia, Hystricognathi)

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Abstract

Intraspecific craniometric variation in a population of *Ctenomys minutus* (2n = 46, 47, and 48) from a hybrid zone was studied using univariate and multivariate techniques. The study showed greater morphological variation among females than among males. Analysis of populations that contain hybrid forms suggest some degree of morphological divergence among cytotypes.

Key words: *Ctenomys minutus*, hybrid zone, skull morphology

Introduction

Ctenomys is a genus of fossorial rodents endemic to southern South America which comprises about 56 species (Woods 1993). Regarding both morphology and ecology, *Ctenomys* is highly convergent with North American pocket gophers (Geomyidae), Middle Eastern and European mole rats (Spalacidae), and African mole-rats (Bathyergidae) (Nevo 1979). *Ctenomys* species have high karyotypic diversity with diploid numbers varying from 2n = 10 to 70 (Reig et al. 1990).

The four species of *Ctenomys* that occur in the southern Brazilian state of Rio Grande do Sul, are *C. torquatus*, *C. lami*, *C. minutus*, and *C. flamarioni*. They have been reviewed previously (Freitas 1995). *C. minutus* inhabits fields and pastures in the southern Brazilian coastal plain of Rio Grande do Sul and Santa Catarina. In the centre of this distribution a hybrid zone was found with chromosomal numbers varying from 2n = 46 to 2n = 48 (Gava 1996; Freitas 1997).

Hybrid zones of fossorial rodents have been studied in many species from various genera, e. g. *Thomomys* (Thaeler 1974; Patton 1993), *Spalax* (Nevo 1986), and *Ctenomys* (Gava 1996; Freitas 1997).

The aim of this study therefore is to investigate the skull morphological variation in *C. minutus* and ist relation to the chromosomal hybrid zone.

Material and methods

The sample consisted of 108 kariotyped specimens of *Ctenomys minutus* with chromosomal numbers distributed as follows: 53 specimens with 2n = 46 (30 males and 23 females), 8 specimens with 2n = 47 (3 males and 5 females), and 47 specimens with 2n = 48 (25 males and 22 females) (Gava 1996).

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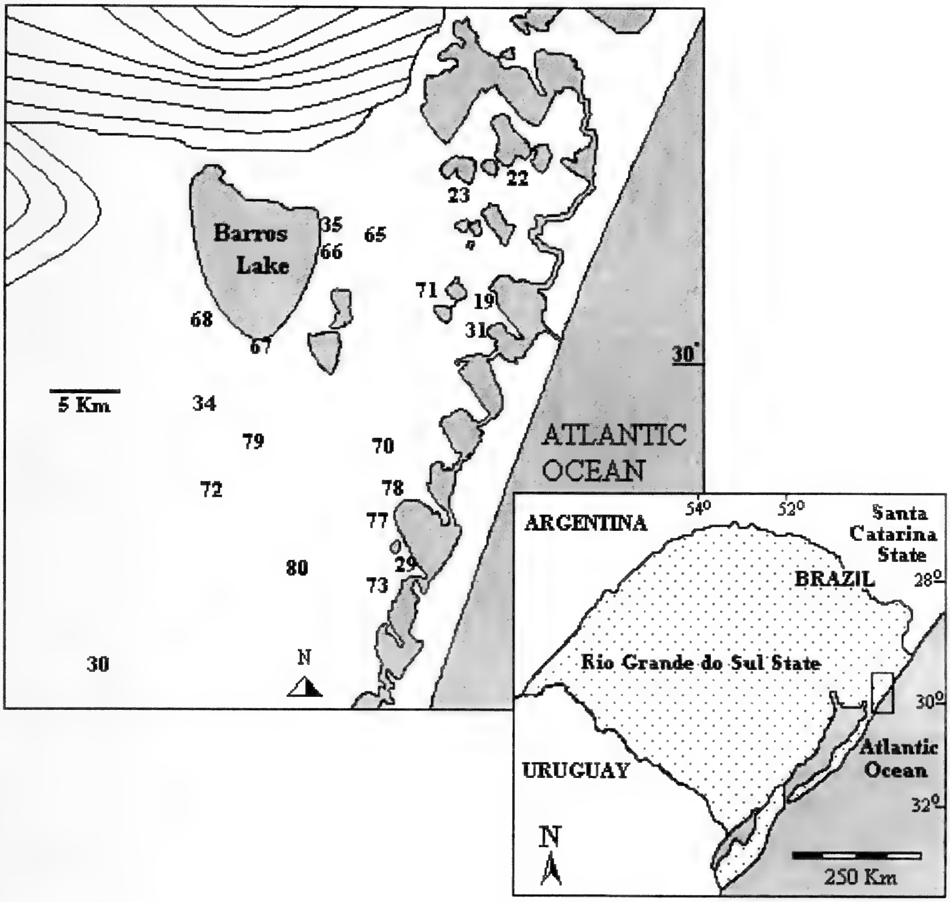

Fig. 1. Map of southeastern Rio Grande do Sul, Brazil, showing the sample localities of *Ctenomys minutus.*

Samples from 18 numbered population localities were plotted on a map of south-eastern Rio Grande do Sul (Fig. 1). The number of individuals by cytotype in each population and the distance between localities were determined by a south-eastern to north-eastern transect, crossing the hybrid zone from locality 30 to locality 22 (Gava 1996).

Eleven standard cranial measurements (Langguth and Abella 1970), in millimeters, were taken as follows: 1) GSL: Greatest skull length, 2) NL: Nasal length, 3) NB: Nasal breadth, 4) BB: Bimeatal breadth, 5) ZYB: Greatest breadth across zygomatic arches, 6) MTB: Greatest breadth across the mastoid, 7) RB: Rostral breadth, 8) POD: Greatest diameter at pre-orbital foramen, 9) DIA: diastema, 10) MSL: Length of molar tooth row, 11) PRL: Length of the palatinum.

All linear measurements were log-transformed to normalise the original measurements. A two-sample t-test was used to evaluate sex-related differences and differences due to variation in chromosomal number (2n = 46, 47, and 48). The statistical analysis of skull morphology was made by two methods, first by univariate analysis and secondly by multivariate analysis. Canonical Discriminant Functions Analysis and Principal Components Analysis were used to classify the three cytotypes separately for males and females. Data from the 11 cranial measurements of the 108 specimens were divided into male and female classes and submitted to univariate analysis separately for males and females. All statistical analyses were made using NCSS 6.0 – Number Cruncher Statistical Systems (Hintze 1995).

Results and discussion

The two-sample t-test showed significant differences in 10 measurements, except for MSL between males and females. A t-test was made for each skull characteristic measurement of the three cytotypes (2n = 46, 2n = 47, and 2n = 48) as is shown in table 1. The only significant difference between 2n = 46 and 2n = 48 was for POD, with POD in 2n = 48 greater than in 2n = 46 ($t = 2.911$, $p > 0.05$).

Multivariate analysis is commonly used to determine systematic positions, morphometric variations, and taxonomic relations e. g. in fossorial rodents such as *Geomys personatus* (Williams and Genoways 1981), *Spalax ehrenbergi* (Nevo et al. 1988; Nevo and Beiles 1989), *Geomys tropicalis* (Williams and Genoways 1977), *Geomys arenarius* (Williams and Genoways 1978), *Geomys pinetis* (Williams and Genoways 1980), *Ctenomys dorbignyi* (Contreras and Scolaro 1986), Bolivian species of *Ctenomys* (Cook et al. 1990), and *Ctenomys talarum* (Bush et al. 1989).

The results of multivariate analysis suggest that females had greater variation than males in Principal Components Analysis (Morrison 1976; Chatfield and Collins 1980). The first factor accounted for 67.2% variation and the cumulative percent for the first three factors accounted for 82.8% of the observed variation. In a correlation matrix, the measurements that showed variation in factor 1 were: GSL, BB, ZYB, DIA, NL, POD, and NB respectively. Measurements that showed variation in factor 2 were: PRL, RB, MSL, and MTB, respectively. Males presented 89.9% of variation in factor 1 and 94.8% considering the cumulative variation of the three first factors. All measurements showed variation in factor 1, as follows: GSL, PRL, BB, ZYB, DIA, RB, POD, NB, NL, MTB, and MSL, respectively. The hybrid form, 2n = 47, presents an intermediate position between the parental karyotypes. Analysis of Canonical Discriminant Functions for the three cytotypes, separately for males and females, showed that females are more variable than males, but in both sexes the separation is distinct and the hybrid shows significant variation in the second score, which represents a shape variable. The classification error of females showed a reduction of 64% compared with 56% in males with hybrids in a peripheral position (Fig. 2). Analysis of Canonical Discriminant Functions for populations that present hybrid forms, considering both males and females, presents a classification error reduced to 59.6% but the peripheral position of hybrids is most evident, suggesting some degree of morphological divergence among cytotypes.

Table 1. Skull measurements of three cytotypes of *Ctenomys minutus*. Mean values ± Standard Deviation and sample size (in parenthesis) are given.

	2n = 46 (53)		2n = 47 (8)		2n = 48 (47)	
Meas[a]	Males (30)	Females (23)	Males (3)	Females (5)	Males (25)	Females (22)
GSL	46.5 ± 4.3	43.5 ± 2.5	43 ± 4.5	43 ± 2.2	47 ± 3	43.7 ± 1.8
NL	16.6 ± 1.8	15.8 ± 1.12	15.1 ± 2.7	15 ± 1	16.7 ± 1.1	15.7 ± 0.8
NB	6.7 ± 0.8	6.1 ± 0.5	5.7 ± 0.7	6 ± 0.6	6.9 ± 0.6	6.2 ± 0.4
BB	26.7 ± 2.2	25.4 ± 1.8	24.8 ± 2.6	25.1 ± 1.3	27.2 ± 1.4	25.8 ± 0.9
ZYB	28 ± 2.5	26.1 ± 1.3	25.6 ± 2.8	26.5 ± 1.3	28.6 ± 1.9	26.8 ± 0.8
MTB	25.8 ± 2	24.6 ± 1.2	24.8 ± 2.1	24.3 ± 1	25.9 ± 1.6	24.6 ± 1.3
RB	11.5 ± 1.2	10.4 ± 0.8	10.4 ± 1.1	10.5 ± 0.6	11.7 ± 0.9	10.8 ± 0.4
POD	9.7 ± 1.1	9.1 ± 0.7	8.6 ± 1.4	9.1 ± 0.7	10.2 ± 0.8	9.5 ± 0.5
DIA	13.5 ± 1.6	12.5 ± 0.9	12.2 ± 2.1	11.9 ± 1.1	13.6 ± 1.1	12.5 ± 0.8
MSL	9.4 ± 0.8	9.1 ± 0.6	8.6 ± 1.5	9.4 ± 0.5	9.6 ± 0.6	9.3 ± 0.4
PRL	21.9 ± 2.4	20.4 ± 2.3	19.8 ± 3.3	19.5 ± 1.4	22.1 ± 1.8	20.5 ± 1.1

[a] Measurements. Abbreavations are spelled out in text.

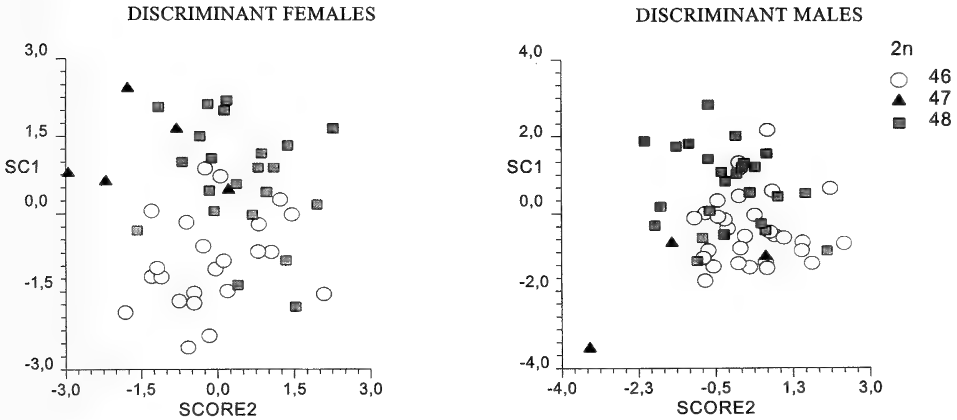

Fig. 2. Comparison of samples of three different cytotypes of *Ctenomys minutus.* The abscissa is the second Discriminant Function and the ordinate is the first Discriminant Function.

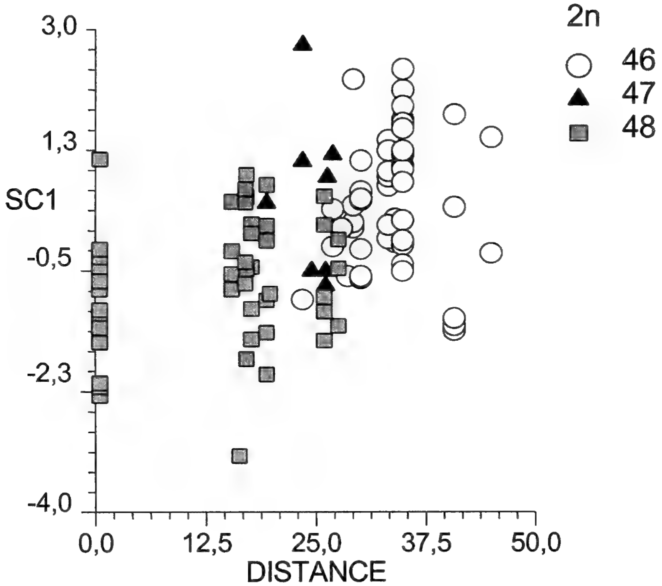

Fig. 3. Individual distribution of first scores of Discriminant Analysis plotted according to transect length among population sites. Distance between populations plotted in a south-eastern to north-

The hybrid zone is approximately 10 km wide (Gava 1996) and the individual scores in Canonical Discriminant Functions were plotted according to the distance in km. Figure 3 shows the variation of the animal scores according to their cytotype in the study area. The position of hybrid forms and a change from negative scores (2n = 48) to positive scores (2n = 46) can be clearly observed.

Despite the cytogenetic difference, the hybrid male meiosis produces a trivalent and, since there is evidence denoting the possibility of balanced segregation and normal fertility in simple Robertsonian heterozygotes, the width of the hybrid zone is a function of the dispersal capability of each individual and the time since secondary contact (Gava 1996).

The geographic range of *Ctenomys minutus* is accompanied by chromosomal variation and intraspecific craniometric variation, mostly among females. This could be explained by historical factors such as populations having been separated by ancient geographic barriers which no longer exist today thus allowing contact among individuals with different diploid numbers (Villwock and Tomazelli 1995).

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Zusammenfassung

Intraspezifische craniometrische Variation in einer chromosomalen Hybridzone von Ctenomys minutus (Rodentia, Hystricognathi)

Die intraszpezifische craniometrische Variation einer Population von *Ctenomys minutus* aus einer Hybridzone ($2n = 46$, 47 und 48) wurde mittels univariater und multivariater Methoden untersucht. Es zeigte sich eine größere morphologische Variabilität innerhalb der Weibchen gegenüber den Männchen. Die Analyse von Populationen, die Hybridformen einschließen, belegen ein gewisses Ausmaß morphologischer Divergenz zwischen den Cytotypen.

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Changes in group size in *Kobus kob kob* (Bovidae) in the Comoé National Park, Ivory Coast (West Africa)

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Abstract

During a 30 month study in the Comoé National Park, Ivory Coast, it was revealed that median size of kob antelope groups which contained a majority of adult females varied between as well as within seasons. Group size was smallest at the height of the rainy season and greatest at the beginning of the rainy season. Whereas increase in group size in the beginning rainy season might have been related to the improving feeding conditions and to reproductive behaviour, reduction of number of animals per group at the height of the rainy season was probably influenced by grass height. In addition to grass height, other factors influencing visibility such as vegetation density, time of the day (day/night) and moon light intensity at night effected group size. While long term trends in group size changes are effected by food availability and reproduction, we assume visibility to be the proximate factor influencing short term (1–24 hours) group size changes in kobs in the study area. We presume avoidance of predator attacks to be the ultimate cause for these changes.

Key words: *Kobus kob*, Ivory Coast, group size variability, visibility

Introduction

During a study on the eco-ethology of kob antelope (*Kobus kob kob*) in the Comoé National Park. FISCHER (1998) found that groups dominated by females in terms of number showed a high fluidity in group size Approximately 70% of all groups encountered contained a majority of adult females and were therefore called female groups. Only those groups have been included in our investigation. Composition of such groups could never be predicted. Beside observed short-term fluidity of the groups, long-term changes in the average group size were obvious in the course of the year. The aim of our study was to collect information about group size changes and come up with possible explanations for the underlying forces.

Materials and methods

Study site

The data were collected during 30 months of field observations of kob antelope in the Comoé National Park (FISCHER 1995, 1996, 1998). The park is located in the north-east of the Ivory Coast between 9°6′ N–8° 5′ N and 3°1′ W–4°4′ W. The study area is situated in the southern part of the park, at the eastern bank of the Comoé river (Fig. 1).

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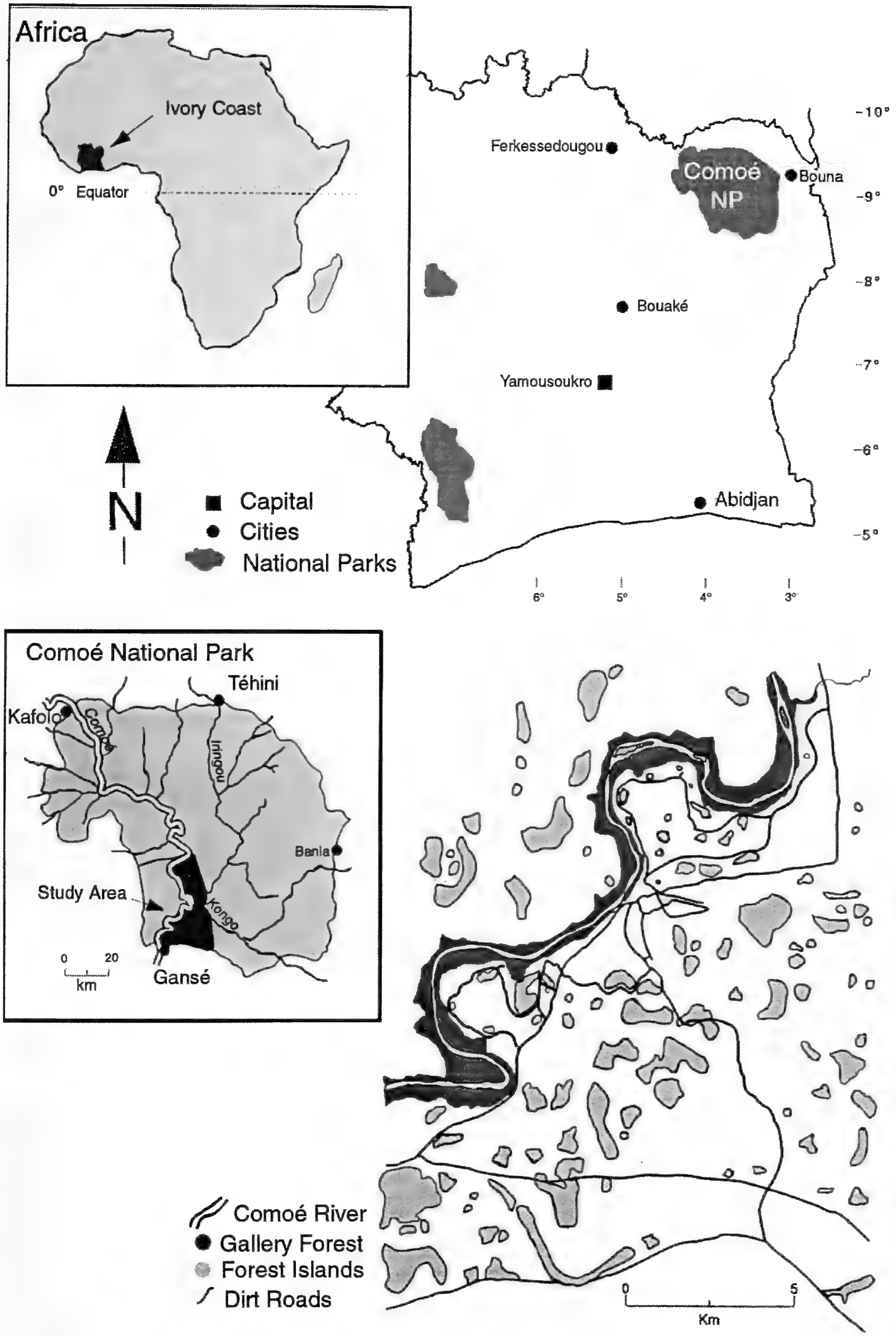

Fig. 1. Map of Africa and Ivory Coast. Below map of the Comoé National Park and the observation area.

The habitat is a tree-shrub savannah, which has been described in detail by Porembski (1991). Open areas are dominated by the following grasses *Loudetia simplex*, *Schizachyrium sanguineum*, and *Andropogon canaliculatus*. The Comoé river is bordered by gallery forest 50 to 200 m in width. Great variation in rainfall patterns within and between years, differences in vegetation height between the seasons and annual bush fires make the southern part of the Comoé National Park a strongly seasonal habitat with unpredictable and sometimes rapidly changing conditions.

Natural predators of the kob, as e. g. leopard (*Panthera pardus*), hyena (*Crocuta crocuta*), and lion (*Panthera leo*) occur in the study area, with the latter being very rare. No signs of caracal (*Felis caracal*), side-striped jackal (*Canis adustus*) or wild dog (*Lycaon pictus*) could be found, although the Comoé National Park is in the range of their distribution area (Haltenorth and Diller 1977; Kingdon 1997). The presence of serval (*Felis serval*) is doubtful. There is heavy poaching on kob antelopes with severe impact on the population (Fischer 1996).

Seasons

Most of the rains (89.7% ± 2.3%) in all years of the study period fell between April and November. The duration and intensity of the dry and rainy seasons in the study area show a high variability between years. Rain may fall in all months during the dry season, may be very rare during certain months of the rainy season, and is highly variable in temporal as well as spatial distribution and quantity. The rainy season is interrupted by a short dry period in July.

Since ecological conditions changed considerably within the wet season, we did not only discriminate between the rainy and the dry season, but further divided the wettest months in two periods, called the beginning rainy season and the height of the rainy season. In order to faciliate data comparison between periods, we distinguished between three seasons of equal length. Even though only little rain fell in November, it was considered a wet month, since water was found in almost every pond in the savanna and the soil was moist. Table 1 shows the definitions for the three seasons.

Table 1. Definition and description of seasons for the southern Comoé National Park applied during the kob study. I = dry season; II = beginning rainy season; III = height of the rainy season; Tse-Tse density refers to the abundance of blood suckling flies of the genus *Glossina*.

season	period (months)	rainfall	grass height	grass age	water is available	Tse-Tse density
I	Dec–Mar	low	low	young	river only	low
II	Apr–Jul	high	intermediate	intermediate	river and savannah	intermediate
III	Aug–Nov	high	high	old	river and savannah	high

Animal observations and data sampling

Animals were observed and counted from a four-wheel-drive car on a 6.3 km long and 200 m wide road strip. Kob densities were calculated using King's road strip method (Mühlenberg 1993).

Social groupings were defined following Underwood's (1982) definition of ungulate groups. All animals closer than 50 m to their nearest neighbour moving in the same direction or synchronizing their behaviour otherwise were assumed to belong to one group. In all tests group sizes include all animals of such aggregations. Only groups with a majority of adult females were used in this study. These groups were then counted in total, including all members. Animals were identified and counted using binoculars (10×40 Zeiss). Occurrence of mating behaviour, group size and composition, as well as location in the area (category of vegetation density) were noted on a prepared form. Horn shape and dimension in males and body size in females were used to determine the animals' age, with the following classes being distinguished: adult females, adult males, subadult males, juvenile females, juvenile males and calves. Groups were also scanned for known individuals (13 adult males, 9 adult females, 2 subadult males) which could be recognised either by natural (ear notches, horn shape, colour) or artificial markings (ear tags, radio collars). Ear tags and radio collars were attached to animals captured in 1994, 1995, and 1996. Night counts were carried out using two 100 Watt headlights held up by two assistants from either side of the car to spot the animals by light reflection of their eyes. Observation distances ranged from less than 20 m up to 200 m (mean: 60 m).

To estimate vegetation density, the number of trees with a height of at least one meter was measured at 30 sites using the Point-Centred-Quarter-Method (Müller-Dombois and Ellenberg 1974). This led to the distinction of three different categories of vegetation density (open: < 0.5 tree/100 m^2; semi-dense: 0.5–5 trees/100 m^2; dense: > 5 trees/100 m^2).

Day/night comparisons were made between successive day/night periods, so that for each day sampled, only data from the following night were used in the analysis. Data collection at night took place in periods comprising one clear new or full moon night and the two preceding and following nights.

At night and during the day prostrate kobs got up within one or two minutes after a car stopped in their vicinity to look at the intruder. Counts in dense vegetation were performed at the beginning rainy season only, when grass height is not sufficient to conceal a standing kob. We therefore assume that only a negligible number of kobs have been overlooked.

Rainfall was measured to the nearest mm after every rain event and grass height to the nearest cm once per month at one site in the savannah. Mean rainfall and mean grass height per month were calculated from data collected in each month between March 1993 and Dezember 1998.

Statistics

All statistical tests are two-tailed and were performed with SPSS for Windows or calculated by hand. Medians are given with their 95% confidence limits. Kolmogoroff-Smirnoff-Test was used to compare different group sizes (Sachs 1984). Wilcoxon-Matched-Pairs-Test was used in the comparison of night and day data, to test if individually known females changed their preference for group size within 12 hours. Spearman-rank-correlation was performed to test if median group size was correlated with grass height or rainfall. Chi^2 test was used to test if distribution of reproductive behaviour in certain months differed from an equal distribution.

Results

Rainfall and Vegetation

Grass growth is triggered by annual burning of most of the savannah and is accelerated at the onset of the rainy season. Figure 2 shows the mean monthly rainfall and the mean grass height for 1993–1998. Total rainfall was 1032 mm in 1993, 856 mm in 1994, 1071 mm in 1995, 1124 mm in 1996, 1022 in 1997, and 1248 in 1998. During the five years of the study the following patterns of rainfall, water, and food availability were found: In January the dry season in the study area was at its peak. Water was still available in the Comoé River, but no free water occurred in the savannah. Up to 100% of the grass plains had usually been burnt by then and food was scarce since grass started to grow only slowly after the burns. Only in 1994 and 1998 rain did fall in January with 2 mm and 74 mm respectively. In February young grass still grew slowly, but with the beginning of the rains in March grass growth accelerated. Grass grew rapidly from March till May on all burnt plots. After the rains of February and March small ponds in the savannah were formed, usually only for a couple of days or even hours. Heavier rains in April filled ponds and pools in the savannah, and small streams began to run. Dependence of kob on drinking opportunities at the Comoé River lasted usually until April. Rains through October promoted grass growth until November. In December rain fell only in 1995 (10 mm) and 1998 (18 mm), and poachers started to burn the plains where grass was already dry.

Population density

The population of kob antelope in the study area has declined by about 80% since 1978 and during the study period from 8.6 ± 0.53 to 6.1 ± 0.7 animals per km^2 (GTZ/FGU 1979; Fischer 1998). This decline is presumably due to intensive poaching in the area (Fischer 1996).

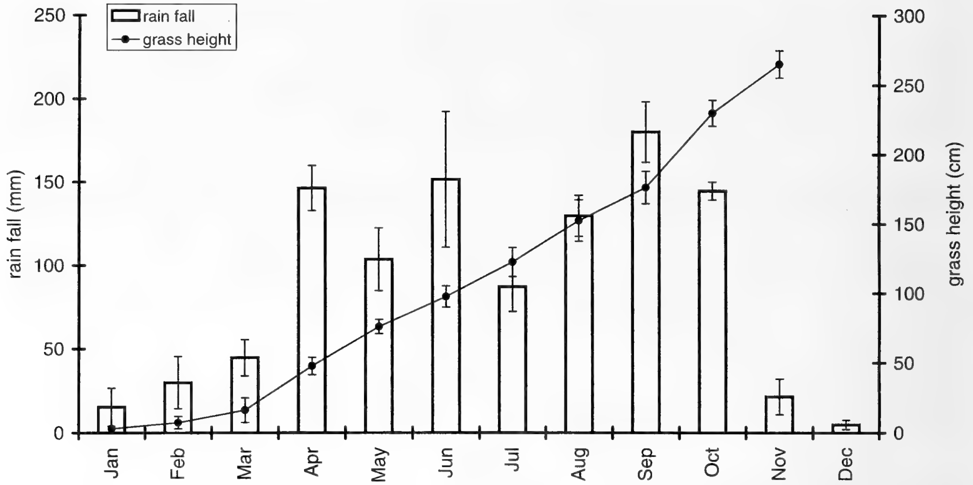

Fig. 2. Mean monthly rainfall and mean grass height in the study area in the southern Comoé National Park during the study period. Vertical bars indicate standard errors.

Reproductive behaviour

Mating and calving was observed throughout the year. Compared to the annual mean an increase of mating behaviour was observed in February (Chi^2 $6.2487 > 3.8415$, $p < 0.05$) and March (Chi^2 $6.8514 > 3.8415$, $p < 0.05$). Fewer matings took place in June (Chi^2 $4{,}9307 > 3.8415$, $p < 0.05$). In all other months mating behaviour showed no deviation from the annual mean.

Annual cycle of group size

Females were found alone or in mixed groups of up to 72 animals. Median size of such groups encountered during daytime changed in the course of the year, leading to a rather regular annual cycle which is shown in figure 3 in relation to grass height. Combining the data of all study years, the following pattern was revealed: female kob aggregated in groups with a median of four animals in January and February. The size of the average female group rose in March to a median of five and peaked in April and May resulting in groups of about six animals. After this peak the number of animals per group declined constantly to a median of five in June, four in July and August, three in September and two in October. Lowest numbers occurred in November with the median of one animal per group. We did not collect data for group size in December.

Median group size was largest at the beginning of the rainy season in April and May when grass on fresh burns grew rapidly to medium heights. The smallest groups were found at the end of the rainy season in November when grass was dry and of maximum height resulting in reduced visibility. It was neither correlated to grass height (Spearman-rank-correlation: $n = 30$, $p = 0.176$, $r^2 = -0.254$) nor to rainfall (Spearman-rank-correlation: $n = 30$, $p = 0.528$, $r^2 = 0.120$). Kolmogoroff-Smirnoff-Test showed that median group size differed significantly between the beginning (April–July) and the end (August–November) of the rainy season (Tab. 2). Since median group size was lowest when visibility was scarce due to grass height, we investigated whether reduced visibility in general leads to a reduction in group size. We collected data on size of female groups with relation to grass height, vegetation density, time of day, and light intensity during nights. Medians with their 95% confidence intervals are shown in figure 4 for all comparisons.

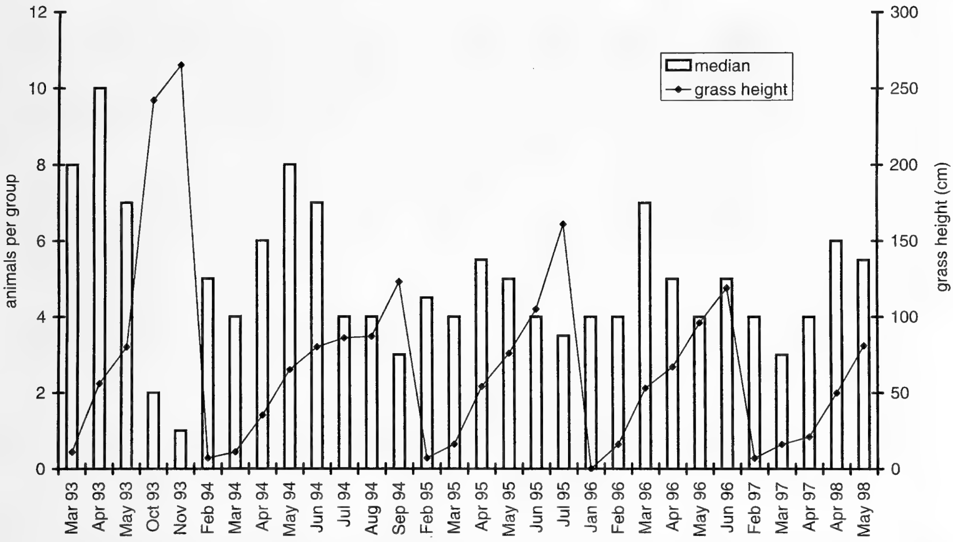

Fig. 3. Annual cycle of median group size of *Kobus kob kob* and grass height for the 30 months sampled in the southern Comoé National Park.

Table 2. Factors influencing group size of *Kobus kob kob* in the southern Comoé National Park including results of Kolmogoroff-Smirnoff-Tests

factors compared	D alpha	D^	significance	group size larger at
season II versus season III	0.088	0.324	+	season II
day versus night	0.122	0.297	+	day
full moon versus new moon nights	0.023	0.327	+	full moon
full moon versus new moon days	0.167	0.103	–	no difference
dense versus semi dense	0.135	0.042	–	no difference
dense versus open	0.123	0.133	+	open
semi dense versus open	0.095	0.139	+	open

Variation between successive day and night periods

It was tested whether size of female groups varied between successive day and night periods. Included in this analysis are all nights independently of the phase of the moon. In 68 cases in which known individuals were observed twice during 12 hours it could be shown that group size had changed within this time span in 88.2% of all cases, and was significantly smaller during nights (Wilcoxon Matched-Pairs Signed-Rank Test, $Z = -0.3267$, $p < 0.05$). In some cases it was also observed that known females encountered at daytime joined another group at night. This sometimes led to a group of equal size but different composition at night than during day. If these changes are taken into consideration as well, group size and/or group composition changed in more than 90% of all observed cases within 12 hours. Hence day and night counts of groups and group size were

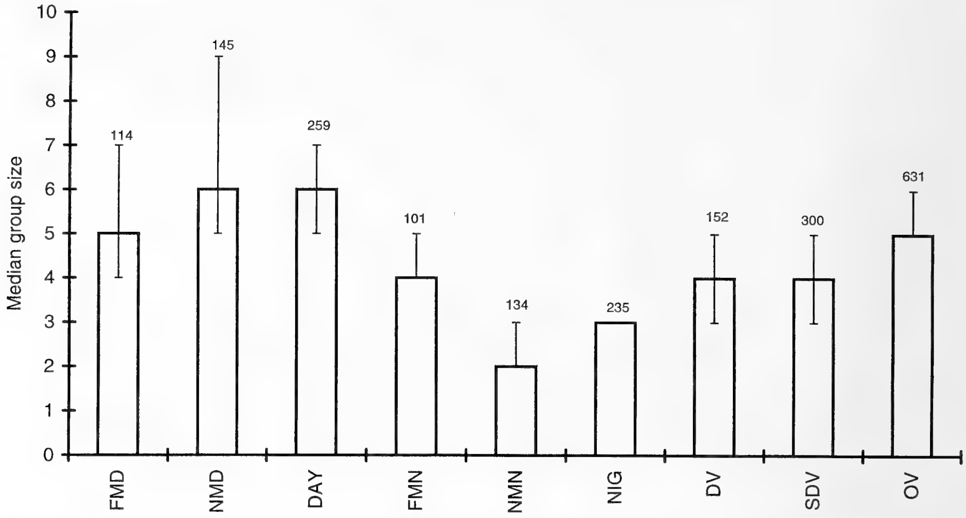

Fig. 4. Median group size of *Kobus kob kob* in the southern Comoé National Park according to various outer parameters related to visibility. Vertical bars indicate 95% confidence limits. Figures above bars give the number of groups included in the analysis. FMD = full moon day; NMD = new moon day; DAY = daytime (6:00 a. m. – 6:00 p. m.); FMN = full moon night; NMN = new moon night; NIG = nighttime (6:00 p. m. – 6:00 a. m.); DV = dense vegetation; SDV = semi dense vegetation; OV = open vegetation.

assumed to be independent of each other, although some members of groups might still have been the same individuals. Kolmogoroff-Smirnoff-Test revealed that groups that contained only unknown females were significantly larger during days compared to nights (n = 494).

Variation between new moon and full moon nights

To test if other factors might have caused group size changes between full moon and new moon periods, group size data collected during nights were compared between full and new moon phases.

Group size was significanfly larger during full moon nights compared to new moon nights. However, no significant differences could be found between full moon and new moon days (Tab. 2, and Fig. 4).

Vegetation density

Of the 1.080 groups observed, 58.1% were found in open vegetation, 27.8% in semi-dense, and 14.1% in dense vegetation.

Kolmogoroff-Smirnoff-Test revealed significant differences in group size between semi-dense and open vegetation as well as between dense and open vegetation. No significant difference between group sizes in dense and semi-dense vegetation could be found.

Discussion

Seasonal changes in African ungulate groups, as we observed, have been detected by RODGERS (1977) and UNDERWOOD (1982). UNDERWOOD (1982) was able to correlate increasing group sizes with rainfall and breeding cycles in different ungulate species. Rodgers (1977) emphasised the effects of social and reproductive behaviour on group size and held territorial behaviour in male impala (*Aepyceros melampus*) and herding activity in male wildebeest (*Connochaetes taurinus*) responsible for increases in group size during the rut. McNaughton (1984) showed that ungulates sometimes establish grazing lawns where grass remains short and biomass high for long periods, thus improving foraging conditions compared to surrounding savannah areas and leading to an increase in group size. Duncan and Vigne (1979) found that group size of horses increased in the presence of large amounts of blood-sucking flies. Do the above results explain our findings in kob antelope?

Group size changes in our study were not correlated to rainfall, and no clear rutting season of kobs exists here. Due to the low population density in our study area, ungulates were not able to establish grazing lawns. However, the beginning of grass growth in February which resulted in small patches of young grass on fresh burns led to aggregations of kob on such sites at the beginning rainy season, which might have added to an increase in group size during that time. Additionally larger groups in February and smaller ones in June might partially be explained by reproductive behaviour (observed more often in February and less in June).

Nevertheless, such behaviour cannot explain the changes of group size in other months. The abundance of tsetse flies (*Glossina* spec.) shows a high variance between seasons in our study area. The tsetse population collapses as soon as the grassland in the area is burnt in December and January, then begins to rise again with the first rains, leading to constantly increasing numbers of tsetse flies from March onwards. Highest numbers can be found between July and November, which following Duncan and Vigne (1979) should lead to an increase in ungulate group size during that time. Instead median group size in the studied kob population decreased from June onwards and was smallest in November.

Since kobs have to drink daily and water availability in the area changes between seasons, it would be conceivable that groups are largest when water is scarce and kobs gather at the rare drinking sites. Since all drinking sites during the dry season are located in the riverbed of the Comoé and can only be reached by traversing the gallery forest, the preferred habitat of leopard and hyena, larger groups during that time may also form in order to reduce vulnerability to those predators. Nevertheless, no correlation between rainfall and hence water availability and group size was found and median group size was smallest at the end of the year when water was only available in the Comoé river.

While increase in group size between February and March might partially be explained by feeding conditions and reproductive behaviour, our findings excluded food and water availability, reproductive behaviour and attacks of blood sucking flies as single explanations for decreasing group size later on. We therefore believe that the hypothesis best fitting our results is, that decreasing visibility due to the higher grass was the reason for smaller median group sizes from June to November.

Provided our assumption is correct, kobs should reduce group size not only in dependence of grass height, but also under other conditions where visibility is otherwise low. According to the hypothesis, groups would be expected to be significantly smaller in dense vegetation, at night and here especially in dark nights (new moon nights). These expectations proved to be correct. However, no difference in size could be found when groups in dense and semi-dense vegetation were compared. Apparently kobs do not distinguish between these two vegetation density categories.

Similar influences of vegetation density on group size was shown by Leuthold (1970) for impala, by Deutsch and Weeks (1992) for Uganda kob, and by Evans (1979) for kudu (*Tragelaphus strepsiceros*). Clarke et al. (1995) demonstrated that eastern grey kangaroos (*Macropus giganteus*) reduced their group size during nights.

Aggregation is generally considered to serve as a protective mechanism against predators hunting by sight (Hamilton 1971; Bertram 1978). If groups are to be attacked, the single individual might decrease the probability to fall victim to the predator due to effects of dilution, position and confusion (Vine 1971; Pulliam 1973; Treisman 1975; Dehn 1990). Under certain circumstances, such as wide and open areas, larger groups might detect an approaching predator earlier or might even be avoided by the predator as Fitz-Gibbon (1990) showed for Thomson's (*Gazella thomsoni*) and Grant's gazelles (*Gazella granti*) hunted by cheetah (*Acinonyx jubatus*). Whereas advantages of dilution and confusion effects increase with larger group size, probability of early predator detection increases with better visibility. Deutsch and Weeks (1992) showed for example that lion hunting success on kob increased with grass height and thicket density. Certain disadvantages are correlated with staying in larger groups when visibility is low. Such groups provide stronger auditory and olfactory signals, are more conspicuous and can therefore be more easily detected by predators like leopards which use those signals to find their prey (Treisman 1975). Additionally, in cases of low visibility prey might depend on acoustic perception of the predator which might be more difficult when groups are larger and thus noisier. There should be a trade-off between advantages and disadvantages of grouping depending on visibility factors. Group size should increase: in open vegetation, in lower grass, during daytime and during full moon nights. Since all statistical tests led to significant results clearly corroborating these predictions, it is assumed that visibility is a factor strongly influencing group size. The preference of kob antelope for high visibility locations was also shown by Deutsch and Weeks (1992), who proved that kob antelopes preferred high visibility leks and territories. The variation of group size in response to visibility factors is thus evaluated as an evolutionary adaptation to the presence of predators. Although lions are rare and wilddogs are extinct in the Comoé, there remain leopard, hyena and human hunters in high abundance. The most effective and dangerous predator of kob antelopes in the study area is man, who hunts during days and more recently during nights as well. Initial results of Gross (pers comm.), tracking five radio collared leopards in the study area showed that these animals have a reversed short-term habitat preference compared to kob antelopes All leopards used open areas of their home-range at new moon nights which they avoided during full moon nights. Leopards also changed their activity pattern in response to season. They were nocturnal at the beginning of the year and switched to be active during days as soon as grass grew higher from June/July onwards.

Because of the low kob population density in the study area, some of the disadvantages of living in groups like increased competition for food resources do not fall into account. This holds especially true because population density dropped about 30% within the last three years without showing any influence on the kobs' grouping behaviour (Fischer 1996).

We conclude that group size is strongly influenced by visibility factors resulting in larger groups when visibility is good. Seasonal changes of group size in kob antelope might well be additionally influenced by other factors related to food availability or reproduction. Fresh grass supply is probably the most important reason for increasing group size at the beginning rainy season. The open herd structure of kob antelopes facilitates seasonal as well as short term changes in group size (Rodgers 1977; Evans 1979). As the cause for these predictable changes in group size, predator avoidance is discussed. The advantages of staying in a large group of conspecifics might be reversed in cases of low visibility due to the hunting pattern of predators who depend at least partially on acoustic perception under these conditions. In the kobs studied here, anti-predator behaviour against hyena, leopard or lion attacks as well as human hunting pressure might have been the reason for grouping and group size changes. Due to heavy poaching on kob antelopes in the Comoé National Park, man is the most dangerous and effective predator of kobs, and has already influenced their behaviour (Fischer and Linsenmair 1999).

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Zusammenfassung

Veränderungen der Gruppengröße von Kobus kob kob (Bovidae) im Comoé Nationalpark, Elfenbeinküste (Westafrika)

Im Rahmen einer 30 monatigen Studie im Comoé Nationalpark, Elfenbeinküste, wurde der Einfluß verschiedener äußerer Faktoren auf die Größe von Gruppen weiblicher Kobantilopen untersucht. Die Größe solcher Gruppen schwankte sowohl zwischen als auch innnerhalb von Jahreszeiten. Sie war am kleinsten zur Hochregenzeit und am größten zu Beginn der Regenzeit. Während Kobantilopen am Anfang der Regenzeit, im Zuge der Fortpflanzung und bei einem verbesserten Nahrungsangebot, größere Gruppen bildeten, stand die Abnahme in der Hochregenzeit vermutlich mit den schlechteren Sichtverhältnissen, hervorgerufen durch hohes Gras, in Zusammenhang. Innerhalb kürzerer Zeiträume hatten Faktoren wie Vegetationsdichte, Tageszeit (Tag/Nacht) und die Mondphase (Vollmond/Neumond) einen Effekt auf die Gruppengröße, wobei schlechtere Sichtverhältnisse zu einer Verringerung der Gruppengröße führten. Wir vermuten, daß bei den Veränderungen der Gruppengröße zwischen Jahreszeiten zusätzlich zu den Sichtverhältnissen die Nahrungsverfügbarkeit und das Fortpflanzungsverhalten eine Rolle spielen, während kurzfristige Schwankungen der Gruppengröße von Kobantilopen (innerhalb von 1–24 Stunden) ausschließlich von den Sichtverhältnissen beeinflußt werden. Den Grund für denWechsel der Gruppengröße in Abhängigkeit von den Sichtverhältnissen sehen wir im Zusammenhang mit derVermeidung von Angriffen großer Beutegreifer.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

A northern and threatened population of *Irenomys tarsalis* (Mammalia: Rodentia) from central Chile

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Key words: *Irenomys tarsalis*, Chile, Maulino forest, fragmentation

Irenomys tarsalis (Philippi, 1900), the Chilean tree mouse or "laucha arbórea", is the single species of a sigmodontine genus endemic to the temperate forests of southern Chile and Argentina (Redford and Eisenberg 1992). The geographic distribution of this rare rodent is poorly known. Along the mountain range of Chile, *I. tarsalis* is known to occur from Chillán (36°54′ S, 71°25′ W) to Puerto Ibáñez (46°04′ S, 72°02′ W). Along the coastal range, *I. tarsalis* reportedly extends from Nahuelbuta (37°58′ S) down to Chiloé (42 °S) and Guaitecas Islands (46 °S; Reise and Venegas 1974, 1987; Pine et al. 1979). The distribution along the Chilean coastal range, however, is very poorly known, and northern limits are regarded as tentative (Kelt 1993). Here we report on a population of *I. tarsalis* 210 km north of its currently known limit, associated to remnants of the endangered temperate Maulino forest, along the coastal range of central Chile (Fig. 1).

Ongoing monitoring of small mammals at a large remnant (approximately 600 ha) of temperate forest, at which National Reserve Los Queules (35°59′ S–72°41′ W, 540–

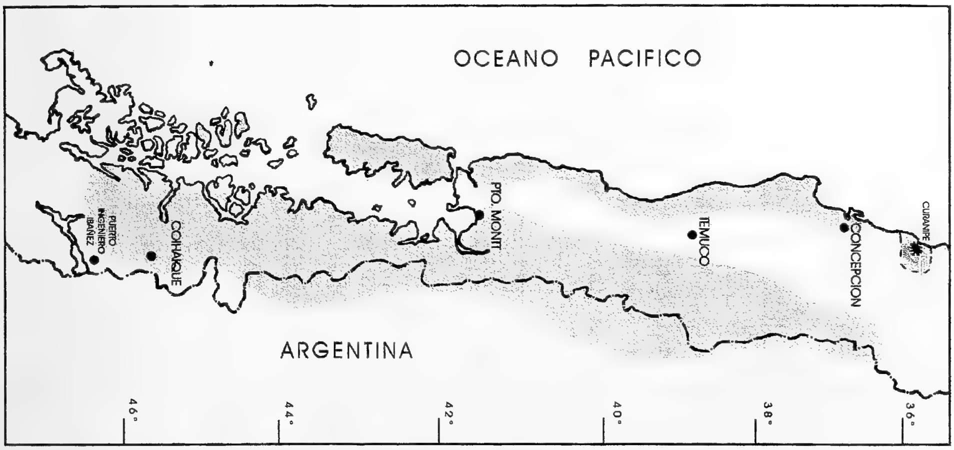

Fig. 1. New distribution of *Irenomys tarsalis* with the present record (asterisk) in the coastal range, extending northern limit approximately 210 km. The southern limit remains unknown (modified from Kelt 1993).

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570 masl) is located, and neighboring forest fragments (Fragment 1: 35°58′ S–72°42′ W, 3 ha, 348 masl and Fragment 3: 35°59′ S–72°41′W, 6 ha, 570 masl) surrounded by pine plantations (*Pinus radiata*), have revealed a small population of *I. tarsalis* at both the Reserve as well as a forest fragment. This is a typical Maulino forest, with *Nothofagus glauca, Aetoxicum punctatum, Cryptocarya alba, Gevuina avellana*, and *Persea lingue* as the dominant tree species (SAN MARTÍN and DONOSO 1995).

Sampling consists of bimonthly live-trapping sessions for at least five trapping nights each time. Since January 1999, at Los Queules National Reserve we operated two grids of 10×5 (3,600 m^2) medium-sized Shermann traps, each trap located 10 m apart. At Fragment 1, we operated a 10×5 (3,600 m^2) grid, half of which is set inside the native forest, while the other half lies into the *P. radiata* plantation. At Fragment 3, we operated a 6×5 (2,000 m^2) trap grid inside the fragment. Additionally, we ran a 10×5 (3,600 m^2) grid in the adjacent *P. radiata* plantation. Traps were baited with rolled oats and checked daily at dawn, as all small mammals are nocturnal.

To date, we have captured, marked and released five adult individuals of *I. tarsalis.* Recaptures have been low, as only three of them were recaptured just once. Four individuals (two males and two females) were captured in Los Queules National Reserve, while one female was found in Fragment 3. No specimen has been captured or recaptured in Fragment 1 or in the *P. radiata* plantation. Captures took place in January, April, and June. Body measurements are: body length 8.9–11 cm, tail length 14.6–15 cm, and hind foot 2.8 cm. All individuals escaped by climbing trees after they were released, corroborating the arboreal habits of the species (PEARSON 1983). Besides *Irenomys*, we also found three other murid species (*Abrothrix longipilis* (Waterhouse, 1837), *A. olivaceus* (Waterhouse, 1837), *Oligoryzomys longicaudatus* (Bennett, 1832), one caviomorph (*Octodon bridgesi* Waterhouse, 1845), and one marsupial (*Thylamys elegans* Waterhouse, 1839). We also captured the introduced black rat, *Rattus rattus* (Linnaeus, 1758) in all forest remnants and pine plantations surveyed (SIMONETTI 1983).

Irenomys tarsalis is regarded as a rare or uncommon species (GREER 1966; PATTERSON et al. 1989, 1990; MESERVE et al. 1991). Its rarity is depicted by the fact that *I. tarsalis* represents only three out of nearly 1,700 capture records from 63 localities in Chile and neighboring Argentina (REISE and VENEGAS 1987). In fact, our trapping success is only 0.16% (out of 4.907 trap/nights), compared to 3.3% of *Abrothrix longipilis*, 2.4% of *A. olivaceus*, and 2.2% of *Oligoryzomys longicaudatus.*

We also found remains of *I. tarsalis* among scats of *Pseudalopex griseus* (Gray, 1837). This fox inhabits the Reserve and uses service roads along the *P. radiata* plantations (ACOSTA and SIMONETTI 1999; MUÑOZ and MURÚA 1990). One out of 22 feces (4.5%) collected in September 1998 and January 1999, contained molars depicting “partial transverse lamination”, clearly attributable to *I. tarsalis* (HERSHKOVITZ 1962). The remains belonged to a single adult individual, found among remains of 25 other rodent specimens of four different taxa, including *Abrothrix* sp., *Phyllotis* sp., and *Octodon bridgesi.*

The presence of *I. tarsalis* over 200 km north of the northern known limits supports the contention that this elusive rodent may have ranged into central Chile, but deforestation could have excluded it except from forest remnants (KELT 1993). Coastal forests of central-south Chile remained less affected by Pleistocene glaciation processes (ARMESTO et al. 1995), probably acting as refuges for *I. tarsalis.* The northernmost population that we discovered, becomes then extremely valuable to test phylgeographic hypotheses and to reconstruct the biogeographic history of small mammalian fauna during the Pleistocene and Holocene in south-central Chile (e. g., MESERVE and KELT 1990). Unfortunately, this northern *I. tarsalis* population might vanish from their northern grounds at the same pace native forests are being eliminated or replaced, due to the scarce representation of Maulino forests in Chilean’s Protected Areas System (SIMONETTI and ARMESTO 1991).

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Spring food preferences of rabbits (*Oryctolagus cuniculus* L., 1758) on the Islet of Alegranza (Canarian Archipelago)

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Rabbits have frequently been introduced into several oceanic islands throughout the world (Monnerot et al. 1994; Callou et al. 1996) and currently it is one of the most widely distributed animal species. They were brought to the Canary Islands during the conquest of the archipelago in the 15th century AD (De Abreu Galindo 1977) and today they are present on all the main islands and islets of the archipelago. This lagomorph species has shown a high capacity of adaptation to insular environments (Cheylan 1984), causing serious conservation problems for the composition and structure of vegetation (Thompson 1994). Despite its wide distribution the diet has been poorly studied on islands, and for the Canarian Archipelago only one specific contribution on this subject matter has been published (Martín and Marrero 1999). However, Nogales et al. (1995) gave some information on the frugivorous role performed by this species in some xeric habitats from the Island of Tenerife.

Two main objectives are pursued in this study: 1) to investigate the spring diet of rabbits and the between-year variation pattern, and 2) to determine whether they show diet selection on an islet of minor dimension and of low plant diversity.

Alegranza is the most northern Islet of the Canarian Archipelago, 17 km from the Island of Lanzarote. It has a surface of 11.7 km^2, a maximum altitude of 289 m a. s. l. and the climate can be characterized as semi-arid (annual precipitation lower than 250 mm and average annual temperature of about 20 °C). It has a xeric, sparse and low vegetation, some of the most common species being, *Chenoleoides tomentosa*, *Salsola vermiculata*, *Salsola divaricata*, *Salsola tetrandra*, *Suaeda vera*, *Euphorbia regis-jubae*, *Lycium intricatum*, *Launaea arborescens*, *Aizoon canariense*, among others.

The present study was carried out in three different areas during April 1996 and 1997. One area was located inside La Caldera volcano while the other two were in Llano del Cortijo (hereafter Llano I and Llano II). Every study area had a size of 4 063 m^2 in which both vegetational coverage and biovolume were measured to estimate plant availability. We collected 280 fresh faeces per areas/spring at random from different latrines. The faeces samples were frozen until they were analysed by use of a microhistological method, based on the plant epidermal resistance to chewing and herbivore digestion (Chapuis 1979). This analysis has been widely used to determine the diet of herbivores (Martínez 1988; Quintana et al. 1994) and although its efficacy has sometimes been discussed (Klein and Bay 1995), Rosati and Bucher (1992) suggested that the impact on the estimated botanical composition will rarely cause significant alterations in diet estimates. A faeces sample (2 g) was homogenized and two drops of this mixture were taken and observed with an optic microscope at 100 to 400 magnification. This process was repeated several times for each study

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area with the aim of obtaining a representative sample of the rabbits' diet. Five fields on each slide were examined for a total of 100 slides per study area, including a total of 3 000 examined fields. Epidermal tissues were identified by comparison with a reference collection of both right and back side of leaves and stems of the vegetation of the islet. Data taken from readings of optic fields ($N = 3\,000$) are expressed as a percentage of frequency of occurrence of each plant species. We used Chi-square and G tests to analyse the variation in rabbits' diet and plant availability in the three study areas and during both springs.

