Mammalian Biology

Zeitschrift für Säugetierkunde

Volume 66
2001

URBAN & FISCHER

Reviews

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Short communications

Mammalian Biology

Zeitschrift für Säugetierkunde

1·2001

URBAN & FISCHER

ISSN 1616-5047
Mamm. biol. · 66(2001)1 · 1-64

www.urbanfischer.de/journals/mammbiol

Mammalian Biology

Zeitschrift für Säugetierkunde

IMPRESSUM
Publisher: Urban & Fischer Verlag GmbH & Co. KG, Branch Office Jena, P.O. Box 100537, D-07705 Jena, Germany; Phone: ++49(0)3641/626-3, Fax: ++49(0)3641/62 65 00, E-mail: journals@urbanfischer.de
Advertisement bookings: Enquiries should be directed to Urban & Fischer Verlag, Advertising Manager: Sabine Schröter, P.O. Box 100 537, D-07705 Jena, Germany;
Phone: ++49(0)3641/62 64 45, Fax: ++49(0)3641/62 64 21.
Advertising rates: The price list from January 1, 2001 is effective at present. **Distribution and subscription agency:**
For customers in the German speaking countries: Please turn to your bookshop or to Urban & Fischer Verlag, Aboservice und Vertrieb: Barbara Dressler, Löbdergraben 14a, D-07743 Jena, Germany; Phone: ++49(0)3641/62 64 44, Fax: ++49(0)3641/62 64 43, E-mail: k.ernst@urbanfischer.de
For customers in all other countries: Please contact your bookshop or The Nature Publishing Group, Linda Still, Brunel Road, Basingstoke, RG21 6XS, UK; Phone: ++44(0)1256/30 26 29, Fax: ++44(0)1256/46 35 70, E-mail: l.still@nature.com Subscribers in the **USA** can call toll free on ++1 800 747 3187.
Terms of delivery (2001): 1 volume consisting of 6 issues.
Subscription rate (2001): DM 498.00*/GBP 200.00. Preference price for personal subscribers: DM 150.00*/GBP 60.00. All prices quoted above are exclusive postage. *Suggested list price. Price are subject to change without notice. Personal subscription orders must be addressed directly to the publisher Urban & Fischer in Jena resp. to The Nature Publishing Group. Subscriptions at a personal rate must include the recipient's name and mailing address. An institutional or business address is only accepted, if the institute or firm has a subscription as well. Personal subscribers can pay by personal cheque or credit cardmentioned below. US dollar prices are converted at the current exchange rate.
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Subscription information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting and printing, binding: druckhaus köthen GmbH

(∞) As of vol. 61, number 1 (1996) the paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Printed in Germany

For detailed journal information see our home page: http://www.urbanfischer.de/journals/mammbiol

Mamm. biol. **66** (2001) 1–12
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Mammalian Biology
Zeitschrift für Säugetierkunde

Review

Genetic heterogeneity of white-tailed deer: management lessons from a long-term study

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Receipt of Ms. 24. 07. 2000
Acceptance of Ms. 20. 10. 2000

Abstract

Genetic data from a long-term (16-year) study of white-tailed deer (*Odocoileus virginianus*) on the U.S. Department of Energy's Savannah River Site (SRS) were examined to evaluate spatial and temporal genetic heterogeneity in this species. Based on our analyses of the long-term data set, three major findings emerged, all of which have important implications for management of white-tailed deer: (1) There exists significant spatial genetic heterogeneity in white-tailed deer based on analyses of allozyme frequencies and mtDNA haplotypes. This heterogeneity exists on a much smaller spatial scale than would be expected for such a large and potentially mobile species as *O. virginianus*. (2) The genetic structure of white-tailed deer at SRS is temporally dynamic and significant heterogeneity exists within demographic units such as age and sex classes. (3) Levels of genetic variation, as measured by multilocus heterozygosity, are frequently correlated to characteristics that are important determinants of ecological function in white-tailed deer populations. These findings are evaluated in the context of a general management model for *O. virginianus* that is also applicable to other wildlife species.

Key words: *Odocoileus virginianus*, allozymes, mtDNA, spatio-temporal heterogeneity, demographic heterogeneity

Introduction

For most of this century, population geneticists and evolutionary biologists have assumed that populations consist of a large number of randomly breeding individuals (panmixia). This view made it easier to mathematically describe the behavior of populations and resulted in a relatively static concept of their genetic characteristics. Little effort was expended in linking genetic and demographic changes in populations. Wildlife biologists considered changes in population numbers, quality of individuals within them, and other demographic parameters as being due to environmental effects, and genetic differences were often not considered at all. Despite this, the environmental or habitat model, which became the almost exclusive population dynamics paradigm in wildlife biology, was very successful in explaining population differences.

1616-5047/01/66/01–001 $ 15.00/0.

The term "genetics" was not even mentioned in most wildlife management texts during the first two thirds of this century. Technological advances in the 1950s and 1960s made it much easier to describe character variation among individuals and to determine the genetic basis of this variation. There was a virtual explosion in the number of studies that provided estimates of genetic variation in natural vertebrate populations (Smith et al. 1982, 1994). As a result of these studies, it became clear that the model of a large panmictic population was not correct for most terrestrial and freshwater vertebrates (e. g. Smith et al. 1978; Avise 1994). However, most of the data, especially for mammals, were from small relatively short lived forms (e. g. Krebs et al. 1973). Data from the white-tailed deer summarized here support the view that genetic heterogeneity over short distances may be common even in large, vagile vertebrates.

Temporal genetic heterogeneity over short time predicts the need for further refinement of habitat management models used in wildlife management. Characteristics of concern to natural resource management, including conservation, need to be thought of as being due to the influences of Environment (E; Habitat) + Genetics (G; Genotype) + Environment-Genetic Interactions (E*G). A holistic perspective would dictate that the enviromnent-genetic interactions would be at least as important in determining the characteristics of wildlife species as the main effects of genotype and environment. Studies that document differential population responses to similar environmental changes may indicate the importance of environment-genetic interaction and/or differences in the genetic composition of the reference populations. This interpretation stresses the importance of genetic factors in formulating management programs for both game and nongame species.

Genetics is most likely to be important if management units have different genetic characteristics from each other and/or they show temporal variations in their genetic characteristics. Our primary objective is to examine existing genetic evidence to see how common spatial and temporal heterogeneity is in white-tailed deer (*Odocoileus virginianus*, Zimmermann). Our purpose is to review the literature on the genetics of the white-tailed deer, present the results of some new analyses of data from a long-term study of this species, and to propose a new perspective on the important conceptual issues.

Sampling considerations

Management decisions based upon data collected from public hunts need to be viewed with caution. Such data must be examined to determine if inferences can be expanded beyond the limits of the available data in time and/or space. Basically this requires that animals are collected randomly with respect to variables of interest such as sex, age, antler morphology, genotype, etc. Deer collected on the Savannah River Site (SRS) in the southeastern United States, because of the limited public access and the details of the hunting methods used, can generally be considered to represent a random sample of individuals from the herd for most variables of interest (Novak et al. 1991). Novak et al. (1991) found no hunter selectivity based upon sex but some selectivity based upon age (older deer being preferentially selected) thus slightly biasing the distribution of ages upwards. Thus age-related genetic changes may be harder to detect than genetic changes related to sexual differences.

Spatial heterogeneity

Many genetic studies have shown that white-tailed deer populations are subdivided spatially. The effect is most noticeable in analyses that encompass large geographic areas (Cronin 1989; Ellsworth 1994 a, b; Hillestad 1984; Kennedy et al. 1987). In these studies F_{ST} (or a similar statistic that estimates the proportion of variance among populations) for both diploid (allozymes) and haploid (mitochondrial DNA

[mtDNA]) genetic markers is large, indicating strong differentiation between local populations.

On a small geographic scale, it is possible that spatial subdivision would not exist for a large, potentially mobile mammal, such as the white-tailed deer. However, a number of studies reject this notion. Spatial differentiation of populations for allozyme frequencies was readily apparent in white-tailed deer from the Adirondack Mountains of New York (Mathews and Porter 1993), northeastern Minnesota (Cronin et al. 1991), and on an even smaller scale, the SRS, South Carolina (Manlove et al. 1976; Ramsey et al. 1979), and Cumberland Island, Georgia (Rowland 1989). When studied, mtDNA markers usually, but not always show greater differentiation than those representing the nuclear genome. For example, Cronin et al. (1991) found the F_{ST} value for mtDNA to be 9 times greater than the F_{ST} for allozymes in mule deer from Montana but found no significant difference between mtDNA and allozyme-derived F_{ST} values for white-tailed deer from Minnesota.

Generally, genetic differentiation of populations is attributed to reduced gene flow, historic events and/or genetic drift (Cronin et al. 1991; Ellsworth et al. 1994 a, b; Leberg et al. 1994). In white-tailed deer, gene flow is influenced strongly by the species' mating system, females being philopatric and males doing the majority of movement among breeding groups (Nelson and Mech 1987). The effect of extirpation in the late 1800s and subsequent restocking have had a profound effect on the spatial pattern of genetic differentiation of white-tailed deer populations over most of their range. However, in

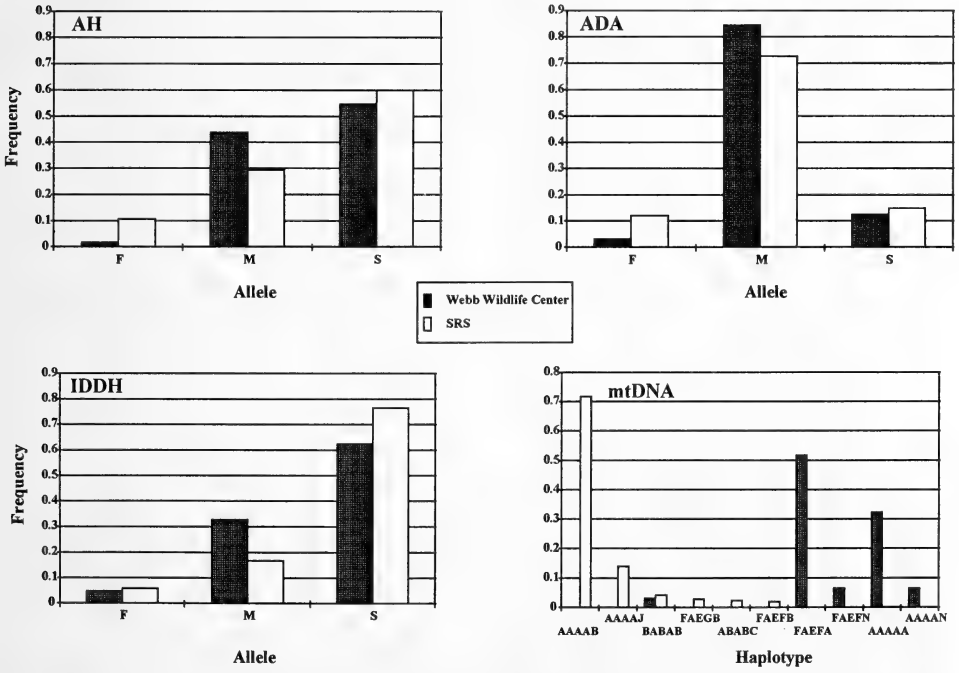

Fig. 1. Comparison of haploid (mtDNA) and diploid (allozyme) genetic markers for white-tailed deer populations collected in 1992 from the Savannah River Site (SRS; $N_{mtDNA} = 215$, $N_{allozym} = 737$) and Webb Wildlife Center (WEBB, $N_{mtDNA} = 31$, $n_{allozym} = 32$). The populations are separated by approximately 100 km. Shown are aconitate hydratase (AH), adenosine deaminase (ADA), and L-iditol dehydrogenase (IDDH) (also known as sorbitol dehydrogenase [SORDH]), the three most variable of the 13 loci sampled. Designations for alleles refer to relative mobility in electrophoretic starch gels. Only haplotypes and alleles with frequencies > 0.01 are shown.

the coastal plain of South Carolina and Georgia, native herds were not hunted to extinction and restocking was minimal. Recent analyses of deer from SRS and Webb Wildlife Center, located 100 km apart on the coastal plain of South Carolina, document significant spatial heterogeneity in both nuclear and mtDNA genomes. Deer sampled from SRS and Webb center display markedly different genetic profiles for nuclear and mitochondrial genes (Fig. 1). This and other studies (KENNEDY et al. 1987) indicate that for allozymes all alleles at a locus are present in most samples, although shifts in frequencies are often observed. In contrast, mtDNA types, which are haploid and maternally inherited, are much more localized. Sometimes, sampling locations separated by only 20 km share no mtDNA types. Female white-tailed deer thus may be extremely philopatric (PURDUE et al. 2000). The role of female philopatry in the maintenance of genetic structure of white-tailed deer can be seen in an inadvertent "experiment" provided by the restocking of deer in Greene county on the piedmont of Georgia. Early in the twentieth century, native deer were extirpated from Greene and surrounding counties and never recolonized the area. In the late 1980s, extensive restocking was undertaken in the area. Northern Greene county was supplied with 60 deer from Ossabaw Island and 7 from adjacent Blackbeard island, Georgia (BLACKARD 1971). The Ossabaw Island deer carry a mtDNA type unique to the island and a few mainland localities on the lower coastal plain. In counties adjacent to Greene, deer were transplanted from Texas and Wisconsin. In 1994, the mtDNA of 20 deer from Greene county were examined. Seven of ten deer sampled in the northern part of the county carried the Ossabaw island mtDNA type. The other three, plus 10 additional individuals from southern Greene county, displayed mtDNA types characteristic of deer from the Midwestern United States. After 40 years and 10–20 generations, female deer from Ossabaw Island have apparently dispersed little beyond their release site. These results reinforce the idea that white-tailed deer are genetically subdivided on a finer geographic scale than is apparent based upon their body size and vagility.

Demographic heterogeneity

Management decisions are usually made for a herd or larger grouping of individuals. However, smaller subsets of individuals (age or sex classes) may be progressing along separate evolutionary trajectories subject to differing ecological challenges. These demographic groups may exhibit different spatial or temporal patterns for both individuals and genotypes. Thus, genetic variability must be analyzed with respect to demographic classes of age and/or sex within a spatio-temporal context. The SRS deer herd provides a unique opportunity to analyze such data because of the size of the data set within years (Minimum = 409, Maximum = 1 999, Total = 14 221 deer), number of years for which data are available (16) and limited public access to the site.

Demographic heterogeneity in the SRS deer herd was analyzed for the years 1974–1989 based upon 7 polymorphic loci available in all years. Data for two highly polymorphic loci, β-hemoglobin and transferrin, were not available for the year 1980, so that year was not included in the analysis. Thus, all deer were categorized for multilocus heterozygosity class based upon 7 loci (HCI was 0, 1, 2, 3 and 4+ heterozygous loci, and H [arcsine of square root HC/Total number loci scored]), year of collection (TIME), age class (AGE) (0.5, 1.5, 2.5, 3.5+ years), sex (SEX), and spatial unit (SPACE) (swamp or upland herd). Expanded definitions of the above variables can be found in SCRIBNER et al. (1985) and NOVAK et al. (1991).

Probabilistic regression (PROBIT) analysis indicates that the distribution of AGE is a function of both TIME and SPACE ($\chi^2 = 61.65$, $P < 0.0001$ and $\chi^2 = 13.09$, $P = 0.0003$, respectively). However, the distribution of SEX is a function of TIME but not SPACE ($\chi^2 = 48.24$, $P < 0.0001$ and

$\chi^2 = 0.69$, $P = 0.4075$, respectively). Thus, analyses of genetic heterogeneity in relation to AGE and SEX must be performed with the appropriate spatial and temporal variables in the analysis.

Probabilistic regression using a Gompertz distribution for HC (GOMPIT) analysis indicates that there are significant SPACE ($\chi^2 = 7.32$, $P = 0.0068$) and TIME ($\chi^2 = 101.64$, $P < 0.0001$) effects, a marginal AGE ($\chi^2 = 6.59$, $P = 0.0863$) effect and no SEX ($\chi^2 = 0.02$, $P = 0.8989$) effect. Unfortunately, interactions among dependent variables cannot be analyzed using a probabilistic regression approach to account for TIME and/or SPACE heterogeneity of SEX and AGE. Therefore, an ANOVA was performed with H as the dependent variables and the main effect of SEX ($F = 0.53$, $P = 0.4676$), AGE ($F = 0.82$, $P = 0.4799$), TIME ($F = 3.84$, $P < 0.0001$), and SPACE ($F = 4.19$, $P = 0.0406$), and the two-way interactions of SEX and AGE ($F = 1.11$, $P = 0.3417$), SEX and TIME ($F = 1.87$, $P = 0.0242$), AGE and TIME ($F = 1.17$, $P = 0.2066$), AGE and SPACE ($F = 0.34$, $P = 0.7930$), and TIME and SPACE ($F = 1.64$, $P = 0.0621$). No higher order interactions were significant, and were therefore not included in the model. The significant interaction of SEX and TIME is due to differenees in H between males and females in different years (Fig. 2). There is no consistent sexual bias in H, 6 years show no significant difference, 5 years show a male bias for higher H, and 4 years show a female bias (Fig. 2).

Previous analysis for the effects of age, sex, year and spatial location on single locus heterozygosity (h) for β-hemoglobin by Chesser et al. (1982) revealed slightly different results. Sex was not found to be an important variable although it is unclear whether a sex by year interaction was tested. This analysis was performed over only a three year time span, for only a single locus and used simple tests of independence that did not analyze variables concur-

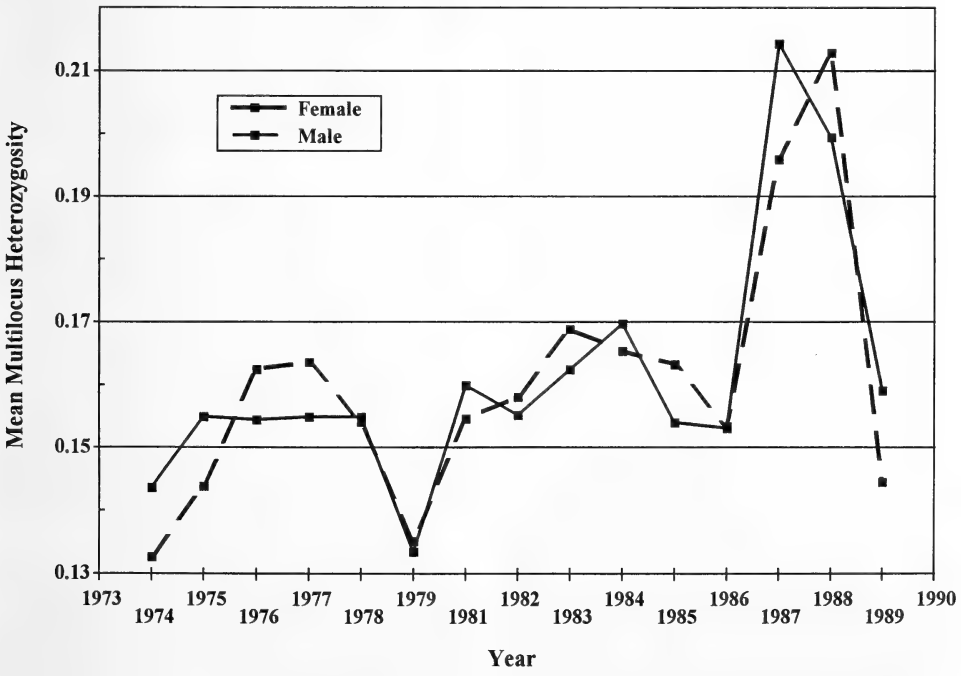

Fig. 2. Multilocus heterozygosity values for male and female deer for the years 1974 through 1989. The year 1980 is not included as indicated in the text.

rently. As indicated by the analyses performed here, there is a much larger range of variation in all variables when analyzed over a longer time span. In addition, longer time series are more likely to include periods of environmental stress. Thus, results based upon data that are limited in time, space or number of loci should be viewed with caution. Differences in results can also be seen in the studies of Smith et al. (1990) where a significant spatial effect was seen and Scribner et al. (1985) where a significant effect of space was not seen. The first study included data from a longer time series (13 years) than the second (6 years) but both estimated H using the same seven loci used here.

The above analyses illustrate the need to examine demographic effects on genetic heterogeneity in light of spatial and temporal variation of both demographic and genetic variables. Management decisions based upon only the main effect, SEX, would not be the same as those based upon the interaction of SEX and TIME. The interaction of SEX and TIME is not surprising for the SRS white-tailed deer herd given the relationships between male body mass and fat levels (Scribner et al. 1989), female fat levels and their relationship to pregnancy (Cothran et al. 1987), conception date of females (Rhodes and Johns 1993) and female age specific body mass (Rhodes et al. 1991). It is unclear if white-tailed deer are unusual for mammals in how they partition genetic variation in space and time. Although other studies have analyzed demographic heterogeneity, few have looked at the interaction of age and/or sex with space and none have analyzed differences over a comparable time span (Smith et al. 1994). The interaction of SEX and TIME has direct consequences for the estimation of genetically effective population sizes and minimum viable population sizes. If different demographic units are present in a population and each is progressing along independent or semi-independent evolutionary trajectories then management plans need to encompass this heterogeneity. Management decisions must be based upon information gathered to assess the additional ecological and genetic dynamics that such population substructuring introduces.

Fitness correlates and energetics

Fitness correlates

A fitness correlate may be defined as a phenotypic characteristic in which the degree of expression is related to the survival and/or reproductive success (fitness) of an individual. Numerous relationships between multilocus heterozygosity (H) and fitness correlates have been demonstrated in a long-term study of white-tailed deer on the SRS (reviewed by Rhodes and Smith 1992). Within age classes of male deer, H is related to (a) body mass and fat levels (Scribner et al. 1989), (b) antler size (Scribner et al. 1989), (c) antler symmetry and Boone and Crocket scores (Smith et al. 1991), (d) frequency of spike antlers (Scribner et al. 1984), and (e) testicle size in fawns (Urbston 1976). H in female deer is correlated with (a) the frequency of twin fetuses (Chesser and Smith 1987; Johns et al. 1977), (b) age-specific body mass (Rhodes et al. 1991), (c) conception date and fetal growth rate (Cothran et al. 1983; Rhodes and Johns 1993), and (d) body fat levels prior to conception and loss of fat during pregnancy (Cothran et al. 1987). Fetal growth rate is also related to the overall H of the fetus (Cothran et al. 1983; Leberg et al. 1990).

Smith and Risenhoover (1993) demonstrated a positive association between H and production of offspring in eight species of cervids. In addition, relationships between H and fitness correlates have been observed in many other organisms (Allendorf and Leary 1986; Mitton and Grant 1984). Thus, H likely integrates many important genetic characteristics of forest organisms.

The general trend of these relationships described for white-tailed deer is for expression of the reference character to increase (e. g., antler size) or decrease (e. g., incidence of spiked antlers) with increasing number of heterozygous loci. However, the

functional relationship varies depending on both the specific character and the age of the deer. In addition, there is evidence to suggest that expression of a reference character may decrease slightly at high H levels compared to that of intermediate levels (e. g., Chesser and Smith 1987) although this may be an artifact of small sample size at older age classes.

In most cases, H explains only a small percentage of the variability in characteristics. For example, H is responsible for only 10–15% of the variability in main beam length and diameter of antlers, number of antler points, and incidence of spiked antlers (Scribner and Smith 1990). Therefore, factors such as age, body condition, habitat, and resource quality, as well as their interaction with H, must be considered when explaining the expression of fitness-related characteristics in individual deer.

Although H may only account for a small amount of the variability in characters, deer with high H generally grow faster, have higher body fat levels and higher reproductive rates than deer with low H. These relationships suggest that deer with various levels of H may partition their energy differently. The potential relationship of H to energetics requires further consideration.

Heterozygosity and energetics

An organism's energy budget can be described by $I = A + E$, where I is the total amount of energy ($Kcal * g\ body\ mass^{-1}$) ingested, A is assimilated energy, and E is egested energy (egestion). Assimilated energy is partitioned into three categories with $A = M + G + R$ where M is maintenance energy and G + R represents assimilated energy used for growth or reproduction (i. e., secondary productivity).

A number of investigations have demonstrated a relationship between H and energetic parameters (reviewed by Mitton and Grant 1984). H has been correlated with decreased rate of oxygen consumption (Koehn and Shumway 1982; Mitton and Koehn 1985; Mitton et al. 1986) and a lower rate of protein turnover (Hawkins et al. 1986). These findings suggest differences in maintenance metabolism among individuals with varying levels of H.

We hypothesize that increased energetic efficiency could explain the effects of H on fitness-related characteristics in white-tailed deer. Hypothetical energy budgets for an organism with varying H are depicted in Fig. 3. In both homozygous and heterozygous individuals, a portion of assimilated energy must be utilized for maintenance metabolism (M) which includes energy used for normal activity. The remaining energy can be used for secondary productivity (G + R). However, in the more heterozygous individual, increased energetic efficiency as a result of higher H could reduce the amount of assimilated energy required for maintenance metabolism (M). A slight decrease in the amount of energy needed for maintenance could permit heterozygous individuals to partition much more energy for growth and reproduction (G + R, Fig. 3 a).

The above hypothesis assumes that ingested energy (I) is relatively constant among individuals. However, individuals with higher H may be able to ingest more energy as a result of aggressive behavior (Garten 1976) or an increased scope of activity (Mitton and Grant 1984). Consequently, assimilated energy would be greater among more heterozygous individuals, providing more energy for growth and reproduction, even if energetic efficiency is not affected by H (Fig. 3 b).

The effect of H on energetics is most likely to result in a selective advantage during periods of stress (Koehn and Shumway 1982; Rodhouse and Gaffney 1984; Teska et al. 1990). Teska et al. (1990) demonstrated that old-field mice of varying H differ regarding feeding efficiency only as food quality is decreased. These results suggest that the effects of temporal variation of H may be to decrease the ability to detect differences in H among individuals during non-stressful periods.

These findings may explain the inconsistency of some relationships between H and fitness correlates observed in white-tailed

deer. For example, a relationship between H and the frequency of twin fetuses was observed among does from the SRS during the 1970s (CHESSER and SMITH 1987; JOHNS et al. 1977) whereas no such relationship was found during the 1980s (RHODES et al. 1991). Future investigations concerned with documenting H effects in white-tailed deer

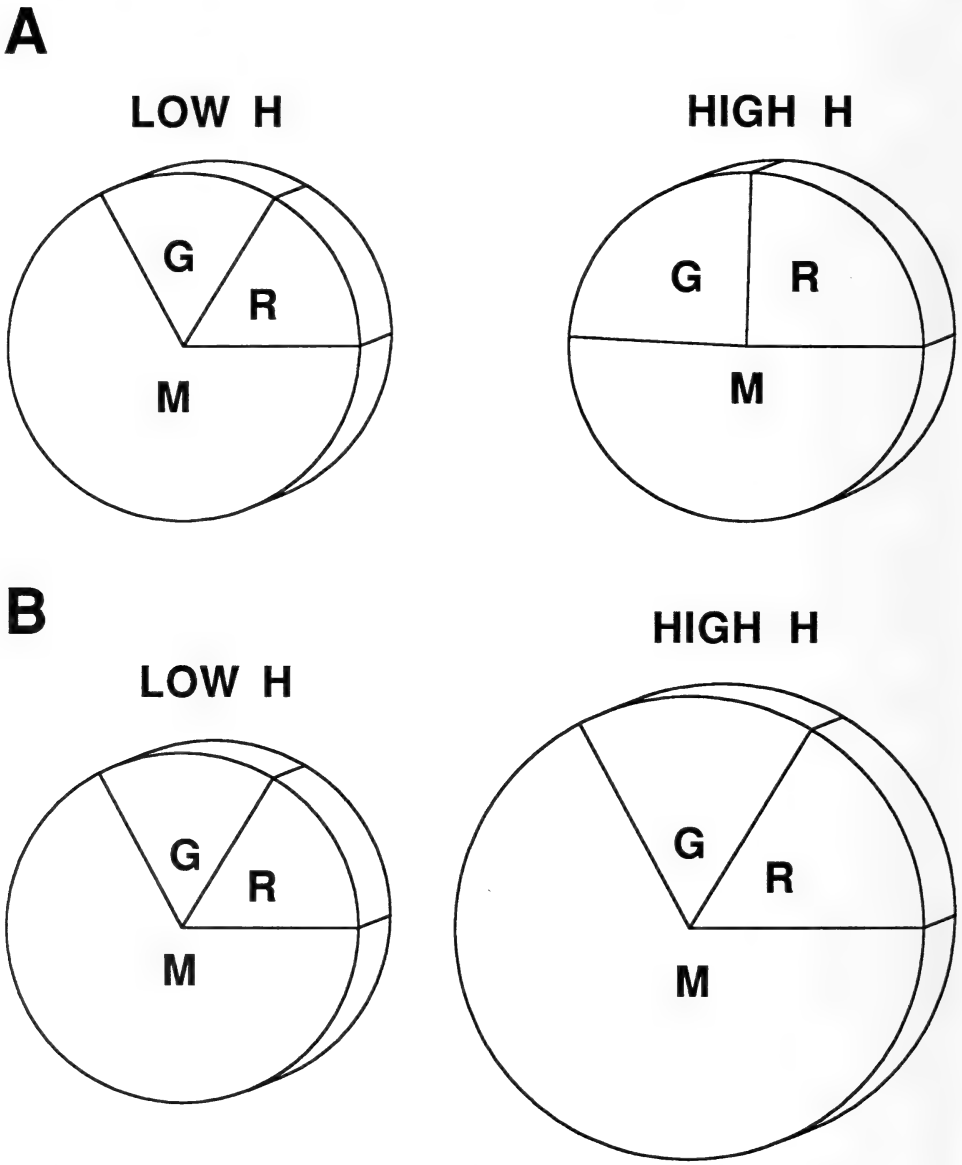

Fig. 3. Hypothetical energy budgets for an organism with relatively low and high levels of heterozygosity (H). High H may increase the amount of energy available for growth (G) and reproduction (R) by: (A) Reducing the percentage of assimilated energy needed for maintenance (M) via effects on metabolic efficiency or: (B) Increasing the amount of assimilated energy via effects on foraging and ingestion. The size of each circle is related to the amount of ingested energy.

should take into account spatial and temporal variation in environmental quality as well as in H.

The influence of H on energetics is related to individual fitness and quality of individuals in a population. Genetic variability could be especially important in allowing forest organisms to persist with increasing levels of anthropogenic and non-anthropogenic stress. Understanding the role of genetic variation has important implications for both conservation and management practices of forest wildlife species.

General management model

Genetic analyses of white-tailed deer populations, as well as other animal populations, have provided insights about their functioning that need to be incorporated in future management plans (Smith et al. 1976). The results of these analyses are especially important to the formulation of management plans. They are as follows: 1) animal populations, especially white-tailed deer, show genetic heterogeneity over relatively short distances and among demographic units within populations, 2) white-tailed deer populations, and probably those of other species, are generally dynamic over short time periods, and 3) levels of genetic variability are frequently correlated to many characteristics that are important determinants of ecological functioning of populations and of concern to natural resource managers. Although the correlation of genetic variability and phenotypic characteristics do not usually explain a large proportion of the total variation, each correlation may be somewhat independent such that the overall effects on the ecologieal dynamics of the population function are very important.

White-tailed deer show a surprising amount of spatial genetic heterogeneity even in areas like the SRS where the habitats are not severely fragmented. In areas where forested habitats are becoming even more fragmented (Harris 1984), spatial heterogeneity in gene frequency may be further increased. Spatial genetic heterogeneity needs to be taken into account in defining boundaries of management units. In addition, conservation efforts need to recognize that many forms of a species having unique combinations of genes may occur in subpopulations separated by short distances. Spatial heterogeneity in gene frequencies has been recognized in a wide diversity of animals, and its management implications have been recognized as important in fisheries management (Ryman and Utter 1987).

Wide scale fragmentation of forested habitat can lead to reduction of census and effective population sizes, which may fall below the minimum viable size (Soulé 1987). One of the most important long-term effects of falling below the minimum viable population size is stochastic loss of genetic variability, which is important for both the future evolution and the ecological functioning of populations. Small populations may also be more susceptible to the effects of inbreeding, especially if population numbers are reduced quickly and kept low for an extended period of time (Thornhill 1993). Although we do not know whether genetic variability causes changes in population parameters and/or is a result of them, it would seem prudent to manage populations in a way that minimizes the chance of losing genetic variability.

The genetic structure of populations is temporally dynamic over time periods that include the length of typical studies (Smith et al. 1990). This dynamic behavior of populations may result from the interactions from smaller groups that differ from each other genetically. Animals that disperse among these subpopulations to breed may have relatively outbred offspring with higher levels of genetic variability and different phenotypic characteristics than those that breed within the subpopulation in which they were born. Management of forest habitats (e. g., maintaining corridors) to allow this type of dispersal among subpopulations may be essential to the long-term health of many of forest animals (Harris 1984), especially large vertebrates.

One measure of the success of various management programs could be the degree to which we maintain the genetic integrity of

the species. Genetic integrity must not be based on a static concept of the genetic characteristics of the species. Populations are extremely dynamic through space and time, and it seems prudent to manage biological resources so that they continue to exhibit their normal variation in both space and time (Norse et al. 1986). Thus, we are trying to manage species that are likely to be genetically different in both space and time, and these genetic differences are likely to have direct relationships with biological characteristics important to both the survival of the species and the production of benefits for humans. As human society continues to increase its impact on every habitat on earth, it will be challenging to devise management and conservation strategies for our precious life support systems, especially forests.

Acknowledgements

We wish to thank all of the people, and especially Paul E. Johns, involved in collecting the electrophoretic data from the SRS herd. This research was supported by contract DE-FC09-96 SR 18546 between the University of Georgia and the U. S. Department of Energy.

Zusammenfassung

Genetische Heterogenität beim Weißwedelhirsch: Für die Wildbewirtschaftung relevante Erkenntnisse aus einer Langzeitstudie

Daten aus einer Langzeitstudie (16 Jahre) an Weißwedelhirschen (*Odocoileus virginianus*) aus dem Savannah River Site (SRS) des U. S.. Department of Energy wurden im Hinblick auf das Vorkommen von räumlicher und zeitlicher genetischer Heterogenität bei dieser Art analysiert. Die Untersuchung erbrachte drei wesentliche Befunde, die auch für die Bewirtschaftung des Weißwedelhirsches von Bedeutung sind: (1) Wie aus der Analyse von Allozymfrequenzen und mtDNA-Haplotypen hervorging, besteht in Populationen des Weißwedelhirsches eine ausgeprägte räumliche genetische Heterogenität, und zwar auf wesentlich geringerem Raum, als man dies bei einer potentiell so mobilen Art erwarten würde. (2) Die genetische Struktur der Weißwedelhirsche am SRS ist zeitlich unterschiedlich und es gibt eine ausgeprägte Heterogenität zwischen demographischen Entitäten wie Alters- und Geschlechterklassen. (3) Die in elektrophoretischen Untersuchungen ermittelte Heterozygotierate ist häufig mit Merkmalen korreliert, die für die ökologischen Beziehungen in Weißwedelhirschbeständen bedeutsam sind. Diese Befunde wurden im Rahmen eines generellen Bewirtschaftungsmodells für *O. virginianus* evaluiert, das auch für andere Wildtierarten anwendbar ist.

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Mamm. biol. **66** (2001) 13–21
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Mammalian Biology
Zeitschrift für Säugetierkunde

Review

Evidence for separate specific status of European (*Capreolus capreolus*) and Siberian (*C. pygargus*) roe deer

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Receipt of Ms. 14. 06. 2000
Acceptance of Ms. 13. 09. 2000

Abstract

Two forms of roe deer, the European (*Capreolus capreolus*) and the Siberian (*Capreolus pygargus*), are widely recognised. Some authors consider these two forms as separate species, while others classify them as merely subspecies or races which are closely related. In this study, we compare the geographic distribution, morphological characteristics, karyotypes, biochemical variability, and potential for hybridisation of European and Siberian roe deer, addressing the question of their phylogenetic status. For most of historical times, the ranges of these two forms have been independent due to physical barriers such as glaciers or flooding. Overlap occurred for a time in the Middle Ages and again more recently, for the last few decades, but even then, the potential hybrid zone was small and hybrids are not thought to have persisted. The Siberian roe deer is substantially larger than its European counterpart in all body measurements, with only the very smallest Siberian individuals and the very largest European deer of approximately equivalent size. Furthermore, the two forms can be reliably distinguished on the basis of cranial shape, due to differential rates of growth of the skull, illustrating the hiatus in morphology between the two forms. All European roe have a karyotype of 2n = 70, while Siberian roe possess between 1 and 14 additional accessory B-chromosomes, increasing clinally from west to east. Changes in karyotype seem to occur at physical boundaries, suggesting the differences are due to partial or total absence of gene flow. On the basis of polymorphism of several enzymes as well as blood and muscle proteins, the genetic distance between the two forms is characteristic of fairly reliable species.
A series of hybridisation experiments have illustrated that, although successful crosses can be achieved, they more often result in stillbirths or birth complications leading to the death of both mother and kid, and reduced or complete infertility among F1 hybrid bucks. It is likely therefore that hybridisation in the wild would be rare or absent, and that hybrids would not persist in the face of immigration of either pure form. We conclude that by all the criteria of classical systematics, the European and Siberian roe deer are separate, good, species, albeit phylogenetically closely related.

Key words: *Capreolus capreolus*, *Capreolus pygargus*, species status, systematics

1616-5047/01/66/01–013 $ 15.00/0.

Introduction

Although roe deer (*Capreolus* sp.) were once classified as belonging to the Cervinae subfamily, it now seems clear that they are in fact part of the Odocoileinae (Groves and Grubb 1987; Grubb 1993). However, taxonomic relationships within this group are far less evident, in particular the status of the various geographical forms of the genus *Capreolus*. Roe deer cover an enormous geographical distribution, ranging from Great Britain and Spain to the Far East and from Kazakhstan and central Asia to northern Scandinavia and Siberia, and a large amount of data has now accumulated which reveals great variation of form over this range. This has lead certain authors to suggest that the genus contains more than one species and perhaps several subspecific forms (Corbet 1978; Danilkin 1986a; Lehmann and Sägesser 1986). Here, we review published data on geographic distribution, morphometry, and genetics of *Capreolus* to conclude whether this genus is monospecific or not.

Geographic range

Fossil records suggest that both the European and Siberian roe deer forms have existed since the Pleistocene period (Danilkin and Hewison 1996). However, it seems that their geographical ranges remained independent due to the glaciation of the Russian plains and the Caspian Sea floods which extended far northward along the Volga. Once these barriers receded, the Siberian roe deer moved west, colonising the plains up to the Dneiper and possibly reaching the northern Caucasus in the Middle Ages (Flerov 1952). Thus, more recently, prior to the twentieth century, the ranges of European and Siberian roe deer overlapped in a small part of their overall distribution, in the northern Caucasus and possibly also in the Dnepropetrovsk, Kirovograd and Orel regions (Fig. 1). Hybridisation may well have occurred here, but due to reproductive barriers (see below) and the predominance of the European form, they almost certainly did not persist. In

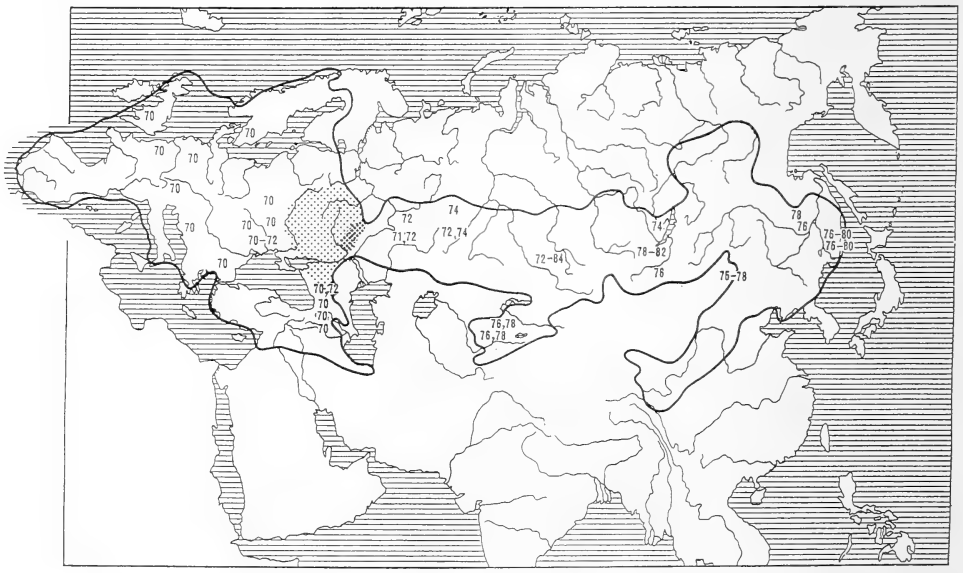

Fig. 1. The distribution of *Capreolus*, showing variation in chromosome number (70–84) across its present geographical range (black line), the extent of historical maximal overlap in range between the European and Siberian forms (⊡) and of present day overlap (▤). The range of the European roe is to the left of this overlap zone and the range of the Siberian roe is to the right. Adapted from Danilkin and Hewison (1996).

modern times, reduction in range and numbers of the Siberian roe due to excessive hunting and the abundance of predators resulted in discontinuities in geographical range and isolation of the European and Siberian populations (Danilkin and Hewison 1996). However, numbers started to recover from the 1930s due to moderation of hunting and a warmer climate and the overall range increased once again. As recently as the 1960s, the advance westward of Siberian roe deer reached the Volga and subsequently the Khoper and Don rivers in the Volgograd region, bringing European and Siberian deer into contact once more during the last couple of decades (Fig. 1).
Thus, the geographic ranges of the European and the Siberian roe deer have been largely independent for much of history, overlapping only in a restricted area during certain periods. The complete isolation of the ranges of these two forms has only very recently been bridged again and the potential hybrid zone remains very small with respect to the total geographic range. Furthermore, there is little evidence that hybrids have persisted in any area, probably due to reproductive isolation between the two forms. Despite the fact that a large number of Siberian deer have been used for introduction programmes within the European roe deer's range, only those introductions that took place where the European form was present in very low numbers or entirely absent have proved successful (Danilkin and Hewison 1996).

Morphology

Despite the fact that there is clearly substantial environmental influence on overall body size and weight of roe deer (e. g. Gaillard et al. 1996; Hewison et al. 1996 a, b), the European form is markedly smaller than the Siberian form in all body dimensions (Fig. 2), including size of antlers (European: length 17–26 cm, span 7–14 cm, Siberian: length >27 cm, span 17–20 cm) and skulls (condylobasal length: European 180–200 mm, Siberian 201–231 mm). Some overlap in size may occur between the very largest individuals of the European form and the very smallest Siberian roe deer, but more generally there is discontinuity in average size between adjacent populations at the range limits between these two forms. This discontinuity is due to differential rates of early growth and development: kids averaged 4 kg weight gain per month for European roe and 6 kg per month for Siberian roe when the two were kept together under identical environmental conditions (Danilkin and Hewison 1996). The difference persisted through to adulthood, when the Siberian roe weighed about 20% more in all seasons.
In addition to simple size variation, European and Siberian roe deer can be distinguished on the basis of cranial shape. Multivariate analyses of 905 skulls from populations over the entire geographical range have identified two well-differentiated morphs, the Siberian and the European (Sokolov et al. 1985 a). Again, this discontinuity appears early in life due to differential growth rates of the skull (Sokolov et al. 1985 b). There are also some indications from this type of analysis that further discrimination within each main group may be possible, particularly for the Siberian morph (northern Siberia and the Far East), perhaps supporting the designation of two or more subgroups (Markov et al. 1985 a; Sokolov et al. 1986 a; see also Hewison 1997). An analogous analysis of antler characteristics was unable to distinguish clearly between European and Siberian forms, presumably because of the pronounced influence of age, condition and environmental factors on these structures which are regrown annually (Danilkin and Hewison 1996).