More than twenty plant species were identified in the *Oryctolagus cuniculus* faeces (Tab. 1), representing over 18 % of the total species present on the Alegranza Islet. The clearly dominant species were *Salsola vermiculata* in La Caldera (> 73 %) and *Chenoleoides tomentosa* in Llano I (> 73 %) and Llano II (> 88 %) during both collection years. In general, a similar between-year pattern consumption of plant species can be observed. Other plants found at high frequency were, in La Caldera, *Aizoon canariense* and *Mesembryanthemum nodiflorum*, and in Llano I and II, *Heliotropium ramosissimum*, *Aizoon canariense*, and some *Poaceae* species. The consumption of plant species was significantly different in the three study areas ($p < 0.05$), except for *Mercurialis annua* ($G = 2.29$; d. f. = 2; $p = 0.31$) and *Nicotiana glauca* ($\chi2 = 1.34$; d. f. = 2; $p = 0.50$) in 1996, and for *Nicotiana glauca* ($G = 4.03$; d. f. = 2; $p = 0.13$), *Salsola divaricata* ($G = 2.92$; d. f. = 2; $p = 0.23$), and *Spergularia fallax* ($G = 1.81$; d. f. = 2; $p = 0.40$) in 1997, whose frequency of occurrence did not vary significantly between the three areas.

Comparing diet vs. availability (Fig. 1), it can be observed that no direct relationship exists between plant species abundance and their consumption from all study areas ($p < 0.001$). Therefore, rabbits clearly selected plants for consumption, and abundant species such as *Euphorbia regis-jubae*, *Lycium intricatum*, *Nicotiana glauca*, and *Suaeda vera* showing low consumption levels.

Table 1. Plant species composition identified in rabbit faecal pellets from Alegranza Islet (Canaries). Values are expressed in % of frequency of occurrence (presence/absence).

Species	La Caldera		Llano I		Llano II	
	1996	1997	1996	1997	1996	1997
Aizoon canariense	8.4	4.8	20.6	23.0	8.4	27.6
Ajuga iva	–	0.6	–	–	–	–
Anagallis arvensis	–	–	1.4	–	1.2	–
Chenoleoides tomentosa	–	–	73.6	76.0	94.0	88.8
Echium lancerottense	–	–	0.2	0.2	–	–
Eurphorbia regis-jubae	1.2	0.2	–	–	–	0.4
Heliotropium ramosissimum	–	1.2	32.0	19.6	5.4	27.6
Ifloga spicata	–	–	–	4.4	–	1.8
Launaea aborescens	–	–	1.8	–	1.6	–
Lycium intricatum	–	1.0	–	–	–	–
Mercurialis annua	0.6	0.2	0.4	–	1.2	–
Mesembryanthemum nodiflorum	0.2	17.8	–	–	–	–
Mesembryanthemum sp.	–	–	0.2	–	–	–
Nicotiana glauca	0.8	0.8	1.6	1.2	1.2	0.2
Patellifolia patellaris	–	1.2	0.4	3.2	–	0.4
Policarpaea nivea	–	–	8.0	–	2.0	–
Salsola divaricata	–	0.2	–	0.6	–	1.0
Salsola vermiculata	83.8	77.8	–	–	–	–
Spergularia fallax	2.6	0.6	1.0	1.4	3.6	0.8
Suaeda vera	–	–	2.6	–	1.6	–
Gramineae	5.8	2.0	2.6	20.2	5.8	15.4
Indeterminate	6.6	5.2	9.8	14.0	3.8	9.0

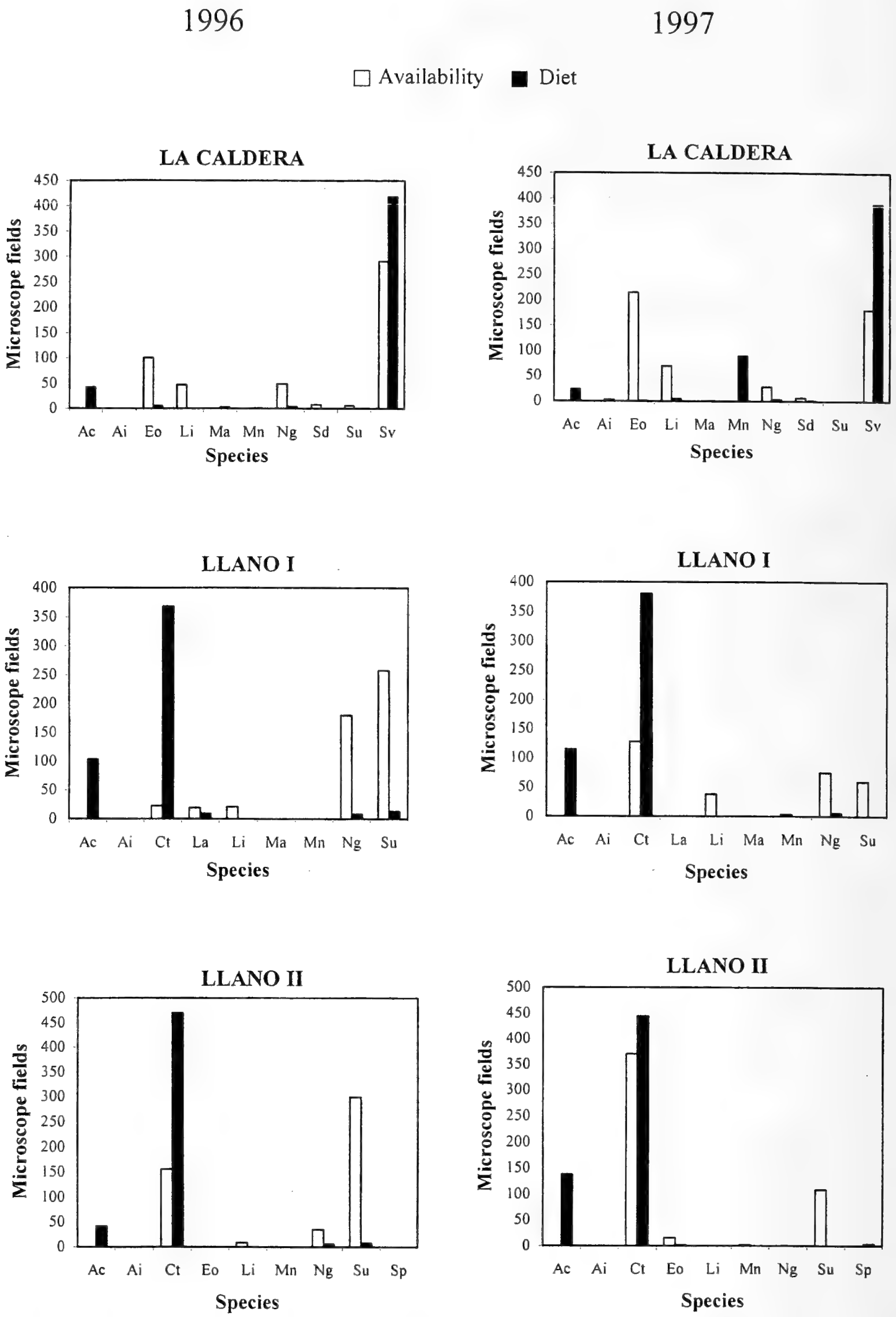

Fig. 1. Comparison between plant availability and diet in the spring of 1996 and 1997 on the Alegranza Islet (Canaries). Data from plant availability were transformed to the same units of optic fields with the aim of relating them to the diet. Ac: *Aizoon canariense*, Ai: *Ajuga iva*, Ct: *Chenoleoides tomentosa*, Eo: *Euphorbia regis-jubae*, La: *Launaea arborescens*, Li: *Lycium intricatum*, Ma: *Mercurialis annua*, Mn: *Mesembryanthemum nodiflorum*, Ng: *Nicotiana glauca*, Sd: *Salsola divaricata*, Sp: *Spergularia fallax*, Su: *Suaeda vera*, Sv: *Salsola vermiculata.* Only the species present in the study areas were included.

Alegranza has an impoverished vegetation because of the continued use of land for agriculture and livestock until 1968, when the island was declared uninhabited (A. Pallarés pers. comm.). Despite this low flora diversity, rabbits consumed at least twenty plant species during the springs of 1996 and 1997. The largest consumption belonged to species included in the Chenopodiaceae family, mainly *Salsola vermiculata* in La Caldera and *Chenoleoides tomentosa* in Llano I and Llano II. These two species do not share the same area, so the rabbits' preference for one of them cannot be estimated. It is interesting to note that Myers et al. (1994) recorded that rabbits avoid Chenopodiaceae species due to the fact that these plants contain a high concentration of salt in arid regions. However, Dawson and Ellis (1979) also reported that this lagomorph consumed these species after a drought period since they have high levels of protein. Furthermore, the low consumption level of some abundant plants in the environrnent, such as *Nicotiana glauca* or *Euphorbia regis-jubae*, may be explained by their content of toxins.

The fact that rabbits select their food could be attributable to the plant features, since other vertebrate herbivores do not compete for this resource on the islet. Despite the fact that rabbits clearly selected two plant species (*Chenoleoides tomentosa* and *Salsola vermiculata*), they consumed vegetables, whose frequency of occurrence varied considerably from one year to the other, e. g., gramineous, *Aizoon canariense*, *Heliotropium ramosissimum*, and *Mesembryanthemum nodiflorum*. Finally, although in general rabbits showed a similar between-year consumption pattern for the main plants in the springs of both years, their diet probably changes during the different seasons of the year according to the state of the vegetation, as indicated by several authors for other areas in the world (Bhadresa 1977; Soriguer 1988; Duffy et al. 1996).

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Comparative investigations on the efficiency of a new live trap for small mammals

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A new type of multiple-capture live trap, the Fribourg trap, was designed to be used in combination with drift fences (Zukal and Gaisler 1992; Kirkland and Sheppard 1994) to capture juvenile fossorial vole *Avricola terrestris* above-ground. Previously, Saucy and Schneiter (1997) have shown that young animals, usually less than two months old and lighter than 65 g, disperse en masse above-ground during rainy nights. The aim of our work was to develop an effective, robust and inexpensive trap to live-trap these dispersers. In this study, we evaluate the efficiency of the Fribourg trap by comparing it to the Sherman trap, model LNA. The Fribourg trap (Fig. 1) is a two-entry trap (9×6×50 cm), made of opaque plastic sheath tubing (Tehalit GmbH, Germany; NFC68–102 667). Both its sides are equipped with slanted doors made of wire netting bent at the base (Fig. 1). This mechanism was designed by Dr. H. Niemeyer and R. Fus (Niedersächsische Forstliche Versuchsanstalt, Göttingen, Germany; Patent No P 19542089.6), and is currently commercialised by Grube KG (Hützel, Germany). Voles and mice will readily push and lift up the one-way, wire netting door, but are unable to perform the opposite movement once caught inside the trap. This mechanism can easily be implemented at the two ends of a trap, thus giving it the aspect of an open tunnel in which light can enter from both ends. The top of the trap is removable which facilitates handling of the animals. The solidity of the trap is enhanced using transversal, narrow plastic bars.

To test the efficiency of the new trap, a comparison with Sherman traps was conducted along the borders of two adjacent 0.5 ha trapping plots (50×100 m), set up in permanent grassland. Drift fences surrounded the two plots to improve above-ground trapping efficiency (Zukal and Gaisler 1992; Kirkland and Sheppard 1994). Trapping was carried out continuously from 28. 4. 98 until 30. 11. 98. Fifty trapping stations were regularly spaced at 6 m intervals along the inner side of each enclosure, thus alternating Fribourg traps (one per station) and Sherman traps (two per station, placed back to back, the entrances in opposite directions). Therefore, a total of 50 Fribourg traps was compared to 50 pairs of LNA Sherman traps, for a total trapping-effort of 32,550 trap nights.

Traps were fastened to the ground with bent iron pegs. No baits were used and traps were checked once a day in the morning. A mirror fixed to a pole was used to examine Fribourg traps. The trapped animals were released outside the plots after having been sexed and marked by fur clipping. Furthermore, *A. terrestris* were classified based on their body weight (Airoldi 1976) as juveniles (< 45 g), subadults (45–64 g) and adults (≥ 65 g).

A total of 1 057 captures was recorded above-ground during 217 consecutive nights, i. e. 4.9 captures/night. Among these 1 057 captures, there were 861 fossorial *Arvicola terrestris* (81.5%), 154 other small mammals (14.6%), 35 amphibians and 7 birds (Tab. 1).

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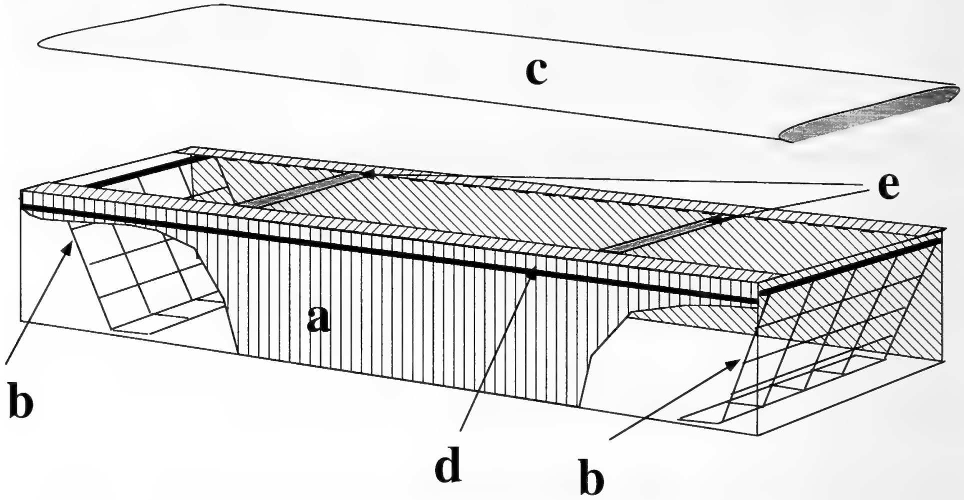

Fig. 1. Design of the Fribourg trap made of plastic electrical sheath tubing. a: body; b: trap-door, rotating around its top axis (Patent No P 19542089.6); c: lid; d: lateral grooves for insertion of the lid; e: tranversal strengthening pieces.

Table 1. Distribution of captures among the two kinds of trapping stations. Sherman: 2 traps per station, i. e. 2 × 50 = 100 traps; Fribourg: 1 trap per station, i. e. 50 traps.

Organisms	Total	Sherman	Fribourg	χ^2	P
Arvicola terrestris	861	335	526	42.4	<0.001
Other small mammals	154	138	16	96.6	<0.001
Amphibians	35	26	9	8.3	<0.05
Birds	7	6	1	–	–
Total	1 057	505	552	2.1	>0.05

Captures of other mammals included mostly *Apodemus sylvaticus* and *A. flavicollis* (N = 84), common and field voles *Microtus arvalis* and *M. agrestis* (N = 40), as well as occasional captures of *Clethrionomys glareolus* (N = 6), *Mus musculus* (N = 6), *Muscardinus avellanarius* (N = 1), *Sciurus vulgaris* (N = 1), *Crocidura russula* (N = 8), *Sorex araneus/coronatus* (N = 2) and stoats (*Mustela erminea* N = 6). Amphibians included the frogs *Rana temporaria* (N = 10) and *R. esculenta/lessonae* (N = 12) and the toads *Bufo bufo* (N = 7) and *B. calamita* (N = 6). Bird captures consisted of three yellow-hammers *(Emberiza citrinella)*, one robin *(Erithacus rubecula)*, two great tits (*Parus major*) and one wren (*Troglodytes troglodytes*).

The 1 057 captures were about equally distributed between Sherman and Fribourg trapping stations, with 505 and 552 captures, respectively ($\chi^2 = 2.1$, df = 1, $p > 0.05$). However, two thirds of fossorial *A. terrestris*, (N = 526, i. e. 61.1%) were caught in Fribourg trapping stations, indicating that single Fribourg traps were significantly more efficient for this species than pairs of Sherman traps ($\chi^2 = 42.4$, df = 1, $p < 0.001$; Tab. 1). Sex ratio ($\chi^2 = 0.9$, df = 1, $p > 0.05$) and weight distribution of *A. terrestris* were not different between the two kinds of trapping stations (mean weight for Sherman: 47.2 g ± 13.8 SD; and for Fribourg: 48.4 g ± 14.3 SD; t = 1.3, df = 826, $p > 0.05$). About 90% of all individuals captured were juveniles or subadults. Unlike *A. terrestris*, other small mammals and amphibians were significantly more abundant in Sherman than in Fribourg trapping stations ($\chi^2 = 96.6$, df = 1, $p < 0.001$ for small mammals and $\chi^2 = 8.3$, df = 1, $p < 0.05$ for amphibians; Tab. 1). Because of their small number, birds were not taken into consideration for further analysis.

The efficiency of the Fribourg trap as a multiple-capture trap was demonstrated by the fact that in 49 cases, two *A. terrestris* were simultaneously caught in the same trap for a total of 98 captures (18.6% of the 526 captures in Fribourg traps). By comparison, only in 19 cases both Sherman traps of a station were occupied ($\chi^2 = 8.2$, df = 1, $p < 0.01$), corresponding to 38 out of 335 captured animals (11.3%). The combinations of sexes in double captures were not significantly different between the two trap types ($\chi^2 = 2.3$, df = 2, $p > 0.05$). We observed a random distribution of the sexes, following the expected frequencies for a sex ratio 1:1 in the population i.e. about 25% female-female, 25% male-male and 50% male-female pairs. Similarly, the combinations of age groups did not differ between Sherman and Fribourg traps ($\chi^2 = 0.4$, df = 2, $p > 0.05$). Double captures consisted essentially of subadults and/or juveniles together. Concerning mortality, we found no difference between the two kinds of traps ($\chi^2 = 0.1$, df = 1, $p > 0.05$).

Among the very large number of traps designed to catch small mammals, there are few two-entry or multiple-capture live traps. Among the former, a wire, two-entry, single-capture trap for *A. terrestris* developed by Pelz (1995) is worth mentioning, while among the latter, the Fitch, Burt and Ugglan multiple-capture traps are commonly used in North America and Europe (Rose et al. 1977; Getz et al. 1993; Jensen et al. 1993). In contrast, the Fribourg trap combines both properties, having two entries and allowing multiple captures. This trap is cheap, easy to build and robust. It uses plastic material, which offers a better insulation than metal traps. In addition, unnecessary handling of empty traps can be avoided by using a mirror for checking. Furthermore, casual observation of the animals' behaviour suggests that the voles are less stressed in Fribourg traps.

Our results clearly indicate that the new mechanism is very selective and efficient for capturing fossorial *Arvicola terrestris*, a rodent whose adult body mass may exceed 100 g (Reichstein 1982). In our study, we mostly caught immature individuals in both kinds of traps. However, this does not indicate a size-selectivity of the traps because adult animals rarely wander above-ground (Saucy and Schneiter 1997).

Our comparison shows that each single Fribourg trap captures 1.6 times more *A. terrestris* than a Sherman trapping station. This difference can be partly attributed to multiple captures in Fribourg traps. In our opinion, two explanations are possible for multiple captures. Firstly, animals inside the trap may attract a second animal. However, no particular affinity between sexes was observed. This is not surprising, because most voles in the traps were sexually immature. Secondly, it is possible that animals following each other enter the same trap together. The mechanism tested in this study is quite silent and may therefore allow for such a behaviour to occur. The same is true for Fitch traps that were also shown to be superior to Sherman traps (Rose et al. 1977). Another explanation for the efficiency of Fribourg traps to catch *A. terrestris* could be their tunnel-like shape, which offers a potential exit to the animals. It is surprising, however, that such a tunnel seems to have no effect on the captures of other small mammals. Yet, the same mechanism may be more efficient for capturing smaller species when narrow entrances and lighter flaps are used. Thus, a similar trap may be designed to achieve an effective sampling of the entire small mammal community.

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Buchbesprechungen

Eisenberg, J. F.; Redford, K. H.: **Mammals of the Neotropics. Vol. 3: The Central Neotropics.** Ecuador, Peru, Bolivia, Brazil. Chicago, London: University Chicago Press 1999. 620 pp., 140 line drawings, 19 colour plates, num. tables. Cloth-only US $ 80.00. ISBN: 0-226-19541-4.

Following vol. 1 from 1989 written by J. F. Eisenberg (see review Z. Säugetierkunde 56, 1991, 128) and vol. 2 from 1992 written by K. H. Redford and J. E. Eisenberg (see review Z. Säugetierkunde 58, 1993, 199–200) this is the third volume on the mammals of the Neotropics dealing with the species of Ecuador, Peru, Bolivia, and Brazil. Thus, concerning the distribution of mammals, the gap in knowledge is now filled also for this median belt region of South America. Following an introduction with general remarks, some concerning the organization of the book, how to use the book, how data for compilations were obtained, and on the geography of the regions,21 chapters are divided into three parts. Part 1 deals with mammalian fauna in the Plio-Pleistocene of Brazil and offers 3 special chapters written by additional authors (S. D. Webb; A. Rancy, C. Cartelle). These give insight into isolation and interchanges of mammalian forms, fossil mammals of the Amazon region and Pleistocene environment, and Pleistocene mammals of the Cerrado and Caatinga of Brazil.

Part 2 is the main part, exceeding nearly 475 pages with the presentation of the contemporary mammalian fauna and the description of genera and species. This follows a general scheme comparable with vols. 1 and 2. 13 chapters deal with New World marsupials (41 pages), and the eutherian orders: Xenarthra (23 pp.), Insectivora (4 pp.), Chiroptera (113 pp.), Primates (49 pp.), Carnivora (Fissipedia) (33 pp.), Carnivora (Pinnipedia) (6 pp.), Cetacea (6 pp.), Sirenia (3 pp.), Perissodactyla (5 pp.), Artiodactyla (24 pp.), Rodentia (162 pp.), Lagomorpha (3 pp.). Each of these chapters starts with a characterization of the order concerning diagnosis, distribution, natural history (including many distinct biological peculiarities), and classification. In the following, the accompanying families and species are dealt with in the same manner. The occurrence of nearly all the species is documented by generalized distribution maps over the region. Dot markings indicate localisation of reports on the maps and likewise the corresponding literature in the reference list. Additionally, many skull drawings from the left side are given as well as drawings of total animals and further anatomical and morphological characteristics. Occasionally, data on body measurements are summarized, keys for species determination are offered and cladograms on the relationship of families or other taxa within the larger orders. There are also nicely prepared colour plates made by Fiona A. Reid, very useful to give an information on the external appearance of some internationally poorly known endemic species. The text is very informative and in most cases clearly states uncertainties or contrary opinions of specialists. Further, it is not only a summary of cited literature but there are also many personal observations of the authors themselves mentioned and personal communications are reported reflecting special views of scientists familiar with certain species (e. g. the fact that Wetzel until his death still was convinced of the existence of a third *Choloepus* species in addition to *C. didactylus* and *C. hoffmanni* in the upper Amazon region although not yet recorded, p. 97, etc.). Of all the chapters in part 2, that on rodents is, of course, the most voluminous one and, as the authors are well aware, most probably also bears several uncertainties evaluated from today. As is commonly known for South America the knowledge of rodent species and their distribution has grown rapidly and increasingly in the last few years and already several new species have been described since the publication of this book and certainly additional ones will be in the future. At least, this is partly documented in the last vols. of this journal. However, the listed and described species give an impressive overview on the adaptive radiation in the biology of rodents.

Part 3 is devoted to five special issues on the biogeography of land mammal written by the authors or guest authors, e. g. on the Galapagos and other South American islands, on biodiversity reconsidered (J. F. Eisenberg), on macrogeography of Brazilian mammals (G. A. B. Da Fonseca; G. Herrmann; Y. L. R. Leite), on the structure on nonvolant mammal communities in different Amazonian forest types (C. A. Peres), and on the contemporary fauna of South America.

In general, concerning the total volume, lists of references are separately attached to each chapter

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instead of a summarising list at the end of the book. This allows rapid orientation and information but very often is connected with repetitions of identical citations over several chapters. It also seems noteworthy that, rather uncommon for US American scientists, a great number of original studies in Spanish, German, and French were considered not only for citation but also in their contents. In this connection, very regrettably, rather one-sided comments are made concerning the domesticated tylopods reflecting some modern (but not necessarily convincing) opinions, although much literature exists in German on this topic. Almost no indication is given on the rather early domestication of *Cavia aperea* during pre-Columbian times or the later occurring farm breeding of endemic *Chinchilla* or *Myocastor* and the biological consequences of this influence. In cases where wild ancestors and their domestic relatives are mentioned this was done in binary nomenclature indicating different species but no new species originated due to domestication. Inconsistencies also occur concerning non-endemic species introduced by man which might have had severe influence on native habitats. Some are dealt with (*Mus, Rattus*) in species description, others (e. g. *Sus, Dama, Lepus*) are not. In this sense, specialists may find some further queries in detail. There were, however, two general problems the authors of this volume were confronted with. Firstly, a great number of species, if not most of them, has a distribution much larger than the characterized central region and were already treated in vols. 1 and 2. In these cases, the accounts are repeated here verbatim, enlarged with new insights or in an abbreviated style. Thus, in special cases this volume is best used in conjunction with the preceding two.

Secondly, concerning taxonomy there are inconsistencies, since vols. 1 and 2 relied on Honacki et al. (1982) while in vol. 3 the authors follow the modern treatise of Wilson and Reeder (1993). Although this was done for reasons of modernisation, some readers might be confused. Therefore, an appendix is added where comparisons are made for key species from vols. 1 and 2 with those of vol. 3.

The above mentioned criticisms are, however, only minor in nature and not heavily with regard to the comprehensive work of vol. 3 and the total three volume set. This is a very informative and modern compilation, long awaited, and very useful for mammalogists in general and those especially interested in the South American fauna.

D. Kruska, Kiel

Ridgway, S. H.; Harrison, R.: **Handbook of Marine Mammals, Vol. 6, The Second Book of Dolphins and the Porpoises.** San Diego: Academic Press (1999). Hardcover, 486 pp., numerous illustrations and tables. £ 69,95. ISBN 0-12-588506-7.

Many mammalogist will be pleased to note that all volumes of the Handbook of Marine Mammals are now available. This is the sixth and last tome of this well established and useful publication. 17 odontocete species – amongst them such well known ones as the bottlenose dolphin (*Tursiops truncatus*), the killer whale (*Orcinus orca*) and the harbour porpoise (*Phocoena phocoena*) – are presented in separate chapters by 28 authors.

As in the previous books of this series each species is described according to a standardised format: First taxonomy, evolution and common names of genus and species are characterised, the geographical distribution, external characteristics and internal anatomy are described, followed by an account of data on life history and population dynamics as well as on abundance in the habitat. Different aspects of behaviour, in some cases presented in remarkable detail, are described and characterised. An account of parasites and diseases follows, with remarks on live maintenance of captive individuals are offered. A final section deals with human effects on the respective species, such as, fisheries, pollution or habitat encroachment. Each chapter is concluded by a detailed list of references, which in some cases considers literature published in the '90s.

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Comparison of reproductive biological parameters in male wolves and domestic dogs

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Abstract

Effects of domestication on the reproductive biology in the species *Canis lupus* were studied by comparing some reproductive biological parameters in male wolves and domestic dogs living under similar conditions.

1. Seasonal changes in the concentrations of the two androgens testosterone (T) and 5α-dihydrotestosterone (DHT) in the peripheral plasma and in the relative testicular weights (testes/carcass weight) were observed in the wolves with maximal values during the winter, their natural mating season. In the domestic dogs such seasonal changes were not seen, androgen concentrations and relative testicular weights were high during all seasons.

2. An allometric comparison of testicular and epididymal weights revealed no differences among the various breeds of domestic dogs studied here. The weights of the testes and epididymides increased almost isometrically with body weight. Compared to the corresponding values in wolves during the mating season the weights of the testes and epididymides had increased by about 40% in domestic dogs.

3. Plasma T- and DHT-concentrations in 4 standard poodles, 2 toy poodles, and 3 wolves rose steeply in their 28th, 32nd, and 34th week of life, respectively. Thus, poodles and wolves living under similar conditions in captivity reach physiological sexual maturity at nearly the same age.

According to these findings domestication had no or little effect on the onset of puberty in the species *Canis lupus*. The seasonality of reproduction as it was observed in wolves, has vanished in the domestic dog and is replaced by the capability to reproduce during any season. The testes, sites of sperm production, and the epididymides, sites of sperm storage, have been enlarged by about 40% during domestication

Key words: *Canis lupus*, domestication, seasonal reproduction, puberty, testicular size

Introduction

Among the numerous effects of domestication the changes concerning the reproductive biology seem to be very striking and have been repeatedly described (Darwin 1875; Keller 1905; Haase and Donham 1980; Price 1984; Herre and Röhrs 1990; Setchell 1992; Benecke 1994). According to Keller (1905, p. 46) the unrestrained function of the reproductive system is a most important precondition for the development of domestic animals.

However, a closer inspection of the literature reveals that many examples for an enhanced reproduction in domestic animals compared to their wild ancestors do not withstand a critical examination since the different performances were achieved under different environmental conditions (see HAASE and DONHAM 1980; HERRE and RÖHRS 1990). Characters that, on the one hand, can effectively influence reproductive performances and, on the other hand, seem to be susceptible to alterations during domestication are the age of puberty and the duration of the reproductive season. Both these characters are amenable to proximate environmental factors (BRONSON and RISSMAN 1986; CATLING et al. 1992), thus emphasizing the necessity to perform comparisons under identical conditions.

The canids kept in the zoological garden at the Institut für Haustierkunde in Kiel live(d) under similiar conditions. Some observations on reproductive biological parameters in male domestic dogs and wolves will be reported in this communication.

Material and methods

The data from 38 wolves (mainly *C. l. lupus* and *C. l. pallipes*) and 90 domestic dogs (36 New Guinea dingoes, 12 hairless dogs, 20 standard poodles, 10 toy poodles, 12 specimens from various breeds, size range: long-haired dachshund to rottweiler) were used for gravimetrical studies. These animals were at least 10 months old. Except for the 12 specimens from various breeds the canids had lived for long periods of times or all their lives in the zoological garden at the Institut für Haustierkunde under the climatic conditions of Kiel (54° N), Germany. They were kept in large outdoor enclosures provided with indoor shelters including heating appliances. After sacrifice they were dissected according to a standard protocol introduced by HERRE 50 years ago. The following data were used for this investigation: 1. gross body weight, taken immediately after death. 2. net body weight = carcass weight, which is obtained by subtracting the weights of the fur (including subcutaneous fat) and the viscera of the thoracic and abdominal cavities from gross body weight. 3. testes weight (left and right combined). 4. weight of the epididymides (left and right combined).

For the estimation of seasonal changes in testicular weight it seemed reasonable to compensate for an expected influence of body weight on gonadal size. For this purpose "relative testes weight" was calculated by dividing testes weight by net body weight. The latter was preferred to gross body weight since KRUSKA (1996) in studies on the effects of domestication on brain size in mammals found it to be a more reliable measure for body size.

Allometric comparisons of testicular and epididymal sizes between the different canid groups were performed using net body weight and – for the reason of comparability with data from the literature – also gross body weight as the independent variable. Logarithmically transformed the allometric power function describes a linear function

$$\log y = b \cdot \log x + \log a$$

where y is organ weight, x is body weight (gross or net), b represents the slope of the regression line and log a the intercept of this line with y-axis at x = 0 and thus the position of the line. Slopes and positions of the regression lines between the canid groups were tested for differences using an analysis of covariance (ANCOVA) and subsequent multiple comparisons (SOKAL and ROHLF 1995). Additionally, all domestic dogs were pooled in one group and tested against the wolves. For reasons of comparability, "relative testes size" as introduced by KENAGY and TROMBULAK (1986) (1.0 representing the average relative testes size in 133 mammalian species), was calculated for domestic dogs and wolves. Due to high age, striking lateral asymmetries, or seasonal involution 13 of the 90 domestic dog specimens and 31 of the 38 wolves were excluded from the data sets for allometric comparisons.

3 wolves (*C. l. lupus*) born around May 15, 4 standard poodles born June 30, and 2 toy poodles from October 26 were used for studies on the onset of puberty. The wolves were hand reared and after weaning kept together with the standard poodles and their female littermates in a mixed group. The toy poodles with their sister and other female canids lived in a separate enclosure. At 3–4 week intervals blood samples were drawn from a brachial vein beginning on June 21 (wolves), November 2 (standard poodles), and December 15 (toy poodles) in their 6th, 18th, and 8th week of age, respectively. The heparinized blood samples were centrifuged and the plasma was stored in a deep freezer until assayed for androgens by radioimmunoassays (RIA) The assay procedure essentially followed the method of WINGFIELD and FARNER (1975) with slight modifications introduced by SCHEDEMANN (1991). Briefly, steroids were extracted from the plasma using Extrelut (Merck) columns and elution

with dichloromethane. Steroids were seperated via Celite column chromatography using 10% and 20% ethylacetate in isooctane for elution of a 5α-dihydrotestosterone (DHT) and testosterone (T) fractions, respectively. Thus, the 2 androgens could be assayed separately using the same antibody (code #EN-5100/4-11/2, kindly provided by Prof E. NIESCHLAG, Münster, Germany). All samples were assayed in duplicate.

Results

Seasonality

In figure 1 relative testes weights of all wolves were plotted against the days of dissection, day 1 corresponding to May 1. A clear annual cycle is evident: from May through October testes were regressed. In November relative testes weights increased and maxima were attained in December and January. Unfortunately, there were no data for February, but in March a decline was observed which continued in April reaching the level typical for the summer months. If the relative testes weights of the domestic dogs were plotted in the same way (not shown) there were no indications for seasonal changes. This statement held for all domestic dogs considered collectively as well as for the single subgroups.

Seasonality and its loss in relative testes weights of wolves and domestic dogs, respectively, kept under similiar conditions were also obvious from the diagram (Fig. 2). The columns representing the average relative testes weight for 3-month-periods showed a seasonal pattern for the wolves with maximal values during the winter. Average relative testes weight of wolves during this period was significantly above those during the other periods. For the domestic dogs the columns were of similar height throughout the year, the relatively short one for the 4th quarter representing 4 specimens only.

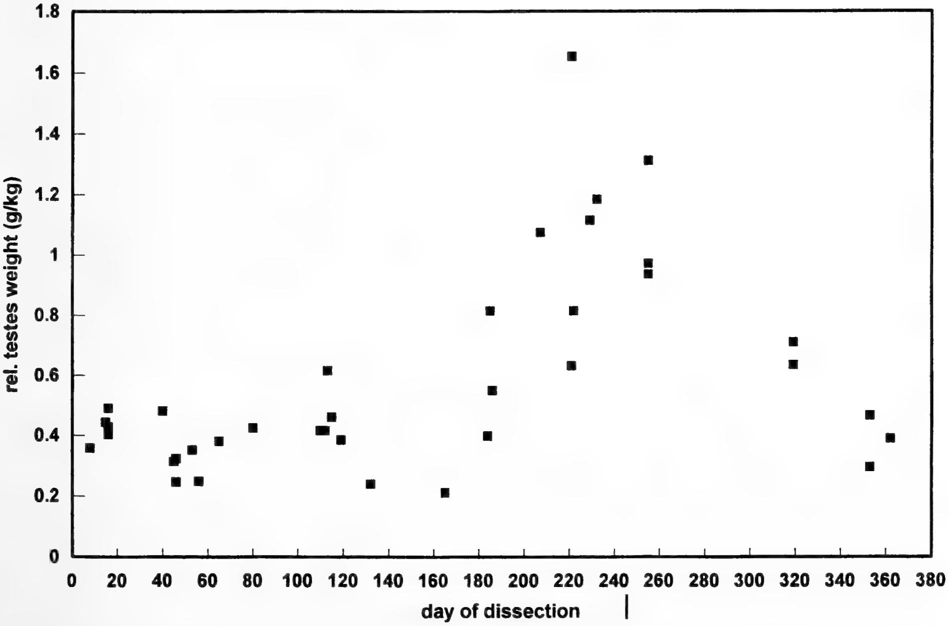

Fig. 1. Relative testes weights (testes weight/net body weight) in wolves plotted against day of dissection, day 1 corresponding to May 1rst (whelping season). Vertical bar underneath abscissa indicates new year. Maximal values were reached during the mating season.

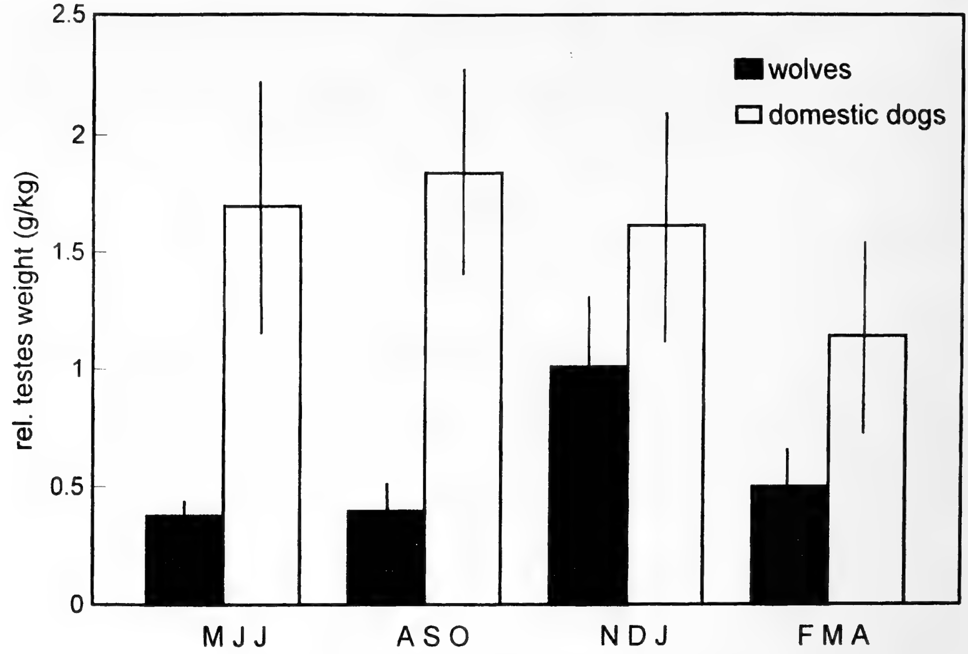

Fig. 2. Relative testes weights (testes weight/net body weight) in wolves (black) and domestic dogs (open). Columns represent mean relative testes weights for 3-months periods. Vertical lines indicate standard deviations.

Allometric comparison

In the sexually mature canids studied here there was a highly significant correlation between testicular weight and net body weight. The slope of the regression line within all canids was b = 0.94 and using ANCOVA no significant differences in the slopes of the regression lines could be detected between the different groups. There were, however, significant differences in the positions of the regression lines. Pairwise examinations showed these differences to concern the wolves compared to standard poodles, toy poodles, and New Guinea dingoes, respectively, but never pairwise compared domestic dogs. If the pooled domestic dogs (b = 0.92) were compared to the wolves (b = 1.06), again, there was no difference between these slopes but a highly significant difference in the position of the regression lines (Fig. 3). Based on the same net body weight testes in domestic dogs were 42.3% heavier than testes in wolves during the mating season.

If the calculations were performed on the basis of gross body weights the results were rather similar. Again, the two variables were correlated with high significance and ANCOVA showed no significant differences in the slopes of the regression lines between the different canid groups (all canids b = 0.98; pooled domestic dogs b = 0.94; wolves b = 1.18). Differences in the position were significant between New Guinea dingoes and wolves and a tendency ($p < 0.1$) for heavier testes was observed in toy poodles compared to wolves. In the pooled domestic dogs the testes were 35.5% larger than in equally sized (gross body weight) wolves during the mating season and this difference was highly significant. In the allometric relation testes weight/gross body weight it was possible to calculate the "relative testes size" in the sense of Kenagy and Trombulak (1986). It was 0.46 in the wolves and 0.54 in the pooled domestic dogs.

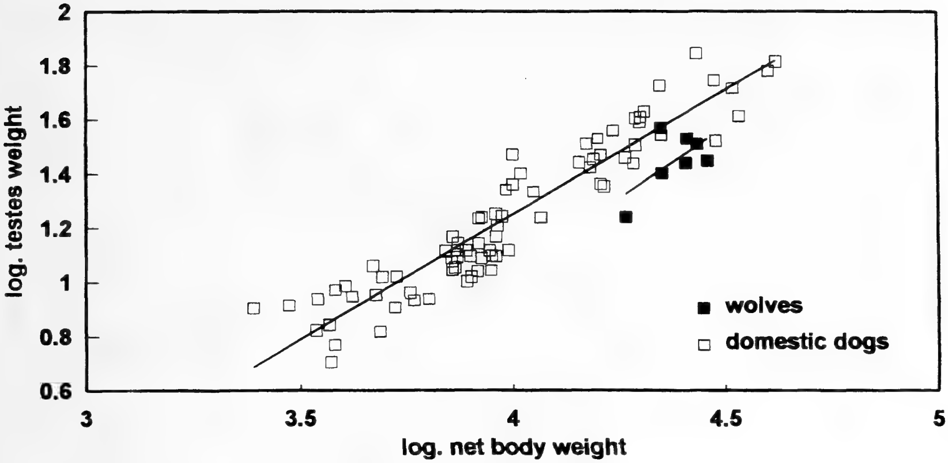

Fig. 3. Allometric comparison of testes weights in wolves during the mating season (black squares) and in domestic dogs (breeds pooled, open squares) in relation to net body weights. Values were logarithmically transformed. The regression lines for wolves and domestic dogs had similar slopes, but differed significantly in their positions resulting in an allometric weight increase of the testes in domestic dogs by 42.3%.

Considering the allometric weights of the epididymides in relation to carcass weights revealed no differences in the slopes but significant differences in the positions of the regression lines between the various canid groups. Pairwise comparisons showed the group "various breeds" to possess heavier epididymides than the wolves and the New Guinea dingoes, respectively, and, there was also a tendency ($p<0.1$) in wolves for smaller epididymides than in standard poodles. For the pooled domestic dogs and the wolves the slopes of the regression lines relating epididymal weights to net body weights were almost identical (pooled domestic dogs $b = 0.88$; wolves $b = 0.94$). The line for the domestic dogs was situated well above the one for the wolves ($p<0.01$) (Fig. 4). On the basis of the same net body weight epididymides of domestic dogs were 42.7% heavier than those of wolves during the mating season.

If epididymal weights were related to gross body weights the results strongly resembled those described above. Again, the pooled domestic dogs ($b = 0.90$) had heavier epididymides than wolves ($b = 1.14$) during the mating season and this allometric increase amounted to 36.1%.

Puberty

In the 4 standard poodles born in June a marked increase in plasma testosterone levels was observed in the 28th week of life (early January). Thereafter, apart form transient depressions average testosterone concentrations remained high (>3 ng/ml) in these dogs (Fig. 5). Similarly, a steep increase of plasma DHT concentrations from 0.058, 0.084, and 0.280 ng/ml in the 18th, 22nd, and 25th week, respectively, to 0.985 ng/ml in the 28th week was seen in the standard poodles with moderate variations around this latter value until the end of the observation period.

In the 2 toy poodles born in October plasma testosterone and DHT levels were low at all sampling dates during the first 28 weeks of life. In the 32nd week (end of May) a severalfold increase was noted in the plasma concentrations of the two androgens (Fig. 6). Apart from some fluctuations high levels persisted until the end of the sampling period.

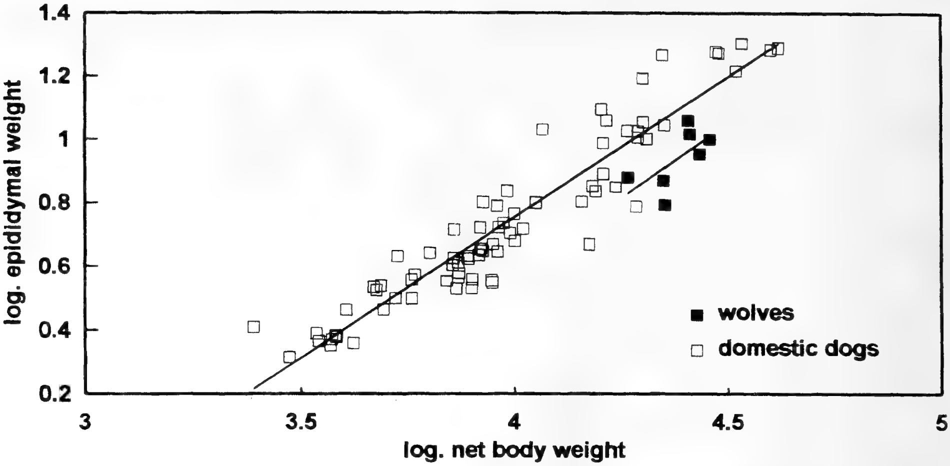

Fig. 4. Allometric comparison of epididymal weights in wolves during the mating season (black squares) and in domestic dogs (breeds pooled, open squares) in relation to net body weights. Values were logarithmically transformed. The regression lines for wolves and domestic dogs had similar slopes, but differed significantly in their position resulting in an allometric weight increase of the epididymides in domestic dogs by 42.7%.

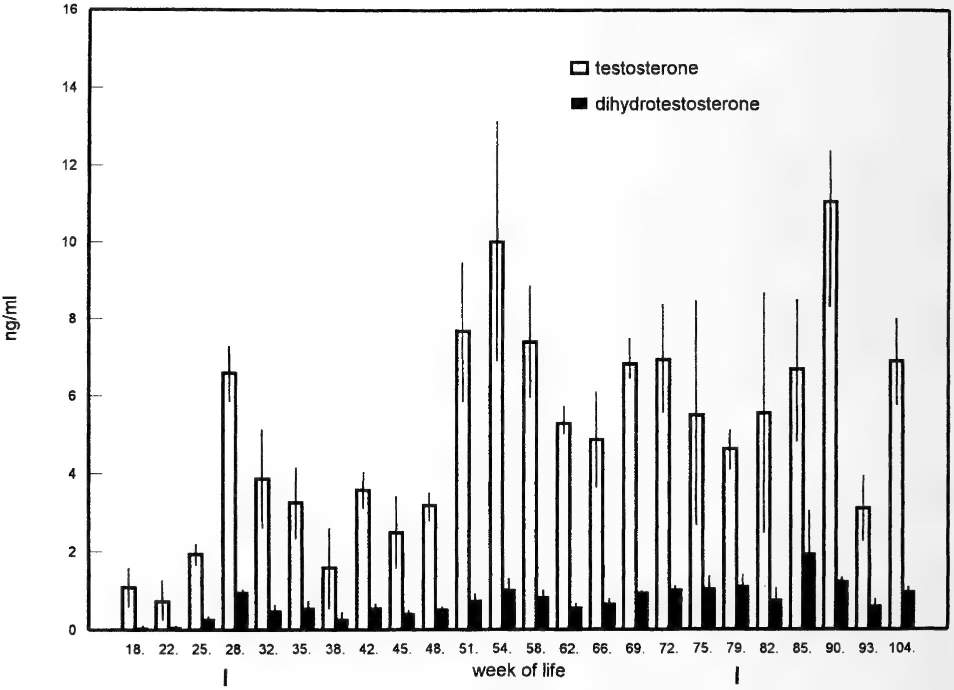

Fig. 5. Concentrations (mean ± SD) of testosterone and 5α-dihydrotestosterone in the plasma of 4 standard poodles (born at the end of June) at different ages. Vertical bars underneath abscissa indicate begin of new calendar years.

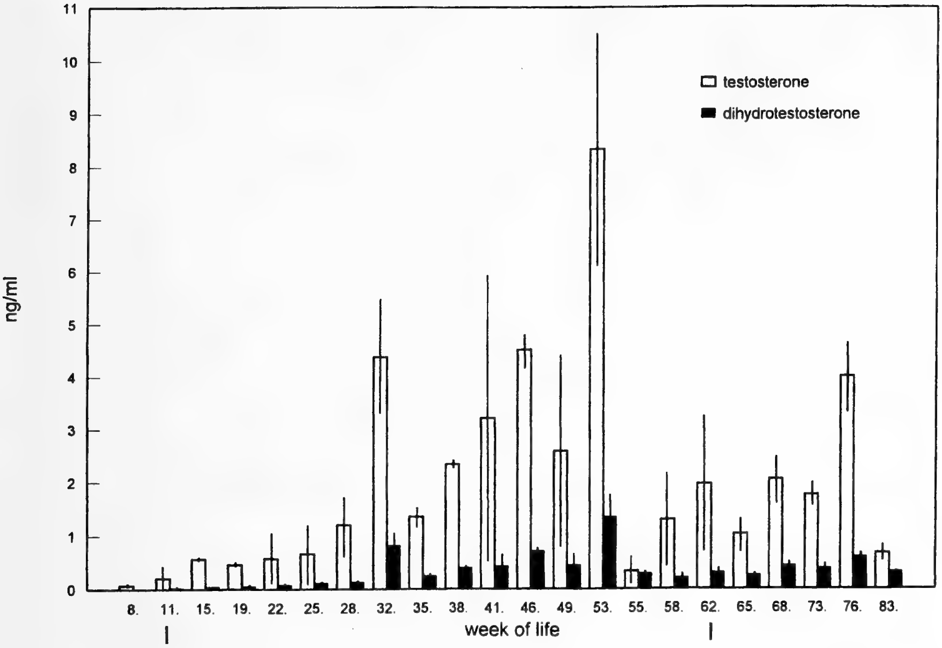

Fig. 6. Concentrations (mean ± SD) of testosterone and 5α-dihydrotestosterone in the plasma of 2 toy poodles (born at the begin of October) at different ages. Vertical bars underneath abscissa indicate begin of new calendar years.

From the 6th through the 31st week of life plasma testosterone and DHT concentrations in 3 wolves born in May remained at low levels. In January (34th week) there was a marked rise in the peripheral androgen levels to about 2 ng/ml (T), and 0.2 ng/ml (DHT) and a further increase took place in February and March. In the following months androgen concentrations fell and reached a new low from May through July. Later in the summer there was a gradual increase which continued during the fall. A second peak was reached during the winter, 12 months after the first one. Subsequently, androgen levels declined steeply in the spring. Thus, in the wolves androgen levels showed a clear seasonal pattern with maximal values during the winter, the natural mating season of the species, and lows during the spring and summer. Interestingly, the first peak commenced at the early age of 34 weeks (Fig. 7).

Discussion

Seasonality

It is widely accepted that seasonal reproduction has evolved as an adaptation to seasonal changes in the environment (Baker 1938; Aschoff 1955; Bronson 1985). In their natural environment wolves like other wild canids reproduce seasonally (Rausch 1967; Ginsberg and Mcdonald 1990; Asa and Valdespino 1998). Depending on the latitude and climatic factors wolves rut between December and April and parturition takes place between March and June (Mech 1970; Heptner and Naumov 1974; Bibikow 1988; Peters 1993). As judged from observations on sexual behaviour and parturition (Mech 1970; Lentfer

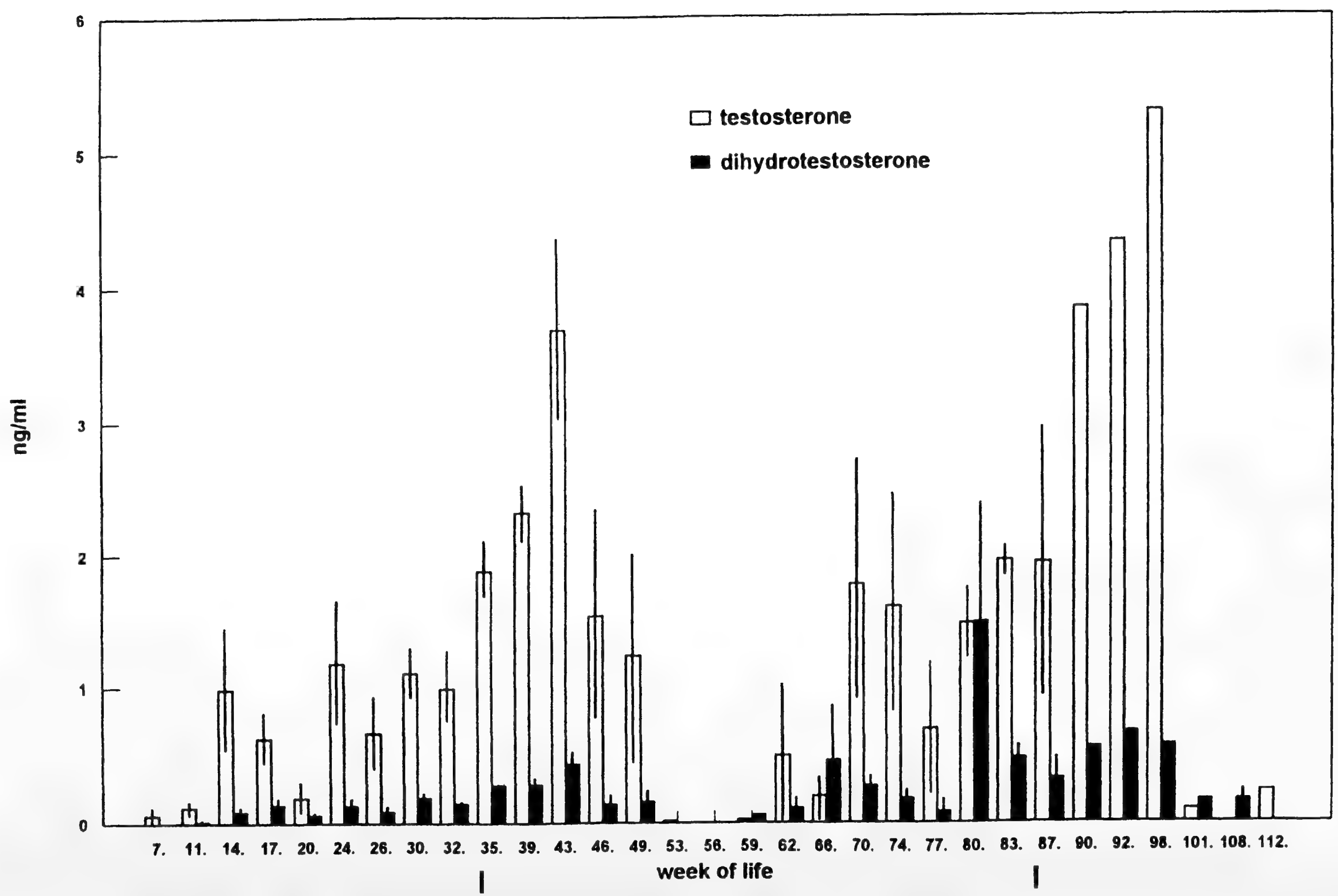

Fig. 7. Concentrations (mean ± SD) of testosterone and 5α-dihydrotestosterone in the plasma of 3 wolves (born at the middle of May) at different ages. Vertical bars underneath abscissa indicate begin of new calendar years.

and Sanders 1973; Seal et al. 1979; Asa et al. 1990) this seasonality of reproduction seems to persist in captivity, and this was also repeatedly observed in the zoological garden at the Institut für Haustierkunde (unpubl.). But like in wild dogs in Australia (Jones and Stevens 1988) a single breeding season each year may not preclude fertility throughout the year in the male.