Genetic and biochemical variability

The karyotypes (chromosomal morphology) of European and Siberian roe deer differ dramatically. All populations of the European form are characterised by an identical karyotype of 2n = 70, while all Si-

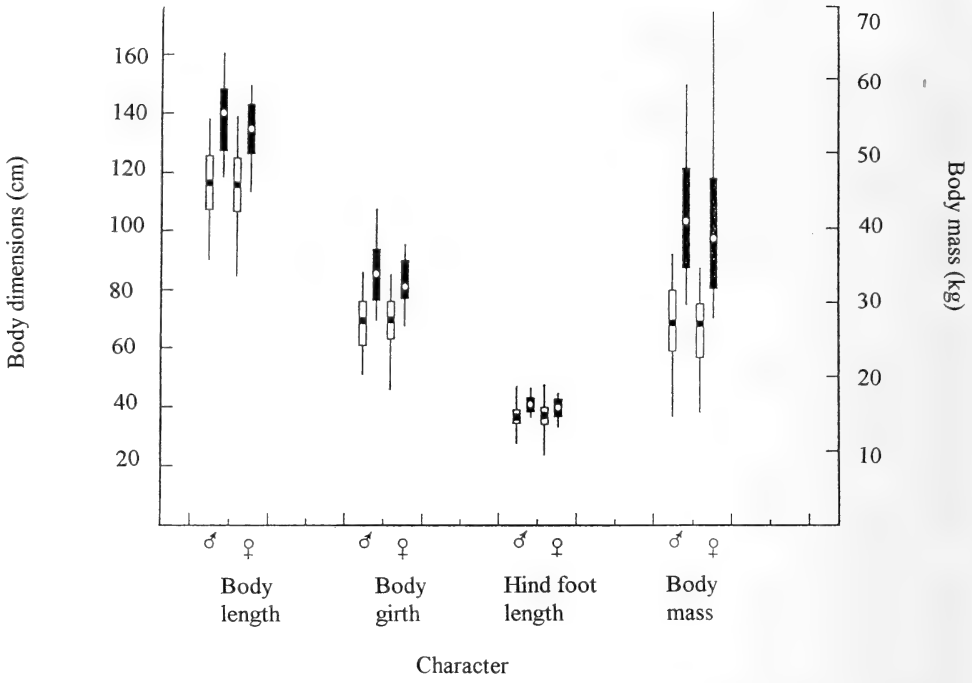

Fig. 2. Variation in total body length, body girth, hind foot length and body mass of European (white bars) and Siberian (black bars) male and female roe deer (adapted from Danilkin and Hewison, 1996). The central dot denotes the average value for each group, the bar gives the limits for population averages and the vertical line shows the range of extreme values of single individuals.

berian populations have karyotypes which contain 1 to 14 additional accessory B-chromosomes, 2n = 70 + (1–14) (Danilkin 1985; Sokolov et al. 1986 b). Furthermore, the Siberian roe deer exhibits mosaicism, particularly in the Far East, where different numbers of B-chromosomes occur within different tissues of the same animal, as well as among individuals of the same population. In addition, all 35 pairs of the main set of chromosomes differ in length between the European and Siberian groups. The number of B-chromosomes present shows clear clinal variation, increasing steadily from west to east (Fig. 1). However, changes in karyotype across the geographic distribution of roe deer are abrupt and seem to occur at physical barriers such as mountain ranges. Hybridisation (see below) leads to inheritance of some B-chromosomes among offspring, but the number inherited is usually less than half the number of the Siberian parent, probably due to unequal segregation during meiosis. At the notional boundary between the two forms in the Ukraine and the northern Caucasus, individuals both with and without B-chromosomes have been identified (Danilkin and Hewison 1996).

At the biochemical level, electrophoresis of certain enzymes has revealed differences in protein polymorphism between European and Siberian roe. Of 14 systems tested, 3 were polymorphic in the European sample, while only two were polymorphic in the Siberian sample and frequency differences between the two forms were found at one particular enzyme locus (Sokolov et al. 1986 c). Isoelectric focusing of blood plasma proteins has identified differences in the pre-albumin zone of the spectrum which are fixed, i. e. all Siberian individuals are different from all European roe. Similarly, differences are also present in the IEF spec-

tra of soluble proteins of the muscle tissue. These different protein fractions probably represent the products of alternative alleles for particular loci. Additionally, immunochemical investigations have indicated that the blood serum of European roe deer contains certain antigens which are characteristic of this group only and may also include two accessory antigens with very different molecular weights (Markov et al. 1985 b).

Hybridisation

A large number of introductions of Siberian deer into areas inhabited by European roe have been carried out with the aim of increasing body weights and improving trophy quality (Danilkin and Hewison 1996). Indeed, those hybrids that are able to survive are heavier and have larger antlers than the pure European form. However, it seems probable that such operations have proved unsuccessful (see above), with even the introduction of a substantial number (several dozen) of Siberian animals resulting in gradual but complete loss of the Siberian form.

Hybrid populations have not developed in the wild due to rather high level of reproductive isolation between the European and Siberian groups, illustrated by a series of experiments on captive deer. In the first experiments (Stubbe and Bruchholz 1979, 1980), two Siberian bucks were mated with a group of European does a total of 32 times. Of these matings, 13 did not result in pregnancy while 19 births were recorded. Caesarean delivery was necessary in 9 cases and another 3 required manual assistance due to the large size of the kid. The level of reproductive isolation between the Siberian and the European roe deer is clearly demonstrated by the fact that 10 subsequent matings between two F1 hybrid bucks and a group of hybrid does did not produce a single offspring. Indeed, it seems that many hybrid bucks are sterile, however, back-crosses between hybrid does and pure bucks of either form did produce viable offspring. Similarly, Sokolov and Gromov (1985) found that European roe does were unable to bare hybrid offspring, often dying in the process of giving birth, while all attempts to cross European bucks with Siberian does were unsuccessful. In yet another set of experiments, Danilkin (1986 b) did succeed in crossing European bucks with Siberian does, however, this resulted in a high proportion of stillbirths. Overall, crosses between the two roe deer forms seems to be possible, but with a much lower level of success than that observed from normal reproduction, with about 20% resulting in the birth of live offspring without the need of some form of assistance (Tab. 1).

Table 1. Some outcomes of experimental hybridization of Siberian and European roe deer (adapted from Danilkin and Hewison 1996)

Cross[1]		Result	
Female × Male	n	Successful Mating[2]	Normal Delivery[3]
Sib. × Eur.	19	7	4
Eur. × Sib.	38	22	8
F1 × Eur.	4	3	2
F1 × Sib.	3	3	3
Eur. × F1	11	1	1
Sib. × F1	2	1	1
F1 × F1	10	0	–
BC1Sib. × Sib.	2	2	1
BC1Eur. × Eur.	2	2	–

[1]Designations for crosses are: Sib. – Siberian roe; Eur. – European roe; F1 – first generation hybrid; BC1Sib. – progeny of F1 doe × Siberian buck cross; BC1Eur. – progeny of F1 doe × European buck cross; [2]successful mating indicates embryos were produced; [3]normal delivery indicates unassisted birth of live kids

Discussion

Species are generally distinguished according to the independence of their geographical distribution, discontinuity in character variation and reproductive isolation. We have highlighted clearly here that the Siberian and the European roe deer have occupied geographically independent ranges during the vast majority of historical times.

The ranges of these two forms have come to overlap again since the 1970s, but this potential hybrid zone is very small with respect to the overall geographic distribution and is unlikely to have had substantial impact due to its recent occurrence. Introductions of the Siberian roe to sites within the range of the European form have generally proved unsuccessful and are of local importance only.

There is discontinuity in a wide variety of morphological or physiological characters between the European and Siberian forms, notably in body size, craniometry (Sokolov et al. 1985 a), including non-metric characteristics (Zima 1989), and basal metabolic rates (Grayevskaya et al. 1980), even between geographically adjacent populations. This discontinuity is also found at the tissue level as cytogenetic, immunochemical and biochemical differences (Sokolov et al. 1986 b, 1986 c) and may include a certain degree of histoincompatibility. Combining the results of studies of biochemical variation suggests that the genetic distance between the European and the Siberian groups is characteristic of fairly reliable species and indicates a rather high degree of reproductive isolation (see Hartl et al. 1998 for comparison of within species gene flow for European roe deer).

The roe deer phenotype seems to vary according to the number of B-chromosomes present, indicating a pivotal role for these accessory structures in roe deer taxonomy and providing a defining character for species designation. Indeed, patterns of B-chromosome distribution may indicate that roe deer originated in central Asia, perhaps in the Altai mountains, and therefore that the Siberian form is the more ancient. It seems likely that the modern European karyotype may have been greatly influenced by the glaciation of the Russian plains which curtailed gene flow, leading to accumulation of genetic differences between the European and Siberian forms and eventually to allopatric speciation and reproductive isolation, although the possibility that this simply represents clinal variation without speciation should be considered.

When crosses produce sterile offspring subgenus status is generally accorded, while when offspring are fertile but have a reduced probability of survival and/or reproduction parental forms are considered good species. Hybrids of several other cerivd species have been reported (Wishart 1980; Bartos et al. 1981) and these are often fertile, forming hybrid populations in the wild (Harrington 1985). However, the data summarised above clearly show that European and Siberian roe deer crosses are associated with a high proportion of stillbirths, the frequent death of both mother and young due to the inability of European roe does to give birth to large hybrid kids and a high level of sterility among hybrid bucks. Thus, in a potential hybrid zone in the wild, we might expect a low rate of successful mixed-pair reproduction and generally low productivity of the hybrid population.

Thus, there is overwhelming evidence for all the criteria of classical systematics that the European and the Siberian roe deer are two distinct species, albeit very closely related. The ecological similarities between the European and Siberian forms in feeding (differences in diet composition are essentially due to contrasting plant availabilities in Asia and Europe), behaviour (communication, sexual and maternal behaviour, ontogeny), social and spatial organisation (group size, family group structure, male territoriality) and dynamics underlines their extremely close phylogenetic relationship. Siberian roe deer are more adapted to living under extreme climatic conditions, particularly deep snow and prolonged periods of low temperatures (Danilkin and Hewison 1996). This may be a result, in part, of physiological differences in energy metabolism, including the presence and activity of regulating hormones such as the catecholamines and enzymes involved in metabolic functions such as glucose-6-phosphatase (Grayevskaya et al. 1980). The further division of this taxonomic group into the northern Siberian form (*C. p. pygargus*) and the southern Tien Shan form (*C. p. tianschanicus*) representing either separate species or subspecies is far less researched and can be

considered rather speculative in view of the current state of knowledge (Danilkin and Hewison 1996). Further research could usefully concentrate on the relationships between European and Siberian roe deer in the zone of overlap (e. g. extent and consequences of hybridisation) in order to advance our understanding of their distinctiveness.

Zusammenfassung

Beweise für den Artstatus von Europäischem (*Capreolus capreolus*) und Sibirischem (*C. pygargus*) Rehwild

Beim Rehwild wird im allgemeinen die Existenz zweier verschiedener Formen, des Europäischen (*Capreolus capreolus*) und des Sibirischen (*Capreolus pygargus*) Rehs angenommen. Einige Autoren betrachten diese beiden Formen als eigenständige Arten, andere betrachten sie lediglich als nahe verwandte Unterarten oder Rassen. Im Hinblick auf eine Überprüfung des Artstatus werden in der vorliegenden Arbeit Ergebnisse über geographische Verbreitung, morphologische Merkmale, Karyotypen, biochemisch-generische Variabilität und die Fähigkeit zur Bildung von Hybriden zwischen dem Europäischen und dem Sibirischen Reh zusammenfassend gelistet und verglichen.
Über den Großteil ihrer Geschichte hinweg war das jeweilige Verbreitungsgebeit der beiden Formen durch Barrieren wie etwa Gletscher oder überflutete Landstriche separiert. Im Mittelalter und in den letzten Jahrzehnten gab es Überlappungen, aber auch dann war eine potentielle Hybridzone klein und es wird nicht angenommen, daß etwaige Hybriden längeren Bestand gehabt haben. Das Sibirische Reh ist in allen Körpermaßen deutlich größer als das Europäische Reh, wobei lediglich die kleinsten Sibirischen Rehe den größten Europäischen Rehen annähernd gleichkommen. Außerdem sind die beiden Formen als Resultat unterschiedlicher Wachstumsraten und aufgrund ihrer Schädelform verläßlich zu unterscheiden. Alle Europäischen Rehe haben einen Karyotyp von 2n = 70, während die Sibirischen Rehe zwischen 1 und 14 akzessorische B-Chromosomen besitzen, in Anzahl klinal von West nach Ost ansteigend. Der Wechsel im Karyotyp scheint an geomorphologischen Barrieren aufzutreten, was auf ein partielles oder totales Fehlen von Genfluß zurückzuführen sein dürfte. Auf der Grundlage von Enzympolymorphismen und von genetischer Variation in Blut- und Muskeleiweißen liegt der genetische Abstand in einem Bereich, wie er üblicherweise zwischen validen Arten gefunden wird. Eine Serie von Kreuzungsversuchen zeigte, daß trotz des Verkommens erfolgreicher Bastardierung, meist Totgeburten auftreten oder Komplikationen bei der Geburt zum Tod von Mutter und Kind führen. Außerdem gab es eine reduzierte oder vollständige Unfruchtbarkeit bei F1-Böcken. Das Vorkommen von Hybriden in freier Wildbahn dürfte daher selten oder überhaupt nicht möglich sein, und ein Überdauern von Hybriden wäre angesichts der Überzahl von Individuen der jeweiligen reinen Formen auch nicht wahrscheinlich. Wir schlußfolgern, daß nach allen Kriterien der klassischen Systematik das Europäische und das Sibirische Reh valide, wenngleich stammesgeschichtlich nahe verwandte Arten sind.

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Mamm. biol. **66** (2001) 22–34
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Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

A report on the community of shrews (Mammalia: Soricidae) occurring in the Minkébé Forest, northeastern Gabon

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Receipt of Ms. 07. 02. 2000
Acceptance of Ms. 19. 05. 2000

Abstract

This report presents the results of a study of the shrew community in the newly created Minkébé Protected Area in northeastern Gabon. The previously unstudied park forms part of the large Guineo-Congolian lowland forest block. The principal technique used to capture animals consisted of pitfall traps with drift fences. Three habitat types (marsh, heterogeneous forest and homogeneous forest) were surveyed. Four to seven species were recorded in each habitat, resulting in a total of eleven species for the study area. Several rare and little-known species occur in the park, such as *Crocidura crenata*, *C. goliath*, *C. grassei*, *Suncus remyi*, and *Sylvisorex ollula*. *Crocidura maurisca* is recorded for the first time from Gabon, far outside its previously known range in eastern Africa.

Key words: Soricidae, community, rainforest, Gabon, Africa

Introduction

Over the past few decades knowledge on the small mammals occurring in the vast and forested Guineo-Congolian region (sensu White 1983) of west-central Africa has increased substantially (Emmons 1975; Emmons et al. 1983; Dubost 1968; Duplantier 1989). This area has been cited as having one of the most diverse biotas on the continent (Sayer et al. 1992). Amongst the largest remaining contiguous areas of forest in the Old World tropics is the zone between southern Cameroon, eastern Gabon, and western Congo-Brazzaville, and contains about 200 000 km^2 of largely intact forest (Brosset 1990). Several reserves have already been designated across this region, including the Dja Faunal Reserve in Cameroon, the Dzanga-Sangha Faunal Reserve in southern Central African Republic, the Odzala National Park in Congo-Brazzaville and the recently named Minkébé Protected Area (6 000 km^2) in northeastern Gabon. In order to document the largely unknown fauna of the Minkebe forest, an area of about 32 000 km^2, and subsequently to put the site into a biogeographic context, a biological inventory was organized in February 1998 in the northwestern portion of this protected area. WWF in collaboration with the Direction de la Faune et de la Chasse, are executing a conservation project of the Minkébé region. Here we report on the

1616-5047/01/66/01-022 $ 15.00/0.

findings of the shrews (Family Soricidae) occurring at this survey site.

Information on the Soricidae of the Guineo-Congolian lowland forest zone, particularly from northeastern Gabon, is not extensive. Over the course of several decades, studies of small mammals, including those on shrews, were conducted in the Ivindo River Basin associated with the Institut de Recherches en Ecologie Tropicale research station at M'Passa (= Makokou, Brosset 1988). This work largely involved studies on the population ecology of numerous species of mammals, but specimens were collected to help identify characters to define species limits. Several species new to science were subsequently described from the region (Brosset et al. 1965 a, 1965 b). The Ivindo forms the drainage of eastern Gabon and is a major tributary of the Ogooué River. This is a different watershed from that of the Ntem River of northeastern Gabon, which drains the western portion of the Minkébé region. More recently field projects on soricid faunas have been conducted in other adjacent regions of this large forest block: Dja Faunal Reserve in Cameroon (Colyn et al. 1996), the Monte Alen National Park in Equatorial Guinea (Lasso et al. 1996), the Dzanga-Sangha Faunal Reserve in Central African Republic (Ray and Hutterer 1995), and the Korup National Park in Cameroon, the westernmost extension of this forest block (Hutterer and Schlitter 1996). Information on the shrews of these sites provides a biogeographic context with regards to the Minkébé fauna.

Material and methods

The Minkébé forest is composed of a large block of Guineo-Congolian lowland forest that drains a vast area (Fig. 1). The northern area of the forest is part of the Ntem River watershed and the balance enters into the Ivindo River. The first action to classify a protected zone in this area was in September 1997 when the Gabonese Government set aside 600 000 ha as the Réserve de Minkébé (De Wachter 1997). In December 1999 this reserve was gazetted as a protected area.

Our study site was near the northwestern boundary of the Minkébé Protected Area in an area of mixed heterogeneous forest and Maranthaceae forest interdigitated between areas of marshland. This region is part of the Aya River drainage, which forms one of the main tributaries of the Ntem River. Our camp was in place between 5 and 17 February 1998 and was located in the Province de Woleu-N'Tem, 28 km ESE Minvoul, 2° 5.2′ N, 12° 22.5′ E, 600 m a. s. l. Access to the forest was along a recent prospection trail cut by a survey group from the International Tropical Timber Organization (ITTO). We commenced our march into the forest from the Baka village of Doumasi, along the Ntem and to the east of Minvoul. Our study site was centered on this transect trail, but we also used the numerous elephant trails throughout the zone for access to other areas.

Three distinct habitat types were found adjacent to the camp: marshlands dominated by *Raphia*, heterogeneous forests, and homogeneous forest composed largely of *Gilbertiodendron*. Marsh areas, which experience extreme seasonal flooding, were interdigitated between the two forest types. Some of these marshes cover areas in excess of 30–50 ha. Our trapping devices were placed within a survey area less than 3 km walking distance from the camp.

The principal technique used to capture soricid shrews consisted of pitfall traps with drift fences. A separate pitfall line was installed in each of the habitat types surveyed (marsh, heterogeneous forest, and homogeneous forest), in order to assess possible variation in habitat utilization by these animals. Each line was 100 m long and consisted of 11 buckets (275 mm deep, 285 mm top internal diameter, 220 mm bottom internal diameter), 10 m apart, in operation for ten complete days. Small holes were cut in the bottom of the buckets to allow water drainage. Buckets were sunk to a depth where the rim was even with ground level. A barrier (drift fence) made from plastic sheeting (0.5 m high and 100 m long) was stapled in a vertical position to thin wooden stakes. The drift fence bisected all of the buckets in the line (Voss and Emmons 1996). A flange of about 50 mm at the bottom of the standing plastic fence was covered with soil and leaf litter to block animals from moving under the barrier. A bucket-day is defined as one of these devices in use for a 24-hour period (dawn to dawn).

The second technique used to capture animals at the site consisted of three different types of small mammal traps. Fifty traps composed of 33 Sherman traps ($9 \times 3.5 \times 3$ inch), 13 National traps

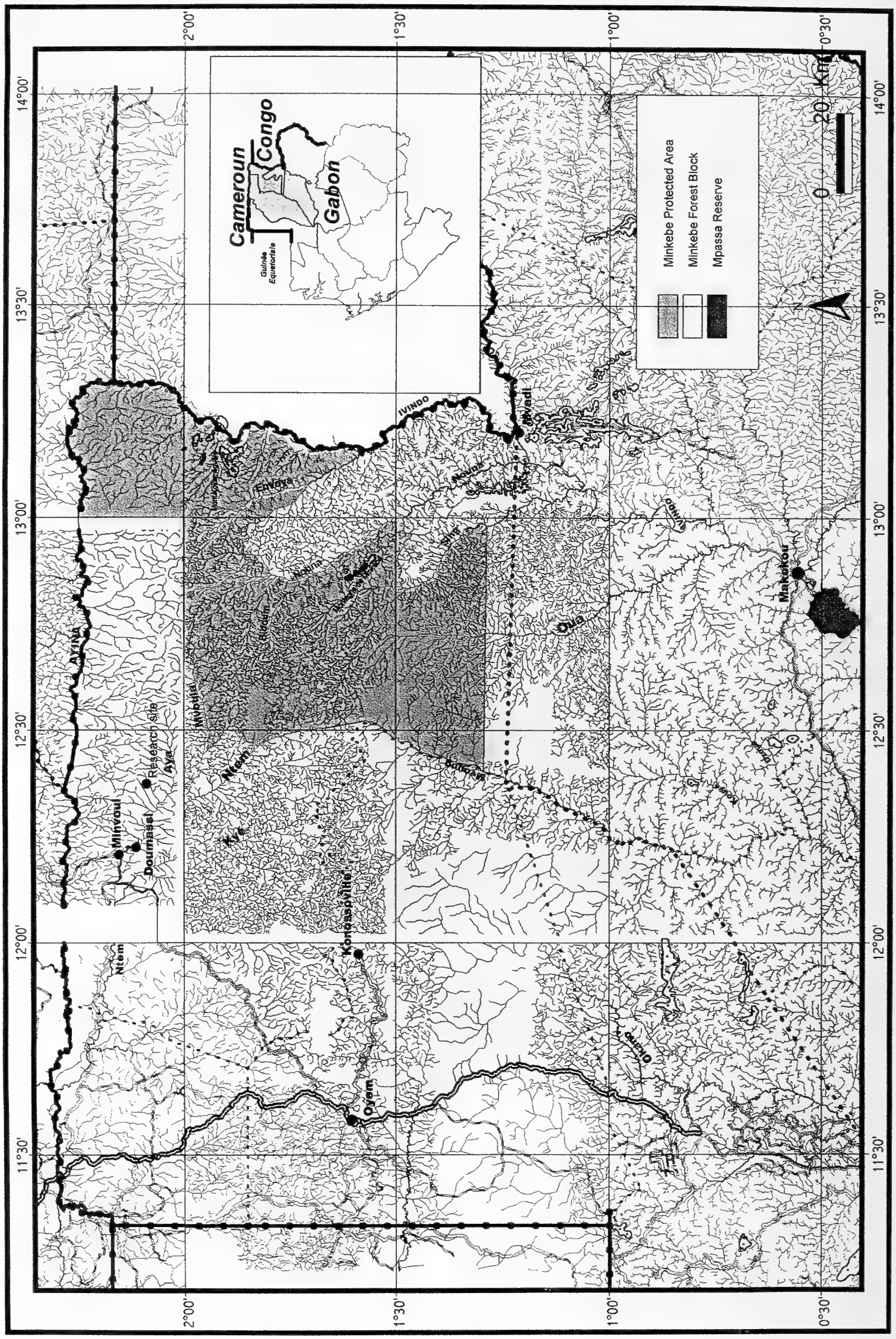

Fig. 1. Map of northeastern Gabon showing the Minkébé Forest Block and the research site; the Minkébé Protected Area is shaded grey.