The findings of this investigation on relative testes weights and on peripheral androgen levels clearly favor the persistence of seasonal fertility of male wolves in captivity. A seasonal pattern of serum testosterone levels after LHRH stimulation and of a testicular size index with maximal values during the winter was reported by Asa et al. (1986, 1990) for captive wolves. For male red foxes captivity seems to have no effect on the seasonality of genital activity (Joffre 1976).

Novikov (1962) stated that in wolves "the weight of the testicles increases fivefold before the rutting season" but unfortunately he provided no data or sources. In the present investigation the lowest and highest testicular weights were 5.6 g (June) and 37.0 g (December), respectively, and from these extremes a 6.6 fold increase could be calculated. However, a more reliable estimation may be gained from relative testes weights. In 7 specimens from the breeding season (which were also used for allometric comparisons) relative testes weight averaged 1.2 g/kg, whereas outside the breeding season it amounted to 0.4 g/kg, thus resulting in a threefold augmentation.

Generally, in domestic dogs, there seems to be no seasonal breeding cycle. According to Engle (1946) the estrus cycle of pure bred dogs of 4 breeds appears rather uniformly throughout the year. The length of estrus intervals in breeding bitches in Britain varied between 16 and 56 weeks with a median of 29 and 32 weeks in non-pregnant and pregnant bitches, respectively (Christie and Bell 1971). In this situation, where the occurrence of the next estrus appears unpredictible, a male would improve his chances to reproduce if he was fertile throughout the year. Relative testes weights and plasma androgen levels in the domestic dogs remained rather high during all seasons indicating a loss of reproductive seasonality during domestication in this species. This result basically agrees with earlier findings in the mallard (*Anas platyrhynchos*) where domestication was shown to flatten the seasonal oscillations of testicular size and plasma concentrations of reproductive hormones (Haase and Donham 1980).

For some domestic dog strains seasonal reproduction has been described: In basenji estrus is under photoperiodic control (Fuller 1956, males not mentioned). In free-ranging dogs in Katwa, West Bengal, pups (64 litters) were born exclusively during the winter (Oct.–March) (Pal et al. 1998, no data on males). In dingoes most females have an annual estrus cycle, whereas males can breed continuously in all habitats except hot and arid regions where they have an annual testis cycle (Corbett 1995). This testis cycle was more pronounced during drought than in flush periods (Catling et al. 1992) and if Central Australian dingoes were housed in Canbarra they did not have a testicular cycle. Here, they exhibited breeding season including elevated testosterone levels, but this was entirely governed by the female (Catling 1979). These findings underline the importance of environmental factors for the expression of reproductive parameters and emphasize the necessity to perform comparisons under identical conditions. There were no signs for seasonal testicular weight changes in the New Guinea dingoes studied here, but it should be mentioned that the overwhelming majority of specimens was sacrificed from July to December.

The timing of reproduction in silver foxes (Forsberg et al. 1989) and basenji dogs (Fuller 1956) is under photoperiodic control and the same very likely applies to wolves. An intraspecific heterogeneity in the response to photoperiodic cues was observed in rodent species and a genetic basis for this variability was documented by selection experiments (Bronson 1985). In this context, the weakening or even loss of reproductive seasonality during domestication may be understood as a consequence of the changed environmental conditions and of the resulting alterations in selection pressure which a species experiences during domestication. When food and shelter are provided by man offsprings which are born outside the original breeding season have a chance to survive and to pass their genes to following generations.

Allometric comparison

The allometric calculations uncovered a highly significant linear correlation between logarithmically transformed testes weights and net body weights. The slope for the regression line was close to 1.0 and this means that in this species testes increase in size in an almost isometric proportion to the increase in net body weight. Thus, "relative testes weight" as it was used in the preceding chapter on seasonality is a rather fair compensation for the influence of body size on testicular size.

Allometrically related to net body weight the testes of domestic dogs irrespective of the breeds studied here were 42.3% heavier than those of wolves during the mating season. In mallards, too, domestication has increased testicular weights (Haase and Donham 1980). According to Kenagy and Trombulak (1986) an increased copulatory frequency should promote selection for larger testes and this should occur with decreasing number of days in which a given number of matings must be accomplished. With other factors being equal Kenagy and Trombulak (1986) predicted that males of a species with a shorter mating season should have larger testes than males with a longer mating season. Obviously, in *Canis lupus* and *Anas platyrhynchos* domestication has lengthened the duration of the reproductive season and at the same time increased testes size. Clearly "other factors" in the sense of Kenagy and Trombulak (1986) were influenced by domestication, too, and of outstanding importance seems to be the mating system. In wolves as in many other wild canid species the mating system is monogamy (Kleiman 1977; Asa and Valdespino 1998). Although preferential mating has been well documented for bitches (Beach and Le Boeuf 1967), a tendency to promiscuity is evident for domestic dogs. The "extreme is the almost totally promiscuous behavior of the Venezuelan Mucuchies dogs; males were observed to line up and breed a female sequentially, with little aggression between them" (Coppinger and Coppinger 1998). Also, in feral dogs in central Italy, Boitani et al. (1995) "found no evidence that exclusive mating occurred within the group's breeding pairs, nor that the males in each pair were the fathers of the female's offspring". Monogamy in wolves includes paternal care (Asa and Valdespino 1998). If under the conditions of domestication man is involved in the care for the pups the reproductive success of a male dog is no longer linked to its paternal care as it was in the wolf. This should facilitate a tendency to promiscuity. Further, in directed dog breeding the mates of a pair are chosen by the breeder. Preferential monogamous mating behavior and refusal to accept the mate chosen by man would often result in reproductive failure, whereas promiscuous behavior would be advantageous under these conditions.

Kenagy and Trombulak (1986) related testes weight to gross body weight in 133 mammal species and calculated a "relative testes size". In the average of all 133 species "relative testes size" was 1.0 and it varied from 0.11 in *Notomys alexis* to 24.65 in *Phocoena phocoena*. If species were grouped according to their mating system mean "relative testes size" was 0.54 and 1.68 for 23 species with a single-male (including monogamous) mating system and 31 species with a multi-male (including promiscuous) mating system, respectively. The authors concluded that a functional relationship exists in many mammals between relative size of the testes and mating system. The value for the wolf reported here (0.46) fits well into this scale. The value for the pooled domestic dogs (0.54) indicates that the increase in relative testicular size during domestication of this species was rather modest compared to the evolutionary changes mentioned above.

The evolution of large testes was, among others, attributed to high sperm production (see Kenagy and Trombulak 1986) and, therefore, a dog probably produces more sperm than an equally sized wolf. The findings concerning the epididymides showed an allometric weight increase in the pooled dogs of 42.7% and 36.1% related to net and gross body weight, respectively, compared to wolves during the mating season. These values are practically identical with those for the testes. Thus, domestication affected the weights of the sperm production site and of the sperm storage site to the same extent.

Puberty

Darwin (1875) was among the first to state that domestic animals sometimes breed at an earlier age than their wild ancestors. Many authors (Mech 1970; Heptner and Naumov 1974; Lentfer and Sanders 1973; Bibikow 1988; Peters 1993; Asa and Valdespino 1998) agree that puberty in wolves usually begins at the age of 22 months. According to Heptner and Naumov (1974) males do not participate in reproduction before their third or fourth year. In the domestic dog, sexual maturity is reached at a much earlier age (6–18 months, Beaver 1977; 6–9 months, Fox 1978).

A spectacular decline in the age of human puberty has occurred in Europe and the United States during the last 100 years and is still going on in the developing countries (Short 1976). These findings point to the role of environmental factors in the timing of puberty and, therefore, comparative studies concerning the onset of sexual maturation should reasonably be performed under identical conditions.

The standards developed by Tanner (1962) as signs of sexual maturation in the human depend on physical characters which are essentially controlled by sexual hormones. The production of testosterone rises sharply at the time of puberty (Setchell 1978). Therefore, in the present study, steep elevations in the peripheral plasma androgen concentrations were used to determine the onset of puberty. According to this criterium, puberty started in the 28th and 32nd week of life in standard poodles and toy poodles, respectively. This means that sexual maturity in poodles begins in the age of 7–8 months, irrespective of the date of birth (June and October) or season. These findings fit well into the data on domestic dogs mentioned above. The slight difference between the two breeds must not be overestimated, especially, since blood sampling was performed in 4 week intervals, only. Nevertheless, it is interesting in this context that skeletal maturation as judged from epiphyseal synostosis was completed later in toy and miniature poodles than in standard poodles (Wiechering 1981).

In the young wolves a steep increase in peripheral androgen levels and, thus, the onset of puberty was observed in the 34th week of life. This unexpected early start of sexual maturation in wolves in captivity markedly contrasts with statements in the literature concerning wolves and seems to fit well with the findings in domestic dogs. The slight difference in the occurrence of increased androgen levels of 2 and 6 weeks to toy poodles and standard poodles, respectively, may be due to differences in the dependence on seasonal cues in the neuroendocrine control of reproduction between wolves and dogs. The external seasonal "zeitgeber" for the timing of gonadal recrudescence and puberty in wolves is probably the photoperiod. In a primitive dog breed, the basenji, seasonal heat was experimentally shown to depend on the photoperiod (Fuller 1956). In another canid species, the silver fox, Forsberg et al. (1989) could shift the seasonal spermatogenetic activity by photoperiodic manipulations. Thus, one may speculate that through appropriate photoperiodic stimulation the onset of puberty in wolves could be advanced by a few weeks leaving no temporal difference to domestic dogs.

In the literature, too, there are some notes concerning the onset of puberty in wolves during their first year. In 2 of 246 pups less than a year old from Alaska Rausch (1967) found Graafian follicles larger than 3 mm. One of 3 captive first-year females studied by

Seal et al. (1979) came into heat and produced a litter, whereas the 2 others only showed elevated LH levels during January not accompanied by significant increases in ovarian activity. A report on vaginal bleeding, estrus, and breeding in several 9 and 10 month-old captive female wolves is given by Medjo and Mech (1976). These authors also reported a 10 month-old captive male who sired a litter. Moreover, in the zoological garden at the Institut für Haustierkunde there were at least 2 pregnancies in first-year wolves during the last 40 years (unpubl. observ.). The two 10 month-old wolves included in chapter "Seasonality" of this study (see Fig. 1 day 319) contained numerous sperm in their epididymides (unpubl.). Thus, sexual maturation seems to be not uncommon in captive first-year wolves.

The early onset of sexual maturation in captive wolves clearly indicates that the genetic potential for an early puberty is inherent in this species. Medjo and Mech (1976) suggested that nutritional and social factors (the animals were removed at an early age from their parents) were important factors for the early breeding in their wolves. The role of a nutritional, especially energetic regulation of puberty was discussed by Short (1976) and Bronson and Rissman (1986). As to the social environment, the 3 young wolves studied here were hand reared and, therefore, inhibiting stimuli from their parents or other members of their family were precluded. Finally, it should be mentioned that the 3 young males did not show overt sexual behaviour during their first winter when, according to physiological criteria, they became sexually mature, whereas the standard poodles, although they were 6 weeks younger and lived in the same enclosure, did show activity (Feddersen-Petersen, pers. comm.). In this mixed group the poodles clearly dominated and the lack of sexual behaviour in the wolves may have been due to suppression. Suppression of sexual behaviour in postpubertal males by social factors was recently shown in common marmosets (Baker et al. 1999). Alternatively, one may suggest that a temporal dissociation between the physical and the mental events of puberty occurs in wolves. Under adequate nutrition physical puberty is reached in the first year. The behavioural development may need another year or more and may be importantly influenced by the social environment. Only under exceptional conditions (as in the case descibed by Medjo and Mech 1976) sexual behaviour may develop in the first year and then result in reproductive activities in first-year males. The frequent use of sexual behaviour and actual reproduction as criteria would explain why in most sources 22 months was named for the onset of puberty. The essential effects of domestication on sexual maturation in *Canis lupus* would, then, seem to concern mainly the behavioural and less the physiological changes.

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Zusammenfassung

Vergleich einiger reproduktionsbiologischer Parameter bei Wolfs- und Haushundrüden.

In dieser Studie sollten Auswirkungen der Domestikation auf die Reproduktionsbiologie der Art *Canis lupus* durch den Vergleich einiger reproduktionsbiologischer Parameter von Haushund- und Wolfsrüden, die unter gleichen Bedingungen lebten, untersucht werden.

1. Bei Wölfen änderten sich die Konzentrationen der Androgene Testosteron (T) und 5α-Dihydrotestosteron (DHT) im peripheren Plasma und das relative Hodengewicht (Hodengewicht/Netto-Körpergewicht) in Abhängigkeit von der Jahreszeit. Maximalwerte dieser Parameter wurden im Winter, der Ranzzeit der Wölfe, gefunden. Bei Haushunden waren derartige saisonale Schwankungen nicht zu erkennen, die gemessenen Größen zeigten zu allen Jahreszeiten hohe Werte.

2. Ein allometrischer Vergleich der Hoden- und Nebenhodengewichte ließ keine Unterschiede zwischen den untersuchten Haushundrassen erkennen. Die Hoden- und Nebenhodengewichte stehen in fast isometrischer Abhängigkeit vom Körpergewicht. Bezogen auf die Werte von Wölfen während der Ranzzeit sind die Hoden und Nebenhoden der Haushunde um etwa 40% schwerer.

3. Messungen der T- und DHT-Konzentrationen im Plasma von 4 Großpudeln, 2 Zwergpudeln und 3 Wölfen während des ersten Lebensjahres zeigten deutliche Anstiege der beiden Androgene in der 28., 32. bzw. 34. Lebenswoche der jeweiligen Gruppe. Unter den gewählten Haltungsbedingungen wurden Pudel und Wölfe in annähernd gleichem Alter physiologisch geschlechtsreif.

Nach diesen Befunden hat sich die Domestikation in der Art *Canis lupus* auf den Beginn der physiologischen Geschlechtsreife nicht oder wenig ausgewirkt. Die Saisonalität der Fortpflanzung beim Wolf ist in der Domestikation der Fähigkeit zur Reproduktion in allen Jahreszeiten gewichen. Der Hoden als Bildungsstätte und der Nebenhoden als Speicher der Spermien sind bei der domestizierten Form um etwa 40% vergrößert.

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Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog *Nyctereutes procyonoides* on native predators in northern Belarus

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Abstract

Feeding habits and dietary overlap among forest generalist carnivores (brown bear *Ursus arctos*, red fox *Vulpes vulpes*, badger *Meles meles*, pine marten *Martes martes*, polecat *Mustela putorius*, and raccoon dog *Nyctereutes procyonoides*) in natural forested landscape of northern Belarus (Gorodok and Rossony districts) were studied. In the warm season (April–October), generalist carnivores were characterized by a fairly wide food spectrum. Predominant items of their diets were fruits, small mammals, insects and birds. Although several pairs of species, such as brown bear-badger, raccoon dog-badger, pine marten-red fox, and pine marten-raccoon dog, had considerable dietary overlap, there was little evidence of a competition for resources in the generalist guild in the warm season. In the cold season (November–March), the food niches of active generalist predators became narrower and considerably overlapped, which coincided with a substantial decrease in food abundance and availability. In this period of poor food supply, generalists mostly consumed wild ungulate carrion, small mammals, and fruits. By inhabiting the same habitats, several pairs of species, such as pine marten-red fox, polecat-red fox, polecat-raccoon dog, polecat-pine marten, may compete for food. In the harshest period of late winter and early spring, in conditions of deep and/or soft snow cover in forest, it is energetically expensive to move around and the majority of food search fails. Thus, all generalists were forced to feed on carrion, the abundance of which substantially affected all generalist carnivores with the probable exception of raccoon dog. The obtained data on the predator abundance suggest that after the raccoon dog had reached a high population density, the native generalist predators began to decline.

Key words: carnivores, feeding ecology, Belarus

Introduction

In Europe, carnivores characterized by a wide food spectrum, such as badger *Meles meles*, pine marten *Martes martes*, polecat *Mustela putorius*, brown bear *Ursus arctos*, red fox *Vulpes vulpes*, and the introduced raccoon dog *Nyctereutes procyonoides* compose a generalist guild which is an important part of the vertebrate predator communities (Macdonald 1995; Jedrzejewska and Jedrzejewski 1998). There is a considerable number of studies on feeding habits of generalists inhabiting forest ecosystems (Lockie 1959, 1961; Geptner et al. 1967; Goszczynski 1986; Tumanov and Smelov 1980; Kruuk 1989; Weber 1989; Lode 1990, 1991; Pazhetnov 1990; Vaisfeld and Chestin 1993; Neal and Cheeseman 1996; Sidorovich 1997; Jedrzejewska and Jedrzejewski 1998 and references therein). There are, however, fewer publications in which dietary overlap of forest generalists has been estimated (Weber 1989; Lode 1991; Sidorovich 1997; Jedrzejewska and Jedr-

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zejewski 1998). Also, detailed studies of these predators inhabiting natural forested landscapes have been conducted only in the Bialowieza Primeval Forest, Poland (Jedrzejewska and Jedrzejewski 1998). In the extensive transitional zone of temperate mixed forest located between the more southern deciduous and the boreal coniferous forest zones and characterized by a specific combination of habitat conditions for predators, this question has not been studied, with the exception of a preliminary study on the dietary overlap of pine marten and polecat (Sidorovich 1997). Patterns of interspecific sharing of food resources can be best revealed by studying wildlife in pristine ecosystems. Another aspect of this study was to investigate a competition for resources between native predators and the introduced raccoon dog.

Thus, by conducting this study in natural landscape of northern Belarus, we aimed to investigate species-specific features of feeding ecology of forest generalist carnivores and estimate dietary overlap between native predators and the introduced raccoon dog in a seasonal dynamic of habitats, with their implications on population changes of the native species. Another important goal of the study was to reveal possible negative trends in numbers and structure of the native generalist guild in connection with the invasion of the raccoon dog.

Material and methods

The study was carried out in two areas located in northern Belarus. The first study region was an area of approximately 20×40 km at the head of the Lovat river, Gorodok district, Vitebsk region. The second study region was an area of approximately 40×60 km located between the three medium-sized rivers: Drissa, Nischa, and Svolna in Rossony district, Vitebsk region. The study areas are characterised by fairly natural conditions of river network, glacial lakes, large forests, and bog ecosystems on rough glacial terrain.

Both areas belong to the extended transitional region of temperate mixed forest located between the more southern deciduous and the boreal coniferous forest zones. Spruce *Picea abies* and pine *Pinus sylvestris* are dominant species among coniferous trees. Black alder *Alnus glutinosa* and grey alder *A. incana*, birches *Betula pendula*, *B. pubescens*, and aspen *Populus tremula* are the most common deciduous trees, whereas there are few masting deciduous trees such as oak *Quercus robur*, lime *Tilia cordata*, maple *Acer platanoides*, and ash *Fraxinus excelsior*, which produce a large amount of nourishing seeds for rodents. Therefore, in the transitional forest zone rodents have only seasonal fluctuations with no recurrent cycles of outbreaks and crashes (Sidorovich et al. 2000). Also, rodent abundance in this area is significantly lower than in the more southern deciduous forest, such as the Bialowieza Forest (Jedrzejewska and Jedrzejewski 1998). In the study areas, during the warm season other common prey of vertebrate predators are amphibians (Pikulik 1985) and migratory birds (Nikiforov et al. 1997). Wild ungulates are not as common there as in the more southern deciduous forest (Jedrzejewska and Jedrzejewski 1998). Similar to the Bialowieza Forest (Jedrzejewski et al. 1992), wolf predation together with deep snow cover act as important factors affecting wild ungulate mortality, keeping the density of these animals at a lower level than in the deciduous forest. Overexploitation by humans leads to an additional reduction in their numbers (Sidorovich 1989). Lower density of wild ungulates causes scarcity of carrion, which is an important food resource for many species of vertebrate predators in the cold season (Sidorovich 1997; Jedrzejewska and Jedrzejewski 1998).

In northern Belarus, winters are fairly severe. Normally, there is a deep snow cover of 40 to 90 cm, and air temperatures of about –20 °C and lower for several weeks are quite common. During winter and especially in late winter and early spring (when there is still a deep snow cover in forests), food resources are much scarcer, and their abundance decreases and is not renewed.

We studied the diets of forest generalist predators by analysing their scats. The majority of data was obtained over a period of 7 years (1992–1998), with the most intensive study period falling between 1996 and 1998. Scats were collected on a regular basis from latrines (badger, raccoon dog, polecat, pine marten) and main dens (polecat, red fox, pine marten). Identity of the occupants of dens and latrines was well known from the long-term field experience in the study areas (snowtracking, visual observations, identification of tracks, live capturing, radiotracking or trapping). In the cold season, the majority of scats was collected at tracks, when it was possible to distinguish tracks of the abovementioned species. Also, many scats of polecats, pine martens, badgers, red fox, and raccoon dogs were collected during radiotracking studies on these species. A total of 429 excrements of brown bears, 642 of badgers, 789 of red foxes, 653 of raccoon dogs, 831 of pine martens, and 437 of polecats were gathered and analysed.

By analysing the scats, we tried to determine as many different individuals of prey and other food items (bird eggs, fruits, and herbs) as possible by means of both identification of species and size difference. The contents were identified microscopically, using the published keys of mammalian hair (Debrot et al. 1982) or teeth (Pucek 1981), fish scales, teeth, and vertebrates (Galkin 1953; März 1987), amphibian bones (Böhme 1977; März 1987), reptilian bones and skin scales (März 1987), feathers and bones of birds (März 1987). Beetles and crayfish were distinguished by remains of their exoskeletons, molluscs and bird eggs by remnants of their shell. In the cases of badger and raccoon dog scats (with the exception of winter scats of raccoon dogs), microscopic search for earthworm chaetae and estimation of their abundance was fulfilled as described by Kruuk (1989).

More detailed research on feeding ecology of generalist carnivores was carried out in the harshest period of late winter and early spring in the condition of deep and/or soft snow cover, when we carried out additional snowtracking to study the feeding habits of these predators. Totally, each species was tracked for longer than 160 km in this season. Each year in late winter, we inspected an area of 5–7 km^2 to find all wild ungulate carcasses. We regularly surveyed wild ungulate carcasses to reveal the species consuming the carrion. A total of 172 carcasses (98 wild boars *Sus scrofa* and 74 elks *Cervus elaphus*) was found and inspected.

As the two study areas are very similar in habitat conditions and seem to be only two parts of the same large forest, the dietary data obtained in these different parts of the forested area were pooled. In calculations of the percentage of occurrence of various food items in the diet (%OC), the total number of scats analysed was used as 100%. The main measure of the diets was the percentage of food biomass consumed (%BC), because it more accurately expresses the proportion of each food item in the total biomass of food consumed by a predator. To obtain the percentage of food biomass consumed, we followed the approach recommended by Jedrzejewska and Jedrzejewski (1998) based on coefficients of digestibility (collected from the literature), i. e. the ratio of fresh weight of a given food item to the dry weight of its remains in scats. To compare the overall dietary diversity (food niche breadth) of generalist carnivores, B index (Levins 1968) was calculated for 16 food categories. B index varies from 1 (the narrowest niche) to 16 i. e. the maximum number of food categories used for calculations (the broadest niche possible). In order to evaluate the overlap of food niches, Pianka's (1973) index α was calculated, which varies from 0 (exclusive niches) to 1 (complete overlap). Both the food niche breadths and dietary overlaps were calculated according to the diets expressed as a percentage of food biomass consumed.

To estimate a possible change in the density of native generalist species as a response to the raccoon dog invasion, we used an abundance index for each species. The abundance index of the species of generalist carnivores was based on the data obtained by counting their track trails which crossed our route. Each year in 1989–1998, we used the same two routes, one of 36 km located in the Gorodok study area, and the other one of 44 km in the Rossony study area. The routes were specially placed across the whole diversity of habitat types such as a variety of forest types, river valley, glacial lake shore, reed and sedge marshes, and pine bog. To evaluate the abundance of badger and brown bear (which are normally inactive in winter in Belarus), we conducted a track survey in early spring, when the species were already active and snow cover still persisted. The abundance index of each carnivore species was calculated as the number of its track trails crossing our route, divided by both the number of kilometres inspected and the number of days passed from the last snowfall, and multiplied by two. As a result of the calculations, we obtained the average number of the tracks per 1 km transect per 2 days.

Results

Feeding habits and dietary overlap

In the warm season, the majority of generalists (pine marten, badger, raccoon dog, and brown bear) consumed a wide spectrum of food (Tab. 1 a). Their food niche breadths calculated by Levins's formula varied from 4.25 to 6.60. Insects (mainly beetles) and fruits (berries and apples) were common food of all these generalists. Badgers mainly fed on earthworms, molluscs, amphibians, small mammals, birds, cereal seeds, and herbs. Brown bears consumed numerous cereal seeds and herbs. Raccoon dogs mainly consumed molluscs, amphibians, birds and their eggs, carrion, and herbs. Pine martens frequently fed on small mammals, honey, birds and their eggs. The above-mentioned predators had large dietary overlaps (badger-brown bear, raccoon dog-badger, raccoon dog-pine marten; Pianka's index = 0.72–0.79) or intermediate dietary overlaps (brown bear-raccoon dog, pine marten-badger, pine marten-brown bear; Pianka's index = 0.45–0.69). Red fox and polecat were characterized by narrower food niches (Levins's index = 2.85 and 3.08, respectively). Red fox basically consumed mammals of small (mainly voles) and medium size (hares, muskrat, red squirrel, and hedgehog), birds, and fruits (mainly billberries and apples), whereas polecat mainly fed on amphibians, small mammals and birds. There was no considerable overlap in the diets of red fox and polecat (Pianka's index = 0.58), and between the two species and the other four generalist carnivores (Tab. 1 a), with the ex-

Table 1. Diet composition (expressed in percentage of occurrence of various food items in the scats analysed (%OC), and in percentage of food biomass consumed (%BC)) of the generalist carnivores in northern Belarus, 1992–1998. B-index of food niche breadth (Levins 1968). α-index of food niche overlap after Pianka (1973). Both B and α were calculated for the sixteen listed food items.

a) in the warm period (April–October)

Food category	Badger		Brown bear		Red fox		Raccoon dog		Pine marten		Polecat	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	82.5	27.3	70.4	18.4	24.3	3.0	67.5	10.9	31.1	14.6	4.7	0.9
Molluscs	10.4	1.0	–	–	–	–	10.6	3.5	0.4	<0.1	1.0	0.1
Earthworms	22.7	11.7	–	–	–	–	1.3	0.4	–	–	–	–
Crayfish	0.6	0.1	–	–	–	–	1.3	0.6	–	–	1.7	0.7
Fish	0.5	0.1	0.5	<0.1	0.5	0.1	5.7	1.5	–	–	2.0	1.2
Amphibians	13.9	4.2	–	–	0.5	<0.1	32.1	13.1	1.8	0.4	67.3	45.8
Reptiles	6.2	0.8	–	–	1.2	0.3	3.2	0.9	2.2	0.3	4.4	1.3
Small mammals	11.8	6.4	0.7	<0.1	70.1	55.7	9.2	6.5	39.8	34.7	32.0	30.6
Medium-sized mammals	1.4	1.1	–	–	13.6	9.1	3.3	2.2	2.2	1.7	–	–
Birds	13.4	7.3	–	–	27.2	16.5	32.7	17.4	24.1	17.5	17.5	13.7
Bird eggs	2.5	0.7	0.5	<0.1	3.6	0.8	8.8	1.7	7.2	2.1	4.7	1.2
Ungulate and other carcasses	5.3	4.8	8.2	7.5	7.3	5.9	11.0	9.3	4.7	4.0	5.1	4.0
Fruits	54.4	21.6	55.9	34.5	19.0	7.7	56.3	27.0	37.5	21.8	1.7	0.5
Cereal seeds	38.8	10.2	35.4	20.1	2.7	0.9	4.4	1.9	–	–	–	–
Herbs	9.7	2.7	40.5	19.3	0.5	<0.1	13.6	3.1	0.6	<0.1	0.7	<0.1
Honey	–	–	0.7	0.1	–	–	–	–	6.9	2.9	–	–
Number of the scats analysed	642		429		441		455		502		446	
Index of food niche breadths B	6.26		4.25		2.85		6.60		4.45		3.08	
Index of food niche overlap α:												
Badger	–		0.79		0.33		0.76		0.65		0.24	
Brown bear			–		0.14		0.69		0.45		0.02	
Red fox					–		0.42		0.89		0.58	
Raccoon dog							–		0.72		0.52	
Pine marten									–		0.51	
Polecat											–	

Table 1. b) in the cold period (November–March)

Food category	Red fox		Raccoon dog		Pine marten		Polecat	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	0.8	< 0.1	11.2	2.0	26.0	10.8	7.0	1.1
Molluscs	–	–	12.7	3.9	–	–	0.4	< 0.1
Crayfish	–	–	0.3	< 0.1	–	–	–	–
Fish	–	–	1.0	0.5	–	–	1.2	0.5
Amphibians	–	–	10.2	3.6	2.5	0.7	30.4	22.8
Reptiles	0.2	< 0.1	4.8	1.0	1.4	0.4	4.7	1.5
Small mammals	80.1	56.4	10.7	6.0	60.3	42.6	38.9	31.9
Medium-sized mammals	9.4	8.2	3.1	2.4	4.9	3.6	0.4	1.0
Birds	8.9	5.4	5.6	2.8	13.1	7.0	3.5	2.3
Bird eggs	–	–	–	–	1.9	0.5	–	–
Ungulate and other carcasses	34.8	28.3	71.5	53.0	19.1	16.3	41.6	38.2
Fruits	7.3	1.7	41.2	21.8	31.4	17.1	1.2	0.7
Cereal seeds	–	–	3.3	0.9	–	–	–	–
Herbs	1.1	< 0.1	14.2	2.1	0.3	< 0.1	1.6	< 0.1
Honey	–	–	–	–	2.7	1.0	–	–
Number of the scats analysed	437		393		366		257	
Index of food niche breadths B	2.47		2.97		3.92		3.34	
	Index of food niche overlap α:							
Red fox	–		0.52		0.92		0.83	
Raccoon dog			–		0.53		0.73	
Pine marten					–		0.74	
Polecat							–	

c) in the harshest period characterized by scarce food supply (either deep snow cover in late winter and early spring or deep and soft snow cover in any time of winter)

Food category	Badger		Brown bear		Red fox		Raccoon dog		Pine marten		Polecat	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	9.6	6.5	14.6	3.4	–	–	5.0	0.8	15.7	6.0	2.0	< 0.1
Molluscs	–	–	–	–	–	–	3.3	0.9	–	–	–	–
Amphibians	13.5	4.9	–	–	–	–	5.0	2.1	–	–	9.1	3.7
Reptiles	1.9	0.6	–	–	–	–	1.7	0.4	2.0	0.7	–	–
Small mammals	3.8	2.2	–	–	38.9	29.4	2.5	2.2	47.1	30.4	30.1	19.9
Medium-sized mammals	–	–	–	–	3.3	3.0	–	–	3.9	3.1	–	–
Birds	–	–	–	–	3.3	2.1	0.8	1.0	6.7	4.7	2.0	1.1
Ungulate and other carcasses	65.4	61.1	73.1	62.5	72.8	64.9	88.4	70.6	55.9	50.1	80.6	75.3
Fruits	23.1	20.5	36.6	22.7	–	–	17.3	11.8	7.8	4.9	–	–
Herbs	15.4	4.2	48.8	11.4	2.8	0.6	28.1	10.2	2.0	0.1	–	–
Number of the scats analysed	52		41		180		121		102		98	
Index of food niche breadths B	2.36		2.19		1.97		1.91		2.84		1.65	
			Index of food niche overlap α:									
Badger	–		0.99		0.87		0.98		0.84		0.92	
Brown bear			–		0.84		0.98		0.81		0.89	
Red fox					–		0.90		0.98		0.98	
Raccoon dog							–		0.85		0.95	
Pine marten									–		0.95	
Polecat											–	

ception of pine marten and red fox (Pianka's index = 0.89) as consumers of voles, birds and fruits.

In the cold season in the conditions of severe climate in northern Belarus, active generalist carnivores such as polecat, pine marten, red fox, and raccoon dog (this introduced species only partly sleeps in winter) mainly consumed carrion of wild ungulates, small mammals and fruits (cranberries, cowberries, and ashberries). The food niche breadth of each predatory species was narrower (Levins's index = 2.47–3.92) than in the warm season. Also in the cold season, red foxes preyed on hares and resident birds; raccoon dogs frequently consumed insects, molluscs, amphibians, and herbs; pine martens fed on insects and resident birds, and polecats consumed many amphibians (Tab. 1 b). The dietary overlaps were either fairly high (pine marten-red fox, raccoon dog-polecat, polecat-pine marten, polecat-red fox; Pianka's index = 0.73–0.92) or moderate (raccoon dog-red fox, pine marten-raccoon dog; Pianka's index = 0.52–0.53).

Table 2 presents the percentages of occurrence of different species of small mammals preyed upon by generalist carnivores in the warm and cold seasons. Microtine voles, bank vole, and mice of the genus *Apodemus* were most important mammalian prey. Red foxes specialized in feeding on microtine voles and striped field mouse, whereas bank vole and mice of the genus *Apodemus* were the main mammalian prey for pine martens. Bank vole, microtine voles, water vole, mice of the genus *Apodemus* and insectivores were fairly equally important for polecats and raccoon dogs.

During the harshest period of late winter and early spring, which is very often characterized by deep and/or soft snow cover, all studied generalists mainly fed on carrion (55.9–88.4% OC and 50.1–75.3% BC, Tab. 1 c). Therefore, they considerably overlapped in the diets (Pianka's index = 0.81–0.99, Tab. 1 c). Also, in this unfavourable period of poor food supply, red foxes, pine martens, and polecats supplemented their diets with mammalian prey, whereas raccoon dogs as well as brown bears and badgers (already active by early spring) frequently fed on cranberries when these fruits were available at pine bogs (Tab. 1 c).

The snowtracking data (Tab. 3) obtained in this harsh period in the forested areas mainly characterized these predatory species as scavengers. After finding an ungulate carcass, they usually stayed at the carrion until it was completely consumed. Different species of carnivores fed at the carcasses found (Tab. 4). Such carrion appeared mainly due to wolf kills (46%, n = 172) and from wild ungulates that had died due to other causes (54%), and

Table 2. Percentage of occurrence of small mammal species consumed by generalist carnivores in the warm (WS) and cold seasons (CS) in northern Belarus, 1992–1998

Species of small mammals	Badger		Red fox		Raccoon dog		Pine marten		Polecat	
	WS	CS	WS	CS	WS	CS	WS	CS	WS	CS
Clethrionomys glareolus	17.4	100	14.3	16.2	8.3	17.6	48.9	63.0	15.1	40.0
Microtus sp.	39.1	–	45.7	30.4	–	17.6	7.6	7.3	37.7	20.0
Arvicola terrestris	–	–	6.3	8.6	8.3	29.5	1.1	–	11.3	10.0
Micromys minutus	–	–	3.2	–	–	–	–	0.8	1.9	–
Apodemus sp.	43.5	–	21.0	32.4	–	–	25.0	16.9	17.0	11.4
Sorex sp.	–	–	0.8	3.8	66.7	17.6	3.3	4.0	5.7	10.0
Neomys fodiens	–	–	–	–	–	–	–	–	1.9	2.9
Talpa europaea	–	–	7.1	8.6	16.7	17.6	4.3	4.0	7.5	4.3
Dryomys nitedula	–	–	–	–	–	–	3.3	1.6	1.9	–
Sicista betulina	–	–	0.8	–	–	–	1.1	–	–	1.4
Chiroptera sp.	–	–	0.8	–	–	–	5.4	2.4	–	–
Sample size (n)	23	2	126	105	12	17	92	124	23	70

Table 3. Feeding habits (in percentage of observations) of generalist carnivores in the harshest period in late winter and early spring according to the snowtracking data (totally 1 679 km) in northern Belarus, 1992–1998

Plausible explanation of feeding habits	Badger	Brown bear	Red fox	Raccoon dog	Pine marten	Polecat
Scavenging (to find carrion or occasionally catch any prey)	49.3	55.2	46.2	20.1	62.7	37.1
Feeding on carrion (mostly of wild ungulate carcasses) and stay around	30.9	20.5	32.3	42.7	18.9	40.8
Hunting on small mammals	0.6	0	14.8	0.9	12.1	11.5
Catching of amphibians	4.7	0	0	5.9	0.1	8.6
Collecting cranberries	10.1	20.4	0.2	12.7	1.0	0
Feeding on herbs	0.8	2.3	0.1	9.2	0	0
Other feeding habits	3.6	1.6	6.4	8.5	5.2	2.0
Length of snowtracking, km	162	304	247	302	379	285

Table 4. Composition of predators (expressed in percentage of track observations) consumed the wild ungulate carcasses found (n = 172) in northern Belarus, 1989–1998

Species of wild ungulate carcasses	Badger	Brown bear	Red fox	Raccoon dog	Pine marten	Polecat	Lynx	Wolf
Elk (n = 74)	5.4	16.2	94.6	60.8	78.4	54.1	5.4	52.7
Wild boar (n = 98)	5.1	8.2	92.8	73.5	62.2	42.9	6.1	30.6

was scarce as a food resource. Usually, in various areas of 5–7 km^2, we found 1 or 2 (up to 4) elk carcasses and 1–4 (up to 9) carcasses of wild boar. Only 6 carcasses (1 elk and 5 wild boars) out of 98 carcasses found (6.1%) were negligibly eaten, 32 carcasses (32.7%) still contained a substantial amount of carrion, but the majority of carcasses (60 out of 98, 61.2%) was nearly totally eaten and mainly contained the skull, other large bones and remnants of skin. Nevertheless, all such poor remnants of wild ungulate carcasses were visited by generalist cernivores, who evidently tried to consume some carrion.

Shift in the abundance of native generalist carnivores

In figures 1 and 2, a pairwise comparison between changes in the abundance of raccoon dogs and the abundance of native species of generalist predators in the Rossony and Gorodok study areas are given. Negative correlation between the raccoon dog abundance and the abundance of polecats was statistically significant for both study areas (Rossony area: $r_s = -0.84$, $P < 0.001$; Gorodok area: $r_s = -0.67$, $P = 0.009$). Also, a statistically significant negative correlation between the raccoon dog abundance and the abundance of other native generalists was found for the Rossony area only (pine marten: $r_s = -0.91$, $P < 0.001$; red fox: $r_s = -0.71$, $P = 0.004$; badger: $r_s = -0.91$, $P = 0.002$; brown bear: $r_s = -0.66$, $P = 0.01$).

Discussion

In the warm season in the natural landscape of northern Belarus, generalist carnivores were characterized by a fairly wide food spectrum. Predominant items of their diets were fruits, small mammals, insects and birds. Although several pairs of predatory species had considerable dietary overlap, there was little evidence of resource competition during the warm season. The diets overlapped mainly concerning non-limited food resources such as

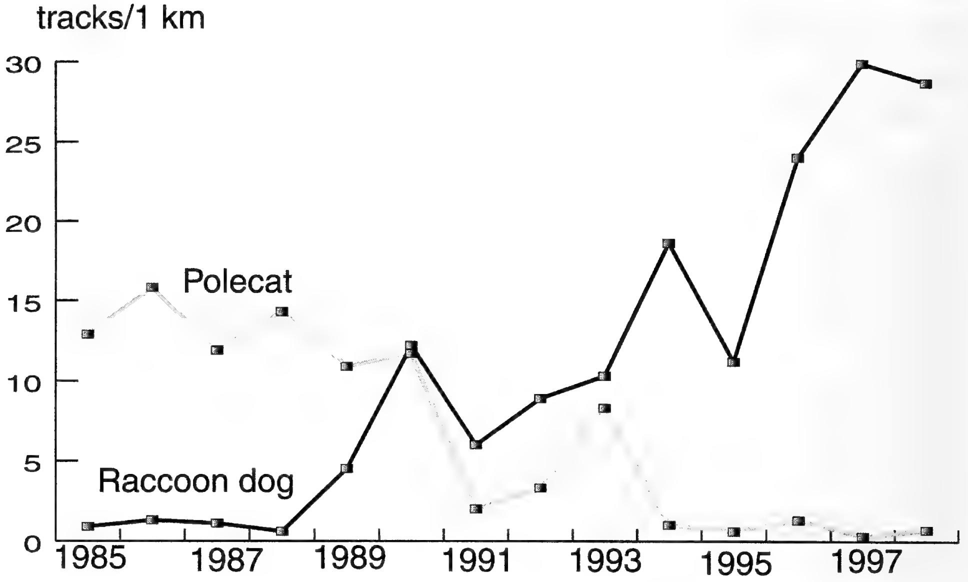

Fig. 1 a.

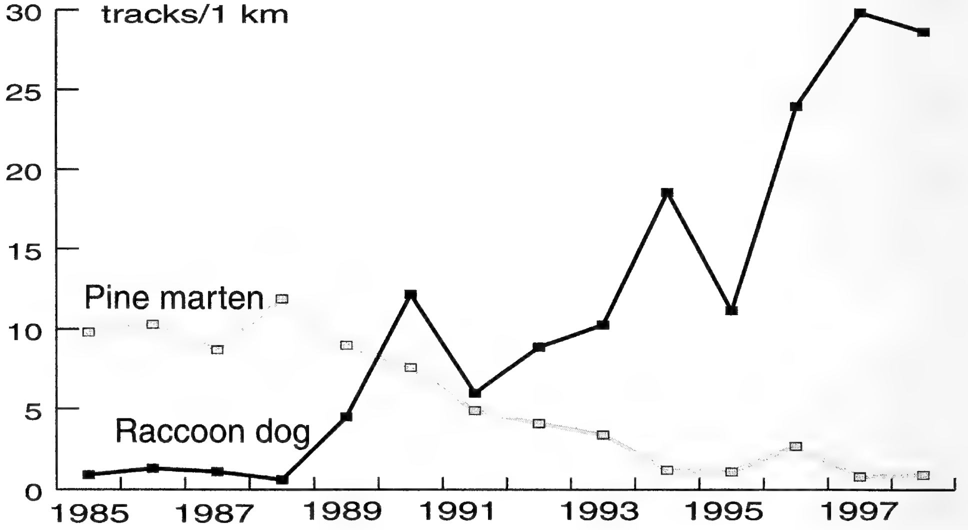

Fig. 1 b.

fruits, cereal seeds, and insects. Also, for most of the warm season, small mammals seem to be a non-limited prey (Sidorovich et al. 2000).

In the cold season, food niches of the active generalist predators became narrower and considerably overlapped, which coincided with a substantial decrease in food abundance and availability. During this period of poor food supply, the observed generalists mainly consumed wild ungulate carrion, small mammals, and fruits, which were markedly limited as a food resource. By inhabiting the same ecosystems, several pairs of predatory species may compete for food. In the harshest period of late winter and during early

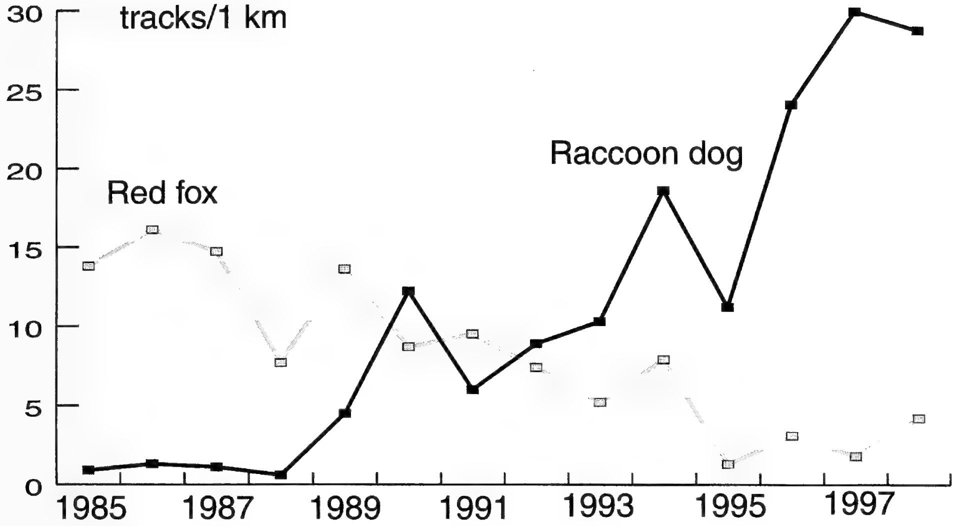

Fig. 1 c.

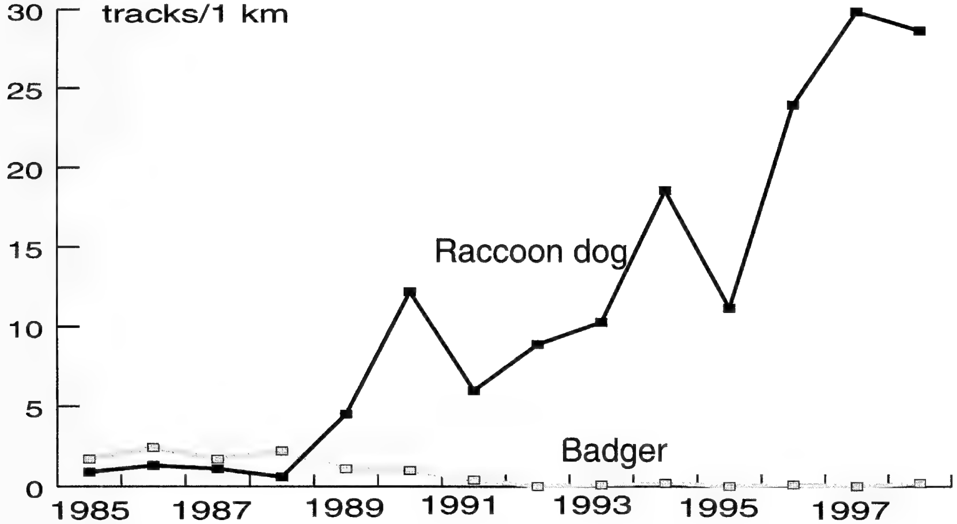

Fig. 1 d.

spring, very often characterized by deep and/or soft snow cover in forests, when it is energetically expensive to move around and the majority of food items is unavailable, all generalists were forced to feed on carrion. During this period, low abundance of carrion may substantially affect all generalist carnivores, with the probable exception of the raccoon dog. This exception appears due to the raccoon dog's capability to save enough internal fat until late winter, to be inactive in harsh conditions, and to consume anything edible food including wild boar scats and herbs as a last choice. Consequently, the feeding of numerous raccoon dogs on carrion leads to a substantial decrease in this very important food resource, which should severely affect the native generalist guild inhabiting the forest ecosystems. This plausibly had a particular impact on the polecat population.

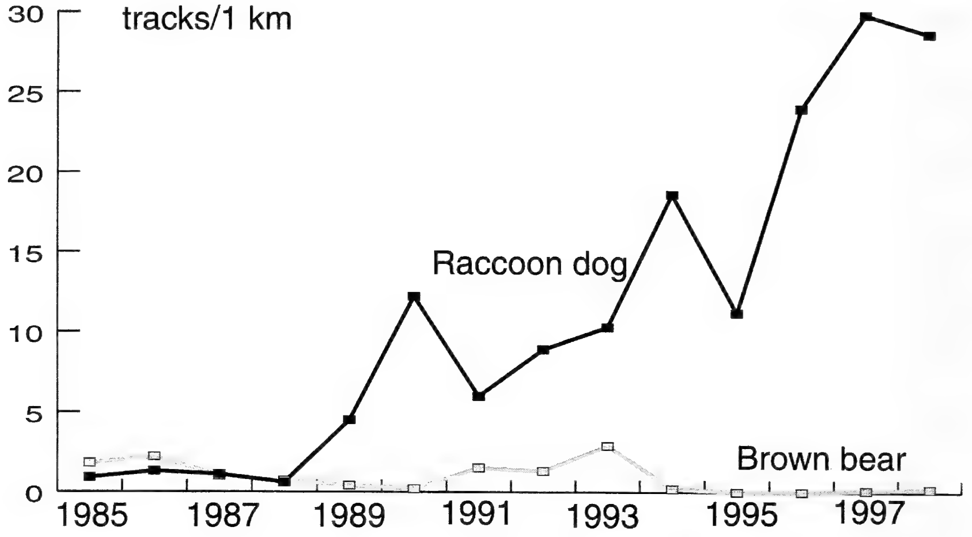

Fig. 1 e.

Fig. 1. Multiannual fluctuations of the abundance of native generalist carnivores (polecat, pine marten, red fox, badger, brown bear) in relation to change in the abundance of raccoon dogs in the Rossony study area, Rossony district, Vitebsk region, northern Belarus, late winter and early spring of 1985–1998. Average number of track trails of a predatory species which crossed 1 km of the inspected route during two days passed after the last snowfall was used as an abundance index of the species.
a) polecat – raccoon dog; b) pine marten – raccoon dog; c) red fox – raccoon dog; d) badger – raccoon dog; e) brown bear – raccoon dog

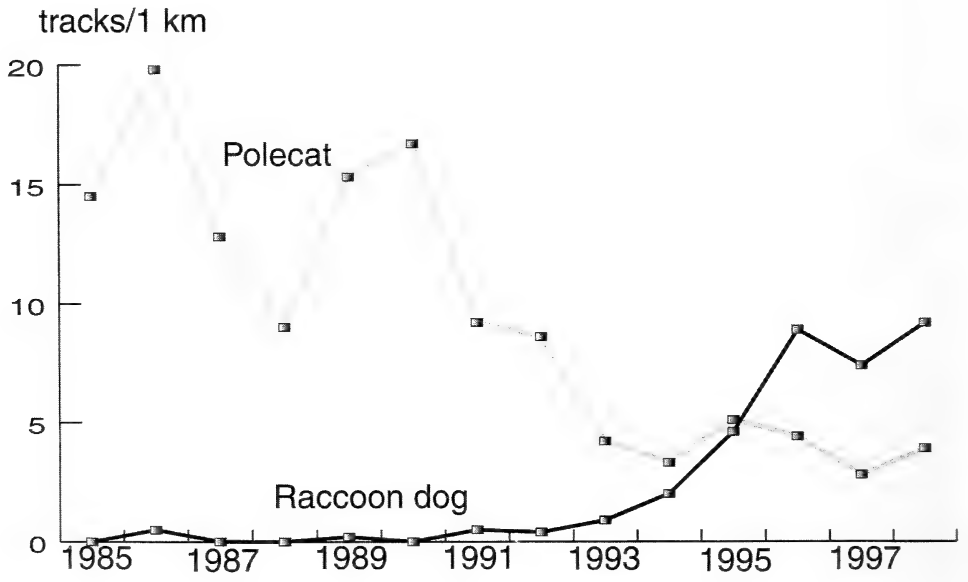

Fig. 2 a.

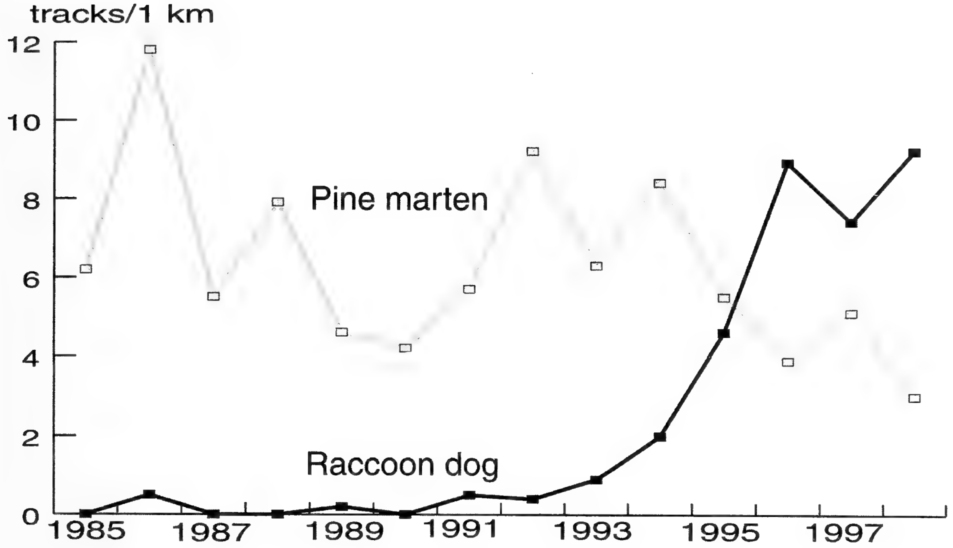

Fig. 2 b.

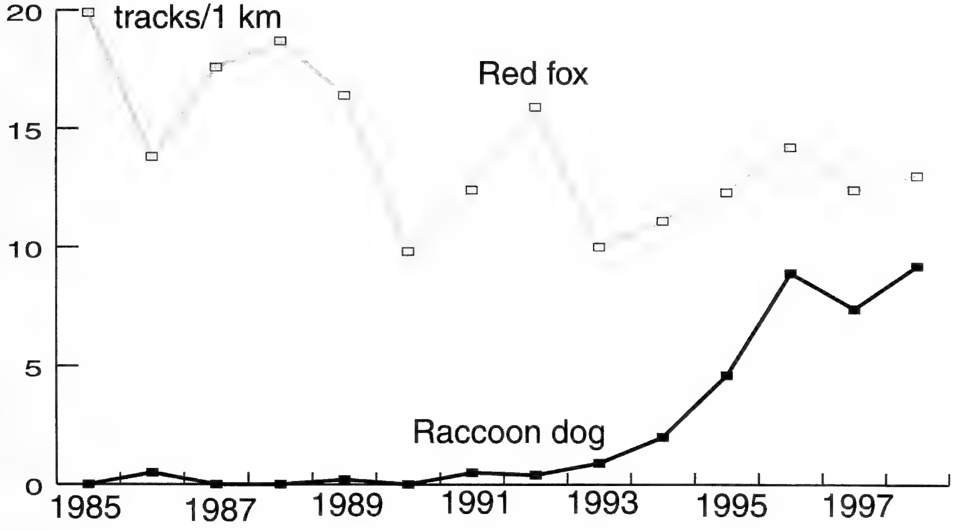

Fig. 2 c.

The obtained data also suggest that in the mixed forests of northern Belarus a specific pattern of sharing food resources between generalist carnivores has developed. Both their feeding habits and dietary overlaps are very different in comparison with those in the more southern Bialowieza Primeval Forest of eastern Poland (JEDRZEJEWSKA and JEDRZEJEWSKI 1998). As regards the differences between these two communities of vertebrate predators both inhabiting temperate forests, the following explanation might be given concerning a substantial difference in habitat conditions.

In the post-glacial landscape of northern Belarus, the soils are fairly poor because of their relatively young age and conditions of a more severe climate than of the more

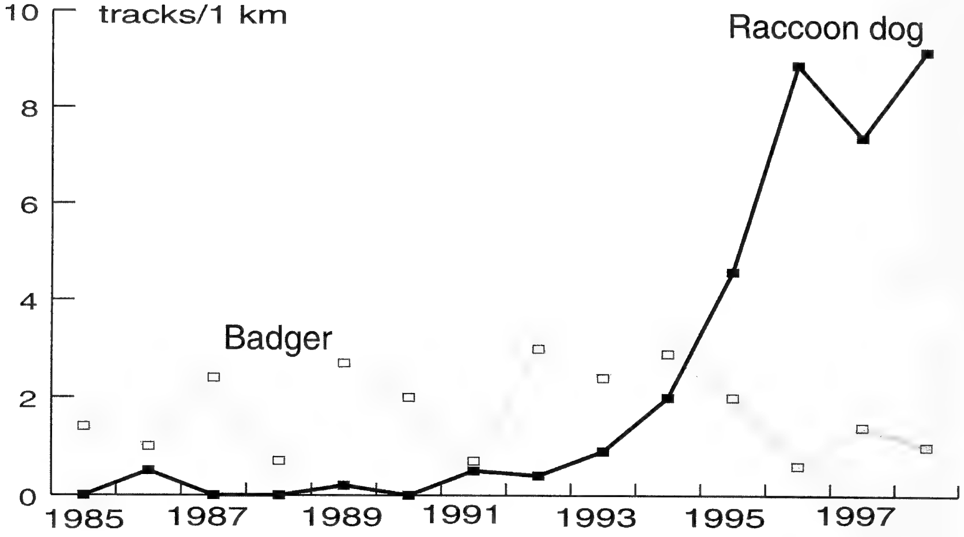

Fig. 2 d.

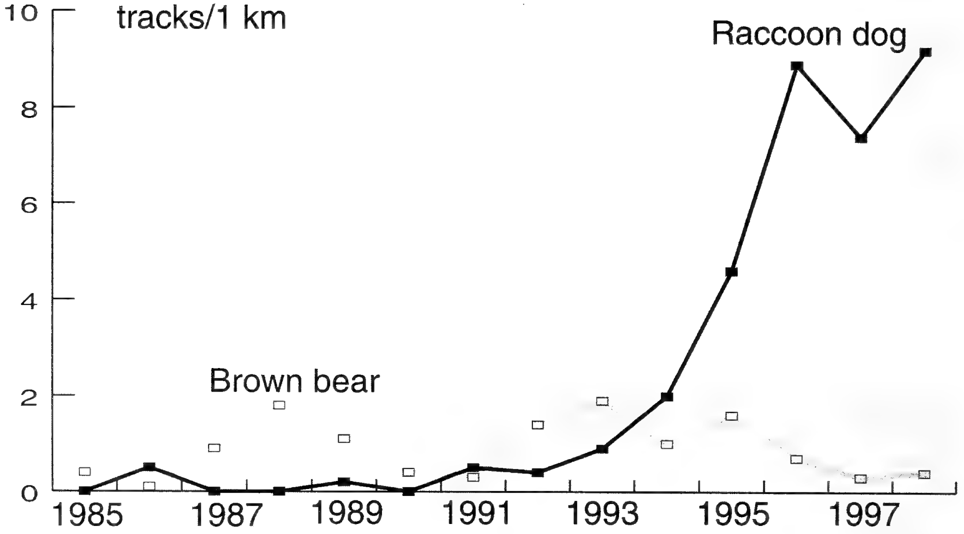

Fig. 2 e.

Fig. 2. Multiannual fluctuations of the abundance of native generalist carnivores (polecat, pine marten, red fox, badger, brown bear) in relation to change in the abundance of raccoon dogs in the Gorodok study area, Gorodok district, Vitebsk region, northern Belarus, late winter and early spring of 1985–1998. Average number of track trails of a predatory species which crossed 1 km of the inspected route during two days after the last snowfall was used as an abundance index of the species.
a) polecat – raccoon dog; b) pine marten – raccoon dog; c) red fox – raccoon dog; d) badger – raccoon dog; e) brown bear – raccoon dog

southern region of forest zone located outside the influence of the last glaciation. In these harsh environmental conditions, mixed forests contain few masting deciduous tree species such as oak and linden and mostly consist of pine, spruce, birches, alders, and aspen. This, in turn, causes a significantly lower number and biomass of small rodents (Sidorovich et al. 2000). Severe winter with strong frost and deep snow cover also makes it difficult for predators to feed on small mammals living under the snow. Therefore, in northern Belarus the habitat conditions of mammalian consumers such as red fox and pine marten are worse than those in the Bialowieza Primeval Forest. Thus, northwards these carnivores more frequently face a shortage of mammalian prey and need to supplement their diets with other food categories (carrion, fruits, birds).

Also, severe conditions of winter time substantially impede polecats from catching amphibians, whereas this predator prefers to feed on frogs in other areas where winter is milder (Weber 1989; Jedrzejewski et al. 1993; Jedrzejewska and Jedrzejewski 1998). In the harsh winter conditions of northern Belarus, polecat acts as a generalist predator feeding on small mammals, amphibians, birds, and carrion. As regards habitat conditions for badgers, invertebrate (especially earthworm) diversity and biomass are substantially lower northwards (Hotko 1993; Neal and Cheeseman 1996; Jedrzejewska and Jedrzejewski 1998). This affects the diets of badgers, which prefer to feed on earthworms (Kruuk 1989; Neal and Cheeseman 1996). In northern Belarus, low biomass of earthworms forces badgers to act as a generalist predator characterized by seasonal feeding specializations on different food items (Sidorovich 1997). This leads to a different pattern of dietary overlap between badger and other generalist carnivores in northern Belarus than in the more southern deciduous forest of the Bialowieza Primeval Forest (Jedrzejewska and Jedrzejewski 1998).

Thus, all the above-mentioned ecological conditions of the large area influenced by the last glacier have determined a different pattern of sharing food resources between forest generalist predators, as well as their feeding habits, in the natural forest ecosystems of northern Belarus compared to those in the more southern mostly deciduous forest in the Bialowieza Primeval Forest (Jedrzejewska and Jedrzejewski 1998). This points out the flexible and highly adaptive nature of the vertebrate community, and at the same time it may indicate their different responses to the influence of introduced species.

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Zusammenfassung

Nahrungsüberlappung bei generalistischen Carnivoren in Beziehung zum Einfluß des eingeführten Marderhundes (Nyctereutes procyonoides) auf die heimischen Prädatoren im nördlichen Weißrußland

Es wurden die Ernährungsgewohnheiten und deren Überlappungen zwischen waldbewohnenden, sich omnivor ernährenden Raubsäugern (Braunbär *Ursus arctos*, Rotfuchs *Vulpes vulpes*, Dachs *Meles meles*, Baummarder *Martes martes*, Iltis *Mustela putorius* und Marderhund *Nyctereutes procyonoides*) in der naturnahen Waldlandschaft Nord-Weißrußlands (Gorodok und Rossony Bezirk) untersucht. In der warmen Jahreszeit (April–Oktober) war für diese generalistisch lebenden Carnivoren ein sehr breites Nahrungsspektrum charakteristisch. Früchte, Kleinsäuger, Insekten und Vögel waren die vorherrschenden Nahrungsbestandteile. Obwohl bei einigen Artenpaaren, wie Braunbär – Dachs, Marderhund – Dachs, Baummarder – Rotfuchs und Baummarder – Marderhund, deutliche Nahrungs-

überlappungen auftraten, gab es in der warmen Jahreszeit in der Gruppe der Generalisten nur kleine Hinweise auf Konkurrenz um Ressourcen. In der kalten Jahreszeit (November–März) wurden die Nahrungsnischen der omnivoren Beutegreifer ohne Winterruhe enger und überlappten sich stärker, was auch mit einer substanziellen Abnahme der Nahrungshäufigkeit und -verfügbarkeit übereinstimmt. In dieser Periode mit schlechter Nahrungsversorgung fraßen die Generalisten meist Aas (Elch und Wildschwein), Kleinsäuger sowie Früchte. Bei Besiedlung gleicher Habitate können so einige Artenpaare, z. B. Baummarder – Rotfuchs, Iltis – Rotfuchs, Iltis – Marderhund, Iltis – Baummarder, um Nahrung konkurrieren. In der härtesten Zeit im Spätwinter und Anfang des Frühjahrs, also unter Bedingungen einer tiefen und/oder weichen Schneedecke im Wald, ist Bewegung energetisch ungünstig und viele Nahrungskomponenten nehmen ab. Dann sind alle Generalisten gezwungen sich von Aas zu ernähren, dessen Häufigkeit diese Carnivoren, mit vermuteter Ausnahme des Marderhundes, deutlich beeinflußt. Die erhobenen Daten zur Häufigkeit der Prädatoren weisen darauf hin, daß mit Erreichen einer hohen Populationsdichte des Marderhundes, die einheimischen Prädatoren seltener wurden.

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Scent marking intensity of beaver (*Castor fiber*) along rivers of different sizes

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Abstract

The intensity of scent marking by territorial beavers could relate to different numbers of transient beavers. Rivers are, most likely, the main paths of beaver dispersal. It is supposed that the intensity of subadult migration depends upon the size of the river because those basins of larger rivers potentially contain a greater number of beavers. Scent marking intensity (the number of scent mounds) and relative abundance (number of beaver activity signs) of beavers were studied in 18 segments of various rivers in Lithuania during the period of subadult dispersal during April and the first ten days of May. The total length of transect was 157 km. The yield of water (Q) of these river segments varied from 0.4 to 32.2 m^3/s.

The Lithuanian beaver population is considered abundant. Even the smallest peripheral water bodies are densely inhabited by beavers, thus making the dispersal of population surplus rather complicated. The highest scent marking intensity (1.78 scent mounds per 0.25 km of shore line) was found in medium-sized rivers (mean $Q = 4.6\ m^3/s$), and the lowest (0.64 scent mounds per 0.25 km of shore line) in the smallest rivers (mean $Q = 0.6\ m^3/s$). Scent marking intensity was significantly positively correlated with the relative abundance in most rivers, excluding the smallest ones. The results are discussed in relation to an appropriate response of territory owners to the different intensity of subadult migration in rivers of differing sizes. The scent mound system seems to be an important mechanism of population self-regulation, preventing an overexploitation of ecological resources in rivers where intensive migration of beavers occurs.

Key words: *Castor fiber*, scent marking intensity, rivers, Lithuania

Introduction

Beavers (*Castor fiber* and *C. canadensis*) occupy family territories along the shore line and live at the same sites for a long periods of time. Being sedentary animals, beavers defend their family territories from conspecific intruders by exhibiting aggressive behaviour against strangers (DJAKOV 1975). An important tool of the territory defence seems to be the scent markings (ROSELL and NOLET 1997; ROSELL et al. 1998). It was hypothesised that seasonal peaks of scent marking activity could be a response related to the increased stream of transient subadults in spring (MÜLLER-SCHWARZE and HECKMAN 1980; ROSELL and NOLET 1997), and the scent mound system serves as an important mechanism of population self-regulation (ALEKSIUK 1968).

Following natural immigration and reintroduction at the beginning of the 1940s to 1967, the expansion stage of the beaver population in Lithuania came to a conclusion in about 1975. During the last few decades, the density of the Lithuanian beaver population

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has been quite high. The average linear density is very similar in different types of water bodies, varying from 0.8 sites/km of river-bed in natural rivers to 1.1 sites/km in suitable canals. Even the smallest peripheral water bodies, such as small streams and small swamps, are densely inhabited by beavers (Ulevičius 1999). From this it may be predicted that the dispersal of subadults would be rather complicated. It is supposed that the intensity of subadult migration depends on the river size. The larger river basins potentially contain more beaver groups, thus producing more young animals.

The aim of this study was to investigate beaver scent marking intensity along rivers of differing sizes during the period of subadult dispersal (from April to the beginning of May) in an abundant population.

Material and methods

The investigated river segments are situated between 22°15′–25°45′ E and 54°10′–55°40′ N in the Middle and Lower Nemunas Basin (Fig. 1). This basin covers approximately 70% of the whole territory of Lithuania. The density of the hydrographical network including artificial canals varies from 0.7 to 1.4 km/km^2. With respect to total length of the hydrographical network, the smallest streams (of up to 10 km long) account for about 70%. The proportion of artificial canals (from land reclaimation) varies from approximately 40 to 85%.

In April and the first ten days of May 1991–1993, 157 km of shore line transects were investigated in 18 river segments, and these divided into 628 cut-offs (length – 0.25 km). The length of the river segments investigated varied from 5.0 to 15.5 km. Only one river bank was studied. 0.25 km was the shortest distance of shore line which could be geographically restricted without a significant error occurring in its length using timing (within 1 minute) and mapping of each beaver sign found during the field work. Maps of 1 : 50 000 scale were used.

River segments were clustered according to their average water yield. Four clusters of different river sizes were distinguished (Tab. 1). The water yield of the smallest river segments (I cluster) varied from 0.4–0.9 m^3/s, the II cluster from 1.9–2.8 m^3/s, the III cluster from 4.2–5.0 m^3/s, and the IV cluster from 14.8–32.2 m^3/s. The yield of water was estimated using the Lithuanian river cadastre (Jablonskis and Lasinskas 1962).

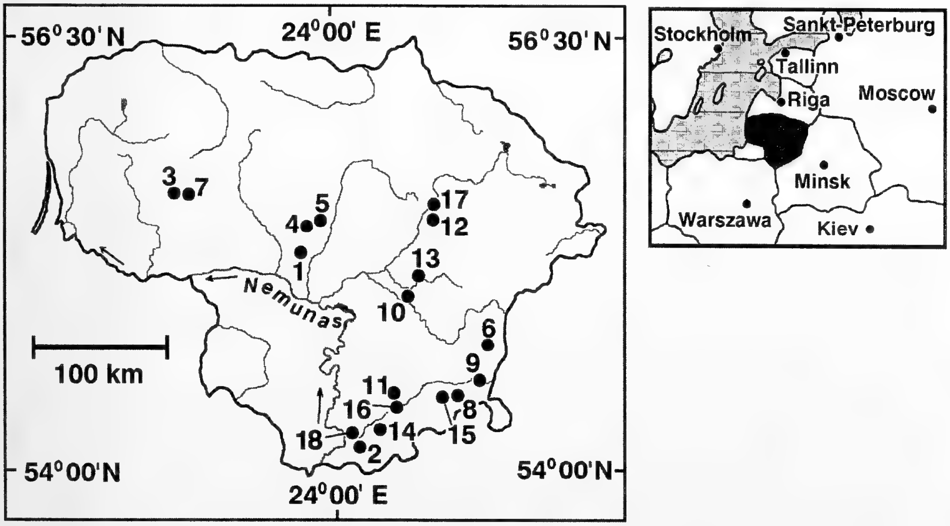

Fig. 1. Study area. The numbers of samples as in table 1.

Table 1. Characteristics and clustering of the river segments investigated

Cluster	No	River	Water yield, m^3/s	Length of segment, km	No of cut-offs
I	1	Aluona	0.4	5.0	20
	2	Skroblus	0.4	6.0	24
	3	Ašvija	0.5	5.0	20
	4	Jaugila	0.7	5.0	20
	5	Dotnuvėlė	0.8	5.5	22
	6	Kena	0.8	11.5	46
	7	Akmena	0.9	4.0	16
Total and average for cluster I			0.6	42.0	168
II	8	Visinčia	1.9	8.5	36
	9	Upper Merkys	2.6	15.5	62
	10	Musė	2.8	6.0	24
	11	Varėnė	2.8	9.0	36
Total and average for cluster II			2.5	39.0	156
III	12	Virinta	4.2	7.5	30
	13	Širvinta	4.3	7.5	30
	14	Ūla	4.8	12.0	48
	15	Šalčia	5.0	8.0	32
Total and average for cluster III			4.6	35.0	140
IV	16	Middle Merkys	18.5	21.0	84
	17	Šventoji	30.0	9.0	36
	18	Lower Merkys	32.2	11.0	44
Total and average for cluster IV			23.9	41.0	164

The number of beaver scent mounds (freshly made, with characteristic odour or without) as well as of other signs of beaver activity (tracks, trails, feeding places) were registered in each 0.25 km cut-off of shore line within an approximately 10 m wide zone from water edge. Two indices – the scent marking intensity (the number of scent mounds per 0.25 km) and relative abundance of beavers (expressed as the number of beaver activity signs except scent mounds per 0.25 km) were analysed. The relation between the scent marking intensity and the relative abundance was investigated using regression analysis. The significance of differences among river clusters was tested using the ANOVA and t-tests with a 5% level of significance.

Results

There was a significant difference in the scent marking intensity between each of the four river clusters (ANOVA test, $\chi^2 = 47.91$, df = 3, $p < 0.000$). It consecutively increased from the smallest rivers (cluster I, 0.6 scent mound/0.25 km) to the medium-sized rivers (cluster III, 1.8 scent mound/0.25 km) (t-test, t = 6.28, df = 307, $p < 0.000$), and then decreased again in the large rivers (cluster IV, 1.0 scent mound/0.25 km) (t-test, t = 3.58, df = 303, $p < 0.000$) (Tabs. 2, 3). The smallest rivers (I cluster) exhibited the most distinct difference in the scent marking intensity compared to the other clusters.

A slightly different pattern was discovered concerning the differences in relative abundance among river clusters (Tabs. 2, 3). Despite statistically significant differences between each of the clusters (ANOVA test, $\chi^2 = 43.41$, df = 3, $p < 0.000$), there was no obvious tendency of increase from cluster I to III. The highest relative abundance was established in the medium-sized rivers (cluster III, 4.8 sign/0.25 km). However, the smallest rivers (cluster I) also exhibited high relative abundance (3.5 sign/0.25 km). The difference between these two clusters was significant (t-test, t = 2.65, df = 307, $p < 0.008$), but lower than in the case of the scent marking intensity. The lowest level of relative abundance was found in the large rivers (cluster IV, 2.4 sign/0.25 km), followed by the small rivers (cluster II, 2.6 sign/0.25 km), and there was no significant difference between these two clusters (t-test, t = 0.79, df = 318, $p < 0.429$). A significant positive correlation between the scent marking intensity and the relative abundance was established by analysing averages

Table 2. Scent marking intensity (mean number of scent mounds/0.25 km) and relative abundance (mean number of other signs of beaver activity except scent mounds/0.25 km) in clusters of rivers of differing sizes

Cluster of rivers	Mean Q, m^3/s	n	Scent marking intensity, x ± SE	Relative abudance, x ± SE
I	0.6	168	0.6 ± 0.088	3.5 ± 0.320
II	2.5	156	1.3 ± 0.166	2.6 ± 0.226
III	4.6	140	1.8 ± 0.167	4.8 ± 0.364
IV	23.9	164	1.0 ± 0.128	2.4 ± 0.210

Table 3. Matrix of significance of differences in scent marking intensity (top right) and relative abundance (bottom left) between pairwise compared river clusters (t; p); df varies from 295 to 330

River clusters	I	II	III	IV
I		3.53; 0.000	6.28; 0.000	2.53; 0.012
II	2.24; 0.026		2.06; 0.040	1.24; 0.217
III	2.65; 0.008	5.17; 0.000		3.58; 0.000
IV	2.94; 0.003	0.79; 0.429	5.93; 0.000	

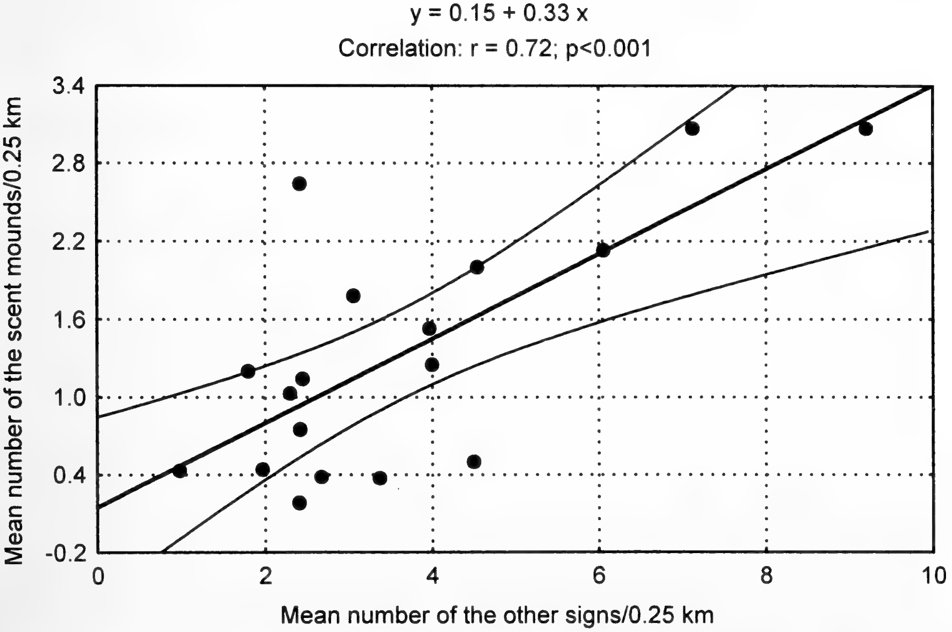

Fig. 2. Relation between the scent marking intensity (y) and the relative abundance (x) of beaver in all the river segments investigated.

Table 4. Correlation between the scent marking intensity and relative abundance per 0.25 km in separate clusters of rivers of different size

Cluster of rivers	Mean Q, m^3/s	n	Coefficient of correlation, r	p<
I	0.6	168	0.02	0.767
II	2.5	156	0.35	0.001
III	4.6	140	0.41	0.001
IV	23.9	164	0.48	0.001

of these indices in the river segments investigated ($r = 0.72$, $p < 0.001$) (Fig. 2). However, some specifities in this relation in separate river clusters were found (Tab. 4). The absolute numbers of the scent mounds and the other signs in 0.25 km cut-offs mostly correlated in the larger rivers (cluster IV, $r = 0.48$; $p < 0.001$). The coefficient of correlation decreased slightly from the large (IV cluster) to small rivers (II cluster), and there was no correlation in the smallest rivers (I cluster, $r = 0.02$; $p < 0.767$).

Discussion

Scent marks are generally considered multifunctional signals (Gosling 1982 for review; Hodgdon and Lancia 1983; Djozhkin et al. 1986; Benhamou 1989). However, one of the most important functions of scent marking is a territory occupancy indication to potential intruders (Gosling 1982; Gosling and Wright 1994; Rosell and Nolet 1997; Rosell et al. 1998). Beavers display very strong and consistent responses to strange scent marks in free-ranging colonies (Müller-Schwarze and Heckman 1980; Müller-Schwarze et al. 1983; Müller-Schwarze and Houlihan 1991; Sun and Müller-Schwarze 1997). In captivity, on the contrary, scent marking activity can be very low, and this can be explained by an absence of motivation (Nitsche 1987). Migrating beavers avoid occupied territories (Aleksiuk 1968). In dense beaver populations, however, the dispersing young very often suffer in encounters with territory owners (Kudriashov 1975).

Scent marking patterns discovered in abundant beaver populations could be explained as a response of territory owners to the differing numbers of transient subadults in rivers of different sizes.

In the smallest rivers, despite high relative abundance, beavers scent marked at relatively low levels. The relatively high isolation of the beaver sites in small streams could be one of the explanations of this phenomenon. The absence of correlation between the scent marking intensity and the relative abundance in small streams also suggests possibly low need for territorial defence. Along the smallest rivers, beaver sites are more isolated from each other and more compactly situated than at the larger streams (Djakov 1975). It has been found in Canadian beaver, that the higher scent marking activity was characteristic for the less isolated beaver families (Butler and Butler 1979; Svendsen 1980). Shallow water and narrow water ways can substantially limit the possibilities of beaver migration. Also, numerous beaver dams in separate sites might be an important impediment for strangers, because dams are intensively controlled by territory owners (Brady and Svendsen 1981). In such conditions, after the first contacts with resident beavers, migrating beavers tend to avoid moving along densely inhabited small streams, and possibly prefer to return to the maternal site or cross watersheds. We have personal reports from Lithuanian foresters and hunters concerning the frequent observations of young beavers in atypical places quite far from water bodies in spring.

There are no beaver dams in the medium-sized rivers, and the water yield conditions are better for migration of transient beavers than those in the smallest rivers. However, the probability of encounters in medium-sized rivers seems to be significantly higher because of the potentially greater number of migrants and the ability to control the whole water area inside the family range by the territory owners. The greater number of migrants possibly initiates more intensive scent marking which is proportional to the beaver activity (relative abundance). In our study this was expressed by the presence of a positive correlation between these two indices.

In the large rivers, a decrease of scent marking might be related to the low probability of contact between the resident and transient beavers. However, in wide open habitats, the scent marking intensity might also be dependent on other factors which can be not so important in small isolated habitats. For example, in large open areas, more so than in compact sites, beavers probably need not only to defend their territories, but also to communicate between the family members by means of scent marking. Beavers can distinguish between the scent mounds marked by relatives from those marked by the unfamiliar non-relatives (SUN and MÜLLER-SCHWARZE 1997). Other aspects that could be related are the higher investigative activity and movement of beavers inhabiting wide territories along large rivers. The olfactory orientation model suggests that most mammals can use their own scent marks to orient themselves within their home range (BENHAMOU 1989).

Our study shows that the scent marking intensity could be an informative index for the evaluation of the migrating state of various intrapopulationary beaver groups inhabiting different systems of the hydrographical network, especially the drainage systems of small to medium-sized rivers.

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Zusammenfassung

Intensität von Reviermarkierungen des Bibers (Castor fiber) an unterschiedlich großen Flüssen.

Biber, die ein Revier bewohnen, reagieren in der Intensität ihrer Markierungen auf die unterschiedliche Anzahl durchziehender Biber. Ohne Zweifel sind Flüsse die Hauptwege für die Ausbreitung von Bibern. Da Einzugsgebiete größerer Flüsse potentiell auch eine größere Anzahl von Bibern beheimaten, ist die Intensität der Abwanderung sub-adulter Biber auch abhängig von der Größe des Flusses. Während der Zeit der Abwanderung sub-adulter Biber vom April bis in die erste Mai-Dekade wurden an 18 Abschnitten verschiedener Flüsse in Litauen die Intensität der Markierung (Anzahl der Markierungsstellen pro 0,25 km Uferlinie) und die relative Abundanz (Anzahl der Aktivitätsanzeichen von Bibern pro 0,25 km Uferlinie) untersucht. Die Wasserdurchflußmenge (Q) der Flußabschnitte variierte von 0,4 bis 32,2 m^3/s. Nach unserer Meinung ist die Biberpopulation in Litauen stark. Gerade die kleinsten Randgewässer sind sehr dicht von Bibern besiedelt und das erschwert die Ausbreitung von Nachwuchs besonders.

Die höchste Markierungsintensität (1,8 Markierungsstellen pro 0,25 km Uferlinie) wurde an den mittelgroßen Flüssen (Q im Mittel = 4,6 m^3/s), die geringste (0,6 Markierungsstellen pro 0.25 km Uferlinie) in den kleinsten Flüssen (Q im Mittel = 0,6 m^3/s) gefunden. Die Intensität der Reviermarkierung war positiv signifikant in Bezug auf die relative Abundanz in den meisten Flüssen, nicht aber in den kleinsten. Die Ergebnisse werden unter dem Aspekt diskutiert, daß Biber in besetzten Revieren unterschiedlich auf die Wanderung sub-adulter Biber an Flüssen verschiedener Größenordnungen reagieren. Das System von Reviermarkierungsplätzen zeigt, das es sich hierbei um einen wichtigen Mechanismus zur Selbstregulation einer Biberpopulation handelt.

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Habitat use by mountain vizcachas (*Lagidium viscacia* Molina, 1782) in the Patagonian steppe

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Abstract

The mountain vizcacha is a hystricomorph rodent of South America that inhabits rocky cliffs and outcrops in the southern Andes and the Patagonian steppe. We investigated habitat use of the mountain vizcacha in the Patagonian steppe by describing characteristics of the rocky cliffs that are associated with use by mountain vizcachas and habitat characteristics associated with their movements away from the cliffs. Steeper portions of the cliffs were more heavily used than less steep portions. Movements away from the cliffs were strongly associated with the amount of rock present. Habitat use by mountain vizcachas both on and away from the cliffs appears to be driven by predator avoidance. Mountain vizcachas can probably more easily escape terrestrial predators on a steep slope. They rarely venture away from rocks which may provide a means for escape from both aerial and terrestrial predators, even when they are away from the cliffs. There is presently very little predation on mountain vizcachas by native raptors and carnivores in this area, and humans are its major predators. The mountain vizcacha's pattern of habitat use, although it may have evolved in response to predation, now makes it very vulnerable to human predation.

Key words: *Lagidium viscacia*, habitat use, predation risk, Patagonia

Introduction

Mountain vizcachas (*Lagidium* spp., family Chinchillidae) are medium-sized hystricomorph rodents which live in rocky habitats in the southern Andes and the Patagonian steppe of South America (Redford and Eisenberg 1992). The mountain vizcachas of the northern Patagonian steppe (*Lagidium viscacia*) consume a variety of grasses, shrubs, and herbs, but select heavily for grasses (Galende et al. 1998; Puig et al. 1998). They may be observed in their rocky habitat during the day, sunning, grooming, and playing outside of their dens in rock crevices. When they are chased or frightened they run across the rocks to hide under rock piles or in crevices. They descend from the rocks to forage during the day and at night.

In the last hundred years, the steppe habitat of the mountain vizcacha in Argentine Patagonia has been greatly altered by grazing of domestic livestock and introduced wildlife. The diets of these exotic herbivores overlap greatly with that of mountain vizcachas (Galende and Grigera 1998). The effects of changes in plant structure and distribution on mountain vizcacha movements have not been studied. Movements of another rock-

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dwelling mammal, the pika (*Ochotona collaris*), have been shown to be affected by availability of food plants, but limited by proximity of those plants to rocks, due to increased predation risk away from the rocks (Holmes 1991).

In this study we described habitat use by mountain vizcachas in the Patagonian steppe of Argentina in two dimensions, by evaluating habitat characteristics of the rocky cliffs they inhabit and also those habitat characteristics associated with their movement away from the cliffs. We hypothesized that habitat use by mountain vizcachas is constrained by distribution of plant foods and predation risk. We predicted that mountain vizcacha presence is associated with habitat characteristics related to food availability and escape and shelter from predators. Potential predators of mountain vizcachas in the study area are buzzard eagles (*Geranoaetus melanoleucos*), great horned owls (*Bubo virginianus*), barn owls (*Tyto alba*), culpeo foxes (*Pseudalopex culpaeus*), pumas (*Puma concolor*), Geoffroy's cats (*Oncifelis geoffroyi*), and minor grisons (*Galictis cuja*).

Material and methods

The study area is in southern Neuquén Province, Argentina. Vegetation is characterized as a grass-shrub steppe with an average ground cover of about 50% (León et al. 1998). There are numerous basaltic rock outcrops, many in the form of cliffs with vertical faces and flat tops. The study was conducted at four sites during the Patagonian summer, from January to March 1996.

We used fecal pellets as an indication of the past presence of mountain vizcachas at a certain place. Mountain vizcachas leave piles of feces at their sunning spots on the rocks and defecate during foraging as well. The use of fecal pellets to determine habitat use is often complicated by differences in defecating behavior among different habitat types or differential visibility of feces. In this study we did not compare different habitat types, but measured habitat characteristics at different points within a single habitat type (within the cliff or within the grass-shrub steppe away from the cliff). Sampling units away from the cliff were small enough ($2\ m^2$) to be inspected thoroughly for feces.

Use of cliffs

We walked transects along the tops of eight cliffs, measuring habitat variables at two randomly-chosen points within each 100 meters of transect. To estimate the amount of use of a point by mountain vizcachas we recorded the number of fresh piles of fecal pellets within 10 meters of the point. Habitat variables measured were the distance between rock crevices, depth and width of rock crevices (assumed to be related to shelter from predators), and height and slope of the cliff (related to escape from terrestrial predators, assuming that these predators are unable to move as rapidly up steep, high cliffs as mountain vizcachas). We performed a multiple regression of the habitat variables measured on the number of fecal piles at a point, it is likely that variables measured at points within the same cliff are spatially autocorrelated. Therefore, we determined significance levels independently of any theoretical distribution (Legendre and Fortin 1989) by bootstrapping the regression 1000 times (Bruce et al. 1995).

In addition, for five cliffs we made mark-resight estimates of population size. We captured several mountain vizcachas from each cliff, placed colored plastic discs in both ears, and released them at the site of capture. Individuals could be identified by unique color combinations of the plastic discs. We returned to the cliffs several days later, counted marked and unmarked vizcachas, and used an unbiased Lincoln-Petersen estimator (Lancia et al. 1994) to estimate the population size (Walker et al. 2000). We did a least-squares regression between the average values for the habitat variables and the estimated number of individuals at each cliff. The small sample size precluded the use of multiple regression for this number of independent variables, so we did a separate regression for each variable. Measurements of the rocks (distance between crevices and width and depth of crevices) were log-transformed to normalize their distributions.

Movement away from cliffs

At ten cliffs we studied habitat characteristics associated with mountain vizcacha movements away from cliffs. We randomly chose two points within each 100 meters of the cliff. From each of these points, along a line perpendicular to the cliff, we randomly located one 2 m×2 m quadrat within each of four strata. These strata were 0–15 m (A), 16 to 50 m (B), 51–85 m (C), and 86–120 m (D) from the top and bottom of the cliff. Within the quadrats we recorded percent cover of rocks (related to escape from predators), shrubs, grasses, forbs (positively related to forage availability), the invasive annual grass *Bromus tectorum*, bare soil, and dead vegetation (negatively related to forage availability). We did an arc-sine transformation of these percentages prior to analysis to improve normality (SOKAL and ROHLF 1995). We also recorded the presence of rock, shrub or grass > 30 cm high (related to shelter from aerial predators), and of feces of mountain vizcachas in each quadrat. We did univariate tests for each variable (univariate logistic regression for continuous and chi-square tests for discrete variables) to determine which to include in a multivariate test. We did a multivariate logistic regression, including all variables with a probability of < 0.10 in the univariate tests, to evaluate which habitat variables were associated with presence of mountain vizcachas within a quadrat (HOSMER and LEMESHOW 1989).

All statistical analyses were performed with the program Statistica (STATSOFT 1995) except for the randomization tests which were performed with the program Resampling Stats (Simon et al. 1995).

Results

Use of cliffs

The extent to which different portions of a cliff were used by mountain vizcachas was related to the width of rock crevices and the slope of that portion of the cliff (Tab. 1). When variables with probabilities > 0.05 in the multiple regression model were excluded, the final regression resulted in coefficients of 0.10 for slope of the cliff ($p < 0.01$), 0.09 for the width of the crevice ($p = 0.01$), and –1.59 for the intercept ($p = 0.83$). The portions of the cliffs that were steeper and had wider crevices were more heavily used than portions that were less steep, with narrower crevices.

The average slope of the cliff was also the variable most strongly related to the number of individual mountain vizcachas at the five cliffs where we had population size estimates (Tab. 2). The steeper cliffs had more mountain vizcachas.

Table 1. Bootstrapped multiple regression of habitat variables of cliffs inhabited by mountain vizcachas and number of fresh piles of mountain vizcacha feces at points along cliffs. Range = range of measurements encountered.

	Range	Coefficient	p-values
Intercept		–2.23	0.89
Distance between crevices	5–226 cm	<–0.00	0.57
Width of crevices	1–40 cm	0.08	0.05
Depth of crevices	5–145 cm	<0.00	0.46
Height of cliff	3–23 m	–0.13	0.95
Slope of cliff	22–59°	0.16	<0.00

Table 2. Regressions of average of habitat variables measured at a cliff and number of mountain vizcachas at a cliff (S. E. = standard error of the coefficient; df = 3 for all tests).

	Coefficient	S. E.	t	p-values
Distance between crevices	0.11	±1.05	0.10	0.93
Width of crevices	0.90	±0.91	0.99	0.41
Depth of crevices	1.80	±1.27	1.42	0.25
Height of cliff	0.20	±0.11	1.80	0.17
Slope of cliff	8.92	±2.31	3.86	0.03

Movements away from cliffs

Mountain vizcacha feces were less likely to be found as distance from the rocky cliff increased. In a logistic regression analysis ($n = 228$) testing the probability of encountering mountain vizcacha feces away from the cliff as compared to the probability of encountering them in stratum A (≤ 15 m from the cliff), coefficients for the strata away from the cliff were negative and increased in magnitude with distance from the cliff (stratum B = –1.67, $p < 0.00$; stratum C = –2.09, $p < 0.001$; stratum D = –2.76, $p < 0.00$). In a logistic regression without stratum A ($n = 169$), there was no difference in use of strata B and C ($p = 0.74$), but signs of mountain vizcachas were less likely to be encountered in D (coefficient = –0.58, $p = 0.04$). Thus, mountain vizcachas used the first 15 meters away from the cliff much more heavily than the area 15–85 meters away, and were even less likely to use areas > 85 meters away.

Because activity of mountain vizcachas was so highly concentrated in the first stratum, we removed this stratum from the remainder of the analyses to facilitate detection of differences associated with habitat characteristics away from the cliff. In the univariate analyses, presence of mountain vizcacha feces in a quadrat was positively associated with percent of rocky cover and the presence of rocks > 30 cm in the quadrat (Tab. 3 and 4). Presence of feces was negatively associated with the percent cover of bare ground, dead vegetation and *Bromus tectorum* (Tab. 3). There was no association between presence of mountain vizcacha feces and amount of vegetative cover (other than that of the invasive *Bromus tectorum*) or the presence of grasses or shrubs > 30 cm tall (Tab. 3 and 4). In the

Table 3. Univariate logistic regressions of presence of mountain vizcacha pellets and percent cover of micro-habitat variables measured in quadrats away from cliffs (Mean = mean percentage of cover within quadrats with and without mountain vizcacha feces; S. E. = standard error of the estimate; df = 167 for all tests).

	Mean without vizcacha feces (±S. E.)	Mean with vizcacha feces (±S. E.)	Estimate	S. E.	t	p-values
Bare ground	21.9 (1.8)	15.3 (2.6)	–1.31	±0.74	–1.77	0.08
Rock	20.5 (1.9)	40.2 (3.8)	2.97	±0.66	4.50	0.00
Dead vegetation	20.0 (1.7)	12.4 (2.1)	–1.96	±0.87	–2.26	0.02
Shrubs	22.0 (2.1)	20.9 (2.8)	0.16	±0.55	0.30	0.76
Grasses	9.3 (0.9)	7.7 (1.5)	–0.71	±1.01	–0.71	0.48
Forbs	2.6 (0.5)	2.8 (0.9)	0.69	±1.35	0.51	0.61
Bromus tectorum	6.7 (0.8)	4.2 (1.2)	–2.81	±1.29	–2.18	0.03

Table 4. Univariate chi-square tests of association of rock, shrub, and grass > 30 cm tall with presence of mountain vizcacha feces in quadrats away from cliffs (df = 1 for each test).

	Number of Unoccupied Quadrats	Number of Occupied Quadrats	Chi-square	p-values
Tall rock	26	16	4.72	0.03
No tall rock	100	27		
Tall shrub	42	15	0.03	0.85
No tall shrub	84	42		
Tall grass	30	7	1.06	0.30
No tall grass	96	36		

Table 5. Parameter estimates and probabilities in multivariate logistic regression of presence of mountain vizcacha fecal pellets in a quadrat and micro-habitat variables with $p < 0.10$ in univariate tests (S. E. = standard error of the estimate; df = 163).

	Estimate	S. E.	t	p-values
Constant	–1.88	0.96	–1.96	0.05
Bare ground	–0.42	0.89	–0.47	0.64
Rock	2.86	0.87	3.29	< 0.00
Dead vegetation	–0.38	1.06	–0.35	0.72
Bromus tectorum	–1.77	1.44	–1.23	0.22
Presence of rock > 30 cm	–0.35	0.48	–0.73	0.47

Table 6. Two-factor ANOVA (Site, Presence of Mountain Vizcachas) with percent of rocky cover as dependent variable (MS Effect = mean square of the independent variable term; MS Error mean square of the error term).

	df Effect	MS Effect	df Error	MS Error	F	p-values
Site	3	0.05	161	0.09	0.58	0.63
Vizcachas	1	1.00	161	0.09	10.75	< 0.00
Site*Vizcacha	3	0.05	161	0.09	0.55	0.65

multivariate logistic regression analysis including those variables with a probability of < 0.10 in the univariate tests, the only variable that was significantly correlated with presence of mountain vizcachas away from the cliff was the percentage of a quadrat which was covered by rock (Tab. 5). A final logistic regression model using only the amount of rocky cover significantly predicted the presence of mountain vizcacha feces in a quadrat ($Chi^2 = 25.07$; df = 1; $p < 0.001$).

To determine if this effect of amount of rock was due to differences or correlations among the four sites within which the ten cliffs were located, we did an ANOVA with two factors, site and presence/absence of mountain vizcachas, and rocky cover as the dependent variable (Tab. 6). This analysis indicated that rocky cover did not differ by site, and that there was no interaction between site and presence/absence of mountain vizcachas. Thus, differences among sites in abundance of mountain vizcachas and/or availability of rock are not responsible for the relationship we found between the probability of presence of mountain vizcachas and amount of rocky cover.

Discussion

Presence of mountain vizcachas was associated with habitat characteristics related to escape and shelter from predators within the cliff. Mountain vizcachas can probably more rapidly escape terrestrial predators on the steeper rocky terrain which they use more heavily than less steep areas, and wide crevices in the rocks of the cliff provide refuge from predators. Away from the protection of the cliff, the ability to quickly return by running over rock appears to be more important than the availability of shelter, as the mountain vizcachas preferred rocky substrate over tall rocks and vegetation.

Mountain vizcacha presence was not related to the amount of vegetation, suggesting that access to vegetation is constrained by its proximity to rocks, as is the case for the pika (Holmes 1991). However, our inability to document any relationship between vegetation and mountain vizcacha movements could be caused by our failure to distinguish among grass species. Puig et al. (1998) suggest that as mountain vizcachas move farther from the cliff they are increasingly selective in their diet. Nevertheless, if such an association was present in our study, movements of mountain vizcachas were still limited to areas with adequate rock cover. If local food sources are reduced or depleted, as may occur with overgrazing by domestic livestock and exotic species, mountain vizcachas may be unable to extend their foraging activities beyond a safe distance from the cliff or rocky areas. This would result in reduced carrying capacities of cliffs and decreased population sizes of mountain vizcachas. Indeed, mountain vizcacha numbers have declined in our study area over recent years, both in numbers of colonies and numbers of individuals within colonies (Walker and Novaro unpubl. data).

Diets of all potential predator species have been studied within the area during the last ten years, without revealing a single case of predation on mountain vizcachas (buzzard eagles: Hiraldo et al. 1995; great horned owls: Donázar et al. 1997; barn owls: Travaini et al. 1997; grisons: Diuk-Wasser and Cassini 1998; great horned owls: Trejo and Grigera 1998; culpeo foxes, pumas, Geoffroy's cat: Novaro et al. 2000). A study done in the area 40 years ago reported consumption of mountain vizcachas by culpeo foxes (Crespo and DeCarlo 1963). The European hare (*Lepus europeaus*) was introduced to Argentina in 1896 (Grigera and Rapoport 1983) and spread into this area of Patagonia a few decades later. It is currently the main component of the diet of most predators, and may have replaced the similarly-sized mountain vizcacha as a prey item in the area (Novaro et al. 2000). Predation on mountain vizcachas by terrestrial predators at a site without hares in the puna of northern Argentina is very heavy (Perovic et al., unpubl. data). Predators at this site include the culpeo fox and puma, as in the Patagonian steppe, but also the Andean cat (*Oreailurus jacobita*), which may be specialized for predation on mountain vizcachas.

Although the mountain vizcacha in this region of the Patagonian steppe is not presently a major component of the carnivores' diets, it probably had a long evolutionary history during which it was. In the absence of heavy predation pressure today its behaviour may continue to be driven by predator avoidance. Very low levels of predation may still be a major threat to already reduced populations of mountain vizcachas, however. As local populations may be very small and dispersal corridors interrupted by human activities, even occasional loss of individuals to predation could contribute to local extinctions due to demographic stochasticity.

Currently, the primary predators of mountain vizcachas in our study area are humans. Mountain vizcachas are frequently hunted by local people for food (Funes and Novaro 1999) and for sport. The behaviors this rock-dwelling species has evolved to avoid predation are not effective for the evasion of human predation. A mountain vizcacha perched on a steep rocky cliff may be inaccessible to terrestrial predators and may see the approach of both aerial and terrestrial predators from far away, but is an easy target for a rifle. Isolated local populations are easily hunted to extinction by humans (Walker and Novaro, unpubl. data). Thus the mountain vizcachas of the Patagonian steppe exhibit a pattern of habitat use which probably helped them avoid predation in the past, but which paradoxically exposes them to greater risk of predation by humans today.

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Zusammenfassung

Habitatnutzung durch Bergviscachas (Lagidium viscacia Molina, 1782) in der patagonischen Steppe

Das Bergviscacha ist ein hystricomorphes Nagetier Südamerikas, das felsige Höhenzüge und Felsengelände der südlichen Anden und der patagonischen Steppe bewohnt. Untersucht wird die Lebensraumnutzung des Bergviscachas in der patagonischen Steppe, indem Charakteristika der felsigen Höhenzüge beschrieben werden, die mit der Nutzung durch das Bergviscacha zusammenhängen, sowie Charakteristika des Habitats, die mit Ortsveränderungen außerhalb der Höhenzüge zusammenhängen. Steilere Felsabschnitte wurden intensiver genutzt als weniger steile. Die Ortsveränderungen außerhalb der Höhenzüge hingen eng mit der Größe vorhandener Felsmassen zusammen. Die Habitatnutzung der Bergviscachas scheint inner- wie außerhalb der Höhenzüge durch die Vermeidung von Räubern beeinflusst.

Bergviscachas können Landraubtieren wahrscheinlich auf einem steilen Abhang leichter entkommen. Sie wagen sich selten von Felsen fort, die auch außerhalb der Höhenzüge Fluchtmöglichkeiten sowohl vor Luft- wie vor Landraubtieren bieten. Es gibt zur Zeit in diesem Gebiet sehr wenig Prädation auf Bergviscachas durch einheimische Greifvögel und Fleischfresser, wodurch der Mensch zum wichtigsten Räuber wurde. Wenngleich das Muster der Habitatnutzung des Bergviscachas als Reaktion auf Verfolgung durch tierische Räuber entstanden sein mag, wird es hingegen sehr anfällig für Verfolgung durch den Menschen.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Genetic diversity within and among populations of the microchiropteran bat *Hipposideros speoris* based on a RAPD analysis

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Key words: *Hipposideros*, bat, genetic diversity, RAPD, PCR

The microchiropteran bat *Hipposideros speoris* inhabits the southern and central parts of India. It prefers to roost in caves and old buildings (Brosset 1962). It lives in colonies with 100–1000 individuals per colony. A colony consists of both sexes with mixed ages. Apparently *H. speoris* breeds throughout the year with maximum number of young between August and October (Radhamani 1996). Based on a survey, the Biodiversity Conservation Prioritisation Project, India, (1998) placed *H. speoris* in the category "Lower risk – near threatened". In the present study we used RAPD – PCR to determine genetic variation within and between populations. The major objective is to provide first information on gene pool differentiation among regional populations in Southern India.

A total of 40 bats was captured using nylon mosquito net and mist net from five local populations (n = 9, 6, 6, 11, and 8 from the five populations, respectively; Fig. 1). Following the puncture of the median vein with a 27 – gauge needle we collected 0.25 ml blood. Blood samples thus collected were immediately mixed with anticoagulant (ACD) and stored in ice in the field and subsequently frozen at –70° C in the laboratory. Total genomic DNA was extracted from the blood and the DNA samples were diluted to 10 ng/µl for experimental use.

The PCR reaction was standardized using a protocol modified from Williams et al. (1990). Total reaction volume of 20 µl was used with a final concentration of 10 mM Tris-HCl (pH 8.0), 50 mM KCl, 1.5 mM $MgCl_2$ and 0.1% (w/v) gelatin; 2.5 mM each of dATP, dTTP, dCTP, and dGTP; 5 pM primers,10 ng of template DNA; and 0.5 unit of Taq DNA polymerase (Pharmacia, Uppsala, Sweden). Amplification was done using a Perkin Elmer Gene Amp PCR system 2400. Amplified products were electrophoresed in 8% polyacrylamide gels. The gels were silver stained and photographed.

A total of 10 arbitrary primers (OPA 3, 4, 7, 8 and 10 and OPB 1, 3, 5, 6 and 7; Bangalore Genei Pvt. Ltd., India.) was tested for five populations. Among them OPA10 (5′ GTGATCGCAG 3′) was found to be ideal for producing RAPD polymorphism in *H. speoris*. The data were scored according to Haig et al. (1994). Based on the known marker size, different polymorphic band sizes were calculated using Kodak Digital Science (ver 2.01. Kodak Scientific Imaging System, Eastman Kodak Company). TFPGA (ver 1.3) (Mark 1997) was used to construct a Nei's (1978) distance matrix for UPGMA cluster analysis. In addition G^2 was estimated for RAPD data with Popgene (ver 1.21) (Yang and Yeh 1993). Subsequently F_{st} was estimated along with contemporary estimates of gene flow (Slatkin and Barton 1989) using the formula $Nm = 0.5\ (1 - F_{st})/F_{st}$. The dis-

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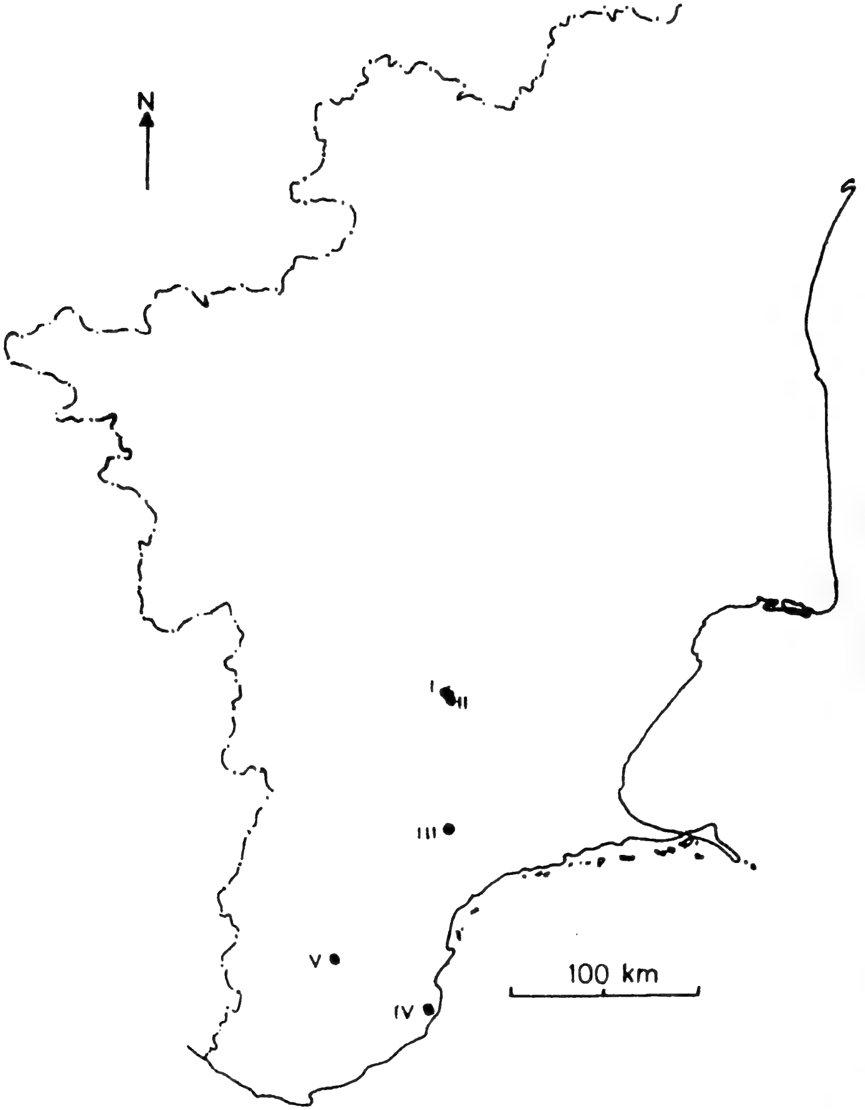

Fig. 1. Map showing the sample localities of the five populations (I to V) of *H. speoris* in South India.

tance matrices were analysed using WINAMOVA (ver 1.55) to estimate the variation among the local populations and individuals within the populations (EXCOFFIER et al. 1992).

RAPD band frequencies varied within and among all estimated populations. Figure 2 shows the representative RAPD pattern obtained with OPA 10 generated from samples of all five populations of *H. speoris*. NEI's (1978 unbiased) genetic index provides genetic diversity within the populations, as follows (Mean ± SE): population I (0.23 ± 0.07), population II (0.21 ± 0.06), population III (0.16 ± 0.08), population IV (0.22 ± 0.09) and population V (0.15 ± 0.07).

In no case did any two individuals share all the scored bands; thus, individuals of 100% similarity were not found. NEI's (1978 unbiased) genetic distance provides a second

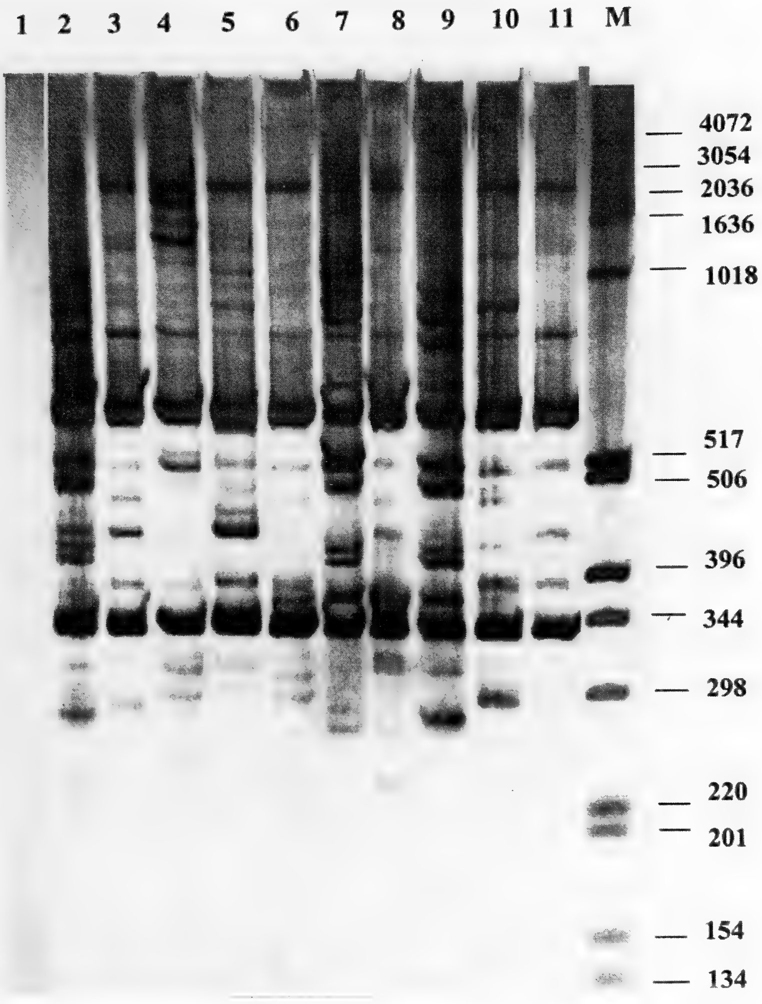

Fig. 2. RAPD amplifications with primer OPA 10 for a representative of five populations of *H. speoris.* Lane 1 is duplicate, M indicates marker, sizes in base pairs. Lanes 2 and 3 indicate population I, lanes 4 and 5 indicate population II, lanes 6 and 7 indicate population III, lanes 8 and 9 indicate population IV and lanes 10 and 11 indicate population V.

index of genetic differentiation between populations and the plotted dendrogram (Fig. 3) shows populations I and II (both were located within 3 km) clustered together as a group. Similarly, population IV and V (200 km apart from population I) clustered into another group. Population III deviated from these two groups.