(16 × 5 × 5 inch), and 4 small snap traps, were placed in each of the three habitat types. These lines were run for 10 nights. Traps were baited daily, generally between 15.00 and 17.00 hours, with oil palm nuts, manioc, finely ground peanut butter or dried fish. On any given day the bait used in all of the trap lines was the same. A "trap-night" is defined as one of these devices in use for a 24-hour period (dawn to dawn). Traps and pitfalls were visited at least twice per day, once at dawn and again in the late afternoon, and captured animals were removed.

Captured animals were prepared as standard museum skins with associated skulls and skeletons, as fluid preserved carcasses, or as full skeletons. Voucher specimens are deposited in the Field Museum of Natural History (FMNH), Chicago, and a representative series will be returned to Gabon. The fieldwork was conducted by SMG and PRN, and the determinations of the collected material were made by RH.

Results

Captures

In total 29 individual shrews of 11 species were captured in the Minkébé study site, covering a body mass range from 1.8 g (*Suncus remyi*) to 76 g (*Crocidura goliath*, Tab. 1). The majority of these individuals were obtained in pitfall traps. Standard small mammal traps yielded only four shrews, and in all cases, except for one,

Table 1. Body mass (g) and external measurements (mm) of eleven species of shrews collected in the Minkébé forest

+ Masses of less than 10 g are accurate ± 0.1 g, between 10 and 50 g ± 0.5 g, and greater than 50 g ± 1.0 g.

* Hind foot measurements do not include the claws.

Species	Museum Number	Sex	Mass+	Total length	Tail length	Hindfoot length*	Ear length
Crocidura batesi	162141	M	15.5	160	61	16	11
Crocidura crenata	162152	F	5.9	165	87	15	11
	162153	M	7.5	165	88	16	11
	162154	M	6.8	166	91	15	10
Crocidura dolichura	162198	M	6.1	152	80	13	10
Crocidura goliath	162144	F	58.0	282	110	25	17
	162145	M	76.0	290	115	27	15
	162184	F	69.0	272	107	26	17
	162185	M	51.0	292	132	26	17
	162186	F	52.0	255	100	23	17
Crocidura grassei	162140	M	14.0	175	85	17	13
	162193	M	11.5	173	83	18	13
Crocidura maurisca	162196	?	7.2	136	57	15	10
Crocidura olivieri	162137	M	23.5	207	85	19	13
	162187	M	24.5	191	75	16	11
	162188	M	33.0	213	95	18	13
	162192	F	29.5	195	80	17	14
Paracrocidura schoutedeni	162142	F	8.1	115	38	14	9
	162146	F	6.7	115	38	11	8
	162194	M	11.5	125	42	12	10
	162195	F	9.5	114	37	12	9
Suncus remyi	162147	F	1.8	70	18	7	5
Sylvisorex johnstoni	162149	F	3.0	84	33	8	8
	162197	M	3.6	92	32	9	9
Sylvisorex ollula	162138	M	17.5	172	65	16	17
	162139	M	22.0	181	71	17	15
	162189	M	17.5	168	77	15	12
	162190	M	18.0	158	59	14	13
	162191	M	16.0	169	63	14	12

Table 2. Species and numbers of Soricidae captured in the Minkébé forest based on habitat type. All animals were captured in pitfall traps or obtained in live traps (second number after /)

	Marsh	Heterogeneous forest	Homogeneous forest
Cumulative pitfall bucket days	110	110	110
Crocidura batesi	0	1	0
Crocidura crenata	1	0	2
Crocidura dolichura	1	0	0
Crocidura goliath	0/1	3/1	0
Crocidura grassei	1	0	1
Crocidura maurisca	0	0	1
Crocidura olivieri	1	0	2/1
Paracrocidura schoutedeni	3	1	0
Suncus remyi	0	1	1
Sylvisorex johnstoni	0	0	2
Sylvisorex ollula	4	0	0/1
Total number of individuals in pitfalls/traps	11	6	11
Total number of species	7	4	7

these were the larger bodied species (*C. goliath* and *C. olivieri*).

The trap effort with both pitfalls and standard mammal traps was equal in the three habitats sampled (marsh, heterogeneous forest, and homogeneous forest). The number of individuals (11) and species (7) captured in the marsh and homogeneous forest were identical (Tab. 2). Fewer individuals and species were obtained in the heterogeneous forest than in the other two habitat types. For species with more than three captures there was no absolute preference for one of the three habitat types. Of the four specimens of *Paracrocidura schoutedeni* captured, three were in the marsh habitat and a single specimen was taken in the heterogeneous forests. Four individuals of *Sylvisorex ollula* were obtained in pitfall devices placed in the marsh habitat and none in the other two habitat types; however, one individual of this species was captured in a Sherman trap set in the homogeneous forest.

Annotated accounts for selected species

Crocidura batesi Dollman, 1915

This species was described from the "Como River" region of Gabon. It has subsequently been recorded in the Belinga Hills, where it was relatively rare in forested habitat (BROSSET 1988); in Equatorial Guinea (LASSO et al. 1996); and in southern Cameroon (SCHLITTER et al. 1999). The species was also listed as part of the fauna of the Dzanga-Sangha region (RAY and HUTTERER 1995). However, a subsequent study of additional specimens from this region has revealed morphological differences which suggest that this population belongs to a yet undetermined species of *Crocidura*.

Our single specimen of *C. batesi* from Minkébé was taken in heterogeneous forest habitat.

Crocidura crenata Brosset, Dubost and Heim de Balsac, 1965 a

The holotype of this animal was obtained in the Belinga area of eastern Gabon and it is also known from near Makokou (BROSSET et al. 1965 a). Subsequently it has been found in the Korup National Park and Dja Faunal Reserve of Cameroon, and regions of the Democratic Republic of Congo (COLYN et al. 1996; HUTTERER and SCHLITTER 1996). The records of *C. crenata* in the Minkébé forest helps to clarify aspects of its geographical distribution in that they provide clear evidence that this species occurs in intermediate areas across this large zone of west-central Africa. This species was not recorded in a recent survey of soricids in the

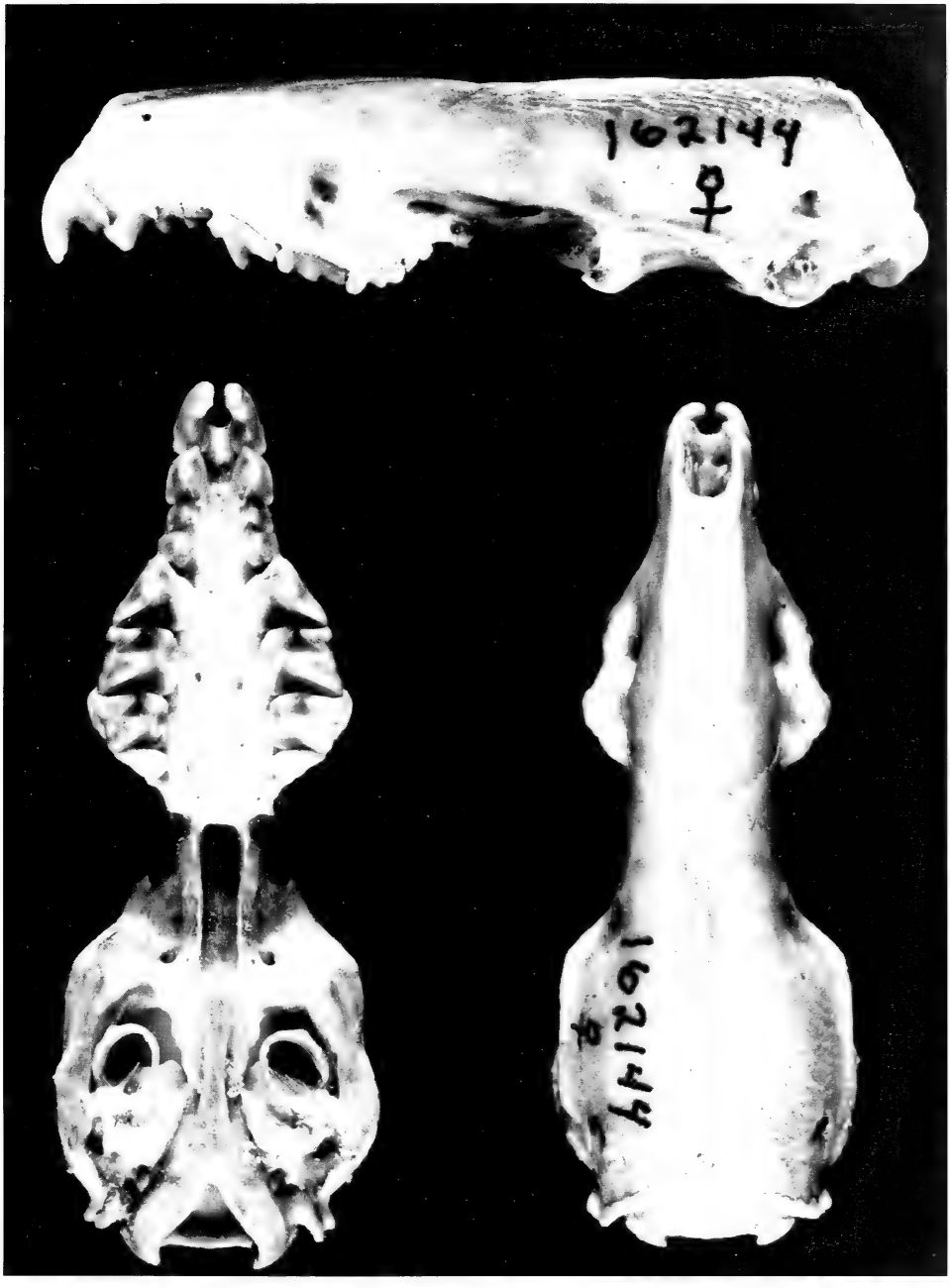

Fig. 2. *Crocidura goliath* (FMNH 162144), female from Minkébé, skull in dorsal, ventral, and lateral view. Condylo-incisive length 38.4 mm.

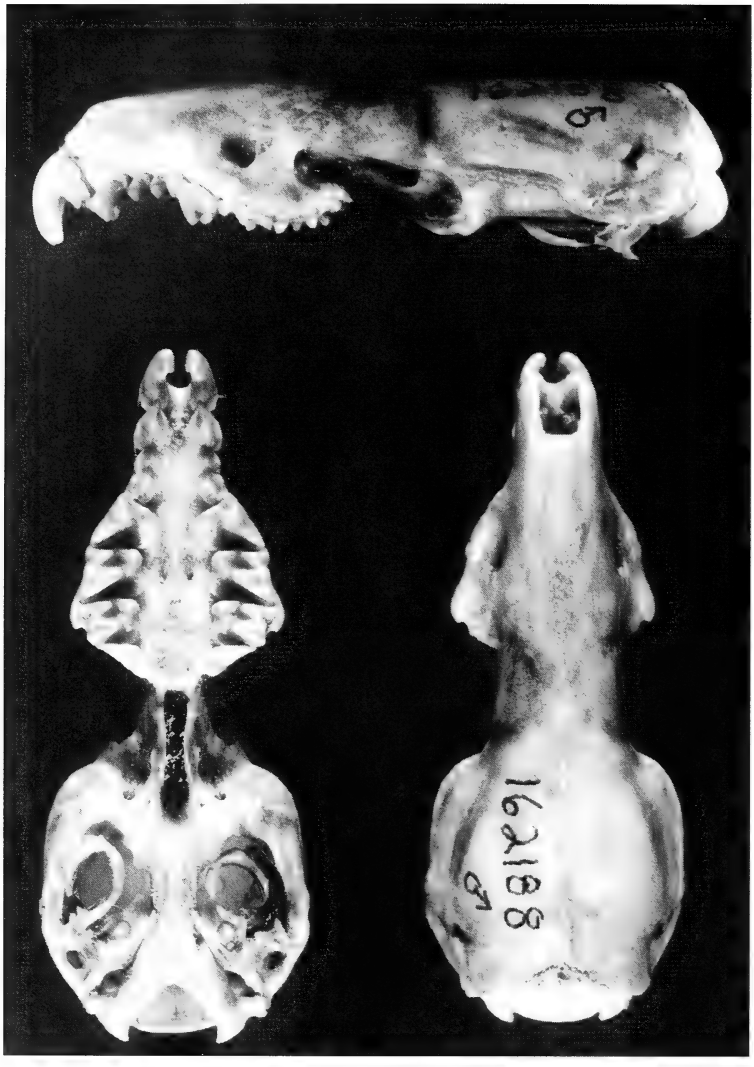

Fig. 3. *Crocidura olivieri* (FMNH 162188), male, skull in dorsal, ventral, and lateral view. Condylo-incisive length 29.6 mm. Compare with *C. goliath*, a species that occurs syntopically in the Minkébé forest.

Monte Alen National Park, Equatorial Guinea (LASSO et al. 1996).

Crocidura goliath (Thomas, 1906)

Several individuals of this giant shrew were taken in both pitfall and Sherman traps in the Minkébé National Park. This included capture sites in both heterogeneous forest and marsh habitat. Of particular interest is that this is the first known syntopic occurrence of this species in primary forest habitat with *C. olivieri*. Specimens of both species were captured in marshland in Minkébé (Tab. 2), thus corroborating the distinct species status of these two giant shrews.

For a considerable period, *C. goliath* had been considered as a large forest variant of *C. olivieri*, the commom African giant shrew (HEIM DE BALSAC, 1970), partly due to its rarity in museum collections. Recent field-

work has shown that both forms are broadly sympatric, with *C. goliath* being restricted to the high forest regions of the Congo Basin (Hutterer 1995; Lasso et al. 1996). The Minkébé survey now offers evidence that both species may live even in the same micro-habitat. The external morphology (Tab. 1) and skulls (Figs. 2, 3) of both species are markedly different in these syntopic populations. Obvious differences exist in the size and robustness of the skull and dentition. Externally, *C. goliath* is distinguished from *C. olivieri* by its long and coarse fur, and a long tail with a low pilosity.

A female *C. goliath* was captured with a single suckling neonate in a Sherman trap placed on the ground next to a downed rotten log.

Crocidura grassei Brosset, Dubost and Heim de Balsac, 1965 b

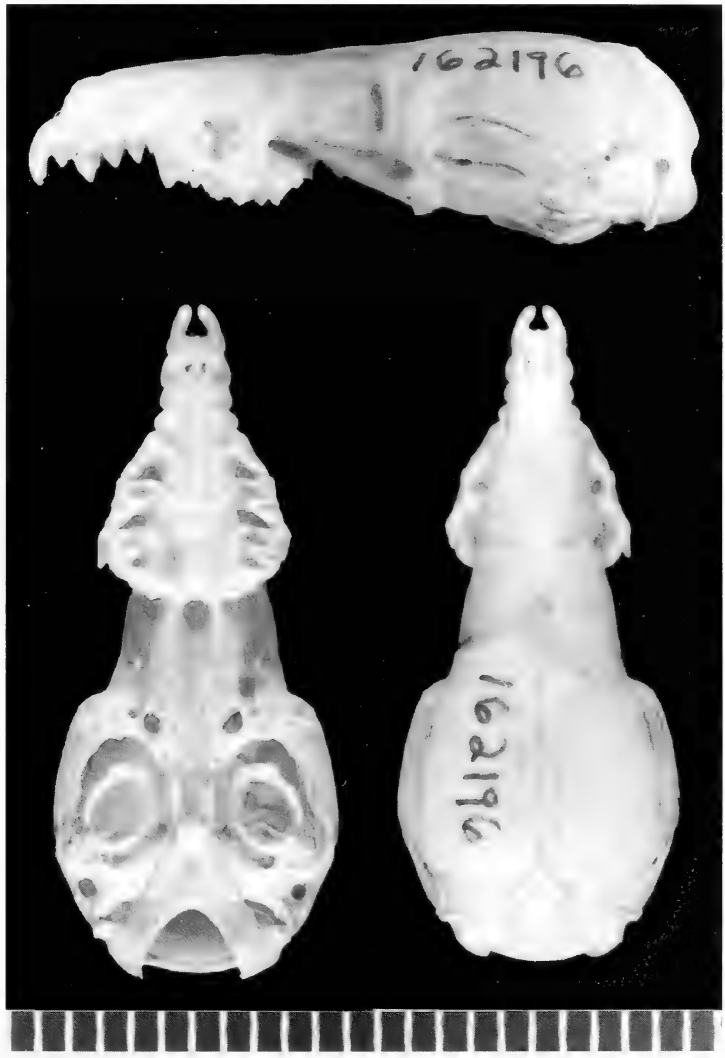

Fig. 4. *Crocidura maurisca* (FMNH 162196) from Minkébé, skull in dorsal, ventral, and lateral view. Condylo-incisive length 21.1 mm.

The holotype of this species was collected at Belinga in eastern Gabon. Subsequently it has been identified from collections made in the Yaoundé region (Cameroon), Boukoko (Central African Republic), Mt. Alen National Park (Equatorial Guinea), and now from the Minkébé region (HUTTERER 1995; LASSO et al. 1996). This is a rare shrew, of which less than ten specimens are known.

Crocidura maurisca Thomas, 1904

The type of this rare shrew was collected at Entebbe, Uganda, and this species has only been documented from Uganda and Kenya (HUTTERER 1995). The single female (FMNH 162196) from Minkébé is a surprisingly new record for Gabon, and extends the range of the species far to the west. This species is characterised by a tail with low pilosity, and by a skull with a slender muzzle and a weak dentition, all of which are expressed in the Gabonese specimen. The skull (Fig. 4) has been compared with typical specimens from East Africa and was found to be very similar, both in measurements and size. Unless further studies, such as biochemical analyses, show otherwise, we consider the Gabonese specimen to represent *C. maurisca*.

HEIM DE BALSAC (1968 a) reported a specimen from Yaoundé, southern Cameroon, as belonging to "*Crocidura* aff. *maurisca* Th.", but later (HEIM DE BALSAC 1968 b; DIETERLEN and HEIM DE BALSAC 1979) changed this identification to "*C. littoralis* subsp.". The specimen, which is not currently available for study, was then discussed by HUTTERER (1982) in the context of the description of a new species from Lake Manenguba, Cameroon Mts. The holotype of *C. manengubae* Hutterer, 1982 was compared with the Gabonese specimen (FMNH 162196) and found to be generally similar but also different in various cranial characters. The correct allocation of the specimen from Yaoundé, geographically half-way between Lake Manenguba and Minkébé National Park, still remains to be solved.

Suncus remyi Brosset, Dubost and Heim de Balsac, 1965 b

Little new information or material of this extremely diminutive species has been available since its description based on material from the Makokou region. It has subsequently been recorded from the Odzala Reserve, Republic of Congo (COLYN et al. 1996) and now from the Minkébé. Interestingly, it was not identified from material obtained in the Dja Faunal Reserve of Cameroon after nearly 7 000 pitfall bucket nights (COLYN et al. 1996).

The single female from the Minkébé collection was obtained in heterogeneous forest. This individual had three enlarged inguinal mammae, an apparently perforated vagina, and no embryos in the uterus. With a body mass of 1.8 g, *Suncus remyi* is equal in size to the European *Suncus etruscus* (Savi, 1822), which is often regarded as the "smallest mammal of the world".

Discussion

The survey of the soricid fauna near the Minkébé Protected Area was rapid and by no means complete. Firstly, only a small fraction of this huge forest block was visited and a limited number of habitats were inventoried. It is almost certain that with more extensive sampling, particularly within other elevational zones and habitats, the number of shrew species known from the park will increase. Secondly, an examination of the number of previously unrecorded species of shrews recorded during each successive night of pitfall trapping indicates that 10 nights of field work were not sufficient to reach an asymptote (Fig. 5).