An overall F_{st} value of 0.21 was obtained. Nm was 1.98, indicating a large amount of gene flow between populations. Similarly, gene frequencies vary significantly across the populations ($G^2 = 16.35$, df = 4, $P < 0.001$). The Analysis of Molecular Variance (AMOVA) permitted to partition the overall variations into two levels (Tab. 1). The individuals within populations accounted for about 76.7% of the total variance component and among populations for 23.3%. They were significantly greater than zero at the 0.05 level.

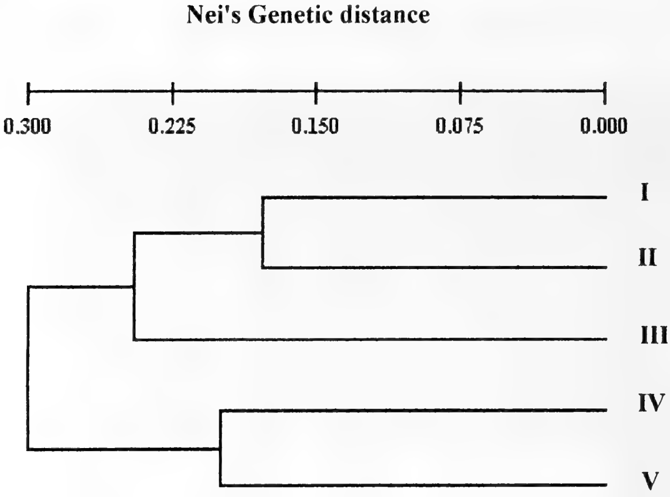

Fig. 3. UPGMA dendrogram constructed by using genetic distance (NEI'S 1978) between the populations of *H. speoris.*

Table 1. Analysis of Molecular Variation (AMOVA) for 40 individuals of *H. speoris.* The total data set contains individuals from five populations. Statistics include sum of squared deviations (SSD), mean squared deviations (MSD), variance component estimates, the percentages of total variance contributed by each component and the probability (P) of obtaining a more extreme component estimate by chance alone.

Source of Variation	SSD	MSD	Variance Component	% Total variation	*P**-value
Among Populations	152.89	38.22	1.37	23.3	< 0.001
Individuals within Populations	536.37	17.23	4.54	76.7	

* After 1000 permutations.

RAPD is one of the methods in the study of population genetics to estimate genetic variability, relatedness, inbreeding level, species verification and pedigree analysis (JAYASANKAR and DHARMALINGAM 1997). It is used to measure the genetic diversity in population studies, based on which numerous conservation efforts have been undertaken in desert fishes (VIRJENHOEK 1995), sea turtles (BOWEN and AVISE 1995) and whales (BAKER and PALUMBI 1995).

Our results enable us to emphasize the genetic diversity in the local populations of *H. speoris.* Similarly, the genetic diversity within and between populations was observed in other bat species such as the little red flying-fox *Pteropus scapulatus* (SINCLAIR et al. 1996), *Tadarida brasiliensis* (McCRACKEN et al. 1994), Australian flying-fox *Pteropus* spp. (WEBB and TIDEMANN 1996) using conventional protein (allozymes) markers and *Myotis myotis* (PETRI et al. 1997) using DNA (mtDNA and simple sequence repeats) markers. SLATKIN (1985) suggested that significant differentiation between populations would be expected only when the Nm value was < 1. The high value of Nm (1.98) in our study indicates a large amount of gene flow between all populations. Similarly, the Nm was low at

0.05 for the megachiropteran *Haplonycteris fischeri*, a species known to have low vagility compared with an Nm of 7.5 for another megachiropteran *Cynopterus brachyotis*, which is an effective seed disperser (PETERSON and HEANEY 1993).

In *H. speoris* the probability of outbreeding in a geographically closely located population is high. In this species, during the reproductive period freshly matured females move away from the native colony (RADHAMANI 1996). Such natal dispersal behaviour influences also the genetic variation in *Oryctolagus cunniculus* (WEBB et al. 1995) and generally avoids inbreeding (PUSEY and WOLF 1996). Our genetic analysis suggests that *H. speoris* should be treated as an interbreeding unit for management purposes.

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Ground squirrel activity during the solar eclipse of August 11, 1999.

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Key words: *Spermophilus citellus*, circadian, solar eclipse, light intensity, telemetry

European ground squirrels (*Spermophilus citellus*) in their natural habitat emerge from their burrows ~4 hours after twilight at dawn and disappear ~3 hours before twilight at dusk (Hut et al. 1999). Entrainment of their endogenous circadian rhythm apparently does not require the perception of twilight. They might, however, respond to the small (average 1 log unit) afternoon decrease in light intensity by retreating in darkness underground, thereby generating a secondary lights-off signal used for entrainment of their endogenous circadian clock.

To test whether ground squirrels respond to a decrease in light intensity in this manner, we exploited the solar eclipse of August 11, 1999. At 12:46 local time, the moon covered 99% of the sun above a field population of European ground squirrels near Vienna. Austria (48°18′ N, 16°22′ E) (Millesi et al. 1999). On August 10, 11 and 12, the number of ground squirrels above ground was counted every 5 min in a 1 ha area, from ~06:00 h until ~20:00 h. Light intensity was measured every 10 min. Around the partial solar eclipse, data were recorded every 1 min. Light intensity was 24 · 103–37 · 10^3 Lux at the appearance of the first ground squirrel above ground, and 20 · 10^3–27 · 10^3 Lux when the last animal retreated (Fig. 1). Rain suppressed above ground activity, and persistent rain on August 10 precluded data acquisition from 16:20 onwards. The sky was clear during the partial solar eclipse. Light intensity before the eclipse (11:16–11:46) was circa 110 · 10^3 Lux and dropped to 1039 Lux at 12:46. From 12:16–13:16 on average 16.3 animals were active above ground. This number was similar, and certainly not decreased relative to either the hour before (15.4) or the hour after the eclipse (16.4).

Five ground squirrels were equipped with light-sensitive radio transmitter collars (Hut et al. 1999) on August 9. Their presence above ground during August 10–12 was recorded every 10 min, and every 1 min around the time of the eclipse. Four of these animals were above ground for most (156–160 min, 20 min absence by rain) of a three-hour period around the eclipse. The remaining animal was underground for two brief episodes of 21 and 12 min, very similar to its activity pattern during the rest of the day.

Thus, the animals did not retreat into their burrows in response to the partial solar eclipse, even though light intensity was reduced by two log units, well below levels normally perceived at the end of activity. It is unlikely that the daily afternoon retreat into the burrow is a response to the change in light intensity in European ground squirrels.

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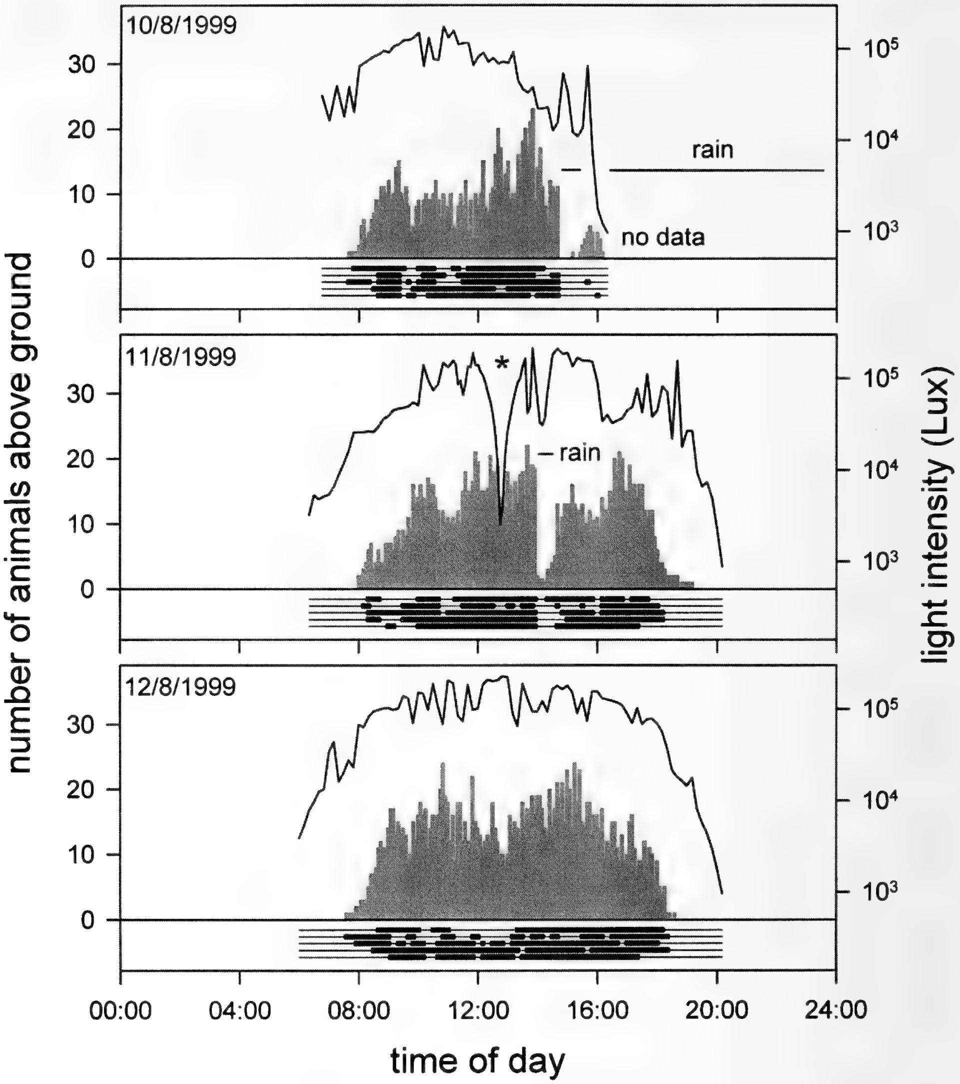

Fig. 1. Number of ground squirrels active above ground and concurrent light intensity (Lux), observed in a 1 ha focal area in a population of European ground squirrels near Vienna, Austria. Bars indicate presence of animals with a radio transmitter above (thick bars) or under (thin bars) ground. * Denotes timing of the partial (99%) solar eclipse at 12:46 local time, on August 11, 1999 (civil twilight dawn 5:07; civil twilight dusk 20:51).

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Contributions to the karyology and taxonomy of *Spalax leucodon nehringi* Satunin, 1898 and *Spalax leucodon armeniacus* Mehely, 1909 (Mammalia: Rodentia) in Turkey

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Key words: *Spalax leucodon*, karyology, taxonomy, Turkey

The subterranean mole rats belonging to the family Spalacidae are widely distributed in southeastern Europe, Asia Minor, Caucasus, Transcaucasus, Ukraine, Armenia, Syria, Palestine, Iraq, Israel, Jordan, and northeastern Africa (Ognev 1947; Ondrias 1966; Lay and Nadler 1972; Corbet 1978; Savic and Nevo 1990; Nevo 1991; Harrison and Bates 1991). To date, about 50 chromosomal forms of *Spalax* have been reported in the literature from these areas.

According to the most recent morphological studies there are two species (*S. leucodon* (Nordmann, 1840) and *S. ehrenbergi* Nehring, 1898) and nine subspecies (*S. l. nehringi* Satunin, 1898; *S. l. armeniacus* Mehely, 1909; *S. l. cilicicus* Mehely, 1909; *S. l. anatolicus* Mehely, 1909; *S. l. turcicus* Mehely, 1909; *S. l. tuncelicus* Coşkun, 1996; *S. l. nevoi* Coşkun, 1996; *S. e. intermedius* Nehring, 1898, and *S. e. kirgisorum* Nehring, 1898) of blind mole rats in Turkey (Kivanç 1988; Coşkun 1996 a, b). However, the results from karyological studies revealed ten karyological forms (2n = 36, 38, 40, 50, 52, 54, 56, 58, 60, and 62) of *S. leucodon* and four karyological forms (2n = 52, 54, 56, and 58) of *S. ehrenbergi* in Turkey, and the number of chromosome arms (NF) for *S. leucodon* and *S. ehrenbergi* varied from 70 to 84 and from 72 to 90, respectively (Soldatovic and Savic 1978; Savic and Soldatovic 1979; Yüksel 1984; Gülkaç and Yüksel 1989; Yüksel and Gülkaç 1992, 1995; Nevo et al. 1994, 1995; Ivanitskaya et al. 1997; Sözen and Kivaç 1998 a, b; Sözen et al. 1999) (Tab. 2). Nevo et al. (1994, 1995) stated that each of the chromosomal forms is a separate biological species. They also examined the populations by using Nei's genetic distance between populations obtained by allozyme electrophoresis and claimed that some populations having identical diploid chromosome numbers are different biological species, presumably representing about 20 such species in Turkey. Later, Sözen and Kivanç (1998 a, b) and Sözen et al. (1999) added 7 karyotypes. These results have increased the total number of alleged biological species of *Spalax* in Turkey to about 30.

The karyotypes of 5 specimens from a site 10 km W of Ardahan, 3 specimens from a site 3 km S of Susuz (Kars), and 3 specimens from a site 20 km E of Erzurum belonging to *Spalax leucodon* were analysed in the present study (Fig. 1, Tab. 1). Chromosome preparations from bone marrow were made in accordance with Ford and Hamerton (1956), and about 30 metaphase cells from each animal were examined. The karyotype preparations and animals examined were deposited in the Department of Biology, Faculty of Science, University of Ankara.

It was determined that specimens have 2 n = 50 and NF = 72 in all populations examined. The X chromosome is a large-sized metacentric, and the Y chromosome is a small

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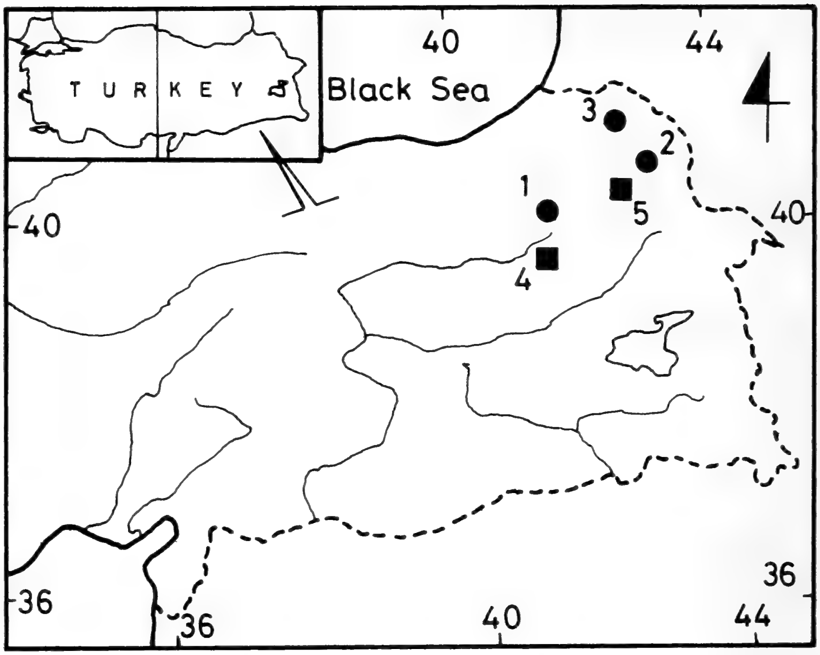

Fig. 1. Geographic distribution of 3 sampling localities (●), and recorded localities (■) by Nevo et al. (1994,1995) in Turkey: 1: 20 km E of Erzurum, 2: 3 km S of Susuz, 3: 10 km W of Ardahan, 4: 80 km S of Erzurum, 5: 14 km W of Sarıkamiş.

Table 1. The location and the number of animals examined

	Spalax leucodon nehringi Satunin, 1898		
Locality	Male	Female	Total
Erzurum 20 km E	2	1	3
	Spalax leucodon armeniacus Mehely, 1909		
Susuz 3 km S	2	1	3
Ardahan 10 km E	2	3	5

acrocentric. The autosomal set has 6 pairs of meta-submetacentrics, 4 pairs of subtelocentrics, and 14 pairs of acrocentrics. The same karyotypes were found by Nevo et al. (1994,1995) in specimens form a site 80 km S of Erzurum and 14 km W of Sarikamiş (Fig. 1, Tab. 2).

Kıvanç (1988) classified the specimens from Ardahan and Susuz as *S. l. armeniacus* and from Erzurum as *S. l. nehringi*. Nevertheless, we determined the karyotype of these populations as belonging to the same karyotypes. This result shows that, as indicated by Savic and Nevo (1990), Nevo (1991), Nevo et al. (1994, 1995), the results of morphological studies at the subspecies level require a modern revision based on chromosome and molecular-genetic data, in addition to their morphology, physiology, and behaviour.

Table 2. Chromosomal records of *Spalax leucodon* (Nordmann, 1840) and *Spalax ehrenbergi* Nehring, 1898 from Turkey
* m: metacentric, sm: submetacentric, st: subtelocentric, a: acrocentric

Spalax leucodon (Nordmann 1840)

Locality	2n	NF	NFa	X	Y	Reference
Bayındır	36	70	–	–	–	Sözen et al. (1999)
Baliikesir and İzmir	38	74	70	st	a	Nevo et al. (1994, 1995)
Havran and Selçuk	38	74	70	st*	a	Savic and Soldatovic (1979)
Beyşehir	40	72	68	sm	–	Nevo et al. (1994, 1995)
Aydın, Erzurum	50	–	–	–	–	Nevo et al. (1994, 1995)
Sarıkamış	50	72	68	sm	–	Nevo et al. (1994, 1995)
Sebil	52	72	68	sm	a	Sözen and Kıvanç (1998 a)
Bolu and Bingöl	54	–	–	–	–	Nevo et al. (1994, 1995)
Yozgat	54	74	70	sm	st	Yüksel and Gülkaç (1995)
Gülek	56	72	68	m	a	Sözen and Kıvanç (1998 a)
Çorlu and Karaevli	56	78	74	sm*	a*	Soldatovic and Savic (1978)
Madenköy	58	72	68	sm	a	Sözen and Kıvanç (1998 b)
Denizli, Pınarbaşı	60	–	–	–	–	Nevo et al. (1994, 1995)
Akşehir	60	76	72	sm	st	Sözen et al. (1999)
Malatya	60	78	74	sm	a	Ivanitskaya et al. (1997)
Malatya	60	78	74	sm	a	Nevo et al. (1994, 1995)
Malatya	60	80	76	sm	st	Yüksel (1984)
Malatya and Yazıhan	60	80	76	sm	st	Gülkaç and Yüksel (1989)
Kırşehir, Nevşehir and Kayseri	60	80	76	sm	st	Yüksel and Gülkaç (1995)
Arguvan	60	82	78	sm	–	Gülkaç and Yüksel (1989)
Ankara	60	82	78	sm	st	Sözen et al. (1999)
Afyon	60	82	78	sm	st	Sözen et al. (1999)
Burdur	60	84	80	sm	st	Sözen et al. (1999)
Kütahya, Afyon, Konya, Sivas, Ankara, Kayseri, Havza, Suşheri	62	–	–	–	–	Nevo et al. (1994, 1995)
Erzurum 20 km E	50	72	68	sm	a	This study
Susuz 3 km S	50	72	68	sm	a	This study
Kars 10 km W	50	72	68	sm	a	This study

Spalax ehrenbergi Nehring, 1998

Locality	2n	NF	NFa	X	Y	Reference
Kilis	52	74	70	sm	a	Sözen et al. (1999)
Birecik, Siverek, Diyarbakır, Elaszığ	52	76	72	sm	–	Ivanitskaya et al. (1997)
Diyarbakır, Urfa	52	76	72	–	–	Nevo et al. (1994, 1995)
Elazığ	52	76	72	sm	st	Yüksel (1984)
Adıyaman, Hilvan	52	76	72	m*	st	Yüksel and Gülkaç (1992)
Urfa	52	80	76	sm	–	Ivanitskaya et al. (1997)
Suruç	54	76	72	m	st	Yüksel and Gülkaç (1992)
Tarsus	56	72	68	–	–	Nevo et al. (1994, 1995)
Tarsus	56	72	68	m	–	Ivanitskaya et al. (1997)
Gaziantep	56	82	78	sm	–	Ivanitskaya et al. (1997)
Gaziantep	56	90	86	m	st	Yüksel and Gülkaç (1992)
Gaziantep	58	82	78	–	–	Nevo et al. (1994, 1995)

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Does environment affect polymorphism of B chromosomes in the yellow-necked mouse *Apodemus flavicollis*?

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Key words: *Apodemus flavicollis*, B chromosomes, environmental variables

B chromosomes are chromosomes additional to the standard complement. Their only consistent feature is that they are not essential for survival of an individual. Contrary to their widespread occurrence in plants and insects, they have been found so far in only 35 species of mammals (Vujošević 1993). B chromosomes are a widespread component of the genetic system of the yellow-necked mouse *Apodemus flavicollis.* In almost all the studied populations animals with Bs were present (Soldatović et al. 1975; Kral et al. 1979; Sablina et al. 1985; Giagia et al. 1985; Vujošević et al. 1991; Nadjafova et al. 1993; Zima and Macholán 1995; Boeskorov et al. 1995) with frequencies varying from 0.11 in Slovenia to 0.94 in the Western part of the Czech Republic.

B chromosomes in *A. flavicollis* are acrocentrics as are the chromosomes of the standard complement. Equilibrium frequencies of Bs were found in the course of year-to-year studies regardless of changes in population density (Vujošević 1992). On the other hand, it was found that seasonal changes in frequency of animals with Bs could be significant under conditions of stress produced by overcrowding (Blagojević and Vujošević 1995) or could follow changes in population density if abundance is moderate and there is no increased competition for food and space (Vujošević and Blagojević 1995). A number of studies in different taxonomical categories has shown that the presence of B chromosomes in certain populations can be associated with certain ecological and climatic variables (Fröst 1958; Bosemark 1956; Brown 1960; Parker et al. 1991, Confalonieri 1995). As Bs are found in different regions throughout the range of *A. flavicollis* at different frequencies, it was of interest to examine whether or not the environment influences their appearance in any way. In this study the status of B chromosomes in Yugoslavian populations of *A. flavicollis* is investigaied concerning correlations to certain environmental variables.

A total of 967 live specimens of the yellow-necked mouse *Apodemus flavicollis* was collected using "Longworth" traps at following localities in Yugoslavia (coordinates of the UTM system are given in brackets): Ada (CQ82), Avala mt. (DQ64), Cer mt. (CQ84), Donji Dobrić (CQ83), Goč mt. (DP82), Fruška Gora mt. (DR00), Jastrebac mt. (EP30), Petnica (DQ10), Maljen mt. (DP28), Lešnica (CQ82), Kopaonik mt. (DN88) and Rudnik mt. (DP68). In this number animals previously studied are also included (Vujošević and Blagojević 1995; Blagojević and Vujošević 1995). Chromosome preparation was done directly from bone marrow cells using the standard technique (Hsu and Patton 1969). G- and C-banding were performed using the slightly modified procedures of Seabright (1971) and Summner (1972). Climatological data (average temperature, average number of tropical days, average number of sub-zero temperature days, rainfall, and snowfall) were obtained from the Federal Hydrometerological Institute and represent

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Table 1. Environmental data for the studied localities (Alt – altitude, AT – average temperature, ANTD – average number of tropical days, ANSD – average number of sub-zero temperature days, RF – rainfall, SF – snowfall

	Locality	Alt. (m)	AT (°C)	ANTD	ANSD	RF (ml/m^2)	SF (cm)
1	ADA	150	11.0	40	25	750	30
2	AVALA	450	10.0	10	35	750	30
4	D. DOBRIĆ	300	11.0	25	15	850	30
5	GOČ	750	7.0	10	60	950	55
6	F. GORA	400	10.5	30	30	750	30
7	JASTERBAC	500	7.0	5	45	850	55
8	PETNICA	250	11.0	40	25	750	30
9	MALJEN	900	7.0	10	50	950	70
10	LEŠNICA	150	11.0	40	25	750	30
11	KOPAONIK	1 700	3.0	0	85	850	130
12	RUDNIK	750	7.5	10	50	950	70

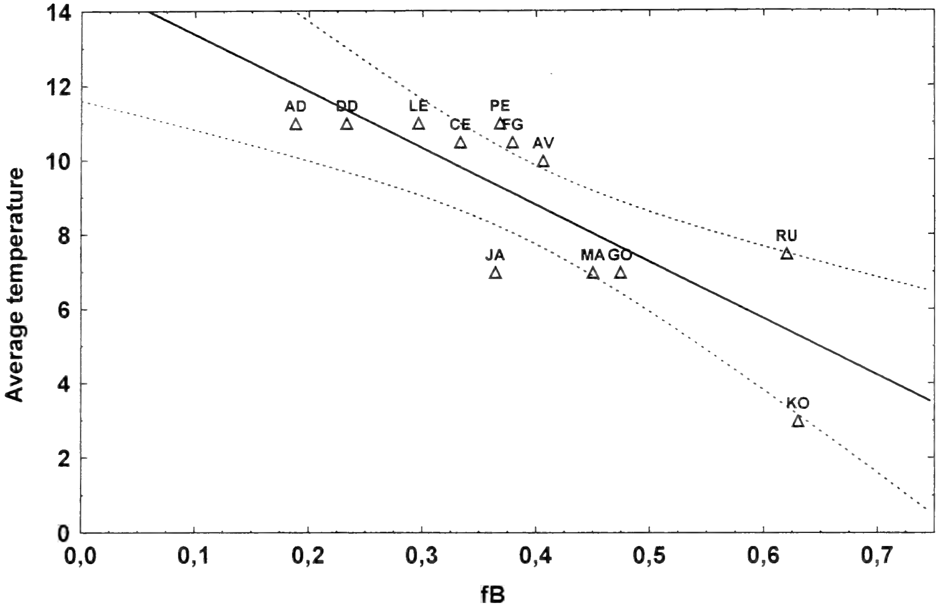
Table 2. Results of analysis for the presence of B chromosomes at different localities (fB – frequency of animals with Bs; fB/B – frequency of Bs per B carrying animal). (*) data from Blagojević and Vujošević (1995); (**) data from Vujošević and Blagojević (1995).

	Locality	N	0 B	1 B	2 B	3 B	4 B	5 B	fB	fB/B
1	ADA	64	52	9	3				0.19	1.25
2	AVALA	32	19	8	4	1			0.41	1.46
3	CER (**)	132	88	30	12	2			0.33	1.36
4	D. DOBRIĆ	43	33	8	1	1			0.23	1.30
5	GOČ	19	10	6	2	1			0.47	1.44
6	F. GORA	29	18	7	1	2	1		0.38	1.73
7	JASTERBAC (*)	530	337	136	47	5	4	1	0.36	1.38
8	PETNICA	19	12	4	1	2			0.37	1.71
9	MALJEN	20	11	4	4	1			0.45	1.67
10	LEŠNICA	44	31	9	4				0.29	1.31
11	KOPAONIK	24	9	13	2				0.63	1.31
12	RUDNIK	11	4	5	2				0.62	1.29
	TOTAL	967	624	239	83	15	5	1	0.35	1.38

average data for fifty years (Tab. 1). Frequencies of B chromosomes were transformed according to the method of Christiansen et al. (1976) which takes into account differences in sample size. The regression analyses was carried out using the software STATISTICA for Windows (StatSoft, Inc. 1995).

B chromosomes were present in all the samples studied with an average of 0.35 and ranging from 0.19 to 0.64 (Tab. 2). Due to the presence of animals with different numbers of Bs, the frequency of Bs per B carrying animals varied from 1.13 to 1.73 in the different populations. Among animals with Bs the most frequent were those with one B chromosome (0.70). Two Bs per animal were found in all populations making a frequency of 0.24 in the sample. Animals with three Bs were absent from four populations, while four Bs were found in two populations only. Only one animal with 5 Bs was found. There was no significant difference between the frequency of Bs in males and females.

The frequency of animals with Bs in the different populations correlated significantly with the environmental variables $R = 0.94$ ($F_{(6,5)} = 6.14$; $p < 0.03$). The average temperature ($r = -0.79$; $p < 0.005$) and the average number of sub-zero temperature days ($r = 0.82$;



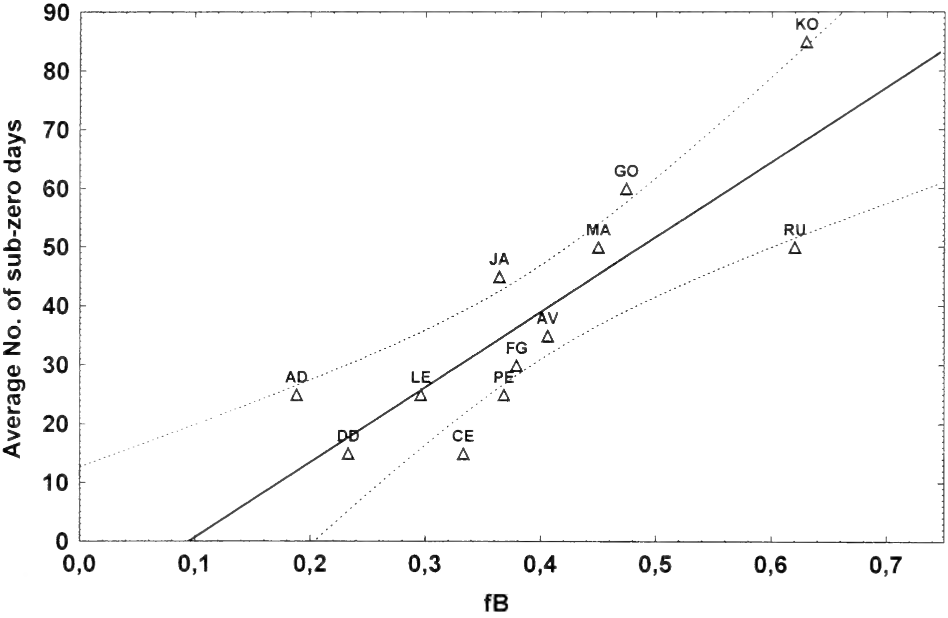


Fig. 1. Correlation between frequency of animals with Bs (fB) and average annual temperature (upper graph) and between frequency of animals with Bs (fB) and average number of sub-zero temperature days (graph below). Populations are labeled with acronyms.

$p < 0.002$) significantly influenced B frequencies. The frequency of B-carriers in populations was negatively associated with the average temperature and positively with the average number of sub-zero temperature days (Fig. 1). Temperature undoubtedly represents the most critical climatic factor and it could be said that *A. flavicollis* with Bs do best at extreme temperatures. As altitude is mainly a measure of the temperature and exposure it is not surprising that with increasing altitude the frequencies of animals with Bs also increases.

Only a small proportion of species possessing Bs has been surveyed extensively. Results of the survey of different plant species (Fröst 1958; Bosemark 1956; Brown 1960; Parker et al. 1991) led to the conclusion that B chromosomes reached the highest frequency under conditions that were most favorable for growth of the species concerned. Barker (1966) and Hewitt and John (1967, 1970) who showed the existence of a negative correlation between B chromosome frequency and rainfall obtained similar results for the grasshopper *Myrmeleotettix maculatus*. Confalonieri (1995) found in an analyses of 25 samples of the grasshopper *Trimerotropis pallidipennis* from Argentina that the frequency of B-carriers in populations was associated with altitude (negatively) and longitude (positively). The author claimed that the higher incidence of B chromosomes was associated with more favorable environments.

Our results show the opposite trend. Frequencies of animals with Bs are highest in extreme climatological conditions. Holmes and Bougourd (1989) described in *Allium schoenoprasum* a situation where B chromosomes conferred a selective advantage to the survival of individuals during the early stages of the life-cycle. Higher frequencies of animals with Bs in peripheral populations were found in the harvest mouse *Reithrodontomys megalotis* (Shellhammer 1969) and pocket mouse *Perognathus baileyi* (Patton 1972). As the most likely explanation Shellhammer (1969) mentioned the general increase in genetic variability towards the periphery of the distribution area of a species. It could be added that high altitude produces similar effects on the genetic structure of species as does the periphery of its distribution. Therefore it is possible that in *A. flavicollis* the presence of Bs increases the ability of the species to occupy such an area. It is difficult to decide whether increased levels of B's are a consequence of stress or whether they provide better resistance against stress.

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Buchbesprechungen

STANFORD, C. B.: **The Hunting Apes. Meat eating and the origins of human behavior.** Princeton, New Jersey: Princeton University Press 1999. Hardcover, 253 pp., 9 photographs, 3 tables and 3 diagrams. DM 52,10, US$ 24,95. ISBN 0-691-01160-5

With his book of 7 chapters and bibliographic references CRAIG STANFORD reviews an extensive body of facts, hypotheses and socio-biological ideas about the meat-obtaining and meat-sharing behaviour of several primates, focusing on apes and human hunters and gatherers. Whoever looks for a survey or for detailed facts concerning this field will profit from the first chapters and the bibliographic references at the end. Some badly reproduced black and white photographs do not serve to illustrate the text.

Unfortunately the author then tries to give his own interpretation of what he sees as the key event opening the door towards the evolution of the special human attributes – meat sharing and the intragroup "politics" about it. He models the old "man-the-hunter" thesis to a "man-the-meat-sharer" thesis and combines it with the "food-for-Sex" idea to a "man-the-co-operative-hunter-for-sex" thesis. STANFORD does not really add new arguments to this old debate, and often he contradicts his own claim of what a good hypothesis is all about. Like some of the contemporary authors he cites, STANFORD searches for one key adaptation initiating the human career, and he expects to find it in the behaviour of modern chimpanzees. But if this "key starter" really can be found in the behaviour of chimpanzees – why then did they remain being vanishing apes instead of becoming bio-genetically successful humans? If there should have been one single key adaptation opening the door to becoming human, we can be sure we will never find it in today's ape behaviour. This simple reflection discharges the idea of hunting, meat-eating or meat-sharing as a central point of interest for understanding the human evolution – but CRAIG STANFORD does not even take notice of this contradiction. Consequently, in the last chapter the author forces his simple ideas into explaining the origin of human patriarchy – a ridiculous attempt.

Like many socio-biologically arguing primatologists that work on great apes, the author focuses completely on chimpanzee behaviour, before defining (or even neglecting?) the differences between apes and humans. The socio-biological ideas about evolution promise important advances in the understanding of our biological history – but we are highly complex animals, and socio-biology needs to be integrated into a much more complex and interwoven mode of thinking!

K.-P. VALERIUS, Giessen

SPINAGE, C. A.: **Elephants.** London: T. and A. D. Poyser Ltd. (1994). 319 pp., numerous black and white pictures and 25 colour illustrations. Hardcover, £ 27.–. ISBN 0-85661-088-7.

This book, which only came to the attention of the members of the editorial office just recently, although it was already published in 1994, deserves to be reviewed in this journal. It is not, in the strict sense of the word, a scientific publication; there are no references in the running text, but information can be traced in 14 pages of "Select Bibliography". The text is fluently written and often spiced with a pleasant portion of British humour. The reader is supplied with detailed and diverse information on the Indian and African elephants (*Elephas maximus* and *Loxodonta africana*).

Palaeontology, taxonomy and distribution of both species are dealt with; anatomy, physiology, reproduction, as well as information on growth and longevity, diseases and parasites are presented and discussed. Of course, the author also deals with social behaviour and with food and feeding of elephants. Their influence on vegetation, effects of overpopulation and population dynamics are thoroughly treated, as well as the structure and growth of the tusks and the problems related to hunting and ivory trade, not to forget management and protection of elephant populations. The last chapter of the book deals with husbandry of both species; contrary to general assumptions, *Loxodonta africana* is, at least, as tractable as the Indian elephant. The book concludes with two appendices, one with

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common and scientific names of plants mentioned in the text and the second with a list of parks in Asia and Africa where elephants can be found. In addition to the above-mentioned bibliography 14 pages of subject index make the information supplied in this book accessible.

"Elephants" by Clive Spinage is an unusual book: The reader cannot help being fascinated by the fluent presentation and the attractive style. It is equally pleasing and rewarding to browse through this book as well as to study it thoroughly and to improve one's knowledge about elephants.

P. Langer, Giessen

Reeve, N.: **Hedgehogs.** London: T. and A. D. Poyser Ltd. 1994. Hardcover, 313 pp., numerous black and white pictures by Ruth Lindsay and 20 colour plates. £ 21.– ISBN 0-85661-081-X.

"The book is the most authoritative work on the hedgehogs yet." This sentence can be found on the dustcover of the book by Nigel Reeve – and the reviewer can agree fully with this statement! The present publication is a remarkable monograph on species of the family Erinaceidae. It is natural that the two best-investigated European species – *Erinaceus europaeus* of west and central Europe and *E. concolor* of eastern Europe are the most referred-to species in this book. In addition, all other species of the genus *Erinaceus*, as well as information on *Atelerix* (Africa), *Paraechinus*, the desert hedgehogs of northern Africa, Arabia and of the Iranian and Indian biogeographical regions, and *Hemiechinus*, the long-eared hedgehogs, which are mainly Asiatic in distribution, are also thoroughly considered. The wealth of data made available in this book for the reader is very impressive!

After the species have been introduced and after a brief account on the anatomical and physiological features given, the following aspects of hedgehog biology are described in separate chapters: Diet and feeding, home range and territoriality, nest construction and nest use, hibernation and energetics, some aspects of behaviour characteristic for different hedgehog species, reproductive biology, as well as demography and diseases. Finally, the relationship between hedgehogs and humans are considered. In a first appendix veterinary information on the treatment of parasites and diseases is given. Two further appendices present the names of hedgehogs in numerous languages. Although representatives of Erinaceidae have a wide distribution in Africa, the only language from that continent mentioned is Afrikaans! Useful British addresses for studies on hedgehogs and their protection are listed. 30 pages of detailed references and a species, as well as a general subject index conclude the book.

It is not the intention of the reviewer to comment on all data supplied in this remarkable book, but a few comments of the sixth chapter "Hibernation and energetics" should be presented as an example for the enormous amount of data the author compiled and discussed: Different physiological parameters for hibernating hedgehog species are presented, for example, the variability of the length of the hibernating season and the distribution of white and brown fat – the latter for thermogenesis –, modifications of heart rate and respiration. Neuro-anatomical and endocrine changes during hibernation, energy metabolism and metabolic changes in carbohydrate composition, as well as aspects of osmoregulation and haematological changes are discussed and interesting information on different aspects of arousal from hibernation are compiled. Not only adaptive specialisations of hedgehog energetics, but also information on their energy and food requirements are discussed. In a short, but stimulating section the author deals with evolutionary aspects of energetics. Although hedgehogs are in many ways conservative mammals, their well-regulated hibernation should be considered as a specialized charactenstic. Not only does the chapter on hibernation and energetics go into considerable detail, but also in other chapters N. Reed has compiled a remarkable amount of data. They are presented by him in a well-composed, clear and sometimes even humourous, but always highly professional, manner. Any reader interested in mammalian biology will read this enjoyable publication with great intellectual profit and pleasure.

P. Langer, Giessen

Mitchell-Jones, A. J.; Amori, G.; Bogdanowicz, W.; Kryštufek, B.; Reijnders, P. J. H.; Spitzenberger, F.; Stubbe, M.; Thissen, J. B. M.; Vohralik, V.; Zima, J.: **The Atlas of European Mammals.** London: Academic Press 1999. 484 pp. DM 130,–. ISBN 0-85661-130-1

The idea to present a modern compilation on the current distribution of mammals in Europe dates back to the year 1988 and arose at a meeting of international scientists hosted by F. G. De Beaufort and V. Vignon at the National Museum of Natural History in Paris. At that time the Societas Europaea Mammalogica was founded. Specialists were elected for each country and authorised to compilate information from their states. Thus, nearly all European nations are represented from north to south and from the west to the east. However, at the eastern border the reported area includes the Kaliningrad region but excludes Russia, Belarus, the Ukraine, and Moldavia. A standard map over all of the considered parts of Europe is used with a large scaled standard UTM (Universal Transverse Mercator) grid system. The Canary Islands, Madeira, Islas Selvageus, Azores, and Spitzbergen archipelago are recognized as three inserts. The distribution of the species is marked by two differently sized blue dots per grid. Larger ones indicate positive records since 1970; the smaller ones are based on data before 1970 with no evidence of later local extinction. The diverse species accounts are arranged in a standard format on the two opposite pages with the distribution map on the right side. The left page shows the scientific name (taxonomically following WILSON and REEDER with only a few exceptions) as heading and a habitus drawing as well as vernacular names in 33 European languages. Furtheron, short notices are added concerning distribution (worldwide or European, with comments on endemism, introduction, former distribution, extinction, or reintroduction), geographic variation (island forms, clines or existence of named subspecies), habitat (ecological requirements and limitating factors), population status, international legal and conservation status, other information, and main literature. These supplemental data are given by different authorities per species. All species of Europe are considered including introduced and feralized forms currently established and breeding in the wild as well as some vagrants but excluding pets or domesticated animals not established in the wild. Besides the one marsupial *Macropus rufogriseus* 193 eutherian species are recorded from the orders Insectivora (28 species), Chiroptera (34), Primates (1), Lagomorpha (8), Rodentia (68), Carnivora (34), and Artiodactyla (20). This atlas is a very impressive and lucid presentation of the recent situation, very welcome for an overview orientation on a large scale. The layout and appearance are of high quality. Only the unusally great number of authors (with names of only some of the national specialists) appears unappropriate and makes citations of this work rather tedious. A publication under the names of the two founders would have been a better choice.

D. KRUSKA, Kiel

GURUNG, K. K.; RAJ SINGH: **Field Guide to the Mammals of the Indian Subcontinent. Where to watch Mammals in India, Nepal, Bhutan, Bangladesh, Sri Lanka and Pakistan.** San Diego and London: Academic Press 1996. Paperback, 140 pp., numerous black and white pictures, 12 colour and 12 black and white plates, numerous maps. £ 17.50. ISBN 0-12-309350-3.

This book has been written with the tourist to the Indian Subcontinent in mind. After an introduction to the geography of the area in general and some mammological aspects, a section with short descriptions of 106 mammalian species follows. The English and the scientific names are given and a view of the left side of the respective mammal is included. A few short remarks on identification, habitat, range, behaviour, diet, breeding characteristics, on the status and on mammals that could be confused with the respective species are presented. Following this section, colour plates present species in side views. Special characteristics of colour, shape or fur structure, as found in other guides, are not given here. Twelve additional plates show the outlines of mammalian tracks. Hereafter, a section follows that can be considered as the central asset for the tourist interested in the mammalogy of the Indian subcontinent: “Where to watch mammals” characterises 23 National Parks or Nature Reserves. A map informs about the general location of the park and identifies important geographical features. Then, a text – generally one page – presents the following information: The size and the year of establishment of the park or reserve, a general description, comments on the best season for a visit, on access to the park, accommodation and facilities, as well as a list of the mammals to be found in the area. The book concludes with a checklist of mammals, a bibliography and indices on common and scientific names, as well as on the parks considered. For the tourist interested in the mammals of the subcontinent the book by GURUNG and RAJ SING can be a helpful source of general information.

P. LANGER, Giessen

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Mouse opossums (Didelphimorphia, Didelphidae) of northwestern Argentina: Systematics and distribution

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Abstract

We present a systematic revision of the mouse opossums of northwestern Argentina; included are three genera and eight species, *Gracilinanus* (new for the region), *Micoureus*, and *Thylamys*. Two subspecies of *Thylamys* are elevated to species. The distribution of each of the taxa was determined using specimen records. External and cranial descriptions, measurements, and comments on the taxonomy and natural history of each species are given.

Key words: Mouse opossums, systematics, taxonomy, distribution, Argentina.

Introduction

The small didelphid marsupials of the Neotropics have been the focus of much speculation with respect to species composition and the taxonomic status of the different forms. The tribe Marmosini (sensu Goin 1995) represents the most important radiation of extant didelphids in the Neotropics. About 33 species are known (Gardner 1993); their distribution is extensive both latitudinally and altitudinally (Tate 1933).

Thomas (1888) united the mouse opossums in the subgenus *Micoureus*, in the genus *Didelphys*. Later, Cabrera (1919, 1957) divided the group into two subgenera, *Marmosa* and *Thylamys*, which were included in the genus *Marmosa*. The most extensive revision of the group was that of Tate (1933), who divided the genus *Marmosa* (sensu Cabrera 1919) into five informal groups: *cinerea*, *murina*, *noctivaga*, *microtarsus*, and *elegans*. More recently, Marshall (1981), Reig et al. (1985, 1987), and Gardner and Creighton (1989) suggested that the genus *Marmosa* be separated into distinct genera based on marked differences in anatomy and genetics.

The recognized genera differ according to the authors; Marshall (1981) and Reig et al. (1985, 1987) recognized *Marmosa*, *Micoureus*, and *Thylamys*; whereas Gardner and Creighton (1989) also recognized *Gracilinanus* and *Marmosops*. The latter taxonomic arrangement currently is the one that is generally accepted (Gardner 1993; McKenna and Bell 1997). Hershkovitz (1992) placed the above genera in the Family Marmosidae.

Until now, two genera of mouse opossums were known for northwestern Argentina, *Thylamys* and *Micoureus* (Gardner 1993; McKenna and Bell 1997). In this study we present a taxonomic revision of the mouse opossums of northwestern Argentina, an area where there has been a general lack of information concerning the distribution of each species and where the taxonomy has been confusing.

Material and methods

Study area: Northwestern Argentina includes the provinces of Jujuy, Salta, Tucumán, Catamarca, and Santiago del Estero (Fig. 1), with an area of about 470 000 km^2. Due to its location in the subtropics and its complex relief, which varies from 500 to 6 000 m in altitude, a number of climates and habitats as well as corresponding variations in vegetation characterize the area. These include the following phytogeographic provinces: High Andean, Puna, Prepuna, Monte, Yungas, and Chaco (Cabrera 1977; Cabrera and Willink 1973; Redford and Eisenberg 1992).

General: We examined 277 specimens from northwestern Argentina. Specimens were examined from the following collections: AMNH: American Museum of Natural History, New York; BMNH: British Museum of Natural History, London; CEM: Colección Elio Massoia y Flía, Buenos Aires, Argentina; CML: Colección Mamíferos Lillo, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina; IADIZA-CM: Colección Mastozoológica, Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina; MACN: Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; OMNH: Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma; and specimens whose final disposition has not yet been determined and that are designated by the acronym of the collector, ARG: Catalog of specimens from Argentina at the Sam Noble Oklahoma Museum of Natural History; PIDBA: Programa de Investigaciones de Biodiversidad Argentina, MMD: M. Mónica Díaz, and PO: Pablo Ortiz. Standard external measurements and characteristics were recorded in the field when specimens were prepared, or copied from labels of museum specimens. Cranial measurements were taken with digital calipers to the nearest 0.05 mm following Barquez et al. (1999) and Myers et al. (1990).

Localities: Localities for each species were plotted using maps of the Instituto Geográfico Militar del Ejército Argentino, the Automóvil Club Argentino, and Keegan and Keegan (1993). The geographic coordinates of the localities were obtained using a global positioning system (GPS) or were determined with maps or from the literature (Paynter 1985). Some localities could not be located because of imprecise citation or lack of data.

Results

Genus *Gracilinanus*

The genus *Gracilinanus* includes nine species and is widely distributed across the forests and woodlands of the Neotropics (Hershkovitz 1992). Gardner (1993) recognized six species in the genus and did not recognize the three species (*kalinowskii*, *longicaudus*, and *perijae*) described by Hershkovitz (1992). In Argentina two species are known, *G. agilis* and *G. microtarsus*. Herein we expand the distribution of *G. agilils chacoensis* to include northwestern Argentina.

Gracilinanus agilis (Burmeister, 1854)

Gracilinanus agilis chacoensis (Tate, 1931)

Distribution in Argentina: This species was known from the provinces of Corrientes, Chaco, Formosa, Misiones, Entre Ríos, and Buenos Aires (Massoia and Fornes 1972; Contreras 1982, 1984); we extend the distribution to include northwestern Argentina based on specimens from the provinces of Jujuy and Salta.

Specimens Examined (n = 21) (Fig. 1): Argentina. Jujuy: Ingenio La Esperanza, 24°14′ S 64°52′ W, 1 (CEM); Santa Bárbara, 1 (AMNH). Salta: Ingenio San Martín del Tabacal, Lote “Milagros”, 23°16′ S 64°15′ W, 18 (CML). Paraguay. Sapucay, 1 (BMNH, holotype).

Description: The snout is short and pointed, and the tail long and prehensile. The pelage is short and velvety. The dorsum is ochraceous brown, the sides the same color as the dorsum; the bases of the hairs are gray. The venter is pale washed with ochraceous or whitish yellow; the hairs are unicolored. Periocular rings are present, moderate in size, dark brown or black; cheek and feet the same color as the venter. Ears are ochraceous brown. The tail is bicolored, the coloration the same as that of the dorsum and venter.

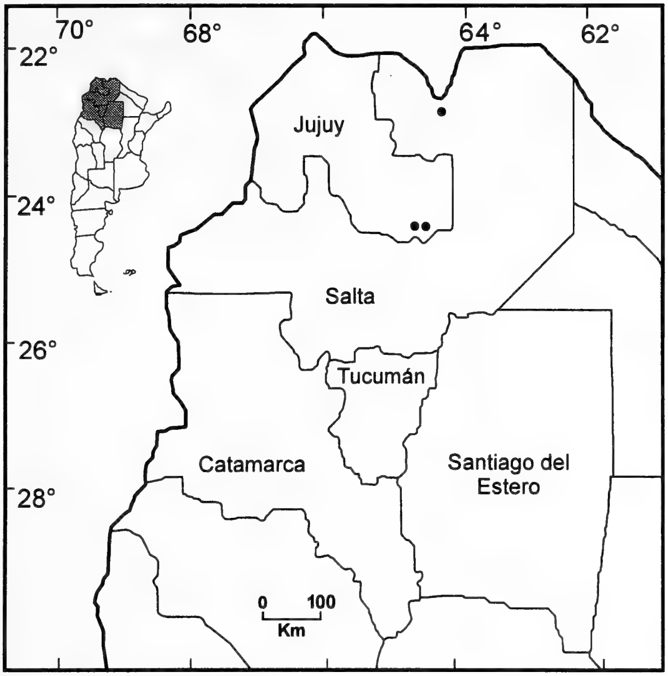

Fig. 1. Localities of occurrence of *Gracilinanus agilis.* Insert indicates the location of the provinces of northwestern Argentina.

The skull is characterized by a short, wide rostrum, and an inflated interorbital region with a marked postorbital constriction. In adult specimens the supraorbital edges are incipient. The nasal bones widen abruptly at the frontomaxillary suture. The third upper premolar is smaller than or subequal in size to the second upper premolar.

Comments: These records are the first for this taxon in northwestern Argentina, although its presence was highly probable due to the proximity of its distribution in western Formosa Province and southern Bolivia (MASSOIA and FORNES 1972; ANDERSON 1997).

In Argentina this species typically inhabits gallery forest, although it may be found to occur in other habitats (OLROG and LUCERO 1981; REDFORD and EISENBERG 1992; EMMONS 1990), such as cultivated areas (MASSOIA and FORNES 1972). Two of the localities, Ingenio La Esperanza and Ingenio San Martín del Tabacal, listed in the Specimens Examined, are in areas where sugar cane is grown. The natural history of this species in Argentina is poorly known; some data were reported by MASSOIA and FORNES (1972) for northeastern Argentina.

Genus *Micoureus*

This genus contains four species, the distribution of two species (*M. constantiae* in the northwest and *M. demerarae* in the northeast) reach the northern limit of Argentina (CABRERA 1957; MASSOIA 1972; GARDNER 1993). EMMONS (1990) did not recognize *M. demerarae* and *M. constantiae* as being different; however, presently they are considered to be different species (GARDNER 1993).

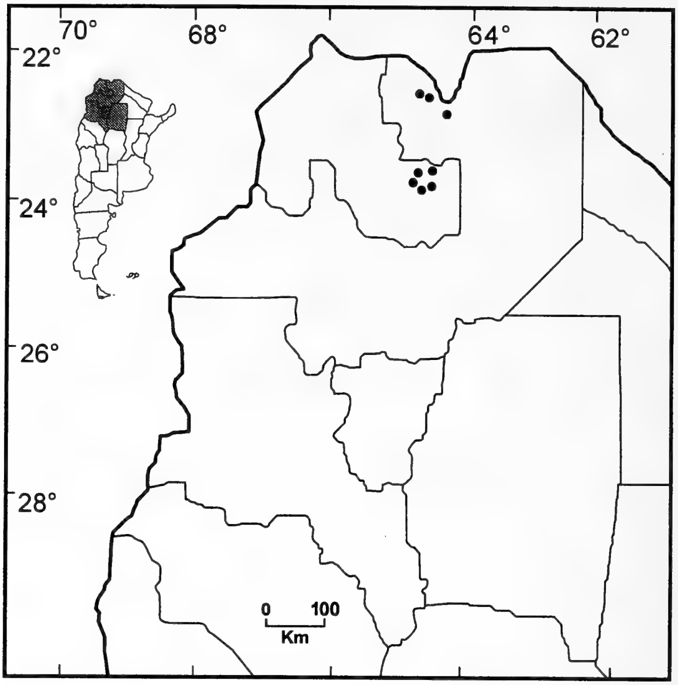

Fig. 2. Localities of occurrence of *Micoureus constantiae.*

Micoureus constantiae (Thomas, 1904)
Micoureus constantiae budini (Thomas, 1919)

Distribution in Argentina: Northwestern Argentina, in the provinces Jujuy and Salta (CABRERA 1957; OLROG and LUCERO 1981; MARES et al. 1989; REDFORD and EISENBERG 1992).

Specimens Examined (n = 11) and Additional Records (Fig. 2): Argentina. Jujuy: Aguas Negras, 23°45′ S 64°56′ W, 5 (2 CML; 3 MACN); Aguas Negras, Camping, Parque Nacional Calilegua, 23°45′ S 64°56′ W (Personal observation of the authors); Caimancito, 23°44′ S 64°36′ W, 1 (MACN); Calilegua, 23°46′ S 64°47′ W, 1 (CEM); Mesada de las Colmenas, 1150 m, 23°42′ S 64°52′ W (HEINONEN and BOSSO 1994); Río San Francisco, altura de Yuto, 500 m, 23°39′ S 64°27′ W, 1 (BMNH holotype). Salta: 43.7 km NW of the Junction of Argentine Highways 50 and 18, on road to Isla de Cañas, 22°57′ S 64°33′ W, 1 (PIDBA); Orán, 23°08′ S 64°20′ W, 1 (CML); Parque Nacional Baritú, desembocadura Arroyo Santelmita, 700 m, 22°31′ S 64°37′ W, 1 (CML).

Description: This is the largest mouse opossum in northwestern Argentina. The tail is long and naked for its entire length, only the part nearest the body is haired, the scales are arranged in a spiral. The dorsal coloration is grayish brown with yellowish hues and becomes brighter on the sides, the bases of the hairs are gray. The periocular rings are broad and dark in color (brown or black). The ears are dark brown. The hairs of the venter are ochraceous, and extend to the cheek, throat, and chin. In some specimens the ochraceous color of the venter is stronger. The feet are ochraceous and the tail is dark brown with light spots at the tip. Unfortunately the type specimen of *Marmosa budini* (BMNH 20.1.7.134) in the British Museum is discolored. In the skull, the rostrum is long and wide; the interorbital region has pronounced pointed supraorbital processes; lambdoidal crests are present, but not very evident; the sagittal crest is absent; the nasal bones expand markedly at the frontomaxillary suture; paraoccipital processes are present, but are not well developed; the tympanic bullae are small.

Comments: Records of this species are scarce and the majority are restricted to protected areas, Parque Nacional Calilegua in Jujuy and Parque Nacional Baritú in Salta. All records are known only from the Yungas phytogeographic province.

At Aguas Negras in June a lactating female, with an ochraceous venter, was captured. At the same locality, stomach contents consisted of hemipterans parts and vegetation. A young individual was captured in August.

Genus *Thylamys*

Unlike the majority of the mouse opossums, which are found in the tropical and subtropical forests, the genus *Thylamys* inhabits principally arid and open areas (Mares 1973; Mares and Braun 2000; Palma 1995; Palma and Yates 1996). This is the most polytypic genus of marsupials in northwestern Argentina and raises the most questions regarding the taxonomic composition of each species. For many years, investigators synonymized the various species and subspecies principally in two taxa, *Thylamys elegans* or *T. venustus*. Currently, five species are recognized: *T. elegans*, *T. pusillus*, *T. macrura*, *T. pallidior*, and *T. velutinus* (Gardner 1993). Some authors consider forms of *T. elegans* in northwestern Argentina as *T. venustus* (Heinonen and Bosso 1994; Palma 1995; Galliari et al. 1996; Díaz et al. 1997; Mares and Braun 2000), restricting *T. elegans* to Chile, thus increasing the total number of species in the genus to six. According to some authors, three species (*T. pallidior*, *T. venustus* and *T. pusilla)* are found in northwestern Argentina (Gardner 1993; Galliari et al. 1996; Díaz et al. 1997; Mares and Braun 2000). This genus is in need of revision as evidenced by the numerons taxonomic problems.

Here we recognized six species for northwestern Argentina: *T. cinderella*, *T. pallidior*, *T. pusilla*, *T. sponsoria*, *T. venustus*, and *Thylamys* sp. *T. cinderella* and *T. sponsoria* were previously considered to be subspecies of *Marmosa elegans* (Thomas 1902, 1921; Cabrera 1957) or *Marmosa venustus* (Tate 1933).

Thylamys cinderella (Thomas, 1902)

Distribution in Argentina: In northern Argentina this species is known in the provinces of Jujuy and Tucumán (Tate 1933); recently specimens from Salta Province have been documented.

Specimens Examined (n = 59) and Additional Records (Fig. 3): Argentina. Jujuy: 4 km W jct Hwys 34 and 3, along Hwy 3, 23°48′ S 64°48′ W, 1 (CM); Caimancito, 400 m, 23°44′ S 64°36′ W, 1 (BMNH); Caimancito, 600 m, 23°44′ S 64°36′ W, 1 (FMNH); Caimancito, 700 m, 23°44′ S 64°36′ W, 1 (MACN); Junction of road to Puesto Viejo and Highway 34, 4 km E, on road to Puesto Viejo, 24°29′ S 64°59′ W, 4 (MMD); Jujuy, 1 258 m, 24°12′ S 65°19′ W, 5 (BMNH); Laguna La Brea, 23°56′ S 64°28′ W, 1 (MMD); Laguna La Brea, 25 km W Palma Sola (Hwy. 1), 23°56′ S 64°28′ W, 1 (OMNH); León, 24°02′ S 65°26′ W (Thomas 1918 as *Marmosa elegans cinderella*); León, 1 500 m, 24°02′ S 65°26′ W, 5 (BMNH); On highway 9 at the border with Salta, at a campground on the way to El Carmen, 4 600 ft., 24°28′ S 65°21′ W, 16 (4 ARG, 6 CML; 6 IADIZA-CM); Oyeros, 3 km N, 24°30′ S 65°00′ W, 1 (MMD); Santa Rita, 2 km NW, on provincial road 1, 24°28′ S 64°50′ W, 2 (MMD); Santa Rita, 4 km NW, on provincial road 1, 24°27′ S 64°50′ W, 1 (MMD); Villa Carolina, 500 m, 24°16′ S 64°43′ W (Thomas 1920 as *Marmosa elegans cinderella*); Villa Carolina, Río Lavallén, 500 m, 24°16′ S 64°43′ W, 3 (BMNH); Yuto, 23°38′ S 64°28′ W, 4 (1 CML; 3 AMNH). Salta: Aguaray, FCCNA, 700 m, 22°16′ S 63°44′ W, 4 (MACN); Güemes, Highway 34, km 1 383, 24°40′ S 65°03′ W, 1 (MACN); Playa Ancha, 1 (MACN); Río Mojotoro, bridge of Ferrocarril Belgrano, 24°40′ S 65°03′ W, 1 (MMD); San Ramón de la Nueva Orán, 23°08′ S 64°20′ W, 1 (CML); Tartagal, Laguna de Las Catas, 22°16′ S 63°52′ W, 1 (CML). Tucumán: Cerro de Raco, 26°43′ S

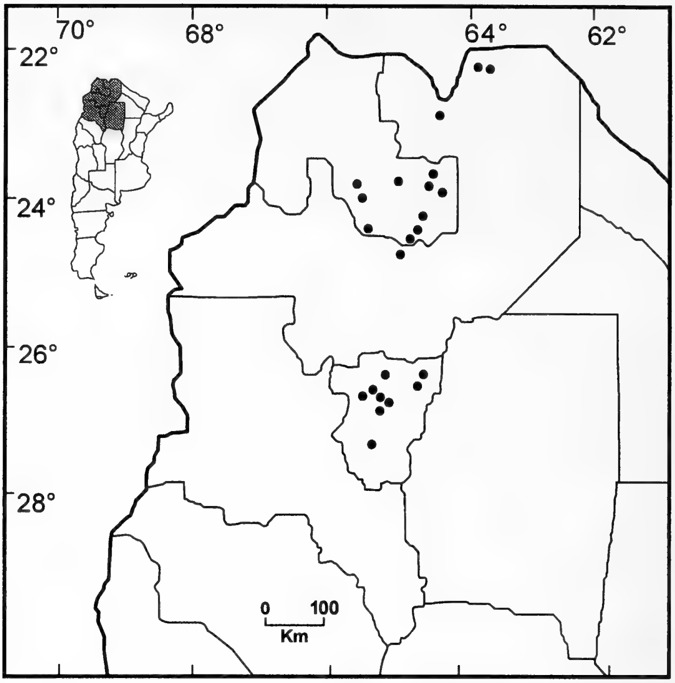

Fig. 3. Localities of occurrence of *Thylamys cinderella*.

65°30′ W; Cerro de Tafí Viejo, 26°44′ S 65°16′ W; Cerro del Campo, 26°35′ S 64°57′ W; Concepción, 27°20′ S 63°35′ W (TATE 1933 as *Marmosa venusta cinderella*); Finca El Jagüel, 4.5 km W provincial road 304, on the way to Requelme, 26°28′ S 64°48′ W, 1 (PIDBA); Ñorco-Vipos (cited as Norreo-Vipos), 26°29′ S 65°22′ W (TATE 1933 as *Marmosa venusta cinderella*); Raco, 1 000 m, 26°38′ S 65°26′ W, 1 (MACN); Tucumán, 450 m, 26°50′ S 65°13′ W, 1 (BMNH holotype); “Tucumán”, no specific locality; Villa Nougués, San Pablo, 26°51′ S 65°23′ W (TATE 1933 as *Marmosa venusta cinderella*).

Description: Dorsal coloration is grayish, although some specimens are somewhat brownish; some specimens have a dark mediodorsal area. The bases of the hairs of the venter are gray and the tips are white or cream; hairs of the chest are unicolored, white or yellowish. The pelage of young individuals is shorter and darker compared with that of adults. Pointed supraorbital processes are present, which are very evident in adult specimens. In young animals these processes are not evident, but the edges of the supraorbital region are pronounced from an early age. The zygomatic arches are well expanded. Lambdoidal crests are pronounced.

Comments: *Thylamys cinderella* has been considered as a subspecies of *venustus*, but here we elevate the taxon to a distinct species based on characters that clearly differentiate it from the other species in the region, *T. sponsoria*, and because the two have been found in geographic sympatry.

TATE (1933), in spite of showing sympatry between *T. cinderella* and *T. sponsoria*, considered the two taxa as subspecies of *T. venustus*. However, there are errors in his specimens examined. Some of the same individuals were listed for both taxa. For example, he cited León and Caimancito (cited as Carmencito) for *T. venusta cinderella* and *T. v. sponsoria*, but in both cases the reference is for the same specimens. The specimens from “Serra de Tucumán” in the AMNH that TATE (1933) identified as *cinderella* are here reidentified as *sponsoria*. Specimens of this species are known, principally, from the Chaco, although some were collected in the Yungas but in arid areas near the Chaco.

On highway 9 at the border with Salta, at a campground on the way to El Carmen, in February, a female with open vagina, a lactating female, and a young individual were collected. Young were also collected at Laguna La Brea in May and at Finca El Jagüel in April.

Thylamys pallidior (Thomas, 1902)

Distribution in Argentina: In arid areas (Prepuna, Puna, Monte, and northern Patagonia), from Jujuy south to Chubut.

Specimens Examined (n = 38) and Additional Records (Fig. 4): Argentina. Catamarca: Belén, 27°39′ S 67°02′ W; Chumbicha, 0.5 km E of Hwy 38 along Hwy 60, 457 m, 28°52′ S 66°14′ W (Mares et al. 1997); Chumbicha, 1.5 km E of Hwy 38, along Hwy 60, 28°52′ S 66°14′ W, 1 (CML); Chumbicha, 600 m, 28°52′ S 66°14′ W (Thomas 1919 a as *Marmosa elegans pallidior*); Chumbicha (cited as Chumbiche), 28°52′ S 66°14′ W; Hualfín (cited as Gualfín), 27°14′ S 66°50′ W (Tate 1933 as *Marmosa pallidior*); Inmed. N Andalgalá, Río Andalgalá, 27°34′ S 66°16′ W; Minas Capillitas, 3 200 m, 27°20′ S 66°25′ W; of Hwy 62, 8 km E jct. Hwy 1 and 62, 27°36′ S 66°15′ W; of Hwy 62, 8 km E jct. Hwy 62 and 1, E of Andalgalá, 27°36′ S 66°15′ W (Mares et al. 1997); Otro Cerro, 28°44′ S 66°17′ W (Tate 1933 as *Marmosa pallidior*); Quirós, 28°45′ S 65°07′ W (Mares and Braun 2000); Rio Andalgalá, 3 km N Andalgalá, 27°34′ S 66°16′ W (Mares et al. 1997). Jujuy: 11 km E of Humahuaca, 2 km E of Pucará on road to Cianzo, 23°12′ S 65°16′ W, 1 (ARG); 9 km NW Bárcena, 23°57′ S 65°30′ W, 2 (ARG); Abra Pampa, 22°43′ S 65°42′ W, 4 (3 CML; 1 MACN); Abra Pampa, 3 500 m, 22°43′ S 65°42′ W, (Thomas 1919 b as *Marmosa elegans pallidior*); Abrapampa, 3 500 m, 22°43′ S 65°42′ W, 1 (BMNH); Alfarcito, 2 600 m, 23°37′ S 65°23′ W, 1 (BMNH); Casabindo, 22°58′ S 66°05′ W (Tate 1933 as *Marmosa pallidior*); Casabindo, 4 000 m, 22°58′ S 66°05′ W, 6 (BMNH); Casabindo, 4 000–4 500 m, 22°58′ S 66°05′ W (Thomas 1919 b as *Marmosa elegans pallidior*); Cerro Casabindo, 4 500 m, 22°56′ S 66°07′ W, 2 (BMNH); Cuesta del Hurón, 29 km W Cineguillas on provincial road 64, 3 835 m, 22°06′ S 66°03′ W, 3 (MMD); Curques, 24 km N Susques, on provincial road 74, 4 100 m, 23°14′ S 66°23′ W, 1 (MMD); Humahuaca, 23°12′ S 65°21′ W (Thomas 1919 a as *Marmosa elegans pallidior*); La Quiaca, 17 km W, 3 km S of road 5, 22°09′ S 65°44′ W, 1 (MMD); Laguna de Pozuelo, no specific locality, 2 (MACN); Maimará, 23°37′ S 65°28′ W (Tate 1933 as *Marmosa pallidior*); Maimará, 2 230 m, 23°37′ S 65°28′ W, 2 (BMNH); Maimará, 2 300 m, 23°37′ S 65°28′ W, 1 (MACN); Maimará, 2 500 m, 23°37′ S 65°28′ W, 2 (MACN); Mina Pirquitas, 31 SE, on road 74 b, Sierra de Quichagua, 22°54′ S 66°19′ W, 4 200 m, 2 (MMD); Miyuyoc, 22°51′ S 65°18′ W, 1 (MMD); Salar Cauchari, 31 km N Cauchari, on road 70, 3 840 m, 23°50′ S 66°47′ W, 1 (MMD); Sierra de Tilcara, 4 500 m, 23°35′ S 65°12′ W, 1 (MACN). Salta: 30 km E Cachi, 2 600 m, 25°09′ S 66°00′ W (Mares and Braun 2000). Tucumán: Near Amaicha del Valle, 26°36′ S 65°55′ W, 1 (PO); Pichao, Sierra de Quilmes, 26°21′ S 66°03′ W, 1 (CML); Tafí del Valle, 26°52′ S 65°41′ W (Tate 1933 as *Marmosa pallidior*). Bolivia. Oruro: Challapata, 3 800 m, 1 (BMNH holotype).

Description: The dorsal coloration is pale gray, although some specimens have brownish tones, the sides are lighter, and the venter is pure white. The feet are white or grayish and the ears are grayish or drab. Periocular ring is black and very thin, and the cheeks are white. The finely haired tail is bicolored, gray or drab dorsally and yellowish-white ventrally. The braincase is globose in form and the zygomatic arches are slightly expanded. The rostrum is long, narrow, and pointed. The interorbital region lacks pronounced supraorbital edges. Tympanic bullae are large and are separated by a small space.

Comments: This species was described by Thomas (1902) as a subspecies of *T. elegans*. Matschie (1916) and Tate (1933) treated the taxon as a valid species; the former within the genus *Thylamys* and the latter in the genus *Marmosa*. Later, it was considered as a subspecies of *T. pusilla* (CABRERA 1957; OLROG 1979), and currently it is considered as a valid species (GARDNER 1993). In Jujuy Province it is found only in the Puna phytogeographic province, whereas further south it occupies other and areas (Monte and Patagonia). The majority of the specimens were collected from rocky areas with little vegetation (spine shrubs, cactus, and grass). In Catamarca Province along the border with the Santiago del Estero Province the distribution overlaps that of *T. pusilla*, which is found typically in the Chaco. PALMA (1995) established the distribution of the species as the rocky hillsides of the Andean Altiplano of Argentina and Bolivia, and broadened the distribution to northern Chile.

The locality of Sierra de Zenta used by Budin on the MACN specimen corresponds to Sierra de Tilcara, which is located east of Maimará. The specimens cited by MARES et al. (1996) as *T. pallidior* for Tucumán Province we considered here as *T. pusilla*.

In February, at Cuesta del Hurón, we recorded a lactating female with an open vagina that had an ochraceous venter. Young individuals were collected in February at Cuesta del Hurón, in March at Cerro Casabindo, 4 500 m and Maimará, 2 230 m; and in April at Alfarcito, 2 600 m.

Thylamys pusilla (Desmarest, 1804)

Distribution in Argentina: In the provinces of Formosa, Corrientes, Chaco, Entre Ríos, Salta, Santiago del Estero, and Tucumán.

Specimens Examined (n = 18) and Additional Records (Fig. 4): Argentina. Salta: 5 km S Tolloche, on Vinalito Rd., 25°30′ S 63°32′ W (DÍAZ et al. 2000; MARES et al. 1981 as *Marmosa pusilla*; OJEDA and MARES 1989 as *Marmosa pusilla*); 6 km W of Piquirenda Viejo, 22°21′ S 63°50′ W (MARES and BRAUN 2000); 90 km NNW of Tucumán (TATE 1933 as *Marmosa pallidior*); Campo Grande, 17 km E Santo Domingo, 24°37′ S 63°20′ W, 1

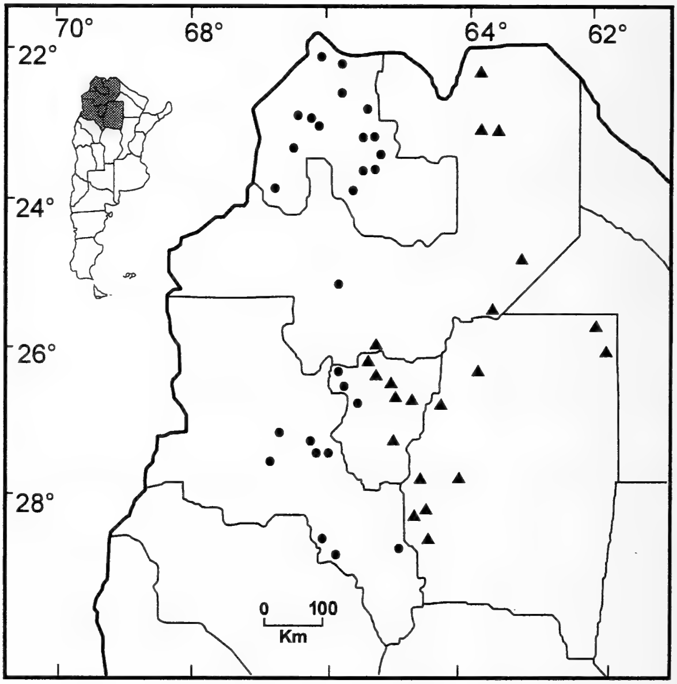

Fig. 4. Localities of occurrence of *T. pallidior* (circles) and *T. pusilla* (triangles).

(CML); Departamento Capital, no specific locality, 1 (MACN); Dragones, 23°16′ S 63°21′ W, 1 (not collected); Hickman, 23°12′ S 63°34′ W, 1 (CML); Los Colorados, 17 km E Santo Domingo, 24°37′ S 63°20′ W, 1 (CML); Puesto Campo Grande, 17 km E Santo Domingo, 24°37′ S 63°20′ W, 1 (CML). Santiago del Estero: 15 km SE Picada de Olmos, on road 16, W of Los Pirpintos, 26°06′ S 62°10′ W, 2 (CML); 6 km S, 2 km E Pampa de los Guanacos, ca. 120 m, 26°17′ S 62°01′ W (MARES and BRAUN 2000); Estancia Guampacha, 27°59′ S 64°45′ W (MASSOIA and LATORRACA 1992 as *Thylamys elegans pallidior*); Estero, 26°37′ S 63°39′ W; Lavalle (cited as La Valle), 28°12′ S 65°08′ W (TATE 1933 as *Marmosa pallidior*); Lago Muyo, not located, 2 (CML); Virgen del Valle picnic area on Highway 64 between Santa Catalina and La Puerta Chiquita, 28°09′ S 64°50′ W, 1 (CML); Robles, 27°55′ S 64°08′ W (CABRERA 1934 as *Marmosa janetta pulchella*); San Antonio, 26°46′ S 64°37′ W, 2 (MACN); Villa La Punta, 28°23′ S 64°45′ W (MASSOIA and LATORRACA 1992 as *Thylamys elegans pallidior*). Tucumán: Cerro Medici, 26°37′ S 65°12′ W (CAJAL 1981); El Bracho, 400 m, 26°59′ S 65°11′ W, 2 (CML); El Cadillal, 26°37′ S 65°12′ W, 1 (CML); Estación Vipos, 26°29′ S 65°22′ W (TATE 1933 as *Marmosa pallidior*); Las Mesadas, 26°27′ S 65°30′ W, 1 (CML); San Pedro de Colalao, 26°14′ S 65°29′ W, 1 (CML); Tapia, 26°36′ S 65°18′ W (TATE 1933 as *Marmosa pallidior*).

Description: This species is very similar in coloration to *T. pallidior*, although the dorsal coloration is browner, and in some specimens grayer. The venter is pure white and this coloration extends to the cheek. The feet are white and the ears are grayish or drab. The periocular rings are black and very thin. The braincase is globose in form and the zygomatic arches are greatly expanded. The rostrum is short and wide. The supraorbital processes of the interorbital region are pronounced. The tympanic bullae are small compared to *T. pallidior*.

Comments: According to PALMA (1995) the species is found in the Chaco and Monte Desert of Argentina. According to our study, specimens from the Monte desert are *T. pallidior*. We restrict the distribution of this species to the Chaco and the area of transition with the Yungas.

Thylamys sp.

Specimens Examined (n = 7) (Fig. 6): Argentina. Jujuy: Cerro Calilegua, El Duraznillo, 3 000 m, 23°28′ S 64°55′ W, 1 (CML). Tucumán: La Higuera, 26°23′ S 65°26′ W, 6 (CML).

Description: The pelage is short and dark, typical of young individuals. The dorsum is grayish brown and is darker along the midline; the specimens from La Higuera are browner. The venter is yellowish gray, grayer in comparison with specimens of *T. sponsoria* and *T. cinderella*. The specimen from Jujuy has black periocular rings and those from La Higuera have brown rings. Cranially, these specimens correspond to young individuals that have a deciduous premolar or an erupting permanent third upper premolar. The skulls are large and are similar to those of adults of others species of *Thylamys* examined. The supraorbital edges are pronounced and the rostrum is well developed.

Comments: The specimen from Jujuy was identified by OLROG (1979) as *Marmosa pusilla pallidior*, but its characters do not correspond to those of this group. HEINONEN FORTABAT and CHEBEZ (1997) cited *T. elegans pallidior* for Parque Nacional Calilegua, probably following OLROG (1979).

The specimens listed as *Thylamys* sp. do not correspond to any of the described species of *Thylamys*, based on the description and comparisons of the different species and subspecies. The specimens are young but the size corresponds to that of (older) adult specimens of other species. The largest species in the genus described to date is *Marmosa janetta*, which was placed in synonymy with *T. elegans* (GARDNER 1993). Because there are few specimens with these characters, it is not possible to make accurate comparisons of the cranium. Additional specimens of adult age are needed to accurately determine to which taxon these specimens correspond.

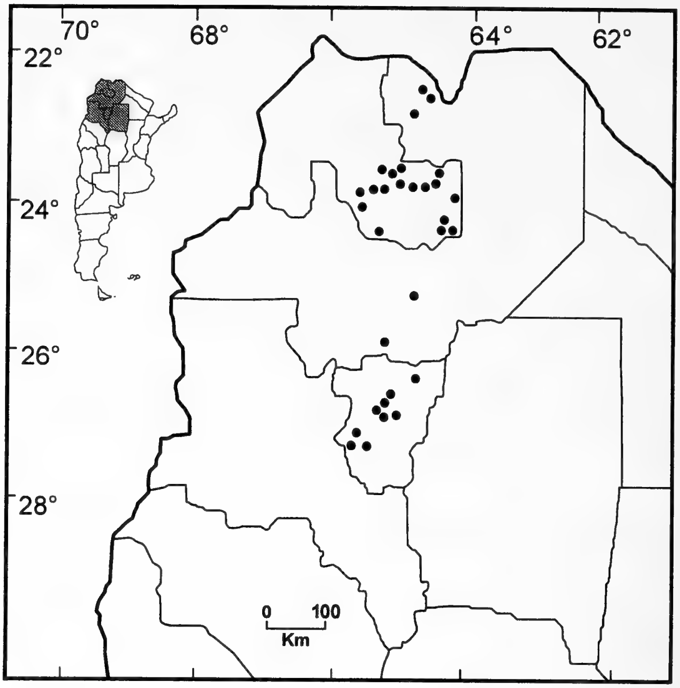

Fig. 5. Localities of occurrence of *T. sponsoria*.

Thylamys sponsoria (Thomas, 1921)

Distribution in Argentina: To date, only known for Jujuy Province. Here we extend the distribution to include the provinces of Salta and Tucumán.

Specimens Examined (n = 118) and Additional Records (Fig. 5): Argentina. Jujuy: 9 km NW Bárcena, 23°57′ S 65°30′ W, 1 (ARG); Abra de Cañas 23°40′ S 64°54′ W, 2 (MACN); Abra de Cañas, 1 700 m, 23°40′ S 64°54′ W (HEINONEN and BOSSO 1994 as *Thylamys venustus*); Abra de Cañas, El Monolito, 1 700 m, 23°40′ S 64°54′ W, 6 (CML); Aguas Negras, 23°45′ S 64°56′ W, 1 (MACN); Aguas Negras, 600 m, 23°45′ S 64°56′ W, 1 (MACN); Arroyo La Horqueta, 3 km SE Laguna de Yala, 2 100 m, 24°07′ S 65°27′ W, 1 (MMD); Arroyo La Horqueta, 6 km SE Laguna de Yala, 2 100 m, 24°07′ S 65°25′ W, 1 (MMD); Arroyo Yuto, 13 km SW Yuto, 23°40′ S 64°37′ W, 2 (MMD); Caimancito, 550 m, 23°44′ S 64°36′ W (HEINONEN and BOSSO 1994 as *Thylamys venustus*); Calilegua, 23°46′ S 64°47′ W, 2 (1 CEM; 1 FMNH); Cerro Hermoso, 23°35′ S 64°53′ W, 3 (MACN); El Simbolar, 25 km SW Palma Sola, 24°11′ S 64°28′ W, 3 (2 CM; 1 OMNH); Higuerilla, 23°36′ S 65°05′ W (TATE 1933 as *Marmosa venusta sponsoria*); Higuerilla, 2 000 m, 6 (BMNH); Mesadas de las Colmenas, 23°42′ S 64°52′ W, 5 (MACN); Mountains W of Yala, no specific locality, 1 (FMNH); Near Yala (cited as Near Vala), no specific locality (TATE 1933 as *Marmosa venusta sponsoria*); On highway 29 (east off of hwy 9), 10 km west of Tiraxi, 23°59′ S 65°23′ W, 1 (ARG); Palma Sola, 24°00′ S 64°19′ W, 1 (AMNH); Parque Nacional Calilegua, no specific locality, 1 (MACN); Río Blanco, 9 km SW San Antonio, 1 443 m, 24°25′ S 65°23′ W 2 (PIDBA); Río Tesorero, 4 km N Tiraxi, on provincial road 29, 23°59′ S 65°18′ W, 2 (MMD); Río Tiraxi, 1.5 km E Tiraxi, on road 29, 23°59′ S 65°19′ W, 1 (PIDBA); Santa Bárbara, 24°17′ S 64°24′ W, 1 (AMNH); Sunchal, Sierra de Santa Bárbara, 24°14′ S 64°27′ W (TATE 1933 as *Marmosa venusta sponsoria*); Sunchal, Sierra Santa Bárbara, 1 200 m, 9 (BMNH, including the holotype); Sunchal, Sierra Santa Bárbara, 1 400 m, 1 (BMNH). Salta: 3.9 km N Potrerillos, along provincial road 6, 26°04′ S 65°30′ W, 1 (ARG); 43.7 km NW of the Junction of Argentine Highways 50 and 18, on road to Isla de Cañas, 22°57′ S 64°33′ W, 6 (PIDBA); Río de las Conchas, 2 km N and 6 km W of Metán, 25°18′ S 61°01′ W, 1 (PIDBA); Río Santa Maria, 1 (MACN); Vado de Arrazayal, 20 km NW Aguas Blancas, 22°33′ S 64°32′ W, 2 (CML). Tucumán: Aconquija, 3 000 m, no specific locality, 1 (MACN); Biological Reserve Horco Molle, near Residencia, 26°45′ S 65°21′ W, 2 (CML); Cerro San Javier, 26°47′ S 65°23′ W, 1 (MACN); Cerro San Javier, 1 000 m, 1 (MACN); Concepción, 27°20′ S 63°35′ W, 14 (MACN); Horco Molle, 26°45′ S 65°21′ W, 1 (CML); Horco Molle, 650 m, 6 (CML); Las Agüitas, El Taficillo, 26°42′ S 65°22′ W, 1 (CML); Parque Provincial El Cochuna, 27°18′ S 65°54′ W, 1 (CML); Piedra Tendida, 8 km W Dique El Cajón, 26°30′ S 64°52′ W, 1 (PIDBA); Reserva Provincial La Florida, 7 km W Ibatín, on Río Pueblo Viejo, 27°13′ S 65°37′ W, 4 (3 ARG; 1 PIDBA); San Javier, 1 000 m, 26°47′ S 65°23′ W, 2 (MACN); San Javier, Estación Biológica R. Schreiter, 1 (MACN); San Miguel de Tucumán, 4 000 ft., 26°50′ S 65°13′ W, 15 (AMNH); San Miguel de Tucumán, 4 500 ft., 1 (AMNH); Villa Nougués, 26°51′ S 65°23′ W, 1 (CML).

Description: This species cannot be differentiated from *T. cinderella* based on coloration, although the structures of the cranium are very different. Unlike *T. cinderella* the supraorbital region lacks pointed processes; only in adult individuals are they slightly pronounced, but they never form processes, and in young individuals there is no evidence of edges. The rostrum is longer and narrower, and the zygomatic arches are less expanded. The lambdoidal crests are less developed compared with *T. cinderella.*

Comments: The majority of the specimen records are from the Yungas. In Jujuy Province, at the locality of 9 km NW Bárcena, an ecotonal area between Yungas and Prepuna, this species was captured with *T. pallidior*, a species typical for higher elevations in the province. On the other hand, we found numerous specimens from the type locality of *T. cinderella* and from areas nearby.

The locality "Near Yala" cited by Tate (1933) for a specimen in the FMNH, is written as "Mountains W of Yala" on the original tag.

A female with a young attached to a nipple was captured in December at Aguas Negras and a lactating female was captured in February at the locality on highway 29 (east off hwy 9), 10 km west of Tiraxi. Specimens with incrassate tails (fat storing) were collected in May at Río Blanco, in June at El Simbolar, and in July at Arroyo La Horqueta. Youngs were captured in January at Horco Molle, in February at Reserva La Florida, in March at San Miguel de Tucumán, and in July at Arroyo La Horqueta.

Thylamys venustus (Thomas, 1902)

Distribution in Argentina: The distribution of the species in Argentina is problematic, since different revisions have treated *T. sponsoria* and *T. cinderella* as belonging to *elegans* or *venusta*. We restrict the distribution in Argentina to northwestern Salta Province.

Specimens Examined (n = 8) (Fig. 6): Argentina. Salta: 27 km W Agua Blanca, 22°45′ S 64°40′ W, 1 (MACN); Angosto del Río Pescado, 22°33′ S 64°32′ W, 1 (MACN); Finca Yakulica, Angosto del Río Pescado, 22°33′ S 64°32′ W, 1 (MACN); Parque Nacional Baritú, Arroyo Santelmita, 22°31′ S 64°37′ W, 1 (MACN); Parque Nacional Baritú, Cerro Chaguar, 22°35′ S 64°37′ W, 1 (MACN); Parque Nacional Baritú, Finca Yakulica, Río Pescado, 22°33′ S 64°32′ W, 2 (CML). Bolivia. Cochabamba: Paratani, 2 800 m, 1 (BMNH holotype).

Description: Size smaller than the other species of *Thylamys.* The dorsal coloration is cinnamon brown with the sides lighter. The venter is cream, the bases of the hairs are gray except on the chin, throat, and along the midline of the chest. The periocular rings are thin and black, the cheeks are yellowish-white, and the ears are brown. The feet are cream. The tail is bicolored, dark brown above and grayish below; the proximal portion is almost unicolored. The rostrum is wide and short; the zygomatic arches are moderately

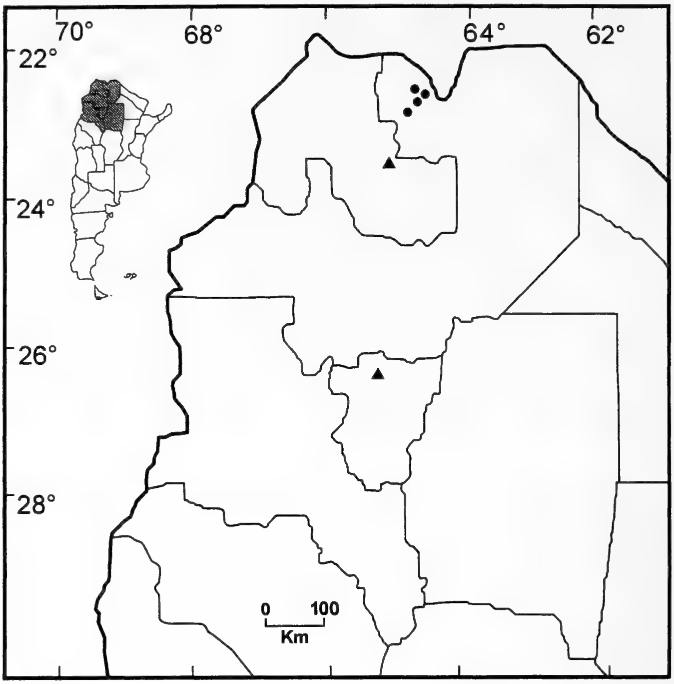

Fig. 6. Localities of occurrence of *Thylamys* sp. (triangles) and *T. venustus* (circles).

expanded. The interorbital region has edges that are slightly pronouced only in adult individuals. The dentition corresponds to old age for the majority of the specimens examined, but the size is smaller in comparison with the other species mentioned above of the same age.

Comments: According to our comparison with the type specimen of *venustus*, the majority of the specimens from northwestern Argentina do not correspond with this species, principally owing to the small size that characterizes this species. Based on our records this species is only present in northern Salta Province along the border with Bolivia.

Tate (1933) proposed a distribution from Cochabamba, Bolivia to the headwaters of the Río Bermejo. Cabrera (1957) suggested that Tate's (1933) results indicated that this area was a zone of overlapping between *M. e. venusta* and *M. e. cinderella*. Olrog (1959) also considered *venusta* as a subspecies of *elegans*, together with *cinderella* and *janetta*, with an allopatric distribution in northwestern Argentina. Anderson (1997) described the southern distribution of the species in Bolivia, along the border with Argentina. However, his sample may have included some of the species mentioned in the present study, based on our examination of the measurements published for some of the specimens. The specimen localities listed in the present study correspond to a distribution similar to that suggested by Cabrera (1957). This area contains relatively undisturbed forest; the known localities are located in Parque Nacional Baritú or in nearby areas.

Key to the species

1. Pelage with a tricolor pattern; tail accumulates fat seasonally; nasal bones more or less parallel, not expanded at the frontomaxillary sutures (Fig. 7 a); third upper premolars larger than the second . . . . Genus *Thylamys*...3

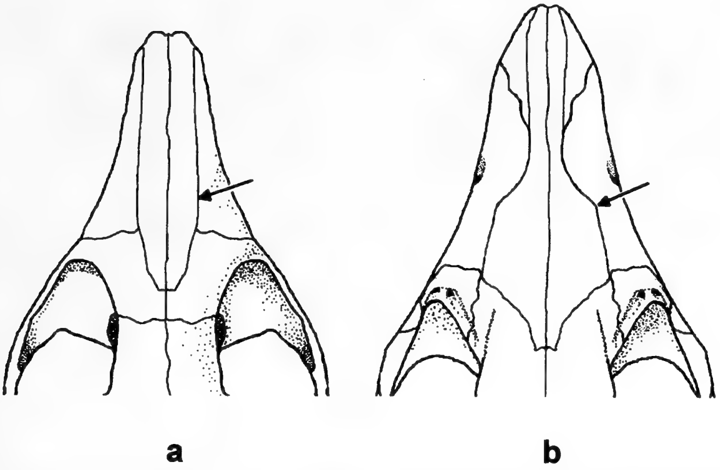

Fig. 7. Dorsal view of the anterior part of the skulls of *Thylamys (a)* and *Gracilinanus (b)* showing the differences in the nasal bones (arrow).

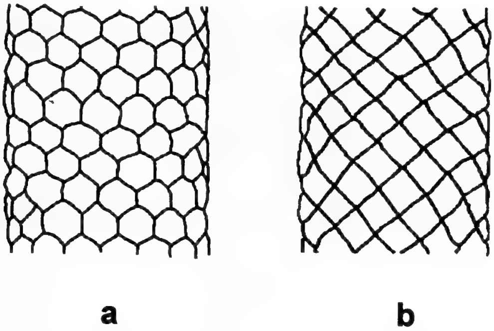

Fig. 8. View of the caudal scales of *Gracilinanus (a)* und *Micoureus (b)*.

1′. Pelage without tricolor pattern; tail does not accumulate fat seasonally; nasal bones expanded abruptly at the frontomaxillary sutures (Fig. 7 b); third upper premolars less than or subequal to the second 2

2\. Caudal scales annular (Fig. 8 a); supraorbital processes absent; greatest length of the skull less than 30 mm; length of head and body less than 110 mm . . *Gracilinanus agilis*

2′. Caudal scales spiral (Fig. 8 b); supraorbital processes well developed; greatest length of the skull greater than 32 mm; length of head and body greater than 130 mm . . . . *Micoureus constantiae*

3\. Hair of the venter pure white; length of head and body less than 95 mm; greatest length of the skull less than 26 mm 4

3′. Hair of the venter with gray bases; length of head and body greater than 100 mm; greatest length of the skull greater than 26 mm 5

4\. Dorsal coloration grayish; interorbital region without marked supraorbital processes (Fig. 9 a); auditory bullae large; snout elongated; found in the Puna, Prepuna, and Monte . . . . *Thylamys pallidior*

4′. Dorsal coloration brownish; interorbital region with marked supraorbital processes (Fig. 9 b); auditory bullae not especially large; snout not elongated; found in the Chaco . . . . *Thylamys pusilla*

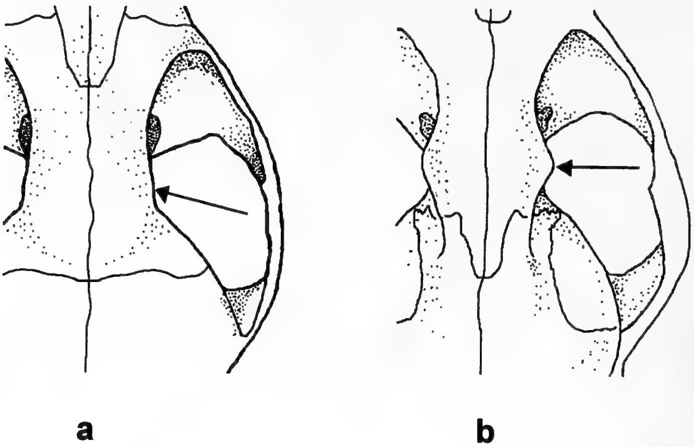

Fig. 9. Dorsal view of the interorbital region of the skulls of *a) Thylamys pallidior* showing the absence of supraorbital processes (arrow), and *b) Thylamys pusilla* showing the well marked supraorbital processes (arrow).

5. Interorbital region with pointed supraorbital processes or pronounced edges (Fig. 9 b); found in the Yungas and the Chaco .... *Thylamys cinderella*
5′. Interorbital region with smooth edges, in adult specimens the edges are slightly pronounced (Fig. 9 a); found in the Yungas 6
6. Adults with condylo-incisive length, in general, greater than 27 mm; zygomatic arch expanded, breath greater than 16 mm........................ *Thylamys sponsoria*
6′. Adults with condylo-incisive length, in general, less than 27 mm; zygomatic arch not expanded, breath less than 16 mm........................... *Thylamys venustus*

Discussion

The taxonomy and distribution of the various taxa of the marsupials of Argentina are in an initial stage of knowledge. This probably is due to the lack of specimens and data for some regions as well as to the lack of collecting efforts. On the other hand, few studies of marsupials have included specimens from Argentina; for this reason the specific identity and the limits of the distribution of the species in Argentina have not been well presented in previous publications (e. g., Palma 1995).

Based on our revision, we include a new genus for northwestern Argentina, *Gracilinanus*, with a new species for the region, *G. agilis*. Two subspecies of *Thylamys* are elevated to species, *T. cinderella* and *T. sponsoria*, which have until now been considered subspecies of *T. venustus*. Therefore, according to this study, eight species are known to occur in northwestern Argentina: *G. agilis*, *M. constantiae*, *T. cinderella*, *T. pallidior*, *T. pusilla*, *T. sponsoria*, *T. venustus* and *Thylamys* sp.

In a comparison of the diversity of marsupials in northwestern Argentina (11 species) to that of the northeast (16 species), the diversity of the latter is greater. However, only four species of mouse opossums are known for the northeast: *G. agilis*, *G. microtarsus*, *M. demerarae*, and *T. pusilla* (Gardner 1993; Mares and Braun 2000); *G. agilis* and *T. pusilla* are species shared between both regions. *Thylamys formosa* has been recorded for northeastern Argentina (Cabrera 1957; Olrog 1959; Olrog and Lucero 1981; Redford and Eisenberg 1992), but this taxon was considered a synonym of *G. agilis* by Gardner (1993) and Hershkovitz (1992).

Table 1. Measurements (in mm, except for weight, which is in g) of species of marmosines. Mean, range (in brackets), and sample size are given for each measurement.

Character	*Gracilinanus agilis*	*Micoureus constantiae*	*Thylamys cinderella*	*Thylamys pallidior*
ToL	197.0	351.9	207.0	196.3
	(178,0–233.0)	(276.0–394.0)	(169.0–251.0)	(169.0–234.0)
	3	11	40	22
TL	108.0	201.8	116.2	100.2
	(98.0–126.0)	(155.0–225.0)	(92.0–140.0)	(87.0–111.0)
	3	11	45	28
HFL	15.3	25.3	13.9	13.0
	(14.0–16.0)	(24.0–27.0)	(11.0–17.0)	(10.0–20.0)
	3	8	46	26
EL	15.7	26.5	21.3	21.5
	(15.0–17.0)	(22.4–29.0)	(15.0–25.4)	(13.0–26.0)
	3	11	46	25
W	12.0	83.4	18.9	18.5
	(12.0–12.0)	(63.0–108.0)	(10.5–34.0)	(12.0–30.0)
	2	5	32	13
CIL	24.2	38.9	27.1	25.6
	(22.9–25.5)	(35.9–41.7)	(22.6–30.6)	(24.1–26.3)
	3	5	26	3
ONL	25.4	40.2	27.4	26.1
	(23.8–27.2)	(37.4–42.8)	(18.8–31.5)	(24.9–26.8)
	6	6	27	3
BB	9.7	14.5	10.7	10.5
	(9.4–10.2)	(13.3–15.4)	(9.5–11.4)	(10.0–10.9)
	6	7	29	3
PC	5.1	6.9	4.5	4.6
	(4.8–5.3)	(6.3–7.2)	(3.8–5.6)	(4.3–5.1)
	6	9	28	3
ZB	13.6	22.0	14.8	13.7
	(12.4–14.3)	(13.7–26.6)	(11.6–17.2)	(13.1–14.1)
	6	7	29	3
MB	9.8	14.5	10.4	10.1
	(9.3–10.2)	(14.2–14.8)	(9.0–11.6)	9.8–10.3)
	5	4	25	3
LR	9.1	15.0	10.3	9.7
	(8.2–9.8)	(14.1–16.7)	(8.3–11.8)	(9.2–10.0)
	5	6	30	3
LN	10.2	18.7	12.9	–
	(8.8–11.1)	(16.3–20.2)	(12.4–13.2)	–
	6	4	3	–
LMxT	9.6	15.9	10.4	11.4
	(9.3–9.9)	(15.3–16.5)	(7.7–11.5)	(9.6–14.0)
	6	7	30	3
PL	12.5	21.0	13.9	13.4
	(11.7–13.4)	(19.2–22.8)	(11.8–15.4)	(12.0–14.4)
	5	6	28	3
C-C	3.9	7.3	4.3	3.9
	(3.4–4.2)	(6.6–8.4)	(3.3–5.0)	(3.8–4.0)
	6	7	30	3
M-M	7.5	12.8	8.2	8.8
	(7.2–7.7)	(11.4–13.6)	(6.6–9.5)	(8.6–9.0)
	6	8	30	3
LM	17.4	29.3	19.2	18.7
	(16.8–18.8)	(24.6–32.1)	(10.1–22.8)	(17.6–19.4)
	5	9	30	3
LMdT	9.8	16.6	10.9	11.2
	(9.4–10.1)	(15.5–17.3)	(9.8–12.0)	(10.3–12.7)
	5	9	30	3

Table 1. Continued

Character	*Thylamus pusilla*	*Thylamus sp*	*Thylamys sponsoria*	*Thylamys venustus*
ToL	185.7	220.6	222.1	220.4
	(141.0–217.0)	(199.0–215.0)	(148.0–271.0)	(200.0–244.0)
	14	7	91	6
TL	97.5	118.4	126.8	128.0
	(75.0–123.0)	(110.0–130.0)	(75.0–151.0)	(115.0–146.0)
	15	7	95	7
HFL	13.6	14.1	15.6	14.0
	(10.0–24.0)	(9.0–15.0)	(7.0–29.0)	(11.1–16.9)
	15	7	75	7
EL	18.2	19.9	21.2	20.5
	(12.0–23.0)	(12.0–25.0)	(11.0–29.5)	(16.5–23.0)
	16	7	92	6
W	16.3	–	26.9	22.5
	(10.0–22.0)	–	(9.0–46.0)	(15.0–28.0)
	12	–	36	4
CIL	24.4	27.6	28.5	27.8
	(20.0–26.9)	(26.7–28.2)	(21.8–31.8)	(26.0–29.2)
	16	6	65	7
ONL	25.1	28.7	29.1	28.4
	(20.9–27.0)	(27.6–29.5)	(23.0–32.3)	(26.6–30.0)
	16	6	65	7
BB	9.9	11.1	11.1	11.0
	(9.3–10.7)	(10.4–11.6)	(9.9–11.9)	(10.4–11.5)
	17	7	67	8
PC	4.7	5.4	5.0	4.8
	(4.2–5.5)	(4.7–5.9)	(4.1–6.6)	–
	19	7	50	1
ZB	14.2	15.6	15.4	15.1
	(13.0–15.3)	(15.1–16.0)	(11.9–17.7)	(14.2–16.7)
	13	6	67	8
MB	9.8	10.7	10.9	10.7
	(9.5–10.1)	(10.3–11.0)	(8.9–11.8)	(10.2–11.5)
	2	6	62	7
LR	8.8	10.7	11.0	10.6
	(8.5–9.1)	(10.3–11.2)	(8.2–12.3)	(9.5–11.5)
	3	7	65	8
LN	10.2	–	12.1	11.7
	(9.5–11.0)	–	(9.6–13.4)	(10.2–12.8)
	3	–	12	5
LMxT	11.7	11.1	11.4	11.1
	(9.2–13.1)	(10.7–11.4)	(8.7–15.0)	(10.7–11.6)
	18	7	74	8
PL	13.0	15.1	15.1	14.7
	(11.5–14.1)	(14.7–15.5)	(12.3-17.1)	(13.7–15.7)
	11	5	60	8
C-C	3.7	4.0	4.4	4.6
	(3.0–4.2)	(3.8–4.1)	(3.3–5.4)	(4.2–5.3)
	19	7	71	8
M-M	7.8	9.2	8.8	8.7
	(6.1–8.5)	(7.8–9.7)	(6.2–10.1)	(8.0–9.7)
	17	7	70	8
LM	18.4	20.5	20.7	20.1
	(16.0–20.0)	(18.7–21.5)	(16.0–29.6)	(18.4–21.8)
	18	7	78	8
LMdT	10.9	11.5	11.6	11.3
	(9.8–11.6)	(11.1–12.0)	(8.8–13.4)	(10.7–11.8)
	19	7	78	8

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Zusammenfassung

Mausopossums (Didelmorphia, Didelphidae) aus dem Nordwesten Argentiniens: Systematik und Verbreitung

Es werden die Ergebnisse einer systematischen Revision der Mausopossums aus dem Nordwesten Argentiniens dargestellt. Drei Gattungen, *Gracilinanus*, *Micoureus*, *Thylamys*, und acht Arten werden behandelt. Die Gattung *Gracilinanus* ist eine neuer Nachweis für diese Region. Für zwei Subspezies von *Thylamys* wird Artrang vorgeschlagen. Für jede Art werden Fundorte, Beschreibungen der äußeren Gestalt und des Schädels, Maße sowie Kommentare zur Taxomonie und zur Naturgeschichte gegeben.

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Reproductive ecology of the bat *Carollia perspicillata* (Chiroptera: Phyllostomidae) in a fragment of the Brazilian Atlantic coastal forest

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Abstract

The reproductive pattern of the bat *Carollia perspicillata* (Linnaeus 1758) was studied in a forest fragment of the Atlantic rainforest in southeastern Brazil from November 1997 to June 1999. *C. perspicillata* showed a seasonal bimodal polyoestrous pattern, with its highest reproductive peaks during the wetter months and lesser peaks during the drier months. Several other aspects were also affected by rainfall: at the end of the dry and wet seasons, number of juveniles was highest (reflecting reproductive peaks), individuals were heavier (indicating better conditions), and activity peaks were shorter and earlier in the night. The influence of rainfall on reproductive patterns is likely to be indirect, its effects being mediated by the availability of food resources, especially fruits, which is probably the factor that does directly affect the reproduction of this species.

Key words: *Carollia perspicillata*, Chiroptera, reproduction, ecology, seasonal dynamics

Introduction

Most acquired knowledge on reproduction of Neotropical bats has come from long-term, detailed studies in Central America (e. g. Baker et al. 1979; Fleming 1988; Fleming et al. 1973; Handley et al. 1991). However, as latitude has some effects on reproductive seasons, results obtained in Central America should not be readily extrapolated to elsewhere in the Neotropics. Several data on the reproduction of Neotropical species have been obtained by studies focusing on other subjects, like communities (Ribeiro de Mello et al. 1999).

On the basis of their classic work in Central America, Fleming et al. (1973) were the first to list four basic reproductive patterns for Neotropical bats, which were later discussed by Taddei (1980), with remarks for Brazilian species: 1. seasonal monestry (family Noctilionidae): single reproductive peak during the year; 2. bimodal seasonal polyoestry (family Phyllostomidae, especially the frugivores): two reproductive peaks during the year; 3. a long reproductive period, with a small period of reproductive inactivity (family Vespertilionidae); 4. reproduction throughout the year (the vampire bats, subfamily Desmodontinae, currently included in the family Phyllostomidae).

The work by Myers (1977), in Paraguay, suggested that there can still be other patterns to be discovered, as in some vespertilionid bats there can be three short reproductive peaks a year, which would correspond to a trimodal seasonal polyoestry.

Several studies have shown that in Brazil the short tailed fruit bat, *Carollia perspicillata*,

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a phyllostomid, shows bimodal seasonal polyoestry (Fazzolari-Corrêa 1995; Ribeiro de Mello and Fernandez 1998; Ribeiro de Mello et al. 1999). This is similar to the pattern *C. perspicillata* shows in Central America (Fleming 1988) and in French Guyana (Charles-Dominique 1991; Cosson and Pascal 1994). Usually there is a higher reproductive peak (almost simultaneously for males and females) during the local wet season, followed by a smaller peak in the dry season. As this pattern is related to climatic seasons, they are inverted in the northern and southern hemispheres, causing predictable differences between Central and South America, in addition to more subtle geographic variation.

The present study aimed to contribute towards further enhancing the knowledge on the reproduction of *Carollia perspicillata*, a bat species pointed out by many authors (e. g. Fleming 1988) as one of the main seed dispersers of pioneer plants, especially understory shrubs, in the Neotropical Region. The Brazilian Atlantic Coastal forest is one of the most endangered ecosystems of the World (Fonseca 1985), which makes it very important to gather more details on its key mutualists. Reproductive condition, age structure, sex ratio, mean mass, and activity cycle were studied in a population of *C. perspicillata*, in order to characterize the variation in these parameters through time and to relate them to climatic patterns, particularly rainfall.

Material and methods

Study area

The study was carried out in a forest fragment (area 15 ha) of the Atlantic coastal rainforest within Poço das Antas Biological Reserve (22°30′–22°33′ S/42°15′–42°19′ W). The fragment is close (<2 km) and thus within flight distance for *C. perspicillata* from the main forest block of the reserve (ca. 3000 ha). The climate of the area is warm and damp; between 1987 and 1998 the mean air temperature was 24.6 °C and the mean annual rainfall was 2.121 mm (Programa Mata Atlântica, unpubl. data).

There is a moderate seasonality in rainfall (Fig. 1). The driest months occur between June and August ("dry" season), and the wettest from September to May ("wet" season). The seasonality of rainfall during the last 10 years is shown in figure 1. There is some yearly variation in the exact duration of the seasons. Therefore we used another criterion to characterize months according to rainfall, especially when analysing hourly activity of the bats (expressed by number of captures). We considered the drier months in 1998 to be May–July, and in 1999 to be May–June, because their rainfall indices were clearly lower than in the remainder of the year (see Fig. 2). This seems to be more consistent with the seasonality of fruit production.

The fragment studied ("H") belongs to a system of eight small forest fragments, and its area is the largest among them. The history of the area has not yet been totally revealed, but there is some evidence that it was a natural island system, becoming drier after the building of a dam in the São João River, which drastically altered the water level. Along the edges of the fragment, as well as in its interior, there are many plant species which have been reported in previous studies as being visited by *C. perspicillata*, such as *Piper* spp. (the most abundant shrub in the edge of the fragment), *Solanum* spp. (very common), *Cecropia* sp.(common in the open area-matrix), and *Passiflora* sp. (present in low abundance) (Bredt 1996; Charles-Dominique 1991, Fleming 1988; Sazima and Sazima 1978).

Compared to the others fragment H has relatively high trees, which support even primate populations of *Leonthopitecus rosalia*, *Cebus apella*, and *Aloutta fusca*. It has a dense understory near the edges, closed canopy (with some gaps) and is connected to a forest "corridor" that leads to the continuous forest. The edges of the fragment are covered by pioneer shrubs (mainly *Piper* spp. and *Solanum* spp.), bracken (*Pteridium* spp.), grass and pioneer trees (like *Cecropia* sp. and *Trema micrantha*), in order of abundance.

Capture and recording

From November 1997 to June 1999, monthly capture-mark-recapture sessions were carried out. Although marking is not useful for the abundance estimation of bats outside large roosts, due to the

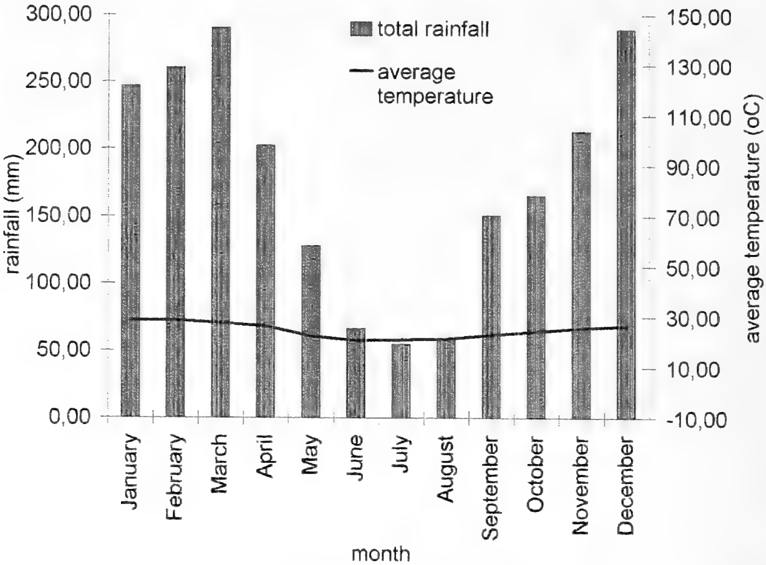

Fig. 1. Variations in rainfall and air temperature for the Poço das Antas Biological Reserve, southeastern Brazil, using the averages for each month for the period 1987–1998.

typical low recapture rates in open areas (Kunz 1982; Kunz 1988; Fleming 1988; Seber 1982), knowing the number of individuals in the total of captures is important in the procedures of non-parametrical statistical tests.