The shrew species richness of 11 species documented during a rapid inventory of a single site in the Minkébé forest during 10 days is comparable to that obtained in a wide variety of habitats over several decades in the nearby Makokou forest. The main difference in the species lists from these sites is that *Crocidura maurisca* was not obtained at Makokou. *Crocidura goliath*, which was relatively common at Minkébé is rare at Makokou (reported under the name *C. odorata* by BROSSET 1988), and

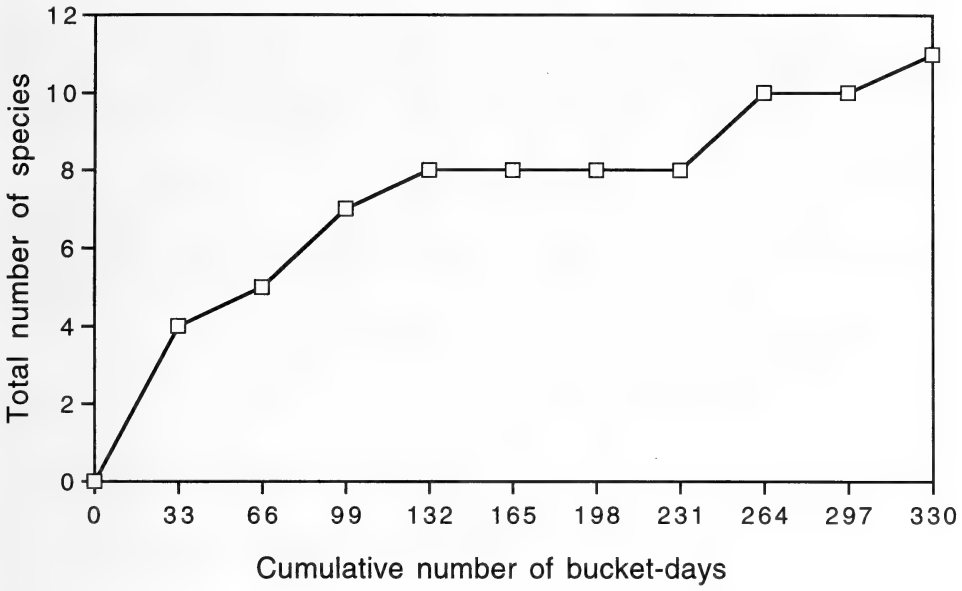

Fig. 5. Species accumulations curve for the shrews over the entire survey period.

C. poensis, the most frequently captured forest shrew at Makokou was not obtained at Minkébé. The latter difference may not be real but merely a result of unresolved taxonomy, as the so-called "*C. poensis* group" is in urgent need of revision. A solution of this problem will require a re-investigation of Brosset's material from Makokou in the context of such a revision. Further our results from the Minkébé forest are close to those obtained at Dja where 12 species of shrews were captured after nearly 7 000 bucket-days (Tab. 3; Colyn et al. 1996). In the case of Makokou, the exact configuration of the "pièges-pots", the type of trap that researchers there used to capture shrews, and most importantly their depth was not specified (Brosset 1988). We strongly suspect they were distinctly smaller than the type employed in our Minkébé study. Further, the dimensions of the pitfalls used in Colyn's et al. (1996) study at Dja were not noted, but they were smaller than those in our study (P. R. Ngnegueu participated in the Dja study). Thus, what seems to be apparent from these comparisons is that larger pitfall buckets are more effective for capturing and retaining a wider variety of shrews. We propose that the bucket size of pitfall devices is an important element in the capture rate of African soricids. A parallel case occurs with the Malagasy tenrecs – large buckets (approximately 15 l) are decidedly more efficient in yielding high capture rates of a greater variety of tenrecs than small buckets (Goodman and Rakotondravony 2000).

Recently an analysis was conducted on the contents of carnivore scats collected in the Central African Republic reserves of Dzanga-Sangha and Dzanga-Ndoki (Ray and Hutterer 1995). These sites are in an area of forest that is part of the large Guineo-Congolian block encompassing the Minkébé and Dja forests. The scats were collected from a wide variety of habitats over the course of two years from an area of 35 km^2. Sixteen species of shrews, including one new to science, were identified from these scats. This is one of the highest diversity of soricids recorded anywhere in the world. We are unaware of any systematic work with pitfall devices at these Central African Republic sites.

It has been previously noted that trap capture rate with pitfall devices for lipotyphlans is generally higher after heavy rain (GOODMAN et al. 1996). The inventory of the Minkébé forest was conducted during the dry season, and on two of the 12 days we were at the site rain fell. During the day of 13 February, a shower dropped 38 mm of rain, and there was no increase in pitfall trap success that same night.

A comparison of six sites that have been surveyed for shrews in the Guineo-Congolian forest block indicates that the fauna of Minkébé and the Makokou/Belinga regions are more similar to one another than either is to any other forest block in this region (Tab. 3). The shrew fauna of Equatorial Guinea is largely a subset of that found at the two Gabonese sites. Further, although the fauna of the Dja is slightly richer than Minkébé there is a large percentage of species shared in common. In contrast, the shrew fauna of the Dzanga-Sangha reserve in Central African Republic is the most diverse and unique of the sites sampled in the region.

Table 3. Geographic distribution (+ recorded, – not recorded) of soricids at several sites in west-central African forests. Taxonomic treatment of species follows HUTTERER (1995).

Site:	Minkébé	Makokou and Bélinga	Equatorial Guinea	Dzanga-Sangha	Dja	Korup
Source of Information:	1	2, 3	4	3	5	6
Species:						
Crocidura sp. indet.	–	–	–	–	+	–
Crocidura attila	–	–	–	–	+	–
Crocidura batesi	+	+	+	+[a]	–	–
Crocidura crenata	+	+	–	–	+	+
Crocidura denti	–	–	–	+	+	–
Crocidura dolichura	+	+	+	+	+	+
Crocidura hildegardeae	–	–	–	+	–	–
Crocidura goliath	+	+	+	+	+	–
Crocidura grandiceps	–	–	–	–	–	+
Crocidura grassei	+	+	+	–	+	–
Crocidura lamottei	–	–	–	–	–	+
Crocidura littoralis	–	–	–	+	–	–
Crocidura ludia	–	–	–	+	–	–
Crocidura maurisca	+	–	–	–	–	–
Crocidura mutesae	–	–	–	+[b]	+[b]	–
Crocidura nigrofusca	–	–	–	+[c]	–	–
Crocidura olivieri	+	+	+	+	–	–
Crocidura poensis	–	+	–	–	+	+
Paracrocidura schoutedeni	+	+	+	+	+	+
Suncus remyi	+	+	–	+	–	–
Sylvisorex johnstoni	+	+	+	+	+	+
Sylvistorex konganensis	–	–	–	+	–	–
Sylvisorex ollula	+	+	+	+	+	+
Sylvisorex pluvialis	–	–	–	+	–	+
Total number of species	11	11	8	16	12	9

Sources: 1 – this study, 2 – BROSSET (1988), 3 – RAY and HUTTERER (1995), 4 – LASSO et al. (1996), 5 – COLYN et al. (1996), 6 – HUTTERER and SCHLITTER (1996).

Comments: [a] – species identy uncertain, [b] – taxonomic status of *mutesae* still unresolved, [c] – the Dzanga-Sangha population of *nigrofusca* may represent a different species; all problems are under study by RH.

Acknowledgements

We are indebted to Mr. Emile Mamfoumbi Kombila, Le Directeur de la Faune et de la Chasse (DFC), Ministère des Eaux et Forêts et du Reboisement, for permits to work in the Minkébé region. The aid and assistance of Hervé Allogho, Pauwel De Wachter, and Olivier Langrand of WWF-Gabon, as well as the local assistance of Sosthene, Ndong, and Obiang is gratefully acknowledged.

Zusammenfassung

Bericht über die Artengemeinschaft von Spitzmäusen (Mammalia: Soricidae) im Minkébé Regenwald, Nord-Ost Gabun

In diesem Bericht werden die Ergebnisse einer Studie über die Artengemeinschaft von Spitzmäusen im Minkébé Regenwald im nordöstlichen Gabun mitgeteilt. Diese bislang unerforschte Region ist Teil des großen Guinea-Kongo Regenwaldblocks. Als prinzipielle Fangtechnik wurden Eimerfallen in Kombination mit Driftzäunen verwendet. Drei Lebensraumformen (Marschland, heterogener und homogener Wald) wurden mit Fallenreihen bestückt. In jedem der drei Lebensräume wurden zwischen vier und sieben Spitzmausarten gefangen, im ganzen Gebiet elf Arten. Einige seltene und wenig bekannte Arten wie *Crocidura crenata, C. goliath, C. grassei, Suncus remyi* oder *Sylvisorex ollula* kommen im Park vor. *Crocidura maurisca* wird erstmals für Gabun nachgewiesen, weit außerhalb des bislang bekannten Areals in Ostafrika.

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Mamm. biol. **66** (2001) 35–47
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Specificity of non-metric parameters of American mink (*Mustela vison*) populations in relation to habitat differences in Belarus

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Receipt of Ms. 16. 02. 2000
Acceptance of Ms. 30. 06. 2000

Abstract

A total of 418 skulls of the American mink *Mustela vison* was examined in a non-metric study to reveal the specificity in 15 remote population fragments and for 4 geographical populations inhabiting the large river basins in Belarus. Also, 14 samples from the present population fragments were compared with the sample closely related to the founders of the naturalised populations of this species. The phenetic (non-metric) distances between the samples were estimated using 22 non-metric traits. High levels of phenetic divergence in the naturalised American mink populations in Belarus were revealed. The founders exhibited significant phenetic differences compared with each of the 14 remote population fragments. Substantial phenetic differences were displayed in half of the pairwise comparisons between remote population fragments. Moreover, among population fragments from a single river basin, there was a significant negative correlation between phenetic similarity and spatial distance. There was no such correlation among population fragments from different river basins. Phenetic distances between all of the 4 geographical populations inhabiting the large river basins were statistically significant. This non-metric differentiation in the naturalised species is discussed with respect to the very diverse and different habitat conditions in which the populations exist. The phenetic plasticity (which marks genetic plasticity) of American mink revealed by our study is an adaptation which determines the high demographic success of this naturalised species demonstrated in many regions of Europe and Asia.

Key words: *Mustela vison*, population variability, non-metrical parameters, Belarus

Introduction

Studies of intra- and interpopulation variation in genetic and morphologic parameters of naturalised mammalian species are important in contemporary population biology (Hartl et al. 1993 a) and conservation biology (e. g. Scribner 1993). There is now a considerable literature on intraspecific differentiation in a wide spectrum of mammals (e. g. Rees 1969; Smith 1981; Yablokov et al. 1983; McLellan and Finnegan 1990; Kozakiewicz and Kanopka 1991; Hartl et al. 1993 b; Ruiz-Garcia 1998).
Phenetic variation in mammals, mostly expressed as a non-metric variation of their

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skulls, is usually used as a simple and cheap way to study morphologic and genetic differentiation and diversity in mammalian populations (see SJØVOLD 1977, for review). Doubts concerning concordance between phenetic and genetic variation have been raised (e. g. HARTL et al. 1993 b), and many authors note the considerable contribution made by both environmental factors and genetics in the prediction of phenetic differentiation (e. g. PETRAS 1967; MARKOWSKI and MARKOWSKA 1988; SOULE and ZEGERS 1996).

The study of intraspecific genetics of introduced species, such as the American mink, *Mustela vison*, is particularly interesting from both practical and theoretical aspects. Primarily domesticated as a valuable fur-bearing animal, the American mink started to naturalise in Eurasia during the 1950s (PAVLOV et al. 1974). In the newly colonised areas, this species exhibited a very high ecological adaptability (GERELL 1967 a, b; DANILOV and TUMANOV 1976; TERNOVSKY 1977; CHANIN and LINN 1980; DUNSTONE and BIRKS 1987; DUNSTONE 1993; SIDOROVICH 1993, 1997; TERNOVSKY and TERNOVSKAJA 1994). Furthermore, relatively short-term morphological responses by American mink to PCB's (BORISOV et al. 1997) and to domestication (KRUSKA 1996; KRUSKA and SCHREIBER 1999) have been revealed.

In Belarus, the very different habitat conditions in different parts of the country lead us to expect complicated genetic responses and morphological divergence in naturalised American mink populations. The aim of this study was to investigate the non-metric diversity of this species in Belarus, and the non-metric divergence of local populations inhabiting river catchments with different ecological conditions. Also, by analysing the skulls from contemporary local populations, we had rare opportunity to compare them with the sample of skulls collected at the time of the beginning of the naturalisation of American mink in Belarus. Thus, we evaluated both spatial and temporal scales of the non-metric skull differentiation in American mink in Belarus.

Material and methods

Most of the sampling areas were located in central and northern Belarus (Fig. 1). Only one study area was in the south-eastern part of the country. We obtained samples from all the four main river basins of Belarus: the Western Dvina, Dnepr, Pripjat, and Neman. Taking into account species-specific features of habitat selection by the American mink, each of these basins consisted of different habitat conditions.

The Western Dvina river catchment is mainly characterised by fast flowing streams of various sizes. Usually, rivers have no or very narrow floodplains. Glacial lakes and brooks were more abundant in this catchment than in the other three. Both the Neman and Dnepr river basins basically have rivers with moderate flow rates and medium-sized swampy floodplains. The Pripjat river basin is located in the lowlands and has only slowly flowing rivers with highly swampy large valleys. There are considerably fewer small rivers and brooks in this river basin than in the other three.

We also sampled the American mink population in the upper reaches of the Lovat, an area which combined all the features of the four main river basins, and in which American mink lived in conditions of a great diversity of habitats.

In 1987–1995, a total of 393 skulls of American mink from 14 localities was sampled (Tab. 1). Also, we had one sample (25 specimens) from a captive population of this species founded by the American mink released in Belarus for the purpose of naturalisation in 1953–1958. This sample originally derived from one of the biggest American mink farms in Belarus (Molodechno district, Minsk region), and was collected about 1960.

Formation of populations of naturalised American mink in Belarus was influenced by introduction in 1953–1958 and consequent northward and southward expansion from the central part of the country. Escaped ranch animals had a certain influence mostly in the central part of Belarus, where the majority of farms is located (SIDOROVICH 1995). Thus, the Lovat, W. Dvina, and Pripjat geographical populations can be considered as the result of expansion.

We used two methods of analysis. First, we carried out a pairwise comparison of the above-mentioned local populations distributed in the sampled areas (Tab. 1), which was used to reveal a non-metric difference depending on the spatial distance. Second, we investigated skull non-metrical variability of the American mink populations inhabiting the main river catchments to reveal

non-metrical specificity of population in different landscapes. In order to compare American mink inhabiting different habitat conditions, we combined samples from the central regions of Belarus (the Neman and Dnepr), because both catchments are characterised by very similar habitat conditions. Phenetic relationship among local population fragments of American mink was studied in two ways: 1) among samples belonging to the same basin of a large river, and 2) among samples derived from the different basins of large rivers (W. Dvina, Dnepr, Neman, Pripjat).

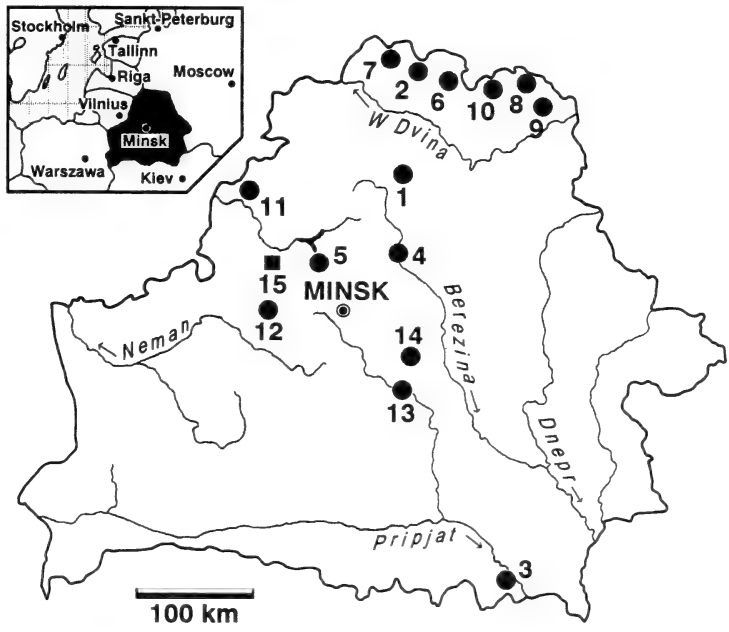

Fig. 1. Study area. Dots show location of samples from the present population fragments; square indicates location of the founder sample. Numbers of samples as in table 1.

Table 1. Information on samples

Sample	n	Sampling period	Rivers in the sampling area	Main river basin
1	10	1991–1992	Ushacha	West. Dvina
2	69	1987–1993	Nishcha, Akhonka, Lemenka	West. Dvina
3	15	1990–1993	Zhelon, Slovechna, Pripjat	Pripjat
4	26	1990–1994	Brodnia, Gaina, Eastern Berezina	Dnepr
5	22	1989–1995	Vyazynka, Konotopka, Ilija, Rybchanka	Neman
6	43	1987–1993	Drissa, Marinets, Cherneya	West. Dvina
7	42	1987–1993	Necherskaya, Studionenkaya, Svolna	West. Dvina
8	75	1990–1995	Lovat, Servaika, Uzhovsky, Skljanka, Prosimka	Lovat
9	18	1990–1992	Vymno, Rjabinka, Luzhesnjanka, Gromot	West. Dvina
10	16	1993–1994	Dubovka, Obol, Usysa	West. Dvina
11	12	1993–1995	Stracha, Golbeltsa	Neman
12	11	1987–1989	Volka, Western Berezina, Neman	Neman
13	12	1991–1993	Ptich	Pripjat
14	22	1990–1994	Svisloch	Dnepr
15*	25	About 1960	American mink farm in Molodechno district, Minsk region	
Total	418			

* founder sample

Zhivotovsky's test (ZHIVOTOVSKY 1979) was used to state the value of a phenetic distance by doing a pairwise comparison of the skull samples. This method is based on estimating both the similarity index (r) and the identity criterion (I). The similarity index, which is the measure of phenetical similarity between two samples, and might be interpreted as frequency of joint morphs (phens, variants of non-metric trait) in both of these samples, has been defined as:

$$r = \sqrt{p_1 q_1} + \sqrt{p_2 q_2} + \ldots + \sqrt{p_m q_m},$$

where p_1, p_2 ..., p_m are the frequencies of the m phens in the variability of the i-non-metric parameter for the first sample ($p_i < 1$), and q_1, q_2, ..., q_m are the frequencies of the same m phens in the variability of the i-non-metric parameter for the second sample ($q_i < 1$). If the samples are compared by k non-metric parameters, then r is calculated as:

$$r = (r_1 + r_2 + \ldots + r_k)/k.$$

The identity criterion, as a tool for evaluation of significance of phenetic distances, has been defined as follows:

$$I = 8\, n_1 n_2 (1 - r - (p_0 + q_0)/4)/n_1 + n_2,$$

where n_1 and n_2 are the sizes of the samples compared; p_0 is the sum of frequencies of phens that are presented in the first sample but not in the second one, q_0 – accordingly, is the sum of frequencies of phens that are presented in the second sample but not presented in the first one. The identity criterion I is distributed as the well known χ-square criterion with the degrees of freedom df = m – 1. By involving k non-metric parameters for the pairwise comparison of samples, I has been defined as:

$$I = I_1 + I_2 + \ldots + I_k,$$

with the degrees of freedom calculated as $df = m_1 + m_2 + \ldots + m_k - k$.

Twenty-two non-metric skull parameters were used for the phenetic study of the American mink. Their variability gives 80 variants i. e. phens as typical states of the non-metric skull parameters (Figs. 2, 3). Number, presence/absence, shape and location of foramina on a particular bone and other bony structures were the basic categories of these non-metric skull variables. In case of bilateral parameters, only the right side of the cranium was taken into account.

In total, 80 phens were revealed (Fig. 3) using the following non-metric skull parameters:

1. Shape of the foramen infraorbitale (front view of the skull): 1.1 – oval; 1.2 – side bend; 1.3 – bottom bend; 1.4 – triangle;
2. Foramen occipitale superior (back view): 2.1 – one foramen directly below crista occipitalis; 2.2 – absent; 2.3 – one foramen located between crista occipitalis and foramen magnum; 2.4 – one foramen directly above crista occipitalis; 2.5 – two foramina located separately horizontally directly below crista occipitalis; 2.6 – two foramina located separately, one – directly below crista occipitalis, another – directly above foramen magnum; 2.7 – three and more foramina directly below crista occipitalis;

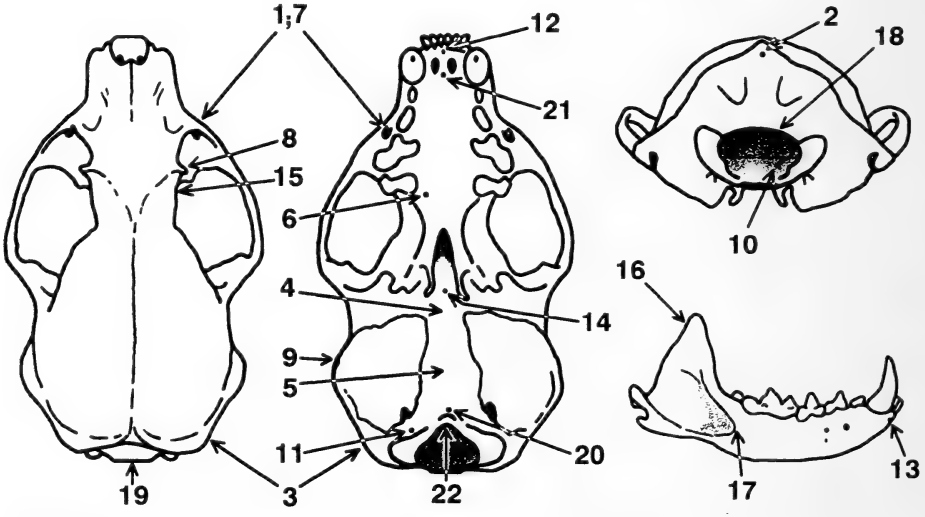

Fig. 2. Location of the non-metric parameters on an American mink skull.