After being examined each bat was individually marked on the forearm with an aluminium-numbered band (provided by A. C. Hughes, Inc.). We used aluminium bands to prevent removal by bats, an usual problem of plastic bands. Marked bats had some eventual injuries, but these could be reduced by using bands larger than the circumference of the forearm. The code contained the letters UFRJ (Universidade Federal do Rio de Janeiro) and three numerical digits.

Three mist-nets (7 m length × 2.5 m height) were placed three or two nights a month, one hour before sundown (approximately 5:00 PM) and closed by sunrise (approximately 6:00 AM). They were positioned along the edge of the fragment, in open trails and near plants attractive to *C. perspicillata*, areas of higher capture probability of this species (Charles-Dominique 1991; Fleming 1988).

Cotton bags were used to keep captured individuals before the examination. The following parameters were observed and recorded (following the methods proposed by Kunz 1988). Species, following Pine (1972), Taddei and Vizotto (1973), and Cloutier and Thomas 1992). Sex. Age – individuals were allocated to age classes by examining the degree of epiphysical ossification of the right digits I to IV (Cosson et al. 1993; Kunz 1988). The degree of ossification was evaluated based on the transparency of the epiphysis; the most representative digit was III. The individuals with epiphyses totally ossified were regarded as adults; subadults were the ones with two bands of cartilage on at least one epiphysis; and juveniles were those whose epiphysis was totally made of cartilage. Total body mass (measured with a Pesola© scale – 100 g/1 g and 300 g/1 g). Length of the forearm and tibia (measured using a digital caliper). The reproductive condition was inferred by the analysis of external characters. Males were classified as either having abdominal or scrotal testis. Females as either pregnant (enlarged abdomen with a detectable foetus), lactating (enlarged nipples, and no hair around them), post-lactating (apparent hairy nipples), and non-reproductive (normal abdomen and nipples not apparent).

Data analysis

All statistical analysis followed Zar (1996). For comparing frequency distributions, chi-square tests were used when possible, and the G test (log-likelihood ratio) was used in analyses that did not meet the assumptions of chi-square. Body mass variations across time were analysed using the Kruskall-

Wallis test, followed by the a posteriori Dunn test (paired), because the distribution of the mass data was not normal. To test the relationship between different data series, such as proportion of reproductive females and average body mass, Pearson correlation was used.

Results

During the twenty months of the study, we found four reproductive seasons in *C. perspicillata*, two with reproductive maxima and two with smaller peaks of reproductive activity. The highest peaks of reproductive females occurred during the rainy season and the smaller ones during the early dry season (Fig. 2). Proportions of reproductive adult females and reproductive adult males were positively correlated with each other ($r = 0.81$, 18 df, $p = 0.0018$). The proportion of reproductive adults varied among months in both sexes (females $G = 107.13$, 19 df; $p < 0.001$, $n = 434$; males $G = 36.84$, 19 df; $0.01 < p < 0.005$, $n = 410$).

In this study as a whole, sex ratio (M/F) for adults was 0.67, differing significantly from 1:1 ($\chi^2 = 30.17$, 1 df; $p < 0.001$, $n = 776$); females represented 60 % of the total of 1,073 captures. Considering adult males and females as a whole, there was no significant variation in the sex ratio among the months studied ($\chi^2 = 23.6$, 19 df; $p = 0.16$).

Age structure did not differ for males and females in the study as a whole ($G = 6.11$, 2 df; $0.025 < p < 0.05$, $n = 932$). Pooling both sexes, there were significant differences between the proportion of age classes among months ($G = 238.04$, 38 df; $p < 0.001$) (Fig. 3). The proportion of juveniles was positively correlated with the proportion of pregnant females three months before parturition ($r = 0.92$, 17 df; $p = 0.00002$). The peaks of lactating females occurred two months after the peaks of pregnant females and one month before the peak of juveniles (Fig. 4).

The mean body mass of adults varied among months in both sexes (females, $H = 129$, 19 df; $p < 0.0001$; males $H = 37.6$, 19 df; $p = 0.0067$), and the greatest differences occurred between months of the dry season and those of the wet season (Fig. 5). Body mass varia-

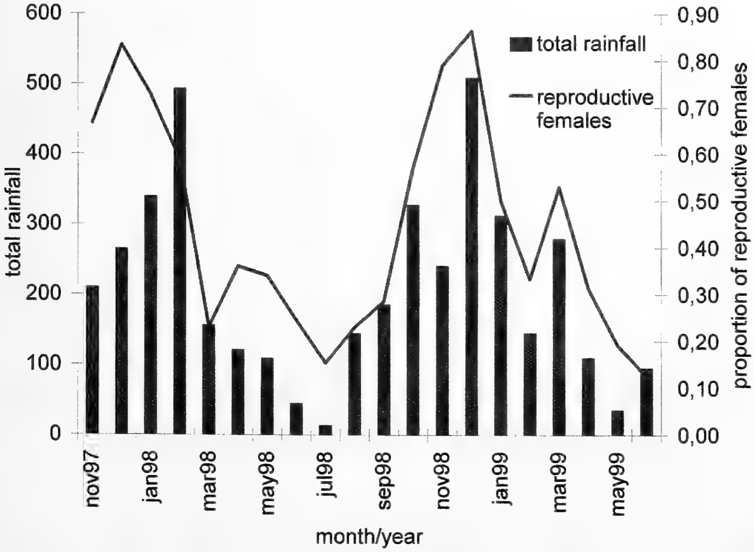

Fig. 2. Monthly rainfall and proportion of reproductive adult females of *C. perspicillata*, during the period studied.

tions in both sexes were correlated with each other ($r = 0.85$, 17 df; $p = 0.0003$). Body mass variation of adult females was positively correlated with the proportion of reproductive adult females ($r = 0.79$, 18 df; $p = 0.0034$).

Regarding activity time, the variations in the numbers of captures of adult females and adult males through the night, were correlated with each other ($r = 0.98$; 10 df,

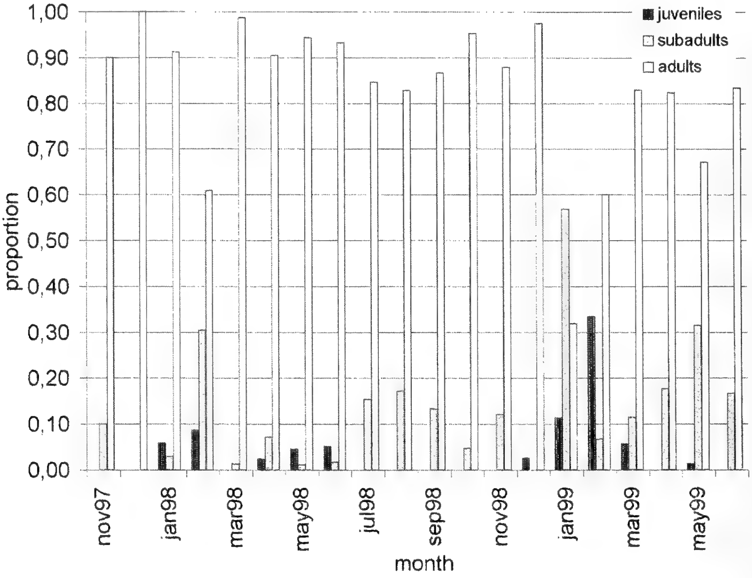

Fig. 3. Monthly variation in the age structure of the *C. perspicillata* population; values are the proportion of captures in each age class in relation to the total number of captures in each month.

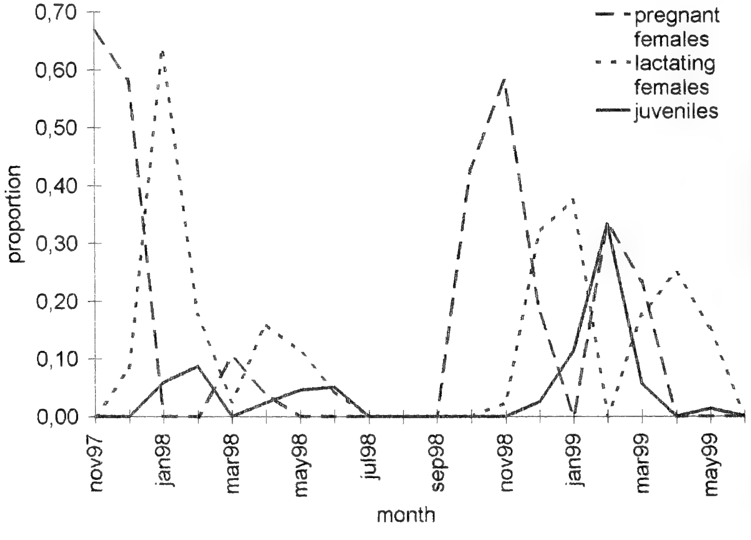

Fig. 4. Monthly variation in the frequency of pregnant and lactating adult females compared to the proportion of juveniles of *C. perspicillata*; values expressed as proportions of the total number of captures in each month.

$p = 8.0 \times 10^{-7}$) (Fig. 6). The sex ratio did not vary throughout the night ($\chi^2 = 5.57$, 11 df, $p = 0.9007$, $n = 853$). Pooling both sexes, the hourly distribution of captures differed significantly between the drier and the wetter months ($\chi^2 = 29.7$, 5 df, $p < 0.0001$, $n = 853$), as the activity was irregular during the drier months, compared to the pattern presented in the wet months (Fig. 7).

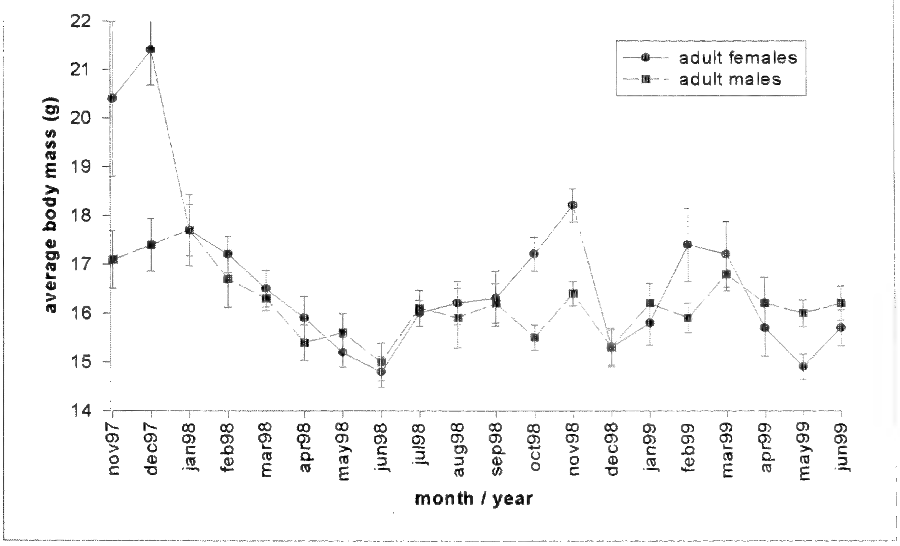

Fig. 5. Monthly variation in the average mass (g) of adult males and females of *C. perspicillata*.

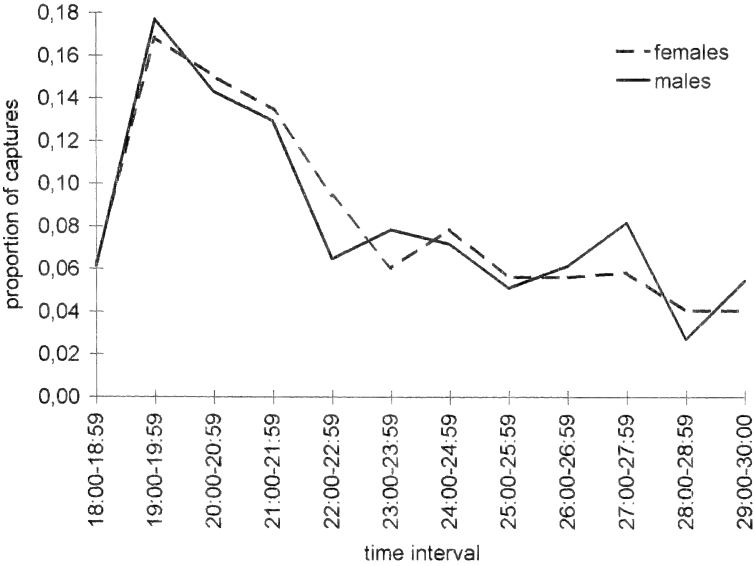

Fig. 6. Variation in the proportion of captures (related to the total) of adult males and females of *C. perspicillata* in different time intervals of the night.

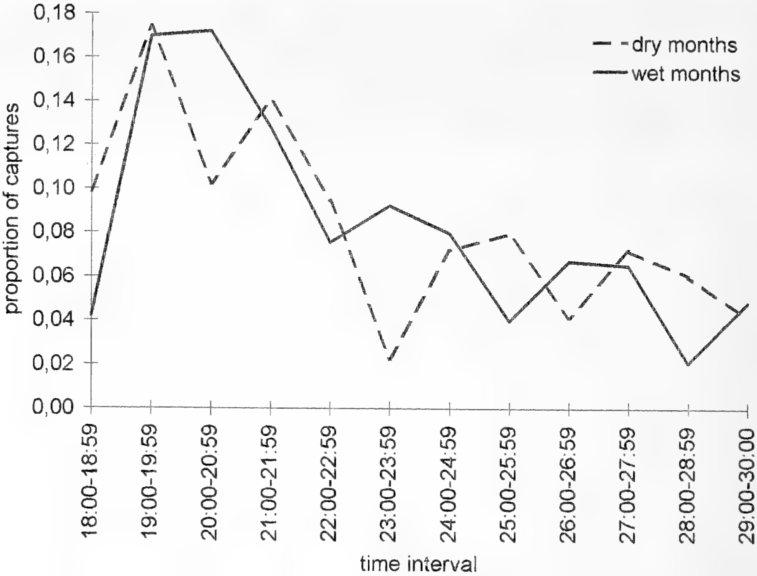

Fig. 7. Variation in the proportion of captures (related to the total) of *C. perspicillata* related in different time intervals during the night, comparing the patterns found in the wet months and in the dry months.

Discussion

The variations in the proportion of reproductive *C. perspicillata* may be best described by a pattern of bimodal seasonal polyoestry, which has already been found for this species in other studies, e. g. in Costa Rica (Fleming 1988), French Guyana (Charles-Dominique 1991; Cosson and Pascal 1994), Panamá (Handley et al. 1991); and Brazil (Fazzolari-Corrêa 1995). The highest reproductive peak for each year occurred during the wetter months, a time of the year where there is probably a greater availability of more nutritional food resources, specially fruits (Marinho-Filho 1991). During the drier months of each year, a secondary peak of reproduction occurred, probably as an effect of post-partum oestrus (Cloutier and Thomas 1992). This is probably the cause of the secondary peak of reproduction a few months after the highest peak, when resources are probably in low abundance, a pattern also proposed by Cosson and Pascal (1994). There is also a temporal relation in the reproductive activity of females and males, which could be interpreted as another evidence of post-partum oestrus. During drier months, *C. perspicillata* tends to increase the proportion of items other than fruits in its diet, especially insects, pollen and nectar (Marinho-Filho 1991), because fruits of its preferred understory shrubs tend to decrease in abundance. Pregnancy lasts three months on average and each female has only one youngster at a time, with very few exceptions (Cloutier and Thomas 1992). This means that each female usually contributes with one or seldom two individuals a year for the population (Cosson and Pascal 1994).

The sex ratio is reverse to what was found in studies based on samplings made close to large roosts (e. g. Fleming 1988) or in small but very crowded roosts (e. g. Cosson and Pascal 1994). There, males accounted for two thirds of the total number of captures. On the basis of the available data, it is not possible to know if this pattern is a consequence of a higher capture probability of females, or if there are really more females in the area. Considering that *C. perspicillata* usually forms harems, and that harem males tend to have smaller home ranges than females, these factors combined could be responsible for the higher capture rate of females.

The direct consequence of the reproductive pattern for the total population is the change of the age structure. The major input of juveniles occurred three months after the peak of pregnancy in both the wet and the dry seasons. Compared to the age structure of other small mammals, the age distribution of this species seems to be very short at the base. Adults accounted for the majority of captures, while juveniles were less abundant. This "inverted pattern" could be explained by the demographic peculiarities of *C. perspicillata* bats: females have normally only one youngster a year, and some juveniles do not survive to reach the adult age. Besides, individuals become adult in about four months, and the mean longevity is approximately 2.5 years (FLEMING 1988). These factors can lead to a higher abundance of adults in *C. perspicillata* populations.

The variation of the body mass of adult females and males seems to be related with the reproductive seasons of *C. perspicillata*. Body mass tended to be higher during the wetter months, the same time when the ratio of females reproducing was higher. This pattern suggests that the wetter months may be the most favourable time for the species to obtain higher quality nourishment in Brazil, corroborating previous studies (e. g. COSSON and PASCAL 1994; MARINHO-FILHO 1991). Females become heavier during the highest reproductive activity, which is a consequence of pregnancy, but males also increase their body mass at the same time, corroborating the hypothesis of a difference in food abundance, as proposed in other works (e. g. COSSON and PASCAL 1994).

Following the general trend of this study, the activity (capture frequency) of *C. perspicillata* also seems to have seasonal patterns. During the wet months, the activity was more regular and concentrated, compared to the dry months, but in both cases it was higher at the beginning of the night. During the wet seasons, *C. perspicillata* concentrates its activity in the first half of the night. Probably, the availability of fruits is higher at this time of the year, and, therefore, *C. perspicillata* tends to reduce drastically its activity after obtaining enough food for their necessities. On the other hand, during the dry season, it becomes necessary to extend the period of activity, because there may be fewer fruits available in the area.

In an overview, in the Atlantic coastal forest *C. perspicillata* seems to have its ecological patterns strongly related to the climatic variations, as in other regions of the Neotropics. It seems reasonable to assume that climatic variations must be the indirect cause of the patterns, the direct cause being the variation in the availability of food, mainly understory shrubs, which is the preferred food source of the species in all the areas where it occurs. The variation in the rainfall seems to affect directly the populations of plants that this bat uses as food, and, consequently, the population of the bats.

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Zusammenfassung

Fortpflanzungsökologie der Brillenblattnasenfledermaus Carollia perspicillata (Chiroptera: Phyllostomidae) in einem Fragment des atlantischen Küstenregenwaldes in Brasilien

Das Ziel dieser Untersuchung war es, das Fortpflanzungsmuster der Brillenblattnasenfledermaus *Carollia perspicillata* (Phyllostomidae) zu erfassen und Faktoren zu bestimmen, die dieses Muster beeinflussen. Die Daten wurden über einen Zeitraum von anderthalb Jahren von November 1997 bis Juli 1999 gesammelt. Die Untersuchung wurde in Brasilien in dem Naturschutzgebiet Poço das Antas (22°30′–22°33′ S, 42°15′–42°19′ W) bei der Stadt Silva Jardim in der Provinz Rio de Janeiro durchgeführt. Die Datenaufnahme im Freiland erfolgte einmal pro Monat in einem 15 ha großen Waldfragment des atlantischen Küstenregenwaldes. Das Untersuchungsgebiet zeichnet sich durch eine reichhaltige Vegetation aus, die als Nahrung und zum Teil als Quartier für Fledermäuse dient. Zum Fang der Fledermäuse wurden Japannetze eingesetzt. Das Fortpflanzungsmuster von *C. perspicillata* ist durch eine jahreszeitliche Rhythmik bestimmt mit einem Maximum in den Regenmonaten (September bis Mai) und einem schwächeren Maximum in den Trockenmonaten (Juni–August). Drei Monate nachdem die meisten Weibchen trächtig waren, kam das Maximum an juvenilen Tieren. Die durchschnittliche Körpermasse der Weibchen und die Aktivitätsrhythmik von *C. perspicillata* veränderte sich von den Regen- zu den Trockenmonaten. Während der Regenmonate trat nur ein sehr ausgeprägtes Aktivitätsmaximum pro Nacht auf. Während der Trockenmonate war die Aktivität gleichmäßig über die Nacht verteilt und es trat kein ausgeprägtes Maximum auf. Diese Muster deuten bei *C. perspicillata* eine Beziehung an zwischen Fortpflanzungsrhythmik und Regen. Die Regenmenge kann die Verfügbarkeit der Nahrungsquellen beeinflussen und folglich auch die Aktivität der Fledermäuse.

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Do arctic and red foxes compete for food?

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Abstract

Overlap and differences in food habits between arctic and red foxes, *Alopex lagopus* and *Vulpes vulpes*, were studied by collecting scats (faeces) at dens above the tree line (alpine region) in northern Norway. Factors other than fox species included den, region, year, height above the sea level, height above the tree line, distance to the tree line, and reproductive status. A total of 5314 scats was analysed, giving n = 34 and n = 33 "den-years" for arctic and red foxes, respectively. Lemming, voles, reindeer, and birds, were major prey of both fox species, and insects were frequent in red fox scats. Small mammals contributed 78% in both arctic and red foxes diet. Arctic foxes consumed more lemmings than red foxes, while red foxes consumed more voles, birds, and insects. Despite such differences, overlap in food habits between the two fox species was high, and consequently, competition for food is likely. Some of the differences may have been caused by environmental rather than intrinsic factors, as red foxes on average occupied dens at lower altitudes than arctic foxes. A high degree of variation was found within fox species, as well as within and between dens, years, and regions. Fox species was most important for the percentage of prey, year and region had smaller effects. The percentage of prey was correlated with height above sea level and height above the tree line as expected, except between the latter and lemming. Competition for food could be one important factor explaining the apparent exclusion of the threatened arctic fox from the home range of the abundant red fox.

Key words: *Alopex lagopus*, *Vulpes vulpes*, diet comparison, Norway

Introduction

Competition between related mammalian carnivores appears to be common, with the larger species generally superior to the smaller (e.g., Lamprecht 1978; Schmidt 1986; Theberge and Wedeles 1989; Johnson and Franklin 1994; Cavallini and Nel 1995; Palomares and Caro 1999). The larger predator may affect the distribution, habitat use, feeding habits, group size, or activity patterns of the smaller predator. Only rarely may two similar-sized predators with similar diet coexist, as, e.g., the badger *Meles meles* and the red fox *Vulpes vulpes* (Ciampalini and Lovari 1985; Fedriani et al. 1999), and perhaps also the red fox and the grey fox *Urocyon cinereoargenteus* (Hockman and Chapman 1983). Direct evidence of competition is difficult to prove without doubt. One set of conditions for ungulates may be that habitat and food overlap exist, and that the shared dietary resources are limited (Putman 1996). This is more difficult for territorial carnivores where interspecific exclusion also takes place, because often only the result of the process of exclusion can be studied and not the process in itself.

The arctic fox *Alopex lagopus* in Fennoscandia (Norway, Sweden, and Finland) is very rare and threatened by extinction, whereas the red fox thrives throughout the re-

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gion. Numerous discussions have pointed to the red fox as a competitor or even predator of the arctic fox (sensu HERSTEINSSON et al. 1989), but the relationship between the two species in the region is still largely unknown. Arctic foxes are restricted to alpine environments, and although a few are still found in most regions, breeding is very rare. Competition for food by the two fox species has been indicated, but lack of data has precluded reliable conclusions (sensu FRAFJORD 1995). Arctic foxes feed largely on lemmings (reviewed by FRAFJORD 1995; compare TANNERFELDT and ANGERBJÖRN 1998; ANGERBJÖRN et al. 1999; ELMHAGEN et al. 2000), but spatial and seasonal diet may vary greatly (e. g., FAY and STEPHENSON 1989; FRAFJORD 1993; ANGERBJÖRN et al. 1994; BANTLE and ALISAUSKAS 1998; STRAND et al. 1998 a). The red fox lives in a diversity of habitats and its diet varies tremendously, but small mammals tend to be important (e. g., LUND 1962; HEWSON and KOLB 1975; JENSEN and SEQUEIRA 1978; CALISTI et al. 1990; CAVALLINI and LOVARI 1991).

The aim of this study is to investigate the food habits of sympatric arctic and red foxes in the alpine region of northern Norway. The main objective is to examine the degree of difference and overlap in the diet of the two fox species.

Material and methods

During the years 1994–1998 arctic fox dens throughout northern Norway were visited for examination and documentation (north of 65° N), and for recording the presence or absence of arctic foxes and arctic fox litters. Presence of red foxes at arctic fox dens was also recorded, as well as all red fox dens found at or above the tree line. I collected fox scats at dens whenever possible, and some samples were also collected by local wardens (Statskog–Fjelltjenesten). The scats were stored in a freezer and dried at 80–100 °C for several hours until completely dry. Each scat was broken up by hand and its content identified according to FRAFJORD (1995). The identification was mainly based on hairs and feathers, with only marginal, additional help from teeth and bones. Hairs from scats were compared under the microscope with hairs from a reference collection made previously. Small mammals (lemmings and voles) were identified on the coloration of the hairs. Focus was placed on the four major prey groups earlier identified as the most important to arctic and red foxes: lemmings, voles, reindeer *Rangifer tarandus* (from carcasses, some hair fragments are almost always ingested), and birds. Although other prey was also identified whenever possible, the scat content was not searched as thoroughly as previously (FRAFJORD 1995) for minor prey items, and a smaller number of samples was studied under the microscope. Consequently, rare or minor prey are likely underestimated slightly in this study (sensu REYNOLDS and AEBISCHER 1991; CAVALLINI and VOLPI 1995). Single fox hairs were ignored, as well as plant material other than berries. No attempts were made to identify shrew (Soricidae) hairs, and only a single shrew mandible was found. No distinction was made between *Mustela erminea* and *M. nivalis*, both are included under the heading *Mustela e/n* (only *M. erminea* were found dead at dens). The mink *M. vison* and hare *Lepus timidus* are also potential prey. Possible voles include *Microtus agrestis*, *M. oeconomus*, *Clethrionomys rufocanus*, *C. rutilus*, and *C. glareolus*. *M. oeconomus* and *C. rutilus* have not been recorded from the south region, the only region where *C. glareolus* has been recorded. A category of "unidentified mammals" is not included in any statistical analysis.

Although the major aim of this study was to compare the food habits of red and arctic foxes, several other factors are included: litter of pups vs. no litter, year of collection, region, meter above sea level, meter above the tree line (nearest forest), and shortest distance to the nearest forest. The three latter factors were taken from topographical maps (1 : 50 000). Northern Norway was divided into four regions (Fig. 1): south (most of Nordland county), central (northern part of Nordland and a large part of Troms county), north (northern part of Troms and western part of Finnmark county) and northeast (eastern part of Finnmark). Year of collection was only used to give an indication of yearly differences, because in many cases the exact year of deposition of the scats was not known (older scats could perhaps be 1–3 years old). Evidence of reproduction was found either by observing pups or by tracks and signs at the den. Species inhabiting the den was recorded by observations or by signs on the den (notably the size of the entrances used). Two arctic fox dens were excluded from all analysis because the inhabiting species was uncertain.

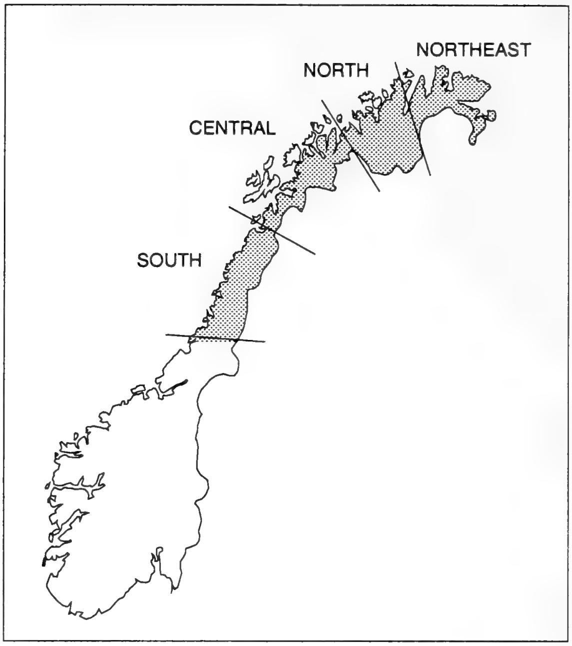

Fig. 1. Map of Norway, showing northern Norway (hatched) with the four regions indicated. Note that the arctic fox distribution range is smaller than the hatched area.

A minimum sample size of 30 scats was attempted, but two cases of smaller samples were included (27 and 28 scats, for the red fox). Smaller samples were lumped by species and region and included in some analyses if the number then exceeded 30 scats. Repeated sampling from the same den during several years was included in the analysis as different den-years. This concerned mostly six arctic fox dens, which were also treated separately. This gave a maximum number of samples (den-years) of 34 for arctic foxes and 33 for red foxes, with average sample sizes (± SD) of 82.5 ± 60.2 and 76.0 ± 43.1 scats, respectively. The total number of scats analysed was 2 805 and 2 509 for arctic and red foxes, respectively. Differences in food habits were tested by the Mann-Whitney U/Wilcoxon rank sum test (z-score) and Kruskal-Wallis H test (χ^2). Univariate ANOVA was used to indicate the relative importance of several factors (F), and Pearson's correlation coefficient (r) was used to study the relationship between prey types and several factors. Only frequency of occurrence is used. The percent of occurrence of every prey identified is given, but included in subsequent analysis are only prey with a frequency of occurrence in at least one fox species of more than 2%, and in most cases 5%. The latter includes only the four major prey items, with the addition of insects. Two indices were calculated to illustrate the magnitude of overlap and difference: percentage overlap (PO = Schoener overlap index; Krebs 1989, p. 381), and difference ($D = \Sigma|px_i - py_i|$, $i = 1 \ldots 5$, px_i = percent of prey i in fox species x, py_i = percent of prey i in species y). In both, only the five most frequent prey were included. PO ranges from 0–100% overlap, D increases with increasing difference in food habits.

Results

Lemming, voles, reindeer, and birds were the major food of both arctic and red foxes, comprising 96 and 92% of the total (100%), respectively. Significant differences in food habits between arctic and red foxes were found for lemming, voles, birds, insects, and berries (Tab. 1), but not for reindeer, bird eggs or hare (D = 93.0%, PO = 61.8%). Arctic foxes consumed nearly twice as many lemmings as red foxes, and only about a fourth the amount of voles. Thus, arctic foxes consumed many more lemmings than voles, while red foxes consumed about equal amounts of lemmings and voles (Tab. 1). Combining lemming and voles, the amounts of small mammals eaten were identical in arctic and red foxes, 78.0 and 78.2%, respectively. Red foxes consumed more birds, insects, and berries than arctic foxes, and appeared to have a more varied diet. Surprisingly, the amount of reindeer eaten was not significantly different despite the fact that the difference between the means was nearly 10%. Large standard deviations of the averages for the five major prey (Tab. 1) indicates large variation among dens within both arctic and red foxes. This was supported by the great range in the percentages for these prey items (Tab. 2). Maximum percentage of lemmings consumed by red foxes was more than 90%, and maximum percentage of voles consumed by arctic foxes was more than 50%. The maximum percentage of birds consumed was equal for arctic and red foxes (Tab. 2).

The number of samples varied greatly among regions and years, and several analyses were performed to outline the importance of the various factors. In one analysis, the samples were not divided by species, but by den, i. e., arctic (n = 51) or red fox (n = 16) dens (many red foxes inhabited arctic fox dens). The differences in the amount of prey eaten were much smaller compared to the results in table 1, with D = 55.5% and PO = 79.3%. Significant differences were still found for lemmings (z = 2.22, p = 0.03), voles (z = 2.46, p = 0.01) and birds (z = 2.89, p = 0.004).

In north Norway, the tree line grows progressively higher from north to south, from sea level in the subarctic northeastern corner to ca. 750 m in the far south. The correlation coefficients were higher for meter a. s. l. than for meter above tree line in all but one

Table 1. Frequency of occurrence (%) of prey in scats from arctic and red foxes, and test between the two fox species. (Unident. m. = unidentified mammals).

	Arctic fox		Red fox			
	Mean	SD	Mean	SD	z	p
Lemming	66.1	21.5	37.5	23.2	4.35	0.000
Voles	11.9	10.3	40.8	27.0	4.97	0.000
Reindeer	28.8	23.9	19.5	18.4	1.64	0.10
Birds	10.0	14.9	31.6	17.8	5.19	0.000
Insects	1.0	2.1	5.5	8.3	3.92	0.000
Bird eggs	1.2	2.7	0.9	1.7	0.39	0.70
Hare	1.9	3.3	1.1	1.7	0.71	0.48
Mustela e/n	0.4	1.2	0.5	1.5	–	
Mink	0.0	0.0	0.3	1.6	–	
Fox	0.3	1.1	0.6	1.3	–	
Shrew	0.0	0.0	0.04	0.2	–	
Berries	0.03	0.2	1.3	2.8	2.82	0.005
Unident. m.	0.0	0.0	0.3	1.3	–	

Table 2. Minimum and maximum percentages of the five major prey for arctic and red foxes.

	Arctic fox		Red fox	
	Min.	Max.	Min.	Max.
Lemming	12.0	94.9	0.9	90.8
Voles	1.5	54.5	3.3	91.8
Reindeer	1.4	88.0	0.0	68.1
Birds	0.0	73.7	2.6	73.4
Insects	0.0	10.1	0.0	43.7

prey (Tab. 3), and lemming was not significantly correlated with meter above tree line. Voles, birds, and insects were negatively correlated with these two factors. The percentages of prey consumed were not correlated with distance to the tree line for any prey (Tab. 3). The majority of the insects found in scats was dung beetles *Aphodius* sp. (Scarabaeidae), but a few other species were also recorded. No correlation between the percentages of insects and reindeer (i. e. carrion) was found ($r = -0.12$, $p > 0.05$, $n = 67$).

When separating arctic and red foxes in the same analysis, only four significant relationships were found. For arctic foxes ($n = 31$), insect prey was related to m a. s. l. ($r = -0.38$, $p = 0.03$), whereas reindeer ($r = 0.47$, $p = 0.008$) and birds ($r = -0.42$, $p = 0.02$) were related to m a. t. l. For red foxes, lemming was related to m a. s. l. ($r = 0.38$, $p = 0.04$, $n = 29$).

In some cases arctic foxes were known to breed or it could be concluded that a litter was born recently. No significant difference was found in the percentages of the five major prey items from arctic fox dens with ($n = 10$) and without ($n = 24$) recent litters ($p > 0.05$), D = 20.9%, PO = 91.1%. In the red fox ($n = 22$ dens with litters and $n = 11$ dens without litters), significantly more scats at dens with pups contained insects (7.1 ± 9.6 vs. 2.3 ± 3.0. $z = 2.01$, $p < 0.048$). The difference was nearly significant for reindeer ($z = 1.87$, $p = 0.06$), and not significant for lemming, voles, and birds (D = 32.4%, PO = 89.9%). Large standard deviations of the percentages indicate great variation among dens.

The red fox used old arctic fox dens, but also made its own den. Arctic fox dens ($n = 48$) were situated higher up in the mountains than red fox dens ($n = 12$, lack of accurate position of some dens reduced the sample size) (m a. s. l.: $z = 2.93$, $p = 0.003$; m a. t. l.: $z = 2.88$, $p = 0.004$) but not more distant to treeline (D t. l.: $z = 1.12$, $p = 0.3$). A similar result was found when considering the fox species that inhabited the den (Tab. 4). Arctic foxes lived much higher in the mountains than most red foxes, which is likely to influence prey availability and consumption. One test of the significance of altitude was to compare food of red foxes in arctic ($n = 16$) and red fox ($n = 17$) dens, but no significant difference was found ($p > 0.05$ for all five major prey; D = 19.2, PO = 94.1%). The actual figures were opposite to what could be expected, with less lemmings and more voles and birds in red fox scats from arctic fox dens.

Table 3. Correlations between percentages of the five major prey and meter a. s. l. (m a. s. l.), meter above the tree line (m a. t. l.), and distance to the tree line (D t. l.). Arctic and red foxes combined ($n = 59–60$). ** $p < 0.01$, * $p < 0.05$.

	m a. s. l.	m a. t. l.	D t. l.
Lemming	0.42**	0.08	0.17
Voles	–0.56 **	–0.34 **	–0.14
Reindeer	0.26 *	0.42 **	–0.03
Birds	–0.51 **	–0.39 **	0.02
Insects	–0.46 **	–0.31 *	–0.17

Table 4. Meter above sea level (m a. s. l.), meter above tree line (m a. t. l.), and distance to tree line (D t. l., km) for dens inhabited by arctic ($n = 31$) and red foxes ($n = 29$) and subject to scat collection.

	Arctic fox		Red fox			
	Mean	SD	Mean	SD	z	p
m a. s. l.	859.7	189.9	557.8	194.9	5.26	0.000
m a. t. l.	241.0	117.5	104.1	84.3	4.05	0.000
D t. l.	8.0	4.0	6.8	4.1	1.35	0.18

Table 5. Numbers of samples (den-years) collected by year and region in arctic and red foxes.

Year	Arctic fox	Red fox
1994	7	7
1995	9	2
1996	4	1
1997	1	8
1998	10	11
Region		
South	20	4
Central	9	9
North	3	16
Northeast	2	4

Table 6. Univariate analysis of the significance of the various factors for the percentages of lemming, voles, reindeer and birds in fox scats.

	Lemming		Voles		Reindeer		Birds	
	F	p	F	p	F	p	F	p
Year	1.70	0.2	13.67	0.001	12.41	0.001	4.01	0.05
Region	0.51	0.5	0.90	0.4	7.70	0.008	0.00	1.0
m a. s. l.	1.39	0.2	4.20	0.05	1.86	0.2	0.12	0.7
m a. t. l.	9.07	0.004	3.33	0.07	1.67	0.2	0.03	0.9
D t. l.	7.46	0.009	2.30	0.1	4.02	0.05	0.15	0.7
Species	11.22	0.002	11.92	0.001	1.25	0.3	9.80	0.003

The samples were skewed among regions and somewhat among years (Tab. 5), and further analyses of these factors were difficult. This was also complicated by the fact that the scats could not always be identified to the correct year of deposition. Instead of analysing these factors separately, all factors were included in a tentative analysis to give an idea of the relative importance of the various factors for the percentage of prey in scats. The significance of the factors varied for the four major prey items (Tab. 6). Fox species was important for lemming, voles, and birds, but not for reindeer. Year was important for voles and reindeer, and region only for reindeer. M a. s. l. was least important. M a. t. l. and D t. l. were significant for lemming (Tab. 6). Thus, fox species and year were the most important of the factors tested.

For a better understanding of the effects of year and den, six arctic fox dens inhabited by arctic foxes with repeated sampling over several years (n = 15 den-years) were analysed separately. The percentage of lemming ($\chi^2 = 10.20$, $p = 0.04$, d. f. = 4) varied significantly across years, but not voles, reindeer or birds ($p > 0.05$). No significant variation across the six dens was found. Relatively high variances indicated large variation both within dens and years. As example, for a single den, minimum and maximum percentages of lemming were 12.0 and 77.5 (variance = 1 189.8). For the single most extreme year, minimum and maximum lemming were 12.0 and 71.3%, respectively (variance = 544.1).

Discussion

Although significant differences in food habits were found, arctic and red foxes had a high overlap and are likely to compete for the same food. Arctic foxes relied heavily on lemmings and reindeer carcasses, while red foxes consumed about equal amounts of lemmings, voles and birds, but less reindeer. Do the red fox have a broader niche and is the arctic fox more a specialist hunter? A large variation in food habits was found within the two fox species, both within and between dens, years, and regions. This variation is, of course, mostly related to the lemming and vole cycles (sensu Elmhagen et al. 2000). During this study period, no great lemming or vole years were experienced in the mountain region, but one year in the central region and two years in the south region had smaller maxima.

The proportions of lemming, voles, reindeer, and birds in the fox diet were related to the height above sea level or above the tree line, consistent with what could be expected, except that lemming was not related to the height above the tree line. Red foxes were on average found in lower areas than arctic foxes. Furthermore, the samples were collected over a large area (north Norway) and over several years, and were not evenly distributed among years and regions. The numbers of voles and birds are supposed to decrease with altitude, much more than the numbers of lemming and reindeer. Consequently, a large portion of the difference in food habits between arctic and red foxes was probably related more to external (environmental) than internal factors. Thus, one may conclude that arctic and red foxes have a high degree of overlap in food habits and will compete for food. Arctic foxes appear to rely more heavily on lemmings than red foxes at similar altitude, and are perhaps a little less opportunistic than red foxes.

Fox species affected the percentages of prey consumed most, and year of collection, region, height above sea level or tree line, and distance to the tree line less. Height above the sea level was thought to be poorly related to the proportion of the different foods consumed in north Norway. Height above the tree line varies less with latitude and should be better related to food habits. But the correlations between the percentages of prey and height above sea level were better than with height above tree line. This result is surprising and difficult to explain. It may have resulted inadvertently from the geographically skewed collection of scats, most arctic fox litters and scats were found in the south, while most red fox litters and scats were found in the north.

In southern Norway (Frafjord 1995), both arctic and red foxes had consumed almost exclusively (min. 95%) small mammals (lemming and voles), and in another study 85% (Strand et al. 1998 a), compared to 78% in this study. Reindeer were notably a larger part of the diet in northern Norway. Some of the samples from north Norway probably included scats from the winter season, when foxes may eat more reindeer carrion. A high mortality among the domestic reindeer in some regions and some years, may have supplied the foxes with additional food than normally available. (Most slaughter offal is today transported away from the mountains to permanent deposits.) This may also have resulted in the birth of some arctic fox litters in years of low numbers of small mammals. A sample of 98 arctic fox winter scats collected at three neighbouring dens in the central region in April 1998, gave frequencies of occurrence of 80.6% lemming, 15.3% voles, 9.2% reindeer, and 10.2% birds. This does not support the hypothesis of a larger proportion of reindeer in the winter diet, but this proportion is likely to vary greatly according to availability (compare Strand et al. 1998 a). In the northeastern region in 1999, 58 red fox scats were collected close to cliffs where sea birds nested (not at dens). These foxes consumed almost exclusively birds, i. e., comparable to arctic foxes in Svalbard (Frafjord 1993): 94.8% birds, 1.7% lemmings, 5.2% voles, and 3.4% reindeer. Obviously, when such opportunistic predators are concemed, large numbers of samples from different regions and years are needed to give a complete picture of their diet.

In this study, I attempted to collect and analyse relatively large samples for each den, and to have a comparatively large number of dens for both fox species (sensu Reynolds and Aebischer 1991), but the sample size was still not sufficient for detailed regional and yearly analysis. Although there are inherent difficulties with the accuracy of scat analysis

(Cavallini and Volpi 1995), these should not affect the comparisons made in this study since all analyses were made in the same manner. However, the method used may possibly underestimate the proportion of voles compared to lemming, and more so at higher percentages of lemmings. The majority of insects found in scats was dung beetles. Some of the beetles may not have been eaten by foxes, and it could be speculated that the larvae had metamorphosed inside the scat (some beetles were indeed undamaged). Other explanations could be that the fox had accidentally (by eating dung) ingested or deliberately eaten the beetles. In one case, a number of dung beetles were found in the few remains of a small fox pup, which indicates that these beetles may also be scavengers. The only berry that is found to any great amount in these alpine regions is *Empetrum hermaphroditum*, its low nutritional value may explain the low frequency of berries in scats. Faeces containing a large number of fox hairs indicate cannibalism.

Despite significant differences in the proportions of the major food items in the diet of red and arctic foxes, the large diet overlap makes competition very likely although it is not strictly a proof (sensu Putman 1996). Although the ranges of the two fox species overlap, this does not necessarily mean that competition is direct. An indirect competition where red foxes exclude arctic foxes from the more productive habitats (which are limited in the alpine region) is more likely (sensu Smits et al. 1989; Hersteinsson and Macdonald 1992; Strand et al. 1998 b). Such an exclusion, or interspecific territorialism, may consequently also work in years (or seasons, habitats) when the dietary resources are not limiting. The red fox may consider an arctic fox as just another, but smaller and inferior, red fox. Competition for food may be the single most important factor involved in the red fox's exclusion of the arctic fox, which may, eventually, lead to the extinction of the arctic fox in Fennoscandia.

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Zusammenfassung

Konkurrieren Polarfüchse und Rotfüchse um Nahrung?

Überlappung und Unterschiede in der Zusammensetzung der Nahrung zwischen Polar- und Rotfuchs, *Alopex lagopus* und *Vulpes vulpes* wurden über Kotanalysen von Bauen oberhalb der Baumgrenze in Nord-Norwegen untersucht. Außer den Fuchsspecies wurden zusätzlich die Faktoren Bau, Region, Jahr, Höhe über Meeresspiegel, Höhe oberhalb der Baumgrenze, Entfernung zur Baumgrenze und Reproduktionsstatus analysiert. Insgesamt standen 5314 Kotproben zur Verfügung in n = 34 und n = 33 „Bau-Jahren" für Polar- bzw. Rotfuchs. Lemminge, Wühlmäuse, Rentiere und Vögel waren Hauptbeute von beiden Fuchsarten, und Insekten waren in Rotfuchskot häufig. Kleinsäuger machten 78% der Nahrung bei beiden Arten aus. Polarfüchse erbeuteten mehr Lemminge als die Rotfüchse, während Rotfüchse mehr Wühlmäuse, Vögel und Insekten verzehrten. Trotz dieser Unterschiede war die Überlappung im Nahrungsspektrum beider Arten groß, und Nahrungskonkurrenz ist wahrscheinlich. Einige der Unterschiede könnten eher durch Umweltbesonderheiten bedingt sein, da Rotfüchse durchschnittlich Baue in geringeren Höhenlagen bewohnten als Polarfüchse. Ein hoher Variationsgrad ergab sich innerhalb der Fuchsarten aber auch innerhalb und zwischen Bauen, Jahren, und Regionen. Die Besonderheiten der Fuchsart war jedoch hauptsächlich bedeutend für die prozentuale Nahrungszusammensetzung, Jahr und Region hatten geringeren Effekt. Die prozentuale Nahrungszusammensetzung war wie erwartet mit der Höhe über dem Meeresspiegel und der Höhe über der Baumgrenze korreliert, ausgenommen zwischen letzterem und Lemmingen. Nahrungskonkurrenz könnte daher ein wichtiger Faktor zur Erklärung der anscheinenden Verdrängung des Polarfuchses aus dem Wohngebiet des überzähligen Rotfuchses sein.

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A long-term analysis of the age structure of otters (*Lutra lutra*) from eastern Germany

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Abstract

The objective of this study was to examine if the increasing number of road-killed otters in eastern Germany affects the age structure of the population over a period of 40 years. A sample of 1 027 otter carcasses from eastern Germany that were collected mainly as roadkills (69%) between 1957 and 1998 was used to reveal possible long-term changes in age and sex composition across regions. Age determination was based on the analysis of cementum annuli of canines. The frequency of juveniles (age class I) amounted to 22%. This is considerably underestimated when compared with living populations. The greatest proportion of otters is represented by middle age class IV (52%) with a maximum age of 15 years. Contrary to the even sex ratio found in living otters from the study range, the present data revealed a significantly higher proportion of males (58%), especially in lower age classes (age class I: 66%, age class II: 71%). Concerning the question on possible effects of increasing numbers of road-killed otters on the population structure, there is no indication of effects on the age structure over the study period. Moreover, there is no time-related difference or significant region-specific deviation between age compositions of the otter samples of seven different regions. These results apply equally for both sexes. There is currently no evidence that an increased mortality affected the age structure of otters from eastern Germany.

Key words: *Lutra lutra*, age structure, road mortality, eastern Germany

Introduction

The otter, *Lutra lutra* (L., 1758), was once widespread throughout Europe and Asia. Today, its European range is strongly fragmented (FOSTER-TURLEY et al. 1990; MACDONALD 1995). In eastern parts of Europe, however, dense populations still exist and eastern Germany constitutes one of the most important refuges in central Europe. There, viable populations exist from north to south in the provinces of Mecklenburg-Vorpommern, Brandenburg, and Saxony, with the river Elbe as the western border of the more or less continuous distribution.

In spite of many investigations on the conservation biology of otters, there are still few data available on age and population structure. HEGGBERGET (1984), KRUUK and CONROY (1991), SIDOROVICH (1991), MADSEN (1996), and ANSORGE et al. (1997) reported on the age composition of otters, based on carcasses that were mostly shot by hunters or killed by traffic. However, there have been only very few attempts to check for possible long-term changes in the population structure, particularly with respect to causes of mortality (e. g. KRUUK et al. 1997).

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Even though hunting, habitat destruction, and pollution caused decline or regional extinction of otters in central Europe, a recent increase of otters is now being noticed in many regions of Europe. This is, however, paralleled by increased numbers of road casualties (MADSEN 1996; PHILCOX et al. 1999). Numbers of road casualties among otters have especially increased in eastern Germany, as a result of increased traffic and road density after the political changes in Germany (HAUER and HEIDECKE 1999; KÖRBEL 1994; ZINKE 1991). Here, we study whether the increasing number of dead otters, that are mainly killed by road traffic, have an effect on the age structure in various regions of eastern Germany over a period of the past 40 years.

Material and methods

Otter samples, periods of collection, and study regions

A total of 1 027 dead otters was collected during 1957–1998 in eastern Germany. According to the necropsies of all carcasses, the main cause of death was road casualties (69%). Carcass collections were initially sporadic but intensified since 1985. For this analysis the material was separated into the following five irregular time periods, to achieve sufficient period-specific sample sizes and to take into account historically and ecologically relevant changes in the study regions: before 1988, 1988–1990, 1991–1993, 1994–1996, 1997–1998. Furthermore, the otter material was assigned to the following seven regions (Fig. 1):

1 – Baltic coast – this approximately 25 km wide stripe of coastal land along the seaboard of the Baltic Sea in eastern Germany includes sandy beaches, shallow bays, and large areas of undisturbed habitat but also has a high road density
2 a – Mecklenburg – a region south of the Baltic coast with few human settlements and large undisturbed habitats with lakes and rivers
2 b – Lake district and Tableland of Mecklenburg/Brandenburg – similar to region 2 a but with many lakes
3 – Oder-Neiße-region – middle part of the German border to Poland; characterized by the rivers Neiße and Oder; with undisturbed habitats and low road density
4 – Lower Lusatia and Brandenburg heath and lakeland – with lower number of ponds, but many settlements and high road density
5 a – Upper Lusatia – most southeastern part of Germany; extensive pond district with many fish farms
5 b – Elbe-Elster-region – delta between the rivers Elbe and Schwarze Elster with intensive agricultural areas; high road density but also a network of ditches

Age determination

After skull preparation a canine or adjacent tooth was extracted. The age in years was determined for each individual by counting the incremental cementum lines of canines produced by low speed sawing of longitudinal root sections (DRISCOLL et al. 1985; ANSORGE 1995). In addition, otters within their first year of life could be distinguished from older ones by various criteria of the skull development, such as obliteration of sutures, development of the postorbital constriction, and the sagittal crest, as well as bone deposition around canine alveoles (HEGGBERGET 1984; STUBBE 1969; VAN BREE et al. 1966).

Years of age of single otters was grouped into the following age classes (AC), mainly based on reproductive aspects, in order to get a better overview in the following analyses:

Age classes (AC)

I: juveniles (within their first year); II: subadults (within their second year); III: younger adults (within their third year); IV: grown adults, middle age (4.–9. year); V: seniors (over 9 years)

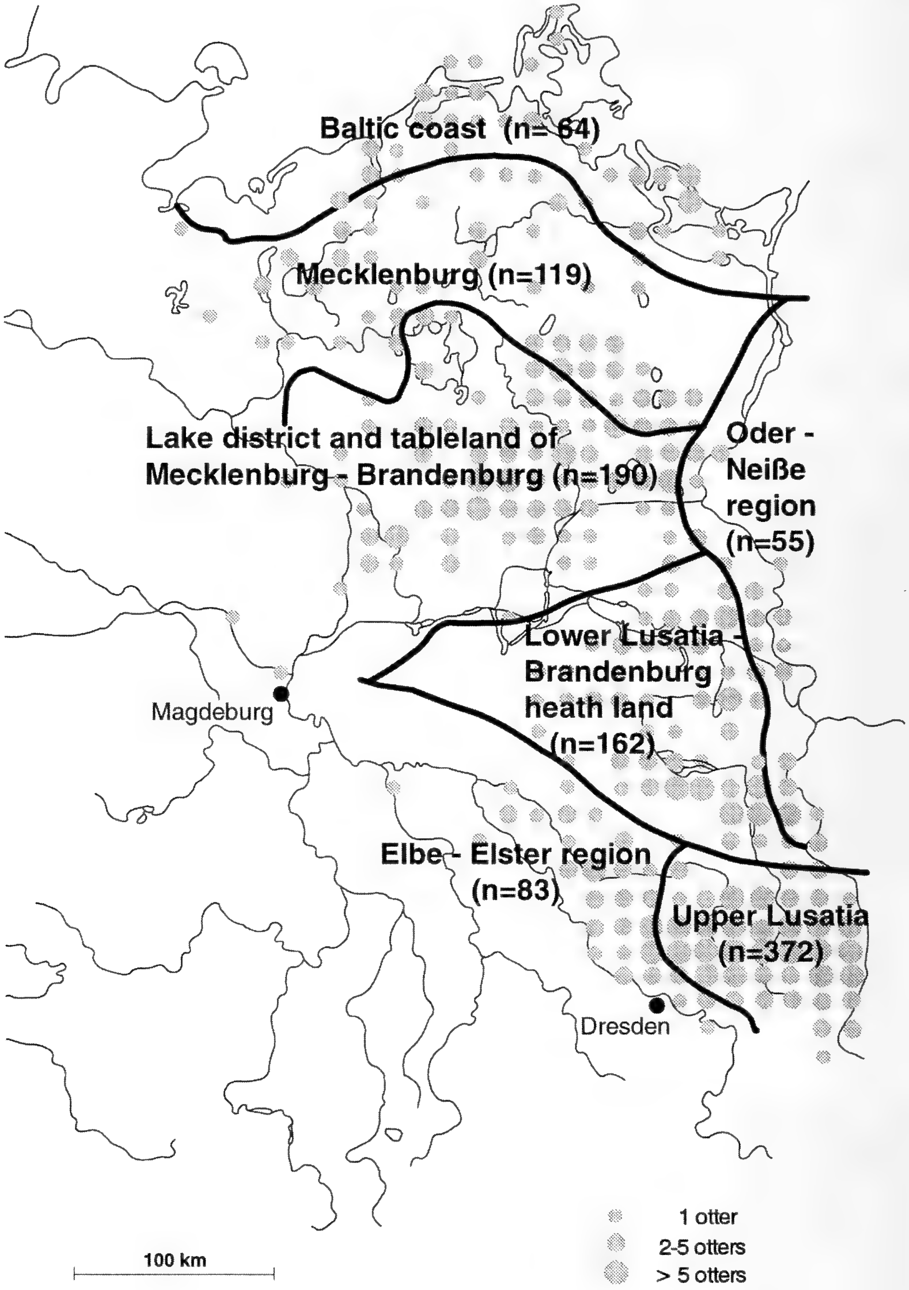

Fig. 1. Map of the sample area including number of investigated otter carcasses studied per topographic grid (grid side length is approximately 11.5 km).