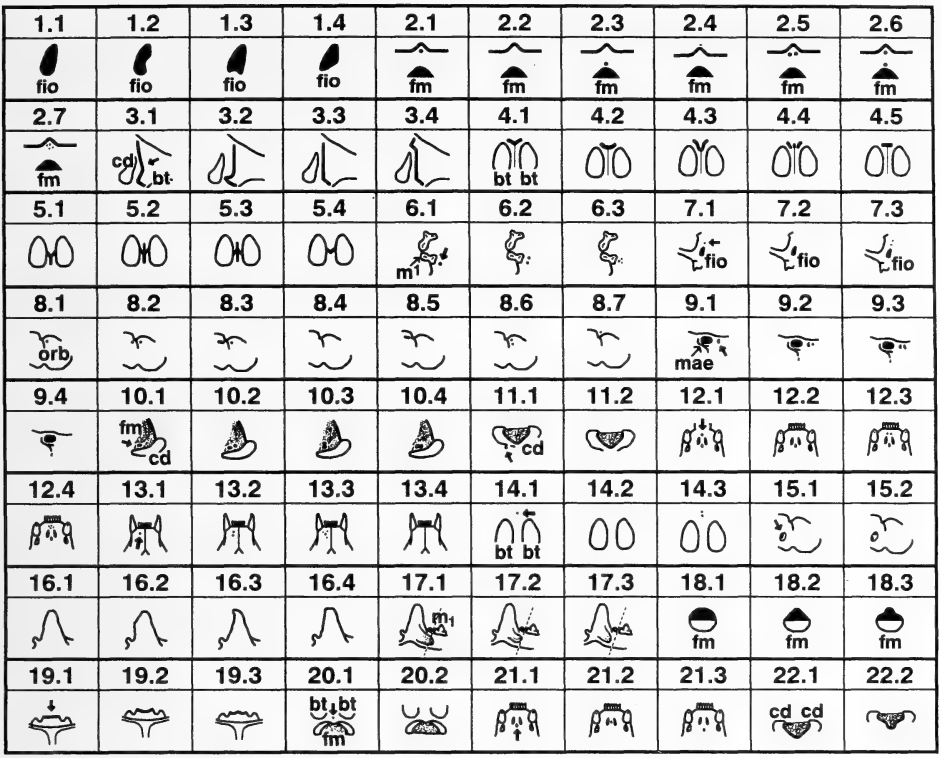

Fig. 3. Variability of non-metric parameters of American mink skulls in Belarus.
fio – foramen infraorbitale, fm – foramen magnum, cd – condylus occipitalis, bt – bulla tympanicum, m^1 – first upper molar, orb – orbita, mae – meatus acusticus externus, m_1 – first lower molar.

3. Profile shape of the processus jugularis ossis occipitalis (side view): 3.1 – proximal bend; 3.2 – lower angle turned up; 3.3 – straight; 3.4 – upper angle turned down;
4. Shape of the bony micro eminencies (estimated by rubbing with an aluminium ruler) on the os sphenoidale in front of the bulla tympani (bottom view): 4.1 – V-shaped; 4.2 – bow-shaped; 4.3 – U-shaped; 4.4 – crown-shaped; 4.5 – dash-shaped;
5. Shape of the bony micro eminencies (estimated by rubbing with an aluminium ruler) on the os sphenoidale between the bulla tympani (bottom view): 5.1 – y-shaped; 5.2 – arrow backwards; 5.3 – arrow forwards; 5.4 – V-shaped;
6. Number of the foramina palatinum posterior (bottom view): 6.1 – one; 6.2 – two; 6.3 – three and more foramina;
7. Number of small foramina located above the foramen infraorbitalis (front view): 7.1 – one; 7.2 – absent; 7.3 – two foramina;
8. Foramen on the processus postorbitalis ossis occipitalis (side view): 8.1 – one foramen located in front of the processus; 8.2 – two foramina, one – in front , another – at the back of the processus; 8.3 – two foramina, one – in front, another – oblong – at the back of the processus; 8.4 – foramen absent; 8.5 – one foramen at the back of the processus; 8.6 – two foramina, both located in front of the processus; 8.7 – one foramen located on top of the processus;
9. Foramen temporale (side view): 9.1 – one foramen; 9.2 – two foramina, the front one is significantly smaller; 9.3 – two foramina of the same size; 9.4 – foramen absent;
10. Foramen canalis condylaris (back view): 10.1 – one foramen; 10.2 – two foramina; 10.3 – one foramen with a rudiment of the horizontal partition; 10.4 – one foramen with a rudiment of the vertical partition;
11. Presence or absence of the foramen hypoglossus (bottom view): 11.1 – present; 11.2 – absent;

12. Number of additional foramina located in front of the foramen incisivum (bottom view): 12.1 – one foramen; 12.2 – absent; 12.3 – two foramina; 12.4 – three and more small foramina;
13. Number of the foramina mandibulae (front view): 13.1 – one foramen; 13.2 – two foramina; 13.3 – three and more foramina; 13.4 – absent.
14. Foramen located on the os sphenoidale in front of the bulla tympani (bottom view): 14.1 – one foramen; 14.2 – absent; 14.3 – two foramina;
15. Number of the foramina opticum (side view): 15.1 – one foramen; 15.2 – two foramina (partition is a little bit deeper);
16. Shape of the processus coronoideus mandibulae (side view): 16.1 – pyramid-shaped with oval apex; 16.2 – with angular hinder margin; 16.3 – with acute and turned back apex; 16.4 – pyramid-shaped with cut off apex;
17. Position of front margin of the fossa masseterica mandibulae with respect to the hinder margin of the M_1 tooth (side view): 17.1 – in front; 17.2 – on the same level; 17.3 – behind;
18. Shape of the foramen magnum (back view): 18.1 – round-shaped; 18.2 – pyramid-shaped; 18.3 – pear-shaped;
19. Shape of bony vault above the foramen magnum (top view): 19.1 – straight; 19.2 – with two eminencies; 19.3 – with three eminencies;
20. Presence or absence of foramen located between the condylus occipitalis (bottom view): 20.1 – present; 20.2 – absent;
21. Position of additional foramen located behind the foramina incisivum with respect to the hinder margin of these (bottom view): 21.1 – on the same level; 21.2 – in front; 21.3 – behind;
22. Shape of bend between the condylus occipitalis (bottom view): 22.1 – V-shaped; 22.2 – with eminencies on both sides.

Skull non-metric variability related to sex was tested using Zhivotovsky's test, and sex-dependent parameters were excluded from further analysis. Out of 22 non-metric parameters of the American mink's skull, only 5 were significantly related to sex (Tab. 2). These were not used in the analysis below. The effect of age was not tested. Distinct changes in size and proportion of mink skulls occur during the first year of life (KRUSKA 1979), thus only skulls belonging to adult American mink aged one year and older

Table 2. Differences between sexes (Zhivotovsky's test) according to the skull non-metric parameters of American mink in Belarus

Non-metric parameter	n of males	n of females	r	I	df	p
1	256	180	0.995	4.55	3	>0.200
2	238	170	0.984	12.47	6	>0.050
3	145	118	0.997	1.60	3	>0.500
4	162	93	0.991	4.26	4	>0.300
5	144	89	0.994	2.46	3	>0.300
6	242	172	0.998	1.34	2	>0.500
7	260	183	0.995	4.49	2	>0.100
8	267	183	0.992	7.16	6	>0.300
9	262	172	0.996	3.72	3	>0.200
10	266	183	0.994	4.79	3	>0.100
11	263	182	1.000	0.00	1	0.999
12*	260	176	0.659	286.64	3	<0.001
13*	249	177	0.986	11.75	3	<0.010
14*	266	178	0.992	7.21	2	<0.050
15	262	184	1.000	0.00	1	0.999
16*	265	184	0.987	11.67	3	<0.010
17	265	184	0.999	0.94	1	>0.300
18	135	109	0.988	5.63	2	>0.050
19	125	97	0.996	1.65	2	>0.300
20	133	110	1.000	0.00	1	0.999
21	119	104	0.988	5.19	2	>0.050
22*	66	56	0.977	5.48	1	<0.020

* differences between sexes are statistically significant

(1+) were used for this study. All skulls having closed sutures (STUBBE 1973 for review) were additionally tested for age using histological sections of the canine teeth (KLEVESAL and KLEINENBERG 1969).

Results

Differences between founders and current local population fragments

Significant differences were found between the founder sample and all other samples derived from current local population fragments of naturalised American mink (Tab. 3). Especially substantial differences were established by comparing the founder sample with the sample 12 from Volka sampling area, Neman river catchment ($r = 0.777$; $I = 126.56$; $p = 0.000$), and with the sample 1 from Ushacha sampling area, Western Dvina river catchment ($r = 0.793$; $I = 128.71$; $p = 0.000$). Lower but significant phenetic differences were discovered between founders and the sample 14 from Svisloch sampling area, Dnepr river catchment ($r = 0.939$; $I = 77.03$; $p = 0.000$).

Table 3. The skull non-metric differences (by complex of all non-metric parameters, df = 39) between the founder and the present local population fragments of the American mink, Belarus

Founders compared with the sample number:	r	I	p
1	0.793	128.71	0.000
2	0.876	241.98	0.000
3	0.874	111.02	0.000
4	0.910	114.22	0.000
5	0.876	126.06	0.000
6	0.850	236.75	0.000
7	0.901	162.86	0.000
8	0.939	124.60	0.000
9	0.884	117.96	0.000
10	0.900	106.33	0.000
11	0.895	87.31	0.000
12	0.777	126.56	0.000
13	0.929	59.61	0.019
14	0.939	77.03	0.000

Differences among local population fragments

There were no significant differences in mean level of phenetic similarity by analysing both groups of samples (Tab. 4). Mean index of similarity was only slightly higher among local population fragments inhabiting the same river basin (0.928 vs. 0.912; $p = 0.128$). Also, there was no difference in rate of significantly dissimilar pairs of samples. Approximately one half of the pairwise comparisons exhibited statistically significant non-metric differences in both groups of samples (45% vs. 55%, $p = 0.5$). However, by comparing local samples belonging to the same basin of a large river, a significant negative correlation between the index of phenetic similarity and spatial distance between two samples was found (coefficient of correlation, $r = -0.77$, $n = 20$, $p = 0.000$; Fig. 4). This correlation was very low and not significant (coefficient of correlation, $r = -0.24$, $n = 71$, $p = 0.842$) when samples belonging to the different basins of large rivers were analysed.

Table 4. Phenetic differences between pairwise compared local samples of American mink from the same (A) and the different (B) basins of large rivers in Belarus

Indicator	A (n = 20 pairs of samples)	B (n = 71 pairs of samples)	Significance of difference, p
Rate of pairs of samples with significant difference, %	45	55	0.500
Mean r ± SD	0.928 ± 0.0324	0.912 ± 0.0430	0.128
Mean I ± SD	64.51 ± 15.680	76.65 ± 33.763	0.123

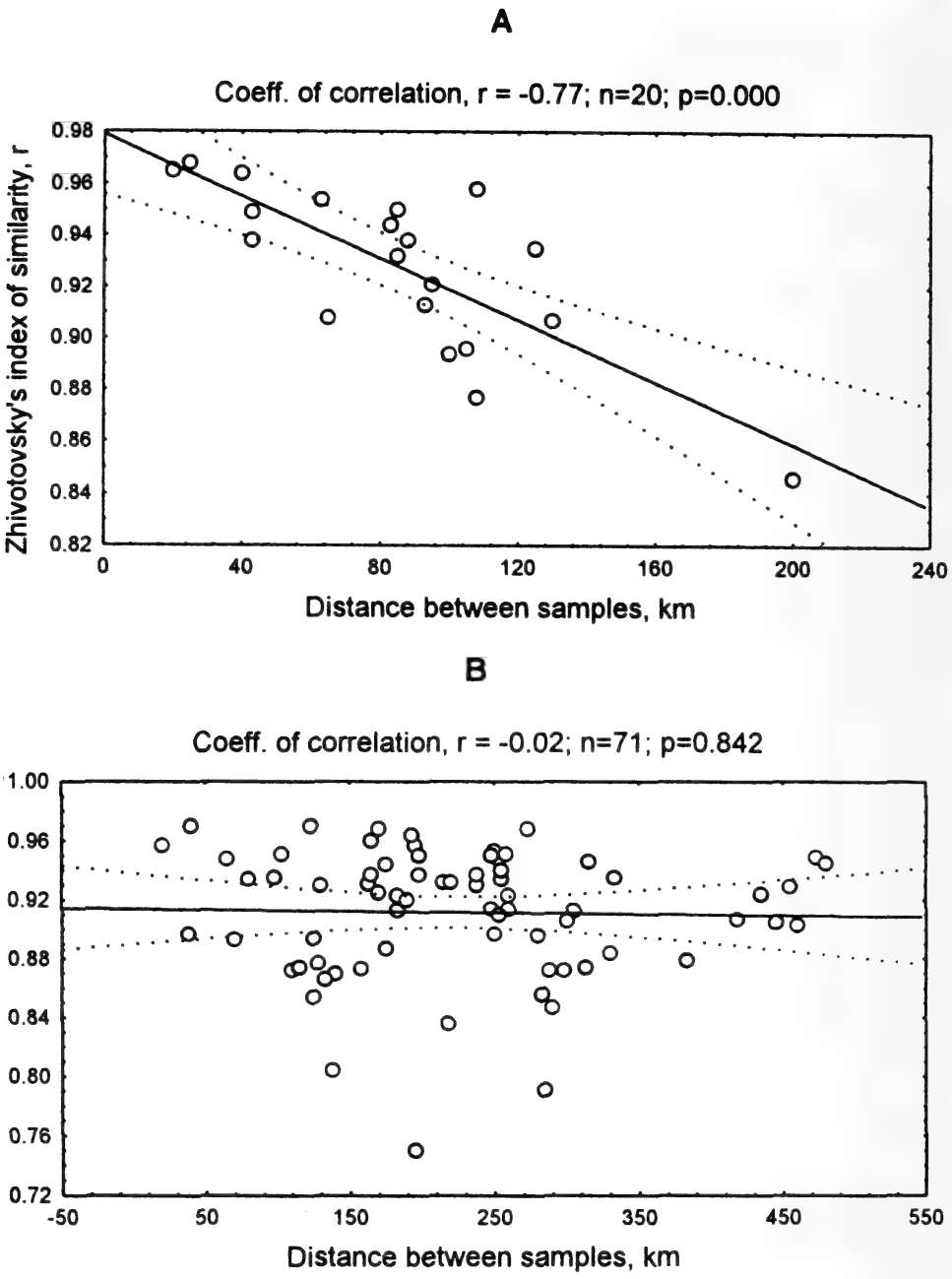

Fig. 4. Correlation between the phenetic similarity and spatial distance among local population fragments from the same (A) and different (B) large river basins (geographical populations) in Belarus.

Table 5. The non-metric skull differences (r; I; p, by complex of all non-metric parameters, df = 39) among pairwise compared geographical populations of American mink inhabiting basins of large rivers in Belarus

Basins	W. Dvina	Neman + Dnepr	Pripjat (n = 28)
Lovat (n = 79)	0.976; 150.8; 0.000	0.977; 102.8; 0.000	0.968; 71,2; 0.010
W. Dvina (n = 222)		0.990; 68,8; 0.020	0.955; 118.2; 0.000
Neman + Dnepr (n = 100)			0.968; 72.3; 0.010

Differences among geographical populations

The non-metric differences were statistically significant, and sufficiently high to be characterised by substantial non-metric specificity between all the 4 geographical populations inhabiting the basins of the large rivers – Lovat, W. Dvina, Neman–Dnepr, and Pripjat (Tab. 5). The greatest difference was found between populations from the W. Dvina and Pripjat river basins ($r = 0.955$; $I = 118.2$; $p < 0.001$). These river basins are characterised by considerably different habitat conditions for American mink.

Discussion

Substantial intraspecific phenetic differentiation was found among American mink within the fairly small area of Belarus (204 000 km^2). After approximately 30–40 years, established local populations were also markedly different in comparison with the founder population. This suggests a high level of adaptability of this naturalised predator to new habitat conditions. High levels of non-metric plasticity could be one of the basic factors which enabled the American mink to adapt to different ecological conditions and spread throughout Europe (Pavlov et al. 1974; Gerell 1967 a, b, 1968; Danilov and Tumanov 1976; Dunstone 1993; Sidorovich 1993, 1997).

In domesticated American mink populations, the absence of strict natural selection as well as deliberate artificial selection could lead to a certain partial "packing up" of the gene pool. In several European countries significantly lower levels of sexual dimorphism were found in domestic American mink in comparison with the feral ones (Lynch and Hayden 1995). It was interpreted as weak sexual selection, absence of competition, and purposeful artificial selection for larger specimens of both sexes. Decrease in size of brain and some other organs in the domesticated American mink may result from reductions of central nervous and circulatory functions in the domesticated organism (Kruska 1996; Kruska and Schreiber 1999).

More diverse selection started when domestic minks were placed in completely different feral conditions. The gene pool of the newly formed populations of American mink was affected by different pressures of natural selection in comparison with ranch conditions. Consequently, the phenetic structure of these populations should change. This could explain our finding that the founder population differs substantially phenetically from all the current local populations.

Non-metric skull differences among contemporary local population fragments of American mink might also be affected by stochastic changes in frequencies of variants of non-metric parameters in small spatial groups of individuals (processes of genetic drift: the bottleneck, founder effect), especially when small samples from different river catchments were compared. Spatially remote local groups of individuals belonging to different geographical populations might be phenetically similar, whereas the neighbouring ones could be phenetically very different. Absence of a correlation between non-metric and spatial distances demonstrate that phenetic relations between population fragments from the different geographical populations are rather stochastic. Such stochastic differentiation has

been reported for many other species (e. g. GREWAL and DASGUPTA 1967; MCLELLAN and FINNEGAN 1990; KOZAKIEWICZ and KANOPKA 1991; LORENZINI et al. 1993; RYAN et al. 1996).

However, presence of a significant correlation between the non-metric differences and the spatial distances among samples from the same geographical population suggests another interpretation. This finding demonstrates a certain regularity in the intrapopulational non-metric (possibly also genetic) divergence rather than the presence of a stochastic factor. Our results also demonstrate that all geographical populations of American mink (inhabiting catchments of large rivers) were phenetically specific, thus having their own "general" vector of selection. Different selective pressures within one geographical population likely result in formation of phenetically different groups of individuals. The rate of gene flow between such groups would depend on the degree of spatial isolation. Spatial distances among intraspecific groups often correlate with phenetic or genetic differences (REES 1969; MCLELLAN and FINNEGAN 1990; ULEVIČIUS 1992). Thus, spatial isolation can influence genetic and phenetic structures.

The social intraspecific structure can lead to considerable genetic differentiation of adjacent social groups, too. It has been established in primates (SCHEFFRAHN et al. 1996). Both genetic and environmental factors might be important for the control of phenetic variability (e. g. PETRAS 1967; HOWE and PARSONS 1967; BERRY and BERRY 1972; see also HARTL et al. 1993 b, for review). Some authors have argued that the genetic variation explains more than 50% of phenotypic variation (SOULE and ZEGERS 1996). A significant part of phenetic variation can be influenced by phenotypic plasticity as a function of the environment. Genetically, plasticity is likely due to both differences in allelic expression across environments, and changes in interactions among loci (SCHEINER 1993).

Results of our study might be interpreted in connection with a very high phenetic plasticity of American mink occupying new and diverse habitat conditions. Other ecological characteristics of naturalised American mink populations in our study area confirmed the distinct ecological plasticity of this species (SIDOROVICH 1993, 1997). It should be emphasised that our data are not in accord with the data from some other populations of American mink. For example, American mink from Norway exhibited relatively little geographic variation in either the metrical measurements or the non-metrical traits thus indicating little genetic variation (WIIG and LIE 1979). Electrophoretical investigations on wild and ranch mink from Canada and Germany, respectively, showed low protein heterozygosity in both groups (KRUSKA and SCHREIBER 1999). These authors also reviewed works of other investigators showing low allozyme heterozygosity of mustelids. In this respect an explanation of phenetic differentiation of American mink in Belarus due to the phenetic plasticity would also be reasonable because the phenetic expression of monomorphic loci may be unequal in different environments.

For a more detailed study of mechanisms of the non-metric differentiation of American mink in Belarus biochemical-genetic investigations are needed. However, the presently discovered substantial non-metric differences in temporal and geographical scales show that an influence of genetic factor was very important.

Acknowledgements

We are very thankful to Dr. F. TATTERSALL for English correction of the manuscript and K.-A. NITSCHE for translation into German.

Zusammenfassung

Spezifität nicht-metrischer Parameter von Mink-Populationen (*Mustela vison*) im Verhältnis zu Habitat-Unterschieden in Weißrußland

Insgesamt 418 Schädel des Mink, *Mustela vison*, wurden durch eine nicht-metrische (phänetische) Studie geprüft um die Spezifität der Einzelheiten von 15 auseinander liegenden und für 4 geographische Populationen der großen Flußbecken in Weißrußland zu untersuchen. Verglichen wurden auch 14 Proben von den derzeitigen Populations-Fragmenten mit einer Probe der regionalen Gründerpopulation dieser Art. Die Distanzen zwischen den Proben wurden unter Benutzung von 22 nicht-metrischen Merkmalen abgeschätzt. Ein hohes Niveau phänetischer Divergenz wurde in den natürlichen Mink-Populationen von Weißrußland festgestellt. Die Gründertiere zeigten bedeutende phänetische Unterschiede, die mit jedem der 14 entfernten Populations-Fragmenten verglichen wurden. Beträchtliche phänetische Unterschiede werden in der Hälfte des paarweisen Vergleiches zwischen entfernten Populations-Fragmenten gezeigt. Es gab außerdem eine signifikante negative Korrelation zwischen der phänetischen Ähnlichkeit und räumlicher Entfernung unter den Populations-Fragmenten an einem einzelnen Flußbecken. Es gab keine derartige Korrelation unter Populations-Fragmenten von unterschiedlichen Flußbecken. Statistisch bedeutungsvoll waren die phänetischen Distanzen zwischen allen 4 geographischen Populationen, welche die großen Flußbecken bewohnen. Die nicht-metrische Differenzierung bei den natürlich lebenden Tieren wird unter dem Aspekt der vielfältigen Habitat-Bedingungen, in der die Population vorkommt, besprochen. Die in unserer Studie dargestellte phänetische Plastizität des Mink (welche die genetische Plastizität kennzeichnet) ist eine Anpassung, die über den hohen demographischen Erfolg dieser freilebenden Art entscheidet, was in vielen Regionen Europas und Asiens gezeigt werden kann.