Statistics

Pairwise chi^2 tests were used to check for differences in age class (AC) compositions between regions and for successive periods of time (5×2 contingency tables, respectively, see also BODKIN et al. 2000). Trends in different frequencies of juveniles over the study period were tested by Spearman-Rank-Correlation-Coefficient. These tests were carried out for combined sex samples and separately for each sex, and significance decisions were based on the Sequential Bonferroni procedure with a nominal $\alpha = 0.05$ to account for multiple and partly dependent tests (RICE 1989).

Results and discussion

Sample structure

The age composition and the sex ratio of the total sample material are illustrated in figure 2. The age pyramid appears relatively stretched because of the small proportion of juveniles and lower age classes and the long life span. Juveniles account for only 22%, while otters in their 2nd (AC II) and 3rd year (AC III) of life are represented with 11%, respectively 10% of the total sample. Otters of age class IV make up a considerable part (52%) of the sample. Only eight percent of the otters are older than nine years, but otters in our study could reach a rather old age, even exceeding 15 years. In contrast to the age structure of females, males show a nearly continuous development with successive decline of year proportions to the top of the age pyramid. Females show reduced frequencies in years 2 and 4.

The sex ratio of the total otter sample from eastern Germany is male-biased with 58% (1.4:1). Males predominate especially in age class I (66%) and age class II (71%).

Above 6 years the sex ratio of 1.2 males (55%) to 1 female is more balanced; and animals older than 9 years have a mean sex proportion of 1.4:1 (58%).

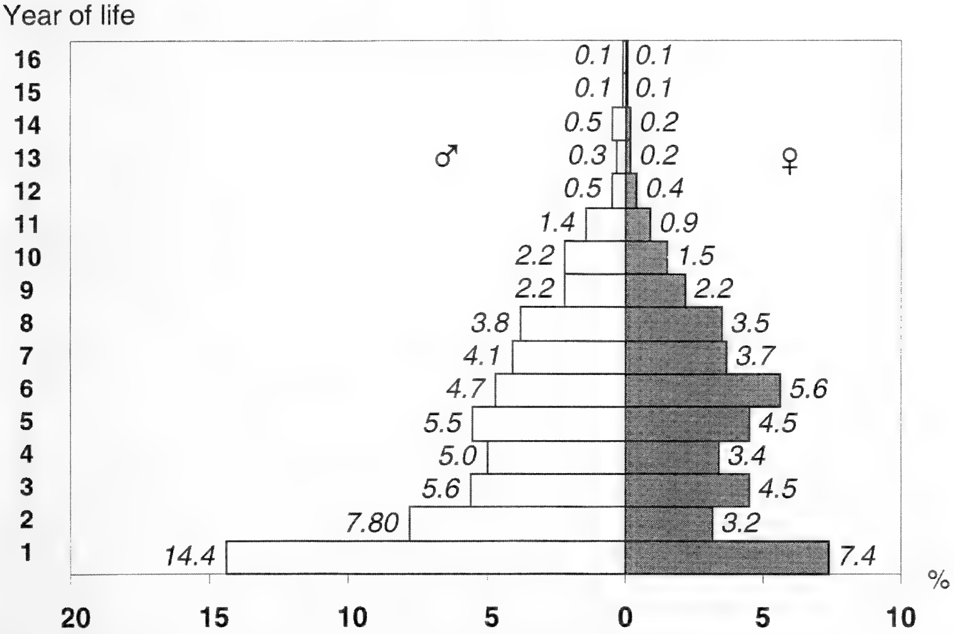

Fig. 2. Sample structure of otters (n = 1027) from eastern Germany, data from 1957–1998 combined.

Despite the frequent use of carcass samples for assessing age and population structures, it has to be emphasized that such samples probably do not reflect the true structure of living populations (GOSSOW 1976). Hence, in interpreting and discussing such data caution is necessary.

Population structure of mustelids based on collection of carcasses is frequently characterized by a male-biased sex ratio (BUSKIRK and LINDSTEDT 1989; VAN BREE 1968). The reason for this could be the larger territorial size and the higher activity level of males of mustelids in general (GOETHE 1964) and therefore an increased exposure to road traffic for male otters (HEGGBERGET 1991; PHILCOX et al. 1999). UTHLEB et al. (1992) hypothesized that increased activity, particularly of young males in connection with searching for a free territory, could increase their risk of mortality. Also, it was assumed that male cubs were more active and curious than female cubs, and thus more endangered. The presently found low number of juveniles, in particular of female juveniles in our sample (Fig. 2) might result from these facts. In contrast to the presently studied carcass sample, females predominate in living otter population as shown by the model of ANSORGE et al. (1997). The low numbers of 2 and 4 year-old females in our study are probably due to stochastic effects.

The age composition of the total otter sample shows a remarkable small proportion of younger age classes (juveniles and subadults) when compared to a population model of otters and reproduction data (ANSORGE et al. 1997). Even though the presently found small fraction of juveniles and subadults is comparable to findings in otter populations from Norway, Scotland, Byelorussia, and France (HEGGBERGET 1984; KRUUK and CONROY 1991; SIDOROVICH 1991; ROSOUX and TOURNEBIZE 1995), it is an underestimation of the real proportion of these age classes within the free-living population. A very high proportion of cubs die non-violent causes, and they are less likely to be found than otters that were killed by road traffic or other violent causes (KRUUK and CONROY 1991). For one study area ANSORGE et al. (1997) developed a model to estimate the real population structure based on the age structure of otter carcasses as well as the analysis of reproduction signs (placental scars, embryo and corpora lutea counts), and field records of cubs per female. According to this model juveniles made up 50% of the living population as opposed to only 24% in the corresponding carcass sample.

Age structure related to time periods

The pairwise comparisons of successive time periods did not reveal any significant differences und thus, changes in the age structure of the eastern German otters.

To exclude the possible influence of different causes of mortality in these tests, a further analysis of changes in age structure over time was carried out using road-killed otters only (Fig. 3). But this approach did not fundamentally change the results.

When possible changes in frequencies of juveniles were analysed, using a Spearman-Rank-Correlation over the time periods there was no significant decline in the proportion of juvenile otters (age class I) after use of the Bonferroni procedure ($\alpha = 0{,}00192$, $p = 0{,}037$; $R = -0{,}9$).

None of the samples show sex-specific differences in age composition.

As in most other central European regions, otters declined continuously before 1988 in eastern Germany and reached their minimum distribution area. However, since the late 1980s a general re-colonisation of regions of former distribution is being noticed (HAUER and HEIDECKE 1999). This range expansion is reflected by the period 1988–1990. From 1990 onward a drastic increase in traffic-mortality of otters has been recorded. This is caused by an enormous intensification of traffic and growth of the road net work (HAUER and HEIDECKE 1999; KÖRBEL 1994). More recent time periods are characterized by an almost constant high level of road mortality. Both re-colonisation of regions and

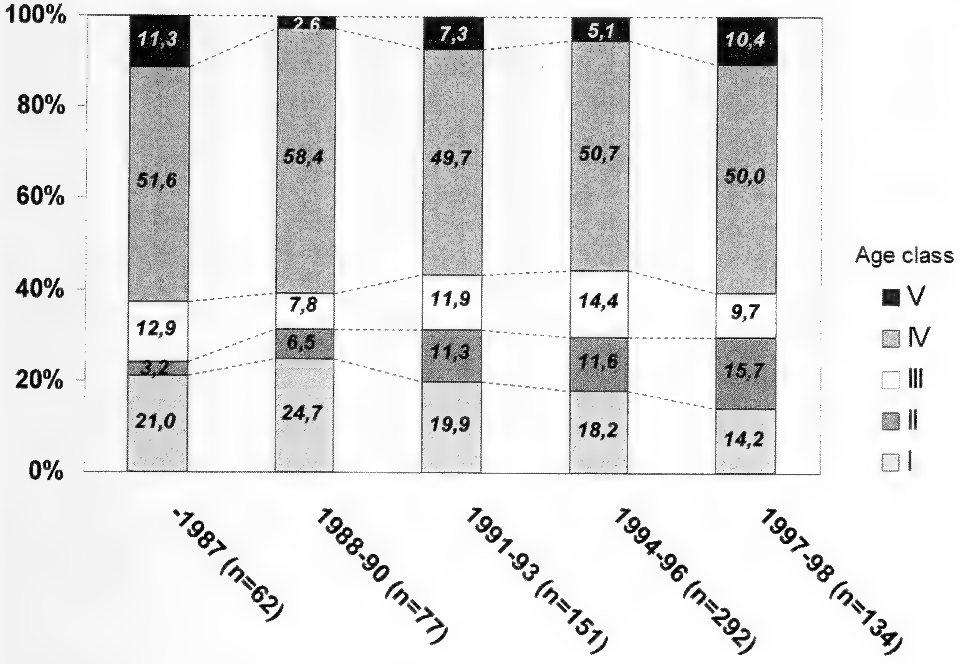

Fig. 3. Age composition of otters related to time periods – traffic-killed only. For age categories, see material and methods.

the increasing traffic mortality were also noticed in other European countries (Philcox et al. 1999). But this increase in road mortality obviously did not alter the age composition of eastern German otters in general.

The slight and not significant trend towards lower juvenile frequencies in the eastern German otters due to road casualties over the last 40 years possibly results from the generally noticed increase of otter populations. In contrast, Kruuk et al. (1997) found a decline of mean age in Scottish otters based on an increasing proportion of immature otters amongst road-kills, and interpreted this as resulting from increased population densities. This contrasting interpretation could be explained, if we assume that the decreasing trend of juveniles in eastern Germany might suggest a more developed population with a higher density than the Scottish populations that might just have begun to build up.

Comparison of the age structure across regions

The age class compositions of the otters killed by road traffic did not differ significantly across the seven regions of eastern Germany (see Fig. 4). This result is the same regarding otters of all causes of mortality.

However, the proportions of age classes III and IV show slight, non-significant deviations for example between region 3 (Oder-Neiße) and region 2 a (Mecklenburg), but the amount of both age classes III and IV achieves 60–70% for each of the regions with the exception of region 4. The lowest proportions of juveniles exist in the regions of the Baltic coast (1) and Oder-Neiße (3) (Fig. 4).

The regional deviations in the proportion of juveniles might result from a lower risk of road mortality for juveniles from undisturbed habitats in the Baltic coast region (1)

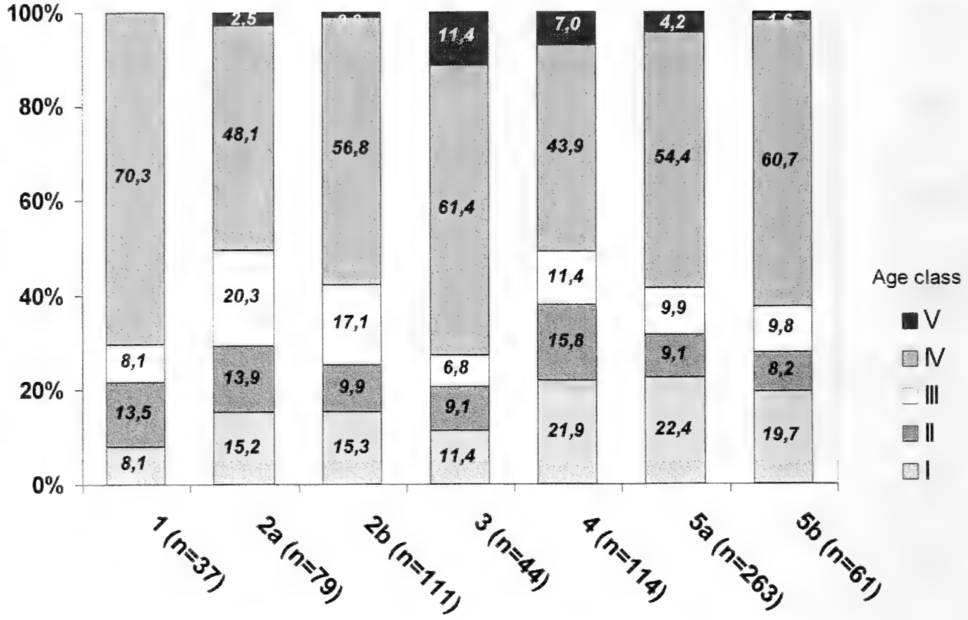

Fig. 4. Age composition of otters in the seven regions of eastern Germany – traffic-killed otters only. (1 – Baltic coast; 2 a – Mecklenburg; 2 b – Lake district and tableland of Mecklenburg/Brandenburg; 3 – Oder-Neiße-region; 4 – Lower Lusatia and Brandenburg heath- and lakeland); 5 a – Upper Lusatia; 5 b – Elbe-Elster-Region)

and the Oder-Neiße-region (3) and correspondingly high proportions of middle-aged otters (AC IV). A higher risk of road mortality would explain the higher proportion of juveniles and subadults in regions with higher road density (4, 5 a) and lower proportions of animals between 3 and 16 years of age (AC III–V). However, all these results do not show significant differences.

Obviously, neither different habitat conditions, nor different levels of disturbances or risks of mortality in the diverse regions do have a significant influence on the age structure of the otter sample.

Population genetic analyses of the otter from eastern Germany did not reveal any strong subdivisions or general isolation among the populations from the regions presently studied (Ansorge and Stubbe 1995; Effenberger and Suchentrunk 1999; Cassens et al. 2000). This suggests some exchange of individuals among the various regions; and this could result in only minor differences in the age structure across large geographic distances.

As we could conclude no significant differences in age structure between several regions in eastern Germany were registrated. The age composition of the otter sample from eastern Germany does not show any indication of increasing mortality since the last 40 years. This is a sign for a long-time stable otter population in eastern Germany.

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Zusammenfassung

Langzeitstudie zur Altersstruktur von Fischottern (Lutra lutra) in Ostdeutschland

Es wurden insgesamt 1 027 Totfunde von Fischottern aus dem östlichen Deutschland aus den Jahren 1957 bis 1998 untersucht und mittels der jährlichen Wachstumslinien im Zahnzement altersbestimmt. Die Haupttodesursache war der Straßenverkehr mit 69%. Ziel war die Charakterisierung der Alters- und Geschlechterstruktur sowie die Untersuchung zeitlicher und regionaler Unterschiede in der Altersstruktur der untersuchten Stichprobe.

Das Geschlechterverhältnis ist deutlich zugunsten der Männchen verschoben (58%), was sich besonders in den unteren Altersklassen (AC I: 66%, AC II: 71%) bemerkbar macht. Als Höchstalter von wildlebenden Fischottern in Ostdeutschland sind 15 Jahre nachgewiesen. Im Vergleich zu freilebenden Populationen ist der Anteil juveniler Tiere in der Untersuchung deutlich unterrepräsentiert (AC I: 22%), den höchsten Anteil stellen Fischotter der mittleren Altersklassen (AC IV: 52%). Das Fehlen deutlicher Änderungen in der Altersstruktur während der letzten 40 Jahre läßt trotz der stark zugenommenen Verkehrsmortalität auf einen großflächig und langzeitig stabilen Bestand in diesem Raum schließen.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

A new subspecies of Miller's long-tongued bat (*Glossophaga longirostris*) from a semiarid enclave of the Venezuelan Andes

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Miller's long-tongued bat, *Glossophaga longirostris* Miller, 1898 (Glossophaginae), inhabits the arid and semiarid regions of northern South America and some Caribbean islands (WEBSTER and HANDLEY 1986; WEBSTER et al. 1998). In Venezuela, this bat species shows a continuous pattern of distribution in the coastal region, and it also inhabits the Llanos region in the states of Anzoátegui, Guárico and Apure, and northern portions of Bolívar and Amazonas. In these areas (Fig. 1), three of the six recognized subspecies (*G. l. longirostris* Miller, 1898, *G. l. major* Goodwin, 1958, and *G. l. campestris* Webster and Handley, 1986) were reported (WEBSTER and HANDLEY 1986; WEBSTER et al. 1998).

An isolated population of this species inhabits the semiarid enclave of Lagunillas, located in the middle Chama river basin in the state of Mérida in the Andes of Venezuela (Fig. 1). This was not described by WEBSTER and HANDLEY (1986). The aim of this study was to investigate the status of this population in Venezuela by multivariate analysis techniques.

Material examined: For the analysis, 204 adult specimens of *G. longirostris* were selected, following the age criteria of ANTHONY (1988). Twenty-two of the specimens came from the Lagunillas, a semiarid enclave in the Venezuelan Andes, and were housed in the Colección de Vertebrados de la Universidad de Los Andes (CVULA). The other 182 specimens, according to the locality from which they were collected, were referred to the subspecies: *G. l. longirostris* (57 specimens), *G. l. major* (61 specimens), and *G. l. campestris* (64 specimens). All the specimens examined were housed in CVULA and the Museo de la Estación Biológica de Rancho Grande (EBRG).

Specimens examined: *Glossophaga longirostris* (Andean population): Estado Mérida (CVULA: I-174, I-387, I-388, I-2 797, I-2 799, I-2 800 to I-2 802, I-2 804, I-2 808, I-2 811, I-2 812, I-2 814, I-2 823, I-2 824, I-2 941, I-3 387, I-3 441, I-3 444, I-3 802, I-3 803, I-4 395). *Glossophaga longirostris campestris*: Estado Amazonas (EBRG: 3 390 to 3 403; 5 817, 5 819, 5 820, 5 815, 5 874, 5 875, 8 242, 8 243, 8 122); Estado Apure (EBRG: 5 750 to 5 754, 5 748, 5 749, 5 755 to 5 763, 5 765 to 5 779, 5 781): Estado Bolívar: (EBRG: 4 271 to 4 273, 17 395, 17 396, 17 413, 5 812, 5 813, 15 859). *Glossophaga longirostris major*: Estado Aragua (EBRG: 1 765, 1 766, 10 311); Estado Cojedes (EBRG: 20 790 to 20 794); Estado Guárico (EBRG: 5 838 to 5 843, 5 845, 5 847 to 5 855, 5 857 to 5 861, 5 836, 5 837, 5 831 to 5 833, 5 834); Estado Nueva Esparta (EBRG: 3 322, 3 323, 3 324 to 3 326, 3 350, 3 357, 5 801 to 5 806, 5 783); Estado Sucre (EBRG: 20 637, 20 638, 20 640, 20 641, 20 643, 5 797, 5 799, 5 800, 20 639); Estado Yaracuy (EBRG: 5 745 to 5 747). *Glossophaga longirostris longiros-*

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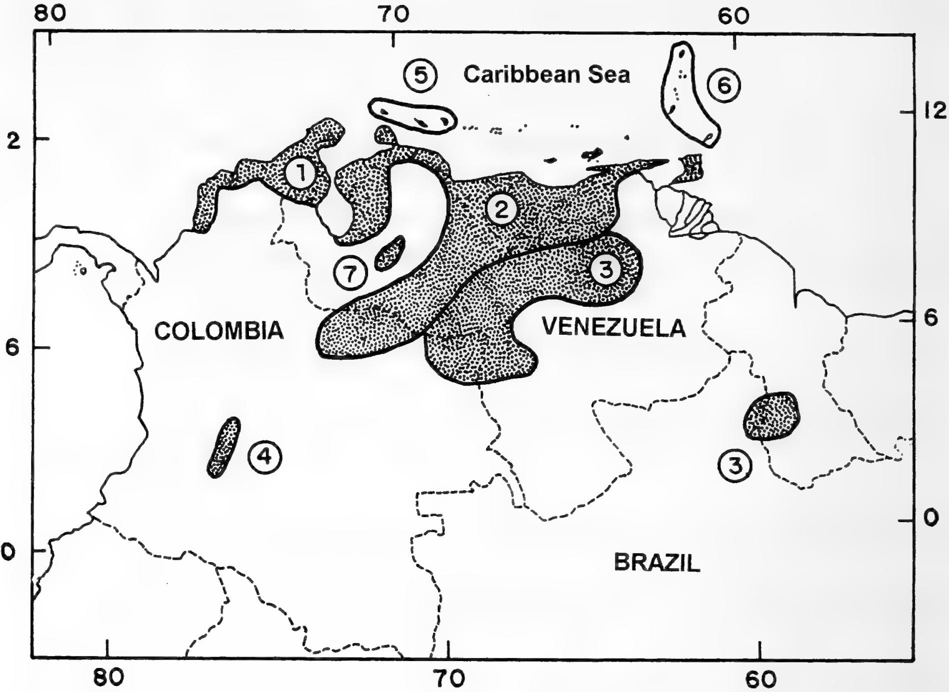

Fig. 1. Geographic distribution of the six previously accepted subspecies of *Glossophaga longirostris* and the isolated Andean population: (1) *G. l. longirostris*, (2) *G. l. major*, (3) *G. l. campestris*, (4) *G. l. reclusa*, (5) *G. l. elongata*, (6) *G. l. rostrata*, and (7) Andean isolated population. (modified from Webster and Handley 1986 and Webster et al. 1998).

tris: Estado Falcón (EBRG: 15 979, 15 983, 20 620, 20 622 to 20 624, 20 625, 20 626, 20 627, 20 628, 2 107 to 2 111, 2 845, 2 846, 2 848, 3 700, 3 701, 5 977, 5 779 to 5 985, 5 993 to 5 997, 6 000 to 6 002, 6 006 to 6 013, 6 045, 6 046, 6 048, 6 050, 6 051). Estado Zulia: (EBRG: 5 975, 5 976, 5 988, 5 989, 5 992, 5 990, 5 991). Measurements: For each selected specimen we took the following eight cranial measurements (in mm): greatest length of skull, including incisors (GLS); postorbital width (POW); mastoid width (MW); breadth of braincase (BB); depth of braincase (DB); maxillary tooth row (MAX); width across upper canines (C1-C1); and width across upper second molars (M2-M2). All cranial measurements were taken with a Mitutoyo digital caliper, with an accuracy of 0.05 mm; with the exception of MAX which was taken by a graduated scale on the ocular lens of a stereoscopic microscope (Leica model Wild M8), with an accuracy of 0.05 mm.

Data treatments: Using the program NTSYS-PC (Rohlf 1993), we carried out a principal component analysis on the eight cranial measurements, based on a correlation matrix from logarithmically transformed data, with the aim to assure the homogeneity of variances (Sokal and Rohlf 1981). This allowed us to determine the principal components and correlation diagrams between the morphometric variables and the principal components. The means of the variables of the four populations were compared by ANOVA. Likewise, we carried out a discriminant analysis, using the program STATISTICA (Stat Soft Inc. 1991), to determine which of the variables allow to discriminate among the four populations.

The analysis of principal components shows an intergradation among the specimens of the Venezuelan populations (Fig. 2); the Andean specimens (a) are located at the lower

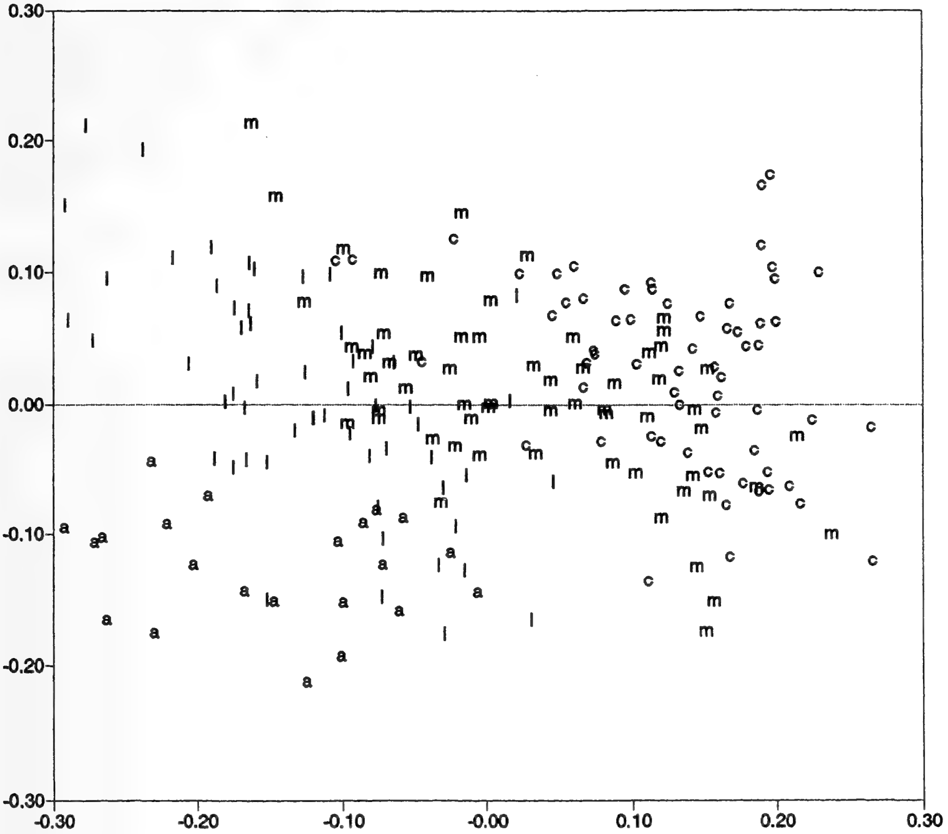

Fig. 2. Disposition diagram of the specimens used in the first plane of the principal components analysis. Each specimen of the Andean population and the previously accepted subspecies are abbreviated as follow: a = Andean population, c = *G. l. campestris*, l = *G. l. longirostris*, m = *G. l. major*.

left extreme of this figure. The correlation diagram of the morphometric variables and the two first principal components (Fig. 3), showed an increase from right to left in all the variables. This result agrees with what Lebart et al. (1979) called a size effect, and indicates that the largest specimens are placed at the left of the plane. In addition, two groups of variables can be observed: the first, conformed by the measurements related with the cranial length (GLS and MAX) and the measurements related with palate width (C1-C1 and M2-M2). The second group is typified by the measurements related with braincase volume (BB, POW and DB).

The small values showed by the angles between each vector pair inside each group in figure 3 indicate a high correlation between these variables. Likewise, we can infer independence between the two described groups by the magnitude of the angle between both (close 90°). On the other hand, the mastoid width (MW) was strongly correlated only with the first principal component, but weakly correlated with the groups described before, which indicates that this variable increases to the same proportion for the specimens of all populations studied. In other words, separation between specimens of the Andean population from those of the remaining Venezuelan subspecies (Fig. 2) is generated simultaneously by the two groups of variables previously described.

The comparisons of the mean values of variables by ANOVA showed that the Andean population exhibits significantly greater values than the remainder of the Venezuelan subspecies in GLS, M2-M2, and MAX (Tab. 1). Our data indicate that specimens of the Andean population have longer skulls, and maxillary tooth row, and broader palate than the other populations considered. Additionally, the Andean population shares with *G. l. longirostris* the greatest values of C1-C1 and MW, which distinguish them from the other populations.

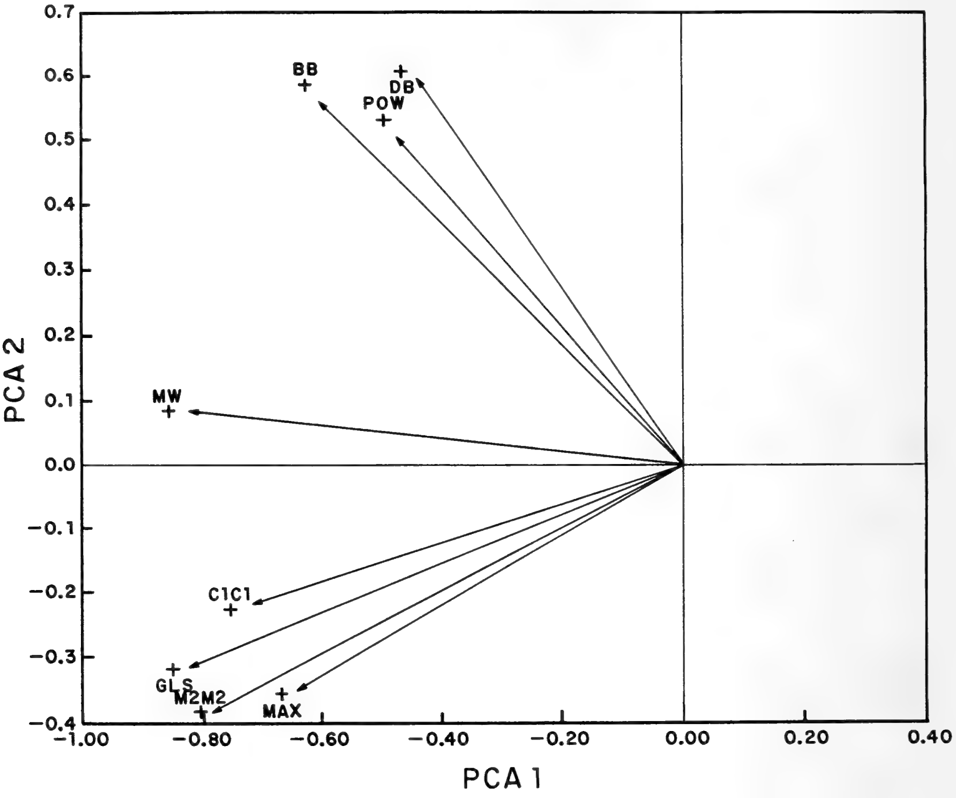

Fig. 3. Correlation diagram between the morphometric variables and the two first pnncipal components. Correlation of all the variables with the principal components were highly significant ($p > 0.005$).

Table 1. Comparison of the characters used in the study among the Andean population and the previously accepted subspecies of *Glossophaga longirostris*. Parentheses show the standard error. Values that have no letter in common are significantly different (ANOVA, $p < 0.05$).

Character	Andean Population	*G. l. longirostris*	*G. l. major*	*G. l. campestris*
GLS	24.6 (0.07) a	23.8 (0.06) b	23.0 (0.05) c	22.4 (0.05) d
POW	4.7 (0.02) a	4.8 (0.02) b	4.7 (0.02) a	4.6 (0.02) a
MW	9.5 (0.04) a	9.6 (0.03) a	9.4 (0.03) b	9.2 (0.02) c
BB	8.8 (0.03) a	9.1 (0.03) b	8.9 (0.03) a	8.8 (0.02) a
DB	8.6 (0.04) a	8.6 (0.03) a	8.5 (0.03) a	8.5 (0.02) a
MAX	8.4 (0.09) a	8.1 (0.04) b	7.9 (0.03) c	7.7 (0.03) d
C1-C1	4.5 (0.04) a	4.5 (0.02) a	4.2 (0.02) b	4.1 (0.02) c
M2-M2	6.4 (0.04) a	6.1 (0.02) b	5.8 (0.02) c	5.7 (0.02) d

According to the results showed herein, we conclude that: i) the Andean population from the semiarid enclave of Lagunillas represents an undescribed subspecies, ii) in absence of biometrical and biogeographic evidence to support the discrimination among the population of *G. l. longirostris*, *G. l. major*, and the Venezuelan fraction of *G. l. campestris*, we propose that all of them belong to the same subspecies referable to *G. l. longirostris*. Based on the evidence of our analysis, we describe the new Andean form of *Glossophaga longirostris* as follows:

Glossophaga longirostris maricelae

subspecies nov.

Holotype: Adult male, skin, skull, and partial postcranial skeleton, CVULA-I-2 812, from Laguna de Caparú, 3 km SE San Juan de Lagunillas, Mérida state, Venezuela, 900 m elevation; obtained on 25 March 1987 by P. J. Soriano and A. Mijares (field number S-1 621). Selected external and cranial measurements (in mm), and weight (in g) of the Holotype are: length of head and body (tail included), 79; length of tail, 4; length of hind foot, 10; length of ear, 15; length of forearm (dry), 38.8; length of tibia, 15.9; greatest length of skull, 24.6; postorbital width, 4.7; mastoid width, 9.6; breadth of braincase, 8.8; depth of braincase, 8.5; maxillary length, 8.4; length across canines, 4.5; length across second upper molar, 6.5; weight, 13 g.

Paratypes: Twenty-one adult specimens from the same locality consisting of 10 males and 11 females: CVULA-I-174, 387–388, 2 797, 2 799–2 802, 2 804, 2 808, 2 811–2 812, 2 814, 2 823–2 824, 2 941, 3 387, 3 441, 3 444, 3 802–3 803, 4 395. Mean and range (in parenthesis) of selected external and cranial measurements (in mm), and weight (in g) of paratypes are: length of head and body (tail included), 71 (64–83); length of tail, 5.3 (4.0–8.0); length of hind foot, 11.5 (10.0–15.0); length of ear, 14.8 (12.0–17.0); length of forearm (dry), 39.2 (37.2–41.2); length of tibia, 15.6 (14.8–16.6); greatest length of skull, 24.5 (24.0–25.5); postorbital width, 4.7 (4.5–4.9); mastoid width, 9.5 (9.1–9.9); breadth of braincase, 8.8 (8.6–9.1); depth of braincase, 8.6 (8.2–8.9); maxillary length, 8.4 (7.4–9.8); length across canines, 4.5 (4.1–4.9); length across second upper molar, 6.4 (6.0–6.7); weight, 13.7 (11.0–17.5).

Diagnosis: This new subspecies is characterized by having the longest and widest rostrum known for the species, as is indicated by its greater values for GLS, MAX, and M2-M2. Likewise, it has a lower value for BB among the Venezuelan populations.

Comparisons: *G. l. maricelae* is distinguished from the other Venezuelan subspecies by having longer skull and maxillary tooth row, broader palate, and less voluminous braincase.

Distribution: This subspecies is endemic of the semiarid enclave located in the middle basin of the Chama river and the Nuestra Señora river basin, Venezuela, between Estanques village at 500 m above sea level and El Morro village at 2 000 m, showing the highest elevational range and altitudinal record known for the species.

Habitat and ecology: This isolated population inhabits the thorn shrub area known as Lagunillas pocket, and is the main pollinator and seed disperser of the columnar cacti *Stenocereus griseus*, *Subpilocereus repandus*, and *Pilosocereus tillianus* (Soriano et al. 1991; Sosa and Soriano 1996). This population shows a bimodally polyestrous reproductive pattern with two extended reproductive peaks throughout the year (Sosa and Soriano 1996).

Etymology: We wish to dedicate the name of this subspecies in honor to the late Maricela Sosa, who studied the feeding and reproductive ecology of this population. The subspecific name is a matronym in the genitive case, singular and of feminine gender.

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Stone marten (*Martes foina* Erxleben, 1777) use of different landscape types in the mountains of central Spain

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Previous studies on habitat selection by stone martens (*Martes foina*) indicate that they occupy a range of different habitats and geographical regions from forest and rocky areas to human environments (Libois and Waechter 1991). In most of central Europe, the stone marten is mainly associated with human environments (Waechter 1975; Skirnisson 1986; Libois and Waechter 1991; Herrmann 1994). In contrast, in central Spain (Mediterranean region), the species prefers forest to human enviromnents in forest-dominated landscapes (Virgós and Casanovas 1998). However, in such landscapes, stone martens may also occur in rocky areas (Heptner and Naumov 1974; Delibes 1983; Libois and Waechter 1991), which is thought to be their preferred habitat in most of the Mediterranean area (Waechter 1975; Delibes 1983). Stone marten preference for forest or rocky landscapes in Mediterranean landscapes, therefore, needs to be evaluated in the field.

In this study, we investigate the presence of stone martens in different landscape types in central Spain during winter, a very restricted season for marten species.

The study was carried out in the mountains of central Spain (Sierra de Guadarrama, 40°40′ N-3°51′ W, Madrid province) over 1 600 km^2. Fifteen relatively homogeneous 4 × 4-km patches (henceforth known as plots) were selected in terms of their rock and tree cover, vegetation formations, and predominant human usage. All plots were located between 1 100 and 1 350 m a. s. l. and were at least 2.5 km apart. The predominant vegetation is pine forest (especially Scots pine *Pinus sylvestris*) as the stone marten is known preferentially to select this forest type in the mountains of central Spain (Virgós and Casanovas 1998). The selected plots have a warm, semi-dry, Mediterranean climate with cool summers and moderately cold winters, with snow being not uncommon but not very persistent (Rivas-Martínez et al. 1987). Human land-use was similar between plots, the most important being weekend recreational use and forestry. Hunting is restricted, only being allowed in the study areas when wild boar *Sus scrofa* populations increase.

Plots were classified as rocky, forested or mosaic according to estimated tree and rock cover (Tab. 1). Thus, we assigned a plot to the forest category when tree cover in that plot was above 50% and rock cover under 10–15%. Similarly, we considered a plot to be located in a rocky landscape when rock cover was over 50% and tree cover under 10%. Landscapes with rock and tree cover not included in the intervals mentioned for rocky and forested landscapes were classified as mosaic.

The study was carried out from November to early March 1996 and 1997, the more restrictive season for martens (Buskirk et al. 1988; Libois and Waechter 1991). Stone marten scat was sampled by walking a series of routes along randomly selected tracks

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Table 1. Mean tree and rock cover, number of sampled sections and frequency of occurrence of scat in the different plots sampled in relation to defined landscape types.

Landscape type	Tree cover (%)	Rock cover (%)	Number of sampled sections	Scat frequency of occurrence
Rocky	5.6	76.4	16	0.06
Rocky	2.0	51.9	10	0.10
Rocky	0.4	50.0	12	0.08
Rocky	2.5	47.7	13	0
Rocky	0.8	54.4	16	0.06
Mosaic	19.4	62.1	15	0.27
Mosaic	49.2	29.1	13	0.31
Mosaic	21.1	45.0	10	0.70
Mosaic	57.2	21.2	16	0.62
Mosaic	52.0	43.0	9	0.44
Forested	57.3	8.9	11	0.64
Forested	45.8	9.9	16	0.19
Forested	74.8	1.2	16	0.06
Forested	50.9	9.1	11	0.45
Forested	66.2	12.5	16	0.06

and paths in the plots (WAECHTER 1975). In order to avoid potential differences in visibility, we sampled tracks of similar width and vegetation characteristics. Minimum and maximum distances travelled were 2.25 km and 4 km, respectively, along a 2 m-wide belt. Each route was divided into 250 m-long sections in which we recorded the presence or absence of stone marten scat and scat number (see CLEVENGER 1993 for similar procedures). Eight of the 15 plots were sampled in both winters to test for possible changes in occurrence patterns within plots between years. The remaining 7 plots were only sampled in the second winter. In addition to scat searches, we estimated both tree and rock cover along each route. Cover estimation of these variables was made at the midpoint of the 250 m sections on each route by visual inspection. The number of 250-m sections sampled per plot is given in table 1.

To study the distribution pattern between the different landscape types, a frequency of occurrence index was used, measured as the number of sections with scats divided by the total number of sections sampled for each plot. To evaluate the potential differences in the frequency of occurrence between the two years, we performed a Fisher exact test applied to a 2 × 2 contingency table with the number of sections with stone marten presence or absence as rows and the years as columns (SOKAL and ROHLF 1981). Stone marten distribution pattern between the different landscapes was analysed using a fixed one-way ANOVA with the numbers of sections with scat (frequency of occurrence) as a response variable and landscape type (rocky, forested or mosaic) as the fixed factor. The frequency of occurrence values were logarithm-transformed to obtain data normality and homocedasticity prior to analyses.

The plots did not show significant differences in the frequency of occurrence values between the two study years (1: $p = 0.99$; 2: $p = 0.39$; 3: $p = 0.99$; 4: $p = 0.11$; 5: $p = 0.21$; 6: $p = 0.20$; 7: $p = 0.99$; 8: $p = 0.99$). Our results indicate that the distribution pattern was fairly constant at least for two consecutive years. Thus, only the data from the second winter with a larger sample were used in the subsequent analyses.

The different values of the frequency of occurrence index between landscape types were highly significant (Fig. 1). The Duncan post-hoc test shows that these differences are due to lower numbers of stone marten in rocky areas compared with mosaic and forested

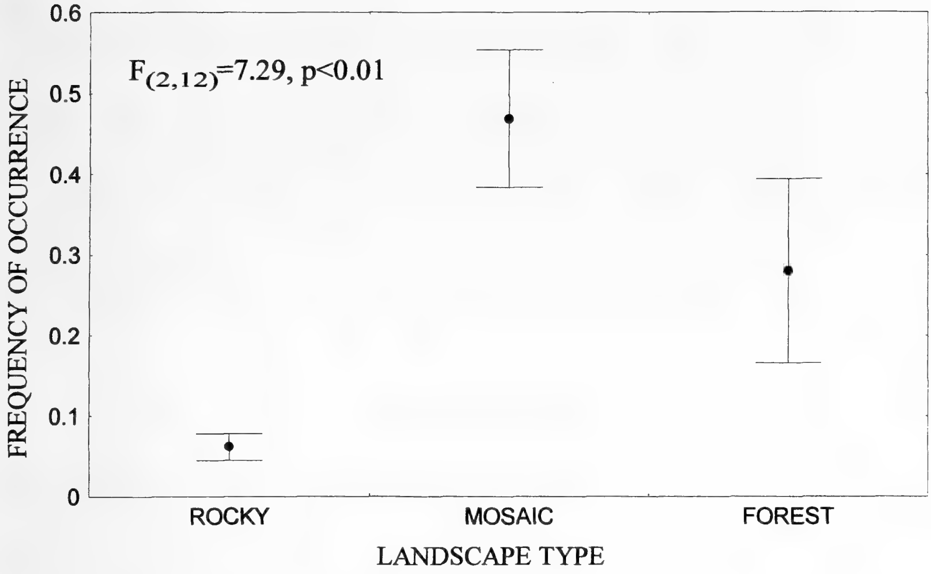

Fig. 1. Results of the one-way ANOVA with landscape type as a fixed factor (three levels) and number of sections in the transects with stone marten scat (frequency of occurrence) as response variables.

landscapes. No statistically significant differences occurred between the forested and mosaic landscapes ($p = 0.12$).

Research on stone marten habitat preferences has focused on radio-telemetry of several marked individuals within small areas (e. g. SKIRNISSON 1986; HERRMANN 1994; GENOVESI et al. 1996), where habitat selection was evaluated at individual levels (e. g. decision-making within home ranges). Our interest in habitat preferences at the population level makes comparisons with previous studies difficult and probably biased. However, several important points can be discussed regarding the results.

In contrast to previous studies (LIBOIS and WAECHTER 1991), the stone marten shows a certain habitat choice in the mountains of central Spain (see also VIRGÓS and CASANOVAS 1998). Thus, on a regional scale, the stone marten is found in greater numbers in the mosaics of forest-rocky areas than in mainly rocky landscapes without forests in contrast to earlier results in other areas (HEPTNER and NAUMOV 1974; WAECHTER 1975; DELIBES 1983). We may suggest that, like other Martes species (BUSKIRK and POWELL 1994), the stone marten presents a definite forest habitat preference when living in forest-dominated landscapes. In contrast, in non-forested landscapes, a habitat shift to open landscapes, such as rocky areas in some Mediterranean areas or buildings in central Europe (see discussion in VIRGÓS and CASANOVAS 1998) would probably be advantageous for the species. Thus, in the non-forested but rocky areas of some Mediterranean regions (e. g. the Spanish plateau) the stone marten may occur in the rocky landscapes of hills or canyons.

The above-mentioned pattern could be explained by a combination of the mechanisms put forth to explain habitat selection in stone martens: food, predation risk, and shelter (LIBOIS and WAECHTER 1991; HERRMANN 1994; THOMPSON and HARESTAD 1994) despite the lack of quantitative estimates for them. We suggest that the low numbers in rocky landscapes could be explained by the high potential predation risk due to low tree cover and high numbers of eagle-owl (*Bubo bubo*), one of the most important predators on stone marten (WAECHTER 1975). Other predators such as red foxes and dogs are widespread and probably may affect stone marten numbers similarly in all landscape types. Therefore, they cannot produce the differences in abundace detected. Food availability (especially rodents, insects, and fleshy fruits) is probably as abundant in rocky landscapes as in forested or mosaic landscapes. Thus, rodents occur in similar numbers in the different landscape types, which are located at the same elevation and in similar scrub composition and cover, both being the main determinants of abundance and diversity of these taxa in mountains (Owen 1990; Alcántara 1992). Fleshy fruits are mainly located along small streams (Rivas-Martínez et al. 1987), which were very common in all the study plots. Shelters (rock holes or hollow trees) were widely available over all plots and landscape types. Therefore, these factors are probably less important than predation risk as a reason for the low numbers of stone marten in rocky areas. On the other hand, the pattern is consistent for the winter season, but the relative value of the different landscape types may change with season.

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The human vomeronasal organ and pheromonal communication: facts and fantasy

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Since the results of some recent studies (Monti-Bloch and Grosser 1991; Berliner et al. 1996) have suggested a functioning vomeronasal organ (VNO) in humans, this topic has drawn much attention. Its involvement in human pheromonal communication is suggested (Weller 1998) and the presence of a well established VNO is almost euphorically postulated. These sort of studies seem to indicate that our VNO never went rudimentary and instead continues to work at a subconscious level.

Some critical remarks on this subject are in order. By comparing the findings in humans (Moran et al. 1991; Smith et al. 1997; Takami et al. 1993) with own results on the VNO in a large number of different mammals (Wöhrmann-Repenning 1984) the suggestions of all previous anatomists have been verified: This accessory olfactory organ has indeed gone rudimentary in the line of catarrhine primates, including man (Frets 1914; Kolmer 1927; Maier 1997). Numerous criteria can be used to illustrate this fact.

It has been well established for a long time that the VNO in humans is always present in the fetus. It shows the greatest differentiation in early embryonic stages and quickly decreases during further development (Boehm and Gasser 1993; Starck 1975). It is for the most part – but not always (!) – present in adult humans as small bilateral pits at the nasal septum (Moran et al. 1991; Kolmer 1927). But in most other mammals, which also includes prosimian and platyrrhine primates (Bergmann 1997), the VNO does rapidly grow during ontogeny increasing in size and in the complexity of its histological structure (Wöhrmann-Repenning and Barth-Müller 1994) (Fig. 1).

The VNO in most mammals is closely associated to an autonomous intranasal system with a complicated morphology, called the vomeronasal complex (VNC) (Wöhrmann-Repenning 1993). Its special anatomy guarantees the functioning of the blind ending, tube-shaped VNO. Humans definitely do not have anything comparable to a VNC. Moreover their VNO has even lost contact with the paraseptal cartilage, which normally surrounds the VNO and near its rostral opening transforms into an intricate structure, often by fusing with other cartilages. In humans the VNO is situated in an unusual position, quite a way above the septal base where the cartilage itself actually has retained its ancestral site.

The vomeronasal nerve normally serves the epithelium of the VNO and connects it with the accessory olfactory bulb (AOB). The VN-nerve bundles are remarkably voluminous and they follow the olfactory epithelial layer of the VNO (Fig. 1). In humans a thorough tracing (Stensaas et al. 1991) is necessary to identify potential vomeronasal axons in the area surrounding the organ. An AOB is present only during early embryonic development, later it quickly regresses and is completely absent in adults (Humphrey 1940). The same situation has been reported for catarrhine primates and in general for all vertebrates lacking a VNO (Humphrey 1940; Stephan 1967; Stephan et al. 1982).

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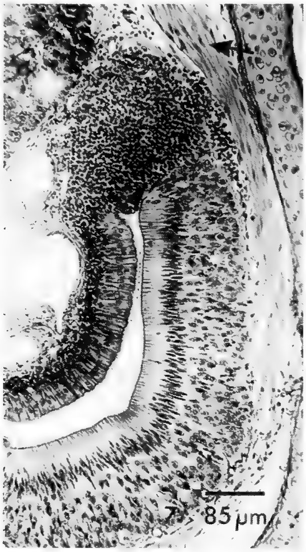

Fig. 1. Cross-section of the VNO of *Tupaia glis*. Note the thick olfactory epithelium, the VN-nerve (arrow) and the vein plexus at the left side. 10 µm. Azan.

All recent studies on the human VNO postulate its involvement in putative pheromone detection (Monti-Bloch and Grosser 1991; Berliner et al. 1996; Weller 1998). The pheromones may reach the organ as airborne substances both under normal (Stern and McClintock 1998) and artificial conditions (Monti-Bloch and Grosser 1991; Berliner et al. 1996). In other mammals the complicated anatomical situation of the VNC guarantees that the olfactory stimuli provided for the VNO are non-volatile molecules (Wysocki et al. 1980) which, suspended in liquid, enter the VNO by means of a vasomotorically induced sucking- and pumping mechanism (Wöhrmann-Repenning 1991). It is suggested that the stimulation of the human VNO takes place on subconscious level. Several behavioral patterns in other mammals indicate that particular attention is given to substances which stimulate the VNO (Bailey 1978; Melese-D'Hospital and Hart 1985) and that the VNO, which plays an important role in social and sexual situations (Estes 1972) and food detection processes (Cooper and Bhatnagar 1976) does not work very selectively (Meredith et al. 1980).

Thus, we should accept that the VNO in humans definitely has gone rudimentary. If it really has retained some form of remnant function, pheromones are carried to it during inhalation. This, however, would generally impede experimental work with humans, because volatile substances are able to reach every receptor cell within the nasal cavity. In addition it seems quite contradictory that a noteworthy percentage of adult humans actually lack the VNO completely without revealing significant sensory deficits. In this sense it is also surprising that during endonasal surgery the patient's VNO can be experimentally removed without any apparent negative effects (Gaafar et al. 1998).

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Buchbesprechungen

Swift, Susan M.: **Long-eared bats.** London: T. and A. D. Poyser Ltd. 1998, Hardcover, 182 pp., numerous black and white pictures and 13 colour plates. £ 24.95. ISBN 0-85661-108-5.

This monographic publication introduces the reader to the biology, ecology, behaviour, protection and research related with two European species ot bats, the brown and grey long-eared bat, *Plecotus auritus* and *P. austriacus.* The author, who is research fellow at the University ot Aberdeen, Scotland, draws on own investigations and on a wide range of international literature, not only concerning the above-mentioned species, but also on other bats, mainly representatives ot the family Vespertilonidae.

After an introductory chapter the morphology is first described, followed by two chapters on food and its procurement. Reproduction, social organisation and behaviour, population biology and hibernation are presented and discussed in subsequent chapters. The author also deals extensively with the relationship between *Plecotus* species and the threats produced by an environment influenced and formed by man, such as timber treatment, street lamps and urbanisation in general. In three appendices the scientific and common English names ot bat species and the care for stranded and injured bats, as well as a list of addresses of British institutions dealing with bat protection and research, are given. 17 pages of references and a detailed subject index conclude the book.

The text is written in a concise, down-to-the-point style; it supplies a wealth of information. Thirteen colour plates – some of them really outstanding photos – illustrate the two considered species and their biotopes. Mammalogists in general and especially chiropterologists will certainly thoroughly welcome this publication.

P. Langer, Giessen

Berta, A.; Sumich, J. L.: **Marine Mammals: Evolutionary Biology.** San Diego: Academic Press 1999: Hardcover, 494 pp., numerous illustrations and tables. £ 39,95. ISBN 0-12-093225-3

This remarkable book gives an overview of the biology of marine mammals with emphasis on their evolution, anatomy, behaviour and their ecology. An aspect of this text worth mentioning is the phylogenetic approach, which supplies additional insights.

After a short introduction the first section deals with the evolutionary history of marine mammals. The authors deal with systematics and classification in general. The two authors, both working in California, initially give an account of the theoretical background and technical aspects of phylogenetic analysis, as well as dealing with questions on taxonomy and classification.

Pinnepeds, cetaceans, sirenians, sea otter and polar bear are considered in this book, but also extinct forms are briefly discussed: Fossils of sirenian as well as carnivoran relatives are dealt with, but the most remarkable form of all is an extinct aquatic sloth, *Thalassocnus natans*, from southern Peru. At the end of the section on the evolutionary history of marine Mammalia, a chapter dealing with the evolutionary biogeography follows. The chapters are structured according to similar principles: After short introductory remarks, the origin and evolution down to the family level are presented and discussed in detail. A summary as well as conclusions follow. All chapters are not only supplemented with an extensive list of references, but the use of these lists is always introduced by a very helpful “weighing” of the references in a special paragraph “Further Reading”, which structures the wealth of information stored in the listed papers.

The second main section deals with evolutionary biology, ecology and behaviour of marine mammals. Pinnipeds and cetaceans are covered thoroughly. A first chapter discusses the integument, and gives an account of the sensory and urinary systems. This chapter reviews older and newer data from the literature. The following chapter deals with the very different types of the musculoskeletal apparatus and, consequently, the very diverse types of locomotion. The subsequent chapter, is concerned with respiration, diving and “breath-hold physiology”, which is necessary for aquatic forms that de-

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pend on air. In this chapter modern data from the physiological literature are presented. An account of sound production for communication, echolocation and prey capture follows; it concentrates on cetaceans. Different aspects of reproduction and population biology in marine mammals are discussed in the following three chapters. Finally, exploitation as well as aspects of conservation are presented. A detailed appendix makes the reader familiar with the classification of marine mammals. A glossary and a detailed index concludes this book.

The wealth of data made available in this publication cannot be discussed sufficiently and in detail in a review of only limited available space. Readers, who want a modern, extensive, clear, well-organised and illustrated introduction into the evolutionary biology of marine mammals, as well as those mammalogists who need a comprehensive source of information and reference to accompany them through their own studies of the fascinating world of marine Mammalia will be well served by the broad approach of ANNALISA BERTA and JAMES L. SUMICH. It is hoped that this book will stimulate other specialist to write similar texts on mammalian groups with emphasis on evolutionary biology!

P. LANGER, Giessen

BOINSKI, S., GARBER, P. A.: **On the Move – How and Why Animals Travel in Groups.** Chicago, London: University of Chicago Press 2000. Softcover or Hardcover, 824 pp., several figures. US$ 35.–/95.– ISBN 0-226-06340-2 (paper) or 0-226-06340-2 (cloth)

There is nothing more boring than effusive patronisation in a book review, raising the impression that the reviewer was corrupted by the publisher. Here, the free of charge review copy alone makes a gratefully appreciated bribe. This book of 22 chapters and more than 800 pages including many diagrams written by many well-known and some famous authors gives an incredible mass of facts on many aspects concerning the social activities of a wide range of animals, including insects, carnivores, whales and humans, but focussing on simian primates. This book never becomes tedious, because facts are taken from a great variety of fields of knowledge relevant for modern evolutionary biology such as ecology, ethology, and socio-biology. Theoretical evaluations are always interspersed with short descriptions of field observations. The reader is guided through this book by a consequent and clearly structured introduction. Chapter titles outline exactly the content. Each chapter is a unit by itself, so that the reader can easily pick out selected chapters of interest. The registers are carefully composed and are a further immense help for orientation. The literature index of nearly 100 pages covers original publications referring to all major statements in the text. For further praise, see the reviews cited on the back cover. They all sound exaggerated but simply state the facts!

Obviously, this enumeration of merits has the danger of becoming tedious, and at this point something negative just has to be constructed to regain the attention of the reader. Why not criticise the title? “On the move – how and why animals travel in groups” is an understatement “par excellence”. Travelling in groups mostly means living in groups – and the authors consequently do not only argue about energetic costs and about who decides where to go in a group, but also expel on general mechanisms of social organisation, on the evolution of cognitive abilities and defence strategies. In the fifth section, comparative aspects of social organisation and travelling of non-primates and human African nomads round off the work.

Summarising all these facts, reading this book is of special interest for all readers interested in the non-molecular mechanisms behind biological evolution – even human evolution, and especially for those who until now are not interested in this field – because after reading this book, they may join the club.

K.-P. VALERIUS, Giessen

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