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Mamm. biol. **66** (2001) 48–59
© Urban & Fischer Verlag
http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Little allozyme and mtDNA variability in brown hares (*Lepus europaeus*) from New Zealand and Britain – A legacy of bottlenecks?

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Reiceipt of Ms. 07. 02. 2000
Acceptance of Ms. 07. 03. 2000

Abstract

We studied cross nuclear and mitochondrial gene pools of brown hares (*Lepus europaeus*) from three local populations in Britain and two in New Zealand, to test the hypothesis of reduced genetic variability in hares from New Zealand resulting from few founders originating from Britain. Multilocus allozyme electrophoresis of 52 protein loci and analysis of restriction fragment length polymorphisms of total mitochondrial DNA based on 16 hexanucleotid-cleaving restriction enzymes were employed in 119 and 36 hares, respectively. Observed and expected average heterozygosities, rates of polymorphism, average numbers of alleles per locus, Shannon-Weaver information indices of allelic diversity, as well as values of haplotype and nucleotide diversity were similar in all regional samples. But hares from both New Zealand and Britain had significantly lower genetic diversity than brown hares from continental Europe studied earlier. Thus, gene pool erosion likely occurred already in British hares, perhaps associated with their probable introduction in Roman times. Theoretically, the small number of alleles found in British brown hares could have been sampled by the few hares that were reported as having constituted the founder stock in New Zealand in the nineteenth century. As expected, rare alleles of British brown hares were absent in New Zealand. But drift had only a slight effect on the gene pool composition of hares in New Zealand.

Key words: *Lepus europaeus*, allozymes, mtDNA, genetic bottleneck

Introduction

In New Zealand, brown hares (*Lepus europaeus*) have higher rates of ovarian tumors and missing posterior upper molars (M^3) than in Europe (Flux 1965, 1980; Parkes 1988; Suchentrunk et al. 1992). This might result from low genetic variability as a consequence of a small number of founder individuals (Flux 1965). Historical documents suggest that brown hares released in New Zealand in the 19th century by various Acclimatization Societies were mostly taken from Phillip Island, Victoria, Australia (Lever 1985; Flux 1990). There, only six hares had built up a population of 200 individuals by 1865, few years after introduction (Flux 1990; Flux et al. 1990; see also Rolls 1969 and Lever 1985). In Australia, brown hares were probably first successfully introduced in 1859 by W. Lyall on the shores of Western Port Bay, Victoria (Lever 1985), and afterwards on Phillip Island (Mahood 1983). In February 1864 an-

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other nine hares were released into an enclosure near Geelong, Victoria by T. Austin, who imported them from England (cf. Lever 1985). All Australian hares are considered originating from Britain (cf., Flux 1990), but no details as to specific regions are given in the available literature (Lever 1985; Flux pers. com.). The exact numbers of hares that have successfully bred after their naturalization in Australia and New Zealand remain unknown. However, the list of importations to New Zealand presented by Lever (1985) suggests limited genetic variability in the founder gene pool (see also Flux 1990).

In this study we compared levels of genetic variability of hares from New Zealand and Britain, to test this genetic bottleneck hypothesis (Flux 1965). Theory and empirical findings (e. g., Fuerst and Maruyama 1986; Leberg 1992; Hartl and Pucek 1994; Tiedemann et al. 1997) predict a smaller effect of bottlenecks on multi-locus allozyme heterozygosity than on other indicators of allozymic variability, such as the rate of polymorphism (P), and mean number of alleles per locus (A). Allozyme heterozygosity may even increase after bottlenecks (e. g., Leberg 1992). Thus, we expected lower P- and A-values for hares from New Zealand than for British brown hares, whereas heterozygosities might be similar. Particularly alleles with low frequencies in British brown hares might have not been sampled by the few founders in New Zealand. Drift effects could have caused shifts in allele frequencies and consequently increased genetic divergence between hares from Britain and New Zealand. We also expected a pronounced reduction of variability in the mitochondrial DNA (mtDNA), because of the lack of recombination in this maternally inhereted genome in post-bottleneck populations (e. g., Giles et al. 1980; Lansman et al. 1981; Avise 1994; Avise and Hamrick 1996; see e. g., Gyllensten et al. 1991 for paternal inheritance of mtDNA). Brown hares from the British Isles are conventionally considered a separate subspecies (*L. e. occidentalis* De Winton, 1898; cf. Corbet and Southern 1977; Arnold 1993). They might be genetically somewhat distinct from mainland European brown hares. Therefore, we compared the present data with adjusted data sets of continental European brown hares published earlier (Hartl et al.1993; Suchentrunk et al. 2000).

Material and methods

Specimens studied

We studied 119 hares from two regions in New Zealand and three in Britain (Fig. 1). In New Zealand, hares were collected in the Wairarapa region (n = 32) of the North Island in September/October 1993 by J. E. C. Flux ("Landcare Research", Lower Hutt), and in the Harper/Avoca catchment (n = 28) on the South Island in October 1993 and March 1995 by J. Parkes ("Landcare Research", Christchurch) and F. Suchentrunk. In Britain, collections were organized by S. Tapper (The Game Concervancy Trust, Fordingbridge, England) in February 1995 in three regions (Wiltshire, southern England, n = 20; Loddington, Leicestershire, central England, n = 19; Duns, Aberdeenshire, Scotland, n = 20). Most hares were dissected by one of the authors (FS). They were sexed by inspection of the internal reproductive organs and aged by checking the lateral epiphysial protrusion of the ulna (Stroh's sign), which separates young of the year (< approx. 7–10 months) from older hares (Suchentrunk et al. 1991). Liver, kidney, and spleen tissue samples were frozen at –20 °C until further use.

Allozymic diversity

We screened allelic variation at 52 hypothetical structural gene loci in 119 hares by standard horizontal starch gel electrophoresis of the following isozymes/-systems (isozyme/-system, abbreviation, E.C. number. and corresponding structural gene loci in parentheses): α-glycerophosphate dehydrogenase (GDC, 1.1.1.8, Gdc), sorbitol dehydrogenase (SDH, 1.1.1.14, Sdh), lactate dehydrogenase (LDH, 1.1.1.27, Ldh-1,-2), malate dehydrogenase (MOR, 1.1.1.37, Mor-1,-2), malic enzyme (MOD, 1.1.1.40, Mod-1,-2), isocitrate dehydrogenase (IDH, 1.1.1.42, Idh-1,-2), 6-phosphogluconate dehydrogenase (PGD, 1.1.1.44, Pgd), glucose dehydrogenase (GDH, 1.1.1.47, Gdh-2), glucose-6-phosphate dehydrogenase (GPD, 1.1.1.49, Gpd), glyceraldehyde-3-phosphate dehy-

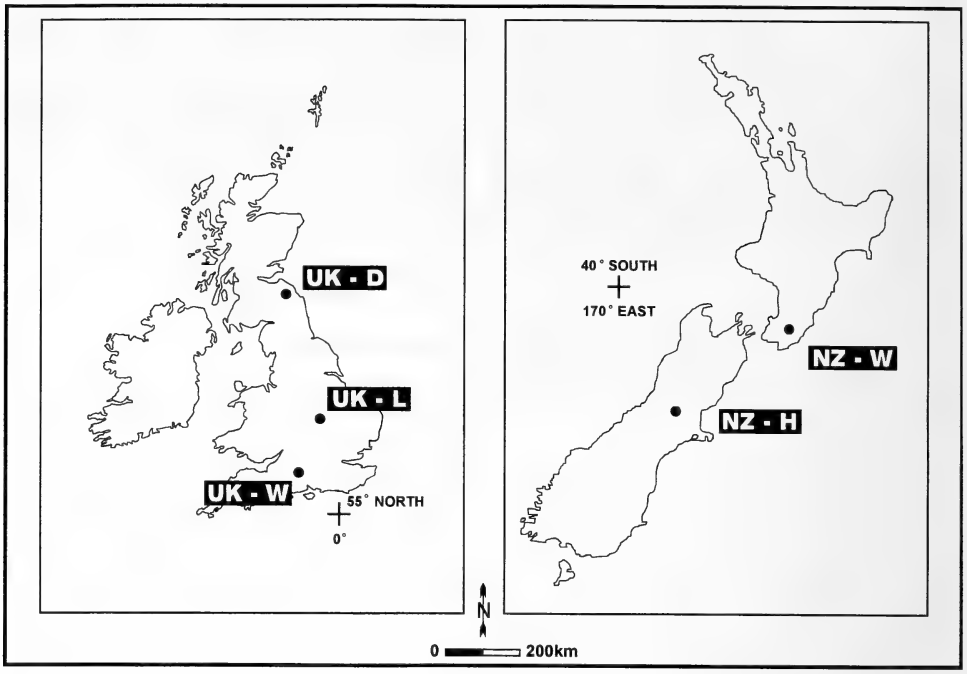

Fig. 1. Sampling regions of brown hares in Britain and New Zealand. Details are given in the text.

drogenase (GAPDH, 1.2.1.12, Gapdh), xanthine dehydrogenase (XDH, 1.2.3.2, Xdh), glutamate dehydrogenase (GLUD, 1.4.1.3, Glud), NADH-diaphorase (DIA, 1.6.2.2., Dia-1), catalase (CAT, 1.11.1.6, Cat), superoxide dismutase (SOD, 1.15.1.1, Sod-1,-2), purine nucleoside phosphorylase (NP, 2.4.2.1, Np), aspartate aminotransferase (AAT, 2.6.1.1, Aat-1,-2), hexokinase (HK, 2.7.1.1, Hk-1,-2,-3), pyruvate kinase (PK, 2.7.1.40, Pk-1), creatine kinase (CK, 2.7.3.2, Ck-1,-2), adenylate kinase (AK, 2.7.4.3, Ak-1,-2), phosphoglucomutase (PGM, 2.7.5.1, Pgm-1,-2,-3), esterases (ES, 3.1.1.1, Es-1; 4.2.1.1, Es-D), acid phosphatase (ACP, 3.1.3.2, Acp-1,-2,-3), fructose-1,6-diphosphatase (FDP, 3.1.3.11, Fdp-1), peptidases (PEP, 3.4.11, Pep-1,-2), guanine deaminase (GDA, 3.5.4.3, Gda), adenosine deaminase (ADA, 3.5.4.4, Ada-2,-3), aldolase (ALDO, 4.1.2.13, Aldo), fumarate hydratase (FH, 4.2.1.2, Fh), aconitase (ACO, 4.2.1.3, Aco-1,-2), mannose phosphate isomerase (MPI, 5.3.1.8, Mpi), glucose phosphate isomerase (GPI, 5.3.1.9, Gpi-1,-2). This suite of isozyme loci is identical to the loci screened by HARTL et al. (1993) for 20 regional samples of brown hares from central Europe, except for Acy-1 and β-Gal, which were not screened presently.

In tissue preparation, electrophoresis, and protein specific staining we followed GRILLITSCH et al. (1992). For resolving allelic variants we made direct side-by-side comparisons of migrating allozymes on the same gels by including samples of brown hares studied earlier in our laboratory, and adopted the allele nomenclature of HARTL et al. (1993) and SUCHENTRUNK (1993). We determined genotypes at polymorphic loci from zymograms according to principles of allozyme electrophoresis (HARRIS and HOPKINSON 1976; ROTHE 1994). In some individuals, however, we could not genotype all polymorphic loci due to poor resolution.

We used the BIOSYS-1 pc package, release 1.7 (SWOFFORD and SELANDER 1989) to calculate allele frequencies, average heterozygosity (H_o – observed, H_e – expected), proportion of polymorphic loci (P, 99% criterion), mean number of alleles per locus based on all 52 loci (A), and for exact tests of deviations of observed genotypes at polymorphic loci from Hardy-Weinberg expectations. As additional index of genetic diversity, we calculated the Shannon-Weaver information index (H′; see HEDRICK 1985) for each regional sample (RS) as the sum of locus-specific information indices based on allele frequencies.

We tested variation of locus-specific allele frequencies between pairs of regional samples by exact Fisher's tests and based significance decisions on Sequential Bonferroni procedure (Rice 1989), to account for multiple testing. Also, we based exact Fisher's tests of variation of allele frequencies between the two age classes (young of the year vs. older animals) and sex on Sequential Bonferroni procedure. In order to evaluate possible drift effects by e. g., founder events and/or long-term low effective population sizes, we calculated pairwise genetic D values (Nei 1978), modified Rogers' distances, and fixation indices (F_{ST}) (Wright 1978) among RSs by the BIOSYS-1 pc program package. Furthermore, we calculated RS-specific F_{IS}-values with this software, to check whether or not possible low genetic variability might result from regional inbreeding. For direct comparison with allozymic variability of brown hares from 20 local samples from Austria (Hartl et al.1993) and eight regional samples from Bulgaria (Suchentrunk et al. 2000), we adjusted all samples to 49 loci by omitting the Acy-1, β-Gal, Ada-2, Ada-3, and Dia-1 loci. All these data sets were produced in our laboratory by using respective marker individuals on the gels, which enabled a direct comparison.

MtDNA-RFLP analysis

We used liver tissue samples of 36 hares (NZ-W = 10, NZ-H = 7, UK-W = 3, UK-L = 13, UK-D = 3) to isolate mtDNA by CsCl/EtBr density gradient ultra-centrifugation and removing EtBr by isoamyl alcohol extraction, basically following the protocols of Lansman et al. (1981) and Rickwood (1987); for details see Hartl et al. (1993) and Nadlinger (1994). We digested total mtDNA of each hare with the following set of 16 hexanucleotid-recognizing type II restriction endonucleases (Roche): ApaI, BamHI, BclI, BglII, ClaI, DraI, EcoRI, EcoRV, HindIII, HpaI, PstI, PvuII, SacI, XbaI, XhoI, and XmnI. The resultant fragments were separated electrophoretically (80 V, two hours) in 0.7% agarose gels with 0.5 µg EtBr/ml and visualized in UV light. In order to validate length estimations of >4 kb long fragments, electrophoresis was continued for two additional hours and fragment measurements were repeated. Fragment length variants <0.4 kb could not be detected by our procedure. Fragment lengths were determined by comparing with Lambda phage DNA digested with HindIII and a 100 bp-ladder (1500–500 bp range). We compared fragments and cleaveage sites deduced from enzyme-specific fragment patterns with those already found in brown hares from Austria (Hartl et al. 1993; Nadlinger 1994). Because our enzyme set was identical with that used already for Austrian brown hares, we could compare our restriction morphs, haplotypes, and indices of mtDNA variability directly with brown hare mtDNA data published by these authors (Hartl et al. 1993). We calculated haplotype diversity (h) and nucleotide diversity (π) (Nei and Li 1979; Nei 1987) to describe RS-specific gene pool variability. We calculated pairwise net nucleotide diversity between RSs based on cleaveage site variations (e. g., Avise 1994) to obtain estimates of mtDNA differentiation among RSs. We compared frequencies of the standard haplotype (i. e., the by far most common type I; Hartl et al. 1993) and other haplotypes (i. e., all others aggregated) between NZ and UK hares by a one-tailed exact Fisher test (hypothesizing lower variability in NZ than UK hares). Finally, we compared RS-specific h- and π-values of NZ and UK hares with the respective values of 18 Austrian brown hare samples (Hartl et al. 1993) by Mann-Whitney U-tests, basing significance decisions on Sequential Bonferroni procedure.

Results

We found di-allelic variation at six loci (Tab. 1) and a significant excess of homozygotes at the Es-1 locus in the NZ-W sample. Except for Acp-1^{50} and Mpi^{84}, all alleles were found earlier in brown hares from central Europe. Allele frequencies did not depend on age category or sex. The indices of genetic variability (H_o, H_e, P, A, H′) are listed in table 1. Overall and locus-specific inbreeding coefficients (F_{IS}) are given in table 2, separately for each RS. Nei's (1978) unbiased D values, Rogers' modified distances, and the fixation coefficients (F_{ST}) appear in table 3, along with the significances of pairwise comparisons of allele frequencies at one or more loci. In table 4, the indices of allozymic variability (based on 49 loci) of the UK and NZ samples are compared to those of 20 Austrian and eight Bulgarian regional samples of brown hares studied earlier (Hartl et al.1993, Suchentrunk et al. 2000).

Thirtyfive (97.2%) hares had the standard mtDNA haplotype I, that was already

Table 1. Allele frequencies at polymorphic loci, sample-specific indices of genetic variability, and mean inbreeding coefficients (F_{IS}) in brown hares from New Zealand (NZ) and Britain (UK); for acronyms see figure 1. Allele designations correspond to those given in HARTL et al. (1989, 1993), SUCHENTRUNK (1993), SUCHENTRUNK et al. (1998), and SUCHENTRUNK et al. (2000). n = number of individuals screened for each locus and regional sample. Indices of gene pool variability (based on 52 loci): H_o = observed average heterozygosity, H_e = expected average heterozygosity, $P_{(99\%)}$ = rate of polymorphism (99% criterion), A = average number of alleles per locus, H′ = Shannon Weaver information index.

Locus	Allele	NZ-W	NZ-H	UK-W	UK-L	UK-D
Idh-2	n	32	28	20	19	20
	100	1.0	1.0	0.975	1.0	1.0
	130	0.0	0.0	0.025	0.0	0.0
Pep-2	n	32	28	20	19	20
	100	0.781	0.536	0.850	1.0	0.875
	104	0.219	0.464	0.150	0.0	0.125
Acp-1	n	32	28	20	19	20
	100	1.0	1.0	1.0	1.0	0.975
	50	0.0	0.0	0.0	0.0	0.025
Ada-2	n	32	6	18	17	18
	100	0.813	0.750	0.694	0.588	0.639
	75	0.187	0.250	0.306	0.412	0.361
Es-1	n	32	28	20	19	20
	−100	0.781	1.0	0.600	0.632	0.650
	−75	0.219	0.0	0.400	0.368	0.350
Mpi	n	32	28	20	19	20
	100	0.938	0.964	1.0	1.0	1.0
	84	0.062	0.036	0.0	0.0	0.0
H_o		0.019	0.013	0.026	0.017	0.023
H_e		0.022	0.019	0.024	0.019	0.023
$P_{(99\%)}$		7.69	5.77	7.69	3.85	7.69
A		1.08	1.06	1.08	1.04	1.08
H′		1.767	1.408	1.829	1.336	1.795

Table 2. Locus-specifc (unbiased) heterozygosities in % (upper values) and inbreeding coefficients (lower values) as well as overall inbreeding coefficients (F_{IS}) for regional samples of brown hares from New Zealand (NZ) and Britain (UK).

	NZ-W	NZ-H	UK-W	UK-L	UK-D
Idh-2	–	–	5.0 −0.026	–	–
Pep-2	34.7 +0.086	50.6 +0.138	26.2 −0.176	–	22.4 −0.143
Acp-1	–	–	–	–	5.0 −0.026
Ada-2	31.0 −0.231	40.7 +0.556	43.7 −0.178	49.9 +0.029	47.5 −0.084
Es-1	34.7 +0.0451	–	49.2 −0.042	47.8 +0.095	46.7 +0.121
Mpi	11.9 −0.067	7.0 −0.067	–	–	–
overall F_{IS}	+0.095	+0.292	−0.117	+0.061	−0.014

found in the majority of central European brown hares (HARTL et al. 1993), and only one hare of the NZ-H sample had a new haplotype. This haplotype deviated from haplotype I by only one additional cleavage site, produced by XbaI at position 14.8 kb of the restriction map published in HARTL, et al. (1993). Values of haplotype (h) and nucleotide diversity (π) were zero for all RSs except for the NZ-H sample; that had an h-value of 28.57% and a π-value of 0.049%. Haplotype frequencies did not differ significantly between the RSs from Britain and New Zealand. Also, RS-specific h- and π-values of the samples from Britain and New Zealand were not significantly lower ($p > 0.05$, one-tailed Mann-Whitney U-tests) than in brown hares from 20 Austrian localities (cf. HARTL et al. 1993). Values of pairwise net nucleotide diversities

Table 3. Matrix of pairwise genetic distances and fixation indices (F_{ST}) among regional samples of brown hares from New Zealand and Britain. NEI's (1978) unbiased D values (first row) and modified ROGERS' distances (WRIGHT 1978) (second row) above the diagonal and F_{ST} values below. F_{ST} values were considered differing significantly from zero with significant allele frequencies for at least one locus in pairwise comparisons (significance based on Sequential Bonferroni procedure; nominal $\alpha = 0.05$, 45 tests). Significance (sig) or no significance (n. s.) is indicated below each F_{ST} value. For acronyms of regional samples see figure 1.

regional samples	(1)	(2)	(3)	(4)	(5)
NZ-W (1)	–	0.001 0.047	0.001 0.033	0.001 0.049	0.001 0.034
NZ-H (2)	0.052 sig	–	0.004 0.071	0.007 0.085	0.004 0.070
UK-W (3)	0.024 n. s.	0.109 sig	–	0.000 0.026	0.000 0.019
UK-L (4)	0.057 sig	0.167 sig	0.016 n. s.	–	0.000 0.019
UK-D (5)	0.026 n. s.	0.106 sig	0.003 n. s.	0.009 n. s.	–

Table 4. Comparison of indices of allozymic and mtDNA variability of regional samples of brown hares from New Zealand, Britain, Austria, and Bulgaria. Allozyme data are based on 49 loci and mtDNA RFLP data on 16 restriction endonucleases (see Material and methods). Means and range (in parentheses) of observed (H_o) and expected (H_e) average heterozygosity, Shannon-Weaver diversity index (H'), rate of polymorphism (P – 99% criterion), average number of alleles per locus (A), haplotype (h) and nucleotide diversity (π) are given for each group of local samples. sig = significance as determined by Mann Whitney tests (d. f. = 1) and sequential Bonferroni procedure ($\alpha = 0.05$), n. s.= not significant.

index	2 NZ and 3 UK regional samples (this study)	20 Austrian (HARTL et al. 1993) and 8 Bulgarian (SUCHENTRUNK et al. 2000) regional samples	sig.
H_o (%)	1.26 (0.9–1.7)	2.83 (1.7–4.2)	< 0.0001
H_e (%)	1.4 (1.0–1.7)	3.06 (2.3–4.7)	< 0.0001
H'	1.029 (0.66–1.29)	2.431 (1.73–3.66)	< 0.0001
$P_{(99\%)}$	4.90 (2.04–6.12)	11.15 (8.16–16.33)	< 0.0001
A	1.048 (1.02–1.06)	1.144 (1.08–1.2)	< 0.0001
H_e/P	0.314 (0.245–0.490)	0.279 (0.172–0.451)	n. s.
h (%)	5.7 (0–28.57)	15.9 (0–69.9)[1]	n. s.
π (%)	0.0098 (0–0.049)	0.0351 (0–0.184)[1]	n. s.

[1] mtDNA values calculated only from data of 18 Austrian regional samples

were zero for the British and NZ-W samples, and amounted to 0.0041% for all pairs involving the NZ-H sample. Respective pairwise values for the presently studied UK and NZ hares and the earlier studied brown hares from 20 Austrian localities (HARTL et al. 1993) ranged between 0.0–0.093%; this was within the range (0.0–0.113%) of net nucleotide diversity between local samples of brown hares from Austria (calculated from data produced in our laboratory, see HARTL et al. 1993).

Discussion

The levels of cross nuclear and mtDNA variability of brown hares from New Zealand and Britain are similar. This is in contradiction to the hypothesis of reduced gene pool variability in hares from New Zealand, owing to an assumed bottleneck during the period of their introduction. Possibly, unrecorded liberations of hares from diverse provenences in Europe in addition to those from the reportedly small number of founders in Australia (LEVER 1985) have increased the effective population size during the founder period in New Zealand. But such additional imports from Europe to New Zealand do not seem very likely, given the acclimatized hares already available in Australia for the Acclimatization Companies.

The essential point to explain the absence of reduced genetic variability in hares from New Zealand as compared to British hares is that brown hares from both New Zealand and Britain exhibit clearly lower allozymic variability than continental European populations. Theoretically, the small number of allozymic alleles found presently in the British brown hares could have been sampled by only few individuals. All common alleles (i. e., those with relative electrophoretic mobility 100/–100) of the British samples were also common in brown hares from diverse regions of continental Europe (HARTL et al. 1989, 1990, 1992, 1993, 1994; SUCHENTRUNK et al. 2000; SUCHENTRUNK et al. unpubl. data). But only 16% of all variant alleles found so far in continental European brown hares with the same set of loci (cf. HARTL et al. 1994; SUCHENTRUNK et al. 2000) occurred in the British samples. Quite several with wide distribution in continental Europe (Pgd^{129}, $Hk\text{-}2^{67}$, $Es\text{-}1^{-42}$, $Es\text{-}l^{-108}$, $Es\text{-}D^{141}$, Mp^{126}) are likely absent in British brown hares. And only one (7.1%) of all mtDNA haplotypes found so far in brown hares from central and southeastern Europe (HARTL et al. 1993, 1994; NADLINGER 1994; SUCHENTRUNK, unpubl. data) could be detected in British brown hares. But quite a number of regional samples of Austrian brown hares did also not display any mtDNA variability (HARTL et al. 1993). British sample sizes are probably too low for such a comparison. Nevertheless, absence of any mtDNA variability of the presently studied brown hares from Britain and the fact that only the standard European mtDNA haplotype I was found in Britain, as opposed to its significantly ($p < 0.0001$, exact Fisher's test) lower frequency on the continent, agrees with the interpretation of generally reduced genetic variability in British brown hares.

The low genetic variability of British brown hares might result from an "ancient" population bottleneck or long-term low effective population sizes associated with their colonization history. It has been hypothesized that brown hares were introduced in Roman times (cf. CORBET 1986; ARNOLD 1993). Deliberate releases of only few individuals or occasional escapes from farms in Roman times or earlier during the Mesolithic (?) or Neolithic occupation periods (cf. JONES and KEEN 1993) could have resulted in a poor gene pool variability of the pioneer population. In addition, a low survival rate owing to a high predation pressure by foxes and other predators, pathogenes, adverse weather conditions etc., could have hampered a quick population growth in the wild. Long-term low effective population size effectively reduces allelic variabililty and heterozygosity (e. g., CHAKRABORTY and NEI 1977; HEDRICK 1985). Contrary to the hypothesis of a deliberate introduction of brown hares to Britain in Roman

times, YALDEN (1982) and ROBERTS (1994) list brown hares along with mountain hares (*Leptus timidus*) as native to Britain since late-glacial times (see also GRIGSON 1983 for the Later Mesolithic excavation site of Cherhill, JONES and KEEN 1993, and citations therein). In this case, brown hares could have lost genetic diversity at low densities under adverse late-glacial climate, or later on in small isolated pockets. STUART (1982), however, lists "*Lepus* sp." as an element of the early Flandrian fauna of Star Charr, and considers only *L. timidus* definitly recorded as fossil in Britain (cf., MAYHEW 1975). As to our knowledge, fossil evidence of *Lepus europaeus* is uncertain in north-central and north-western mainland-Europe during the late-glacial period and early Flandrian, before the formation of the Channel (Strait of Dover, c.8000 years BP cf. e. g., JONES and KEEN 1993). Brown hares might not have roamed mid-latitude Europe during the early Flandrian and not have managed to arrive there before the formation of the Channel (see also CORBET 1986). Alternatively, genetic diversity could have been reduced in fragmented populations with long-term low densities in suboptimal habitats after woodland regeneration in the post-Roman period. But it seems that the distribution of wooded and non-wooded land in Britain has not been altered much in the post-Roman period (ROBERTS 1994).

The low allozymic diversity of British brown hares unlikely results from recent inbreeding in regional populations. This is indicated by quite normal locus-specific heterozygosities, lack of heterozygote deficiencies, and the generally low or even negative inbreeding coefficients. This interpretation is also supported by the absence of a significant gene pool substructuring. Allele frequencies of British brown hares do not differ much across regions. Insignificant fixation indices (F_{ST}) and genetic distance values indicate absence of drift effects among local populations. Obviously, the low amount of genetic variability contained in British brown hares is partitioned among individuals within local populations rather than across larger geographic ranges. The Acp-1^{50} allele occurred exclusively in the Scottish sample and was not found in a large number of brown hares from many regions in continental Europe. It might result from a recent local mutation.

Differentiation between the gene pools of British and central European (Austrian) brown hares (cf., HARTL et al. 1993) is negligible, and virtually nil when based on the detected mtDNA haplotypes. The corresponding pairwise NEI's (1978) unbiased D values (0.000–0.005) fall within the range encountered among local populations from Austria (e. g., HARTL et al. 1993). Despite their conventional subspecific position (*L. e. occidentalis*, DE WINTON, 1898), British brown hares represent only a genetically depauperate version of brown hares from continental Europe. This is confirmed by the absence of any other mtDNA haplotype apart from haplotype I, which has a phylogenetically central position in brown hares and is most widespread in central Europe (HARTL et al. 1993; SUCHENTRUNK, unpubl. data). As indicated by the low genetic distances, no significant genetic drift has occurred between British and continental European brown hare populations. As regards mtDNA, we cannot draw any conclusions on differentiation among the regions studied in Britain, because of too low sample sizes for two regions. Also, the present data do not permit any conclusion as to origins of the British brown hares. This might be achieved by comparing regional population samples and continental European samples with a highly resolving molecular marker system (e. g., microsatellites, mitochondrial d-loop sequences).

The lack of distinct gene pool structuring and the poor allozymic diversity of British brown hares suggest that a relatively high proportion of variant alleles was sampled by the few individuals that supposedly constituted the founder populations in New Zealand. Theoretically, all currently found alleles of the British brown hares could have been contained in the founders.

In New Zealand, hares spread rapidly after their introduction (FLUX 1990). Presently, they occupy large ranges including practi-

cally all types of habitats on the North and South Islands. Although they commonly do not reach those high densities as in Europe, they even have established successful populations in sub-alpine (PARKES 1984) and rather harsh alpine environments (FLUX 1967). Their successful spread in New Zealand might have been particularly favoured by a low level of parasitic or infectuous diseases, a long-term low level of agrochemistry, and relatively little intensification of farming machinery, little road mortality, low predation pressure on adults etc. (see also FLUX 1990). This rapid increase of the founder populations on both main islands, together with repeated imports and subsequent translocations within and between the islands by diverse naturalization companies (FLUX 1990) probably prevented severe loss of genetic variability. Generally, quick population increases following a bottleneck, as was reported for the founder populations of Phillip Island (ROLLS 1969) and New Zealand (FLUX 1990), are counteracting reduction of allelic variability in founder populations (e. g., NEI et al. 1975).

As expected, particularly rare alleles (Idh-2^{130}, Acp-1^{50}) of British brown hares are absent in hares from New Zealand, whereas the common British alleles are common in New Zealand too. Interestingly, the Mpi^{84} allele of both populations from New Zealand was neither present in the British brown hares nor in any of over 900 brown hares from diverse regions of continental Europe studied so far (HARTL et al. 1994; SUCHENTRUNK et al. 2000; SUCHENTRUNK, unpubl. data). It might stem from a recent mutation in New Zealand or Australia. Alternatively, it could be present in regions of Britain or anywhere else in Europe that were not yet sampled, but wherefrom hares were shiped to Australia. The same interpretations apply to the exclusive occurrence of mtDNA haplotype V in the Harpa/Avoca catchment on the South Island of New Zealand. This haplotype is phylogenetically closely related to the basal mtDNA haplotype I of European brown hares, and its evolution can be explained by only one base substitution.

The two local populations on both main islands of New Zealand have differentiated little since their foundations over one hundred years ago. The nuclear and mitochondrial gene pools of hares from New Zealand are very similar to those of British brown hares. Lack of data of allele frequencies in the source population, unknown effective population sizes, and repeated translocations of hares within and between the North and South Islands, that might have changed allele frequencies, prevented us to compare the presently observed allele frequencies with theoretical frequencies as resulting from drift simulations (see e. g., FITZSIMMONS et al. 1997). But both NEI's (1978) D and F_{ST}-values between British and New Zealand populations largely fall within the ranges encountered among regional populations in Europe (D = 0.000–0.019, F_{ST} = 0.00–0.124, re-calculated from adjusted data sets of 49 loci, cf. HARTL et al. 1993; SUCHENTRUNK et al. 2000). In fact, only the F_{ST}-value for the NZ-H and UK-L samples slightly exceeds the range for regional samples from mainland Europe. This marginally increased level of differentiation between these two populations apparently results from the absence of the Pep-2^{104} allele in UK-L and the Es-1^{-75} allele in NZ-H. But in general, we cannot see any marked reorganization in the cross gene pool of hares from New Zealand as compared to British brown hares. Rapid population increases in the local founder populations, repeated releases, and multiple transfers of hares by naturalization companies (FLUX 1990) likely prevented strong genetic drift. However, in spite of apparently well adapted populations in Britain and New Zealand (SUCHENTRUNK et al. 1998), brown hares from these countries harbour less genetic resources for adaptation to future environments than populations from mainland Europe.

Acknowledgements

We are grateful to Dr J. E. C. FLUX (Lower Hutt), Dr J. P. PARKES (Christchurch), Mr HUNTER (Masterton, New Zealand), Dr S. TAPPER (Fording-

bridge), Mr A. Puttik (Middle Woodford, Wiltshire, England), Mr Brockless (Loddington, Leicestershire, England), and to "Bain of Tarves – Catering Butchers, Game and Venison Exporters" (Tarves, Aberdeenshire, Scotland) for organizing shoots and supplying hares. "Manaaki Whenua – Landcare Research" (Lower Hutt and Christchurch, New Zealand) and "The Game Conservancy Trust" (Fordingbridge, Hampshire, England) provided facilities. Mrs M. M. Flux (Belmont, New Zealand), Mr M. Coleman (Christchurch), Mrs M Trebilco, Mr J. Long, Mr S. Moreby, and Mr C. Stoate (Fordingbridge) helped with the organisation work or provided otherwise valuable help. Dr K. Nadlinger (Vienna) helped with comparisons of mtDNA haplotypes found presently and earlier. Priv-Doz Dr D. Heinrich and Mrs R. Lücht (Institut für Haustierkunde, University of Kiel, Germany) helped with archeozoological literature search, and Mr A. Körber (Research Institute of Wildlife Ecology, Vienna Veterinary University, Austria) created the figure.

Zusammenfassung

Geringe Allozym- und mtDNA-Variabilität bei neuseeländischen und britischen Feldhasen (*Lepus europaeus*) – eine Folge von Flaschenhälsen?

Untersucht wurde die Allozym- und mtDNA-Variabilität bei britischen und neuseeländischen Feldhasen (*Lepus europaeus*), um die Hypothese eines Variabilitätsverlustes bei neuseeländischen Hasen infolge eines Flaschenhalsereignisses („Gründer-Effekt") bei ihrer Einbürgerung im 19. Jahrhundert zu überprüfen. Bei 119 Hasen aus drei britischen und zwei neuseeländischen Stichprobengebieten wurde mittels horizontaler Stärkegelelektrophorese ihre allelische Variabilität an 52 Strukturgenloci ermittelt. Bei 36 Hasen wurde anhand von 16 6-Basenschneidenden Endonukleasen der Restriktionsfragmentlängenpolymorphismus (RFLP) in der gesamten mitochondrialen DNA (mtDNA) analysiert. Alle Indices der Allozym- und mtDNA-Variabilität lagen bei den neuseeländischen Stichproben im Bereich jener der britischen Feldhasen. Somit kann die Hypothese zu Verlusten an genetischer Variabilität bei neuseeländischen Hasen im Vergleich zu den britischen nicht aufrecht erhalten werden. Ausgeprägte genetische Drifteffekte zwischen britischen und neuseeländischen Feldhasen konnten ebenfalls nicht festgestellt werden. Jedoch zeigten alle fünf untersuchten regionalen Stichproben signifikant geringere Allozym-Variabilität als Feldhasen vom europäischen Kontinent. Dies läßt die Vermutung eines Verlustes der genetischen Variabilität bei den britischen Feldhasen im Verlaufe ihrer Besiedlungsgeschichte zu. Die nominell als eigene Unterart geführten britischen Feldhasen (*L. e. occidentalis*, De Winton; 1898) erwiesen sich lediglich als genetisch verarmte Varianten der kontinental-europäischen Feldhasen.

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Mamm. biol. **66** (2001) 60–62
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

First record of *Rattus rattus* in Botswana

By K. M. Helgen

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Receipt of Ms. 06. 07. 2000
Acceptance of Ms. 28. 09. 2000

Key words: *Rattus rattus*, Botswana, bubonic plague, commensalism, sylvatic plague

The murid rodents *Rattus rattus* (Linnaeus, 1758) and *Rattus norvegicus* (Berkenhout, 1769) are widely distributed in Africa (Kingdon 1974; Rosevear 1969; Skinner and Smithers 1990) and indeed boast nearly cosmopolitan distributions (Musser and Carleton 1993). These ubiquitous commensals are usually associated with human habitation. Several authors have noted the absence of these rodents from Botswana (Davis 1946; de Graaff 1981; Skinner and Smithers 1990), which may be the last African nation for which there is no published record of either species' presence.

I spent September to December 1999 in Botswana, devoting some time to trapping and preserving rodents, especially in areas inhabited by people, both urban and rural. Four specimens of *Rattus rattus* were trapped in the eastern sector (Fig. 1). All of them were captured in close association with human habitation: one from under a kitchen stove in Mmathubudukwane (Museum of Comparative Zoology No. 62631), a rural village near the border with South Africa; one in a granary at Francistown (MCZ 62632); and two from a basement in Ramotswa near Gaborone (MCZ 62633–62634).

These specimens of *Rattus rattus* (Tab. 1) most likely represent an invasion into Botswana that occurred within the last thirty years. Smithers (1971) noted that it was not recorded in the country despite 5 years of effort during the 1964–1969 Botswana Mammal Survey. He labeled *Rattus rattus* as a "species not recorded but which may occur," noting that despite the absence of specimens from Botswana, it had been trapped nearby at Kariba Dam in Rhodesia (now Zimbabwe), which lies on a railway line that extends into Botswana. Considering its now long-term presence in neighboring South Africa as well, it is rather surprising that the black rat did not invade Botswana earlier. Other common synanthropic rodents have been similarly slow to colonize the country; *Rattus norvegicus* has not been recorded, and Smithers (1971) listed only a single specimen of *Mus musculus* trapped in Botswana. De Graaff (1981) suggested that the aridity of much of the country precludes invasion by exotic rodent commensals like *Rattus*. Other relevant factors discouraging colonization probably include the extremely low population density of the country, its distance from port cities, and, perhaps, the diversity of native rodents

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Table 1. Specimens of *Rattus rattus* collected in Botswana. Measurements are given in millimeters as Total Length – Tail Length – Hindfoot Length – Ear Length.

MCZ No.	Age	Sex	Measurements	Locality	Date collected
62631	adult	M	410–220–35–18	Mmathubudukwane	28 September 1999
62632	adult	F	381–209–35–25	Francistown	6 December 1999
62633	adult	F	383–207–36–25	Ramotswa	15 December 1999
62634	juvenile	M		Ramotswa	15 December 1999

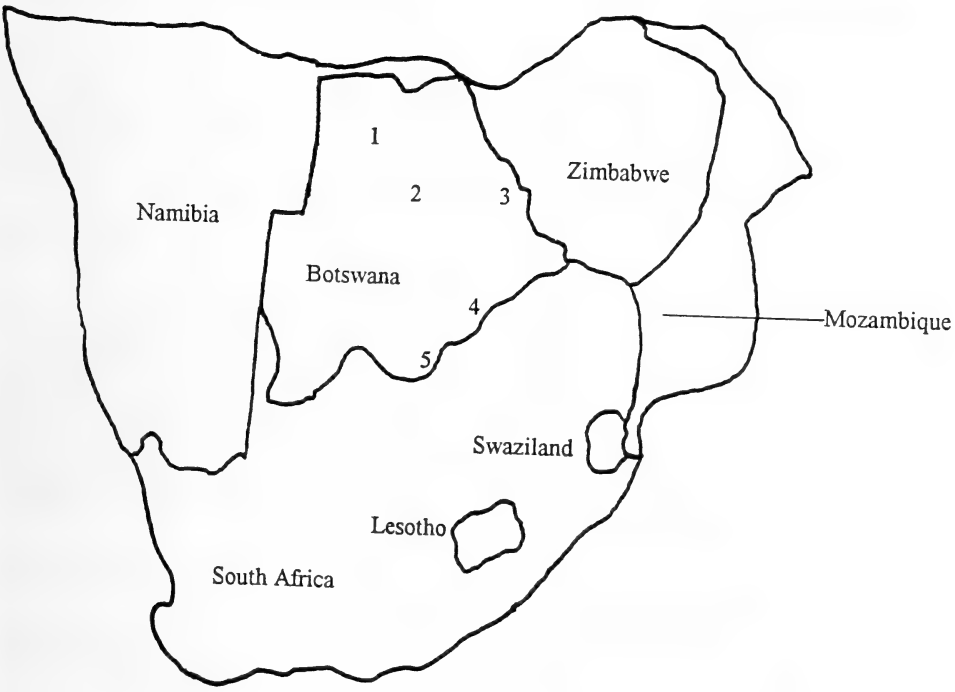

Fig. 1. Localities described in the text; 1, Jao, a small village in the Okavango Delta; 2, vicinity of Toromoja and Xhumo; 3, Francistown, 4, Mmathubudukwane and 5, Ramotswa, sites where *Rattus rattus* has been recorded.

acting as human commensals. Most areas of the country seem to remain free of *Rattus rattus*; at one such locality, a remote village in the Okavango Delta named Jao, I trapped four native rodents – *Aethomys chrysophilus* (de Winton, 1897), *Mastomys coucha* (Smith, 1834), *Saccostomus campestris* Peters, 1846, and *Graphiurus murinus* (Desmarest, 1822), living in or entering huts and outbuildings. The most common rodent in Botswana is the multimammate mouse *Mastomys coucha*, which was caught in both wild and settled areas in the Okavango Delta, the northern Kalahari region, and the eastern sector (from Francistown to the Gaborone area).

Rattus rattus has not been recorded from any areas but the thickly settled eastern sector, and is probably unlikely to invade the Okavango Delta or the more sparsely settled and arid Kalahari region of Bostwana's interior. Despite reports of *Rattus rattus* from the Boteti District that were made by rodent surveyors following the bubonic plague epidemic in Xhumo and Toromoja in 1989–90 (Mokgweetsinyana pers. comm.),

there is no evidence of its existence there. No voucher specimens were preserved, but I have examined survey records at the headquarters of the Ministry of Health in Francistown, and the recorded measurements clearly demonstrate that the animals were not *Rattus* but misidentified *Mastomys*. *Rattus* was thus almost certainly not involved in this epidemic, which as DAVIS (1946) noted for a previous epidemic in the region, was a case of sylvatic plague, implicating native *Tatera* as a permanent reservoir and *Mastomys*, which travels between *Tatera* colonies and human dwellings, as a vector for transmission of plague fleas.

Acknowledgements

I am thankful to S. MOKGWEETSINYANA for access to documents at the Ministry of Health of Botswana, to S. MATALAOTE for administrative assistance regarding permits and travel, to M. MOTSHOME for assistance in collecting specimens, and to D. WILSON for his help in preparing this manuscript. Research costs were defrayed in part with a Barbour Fund grant from the Museum of Comparative Zoology at Harvard University. Collecting was carried out under permit no. WP RES 3/2 XIV (33) issued by the Department of Wildlife and National Parks, Botswana.

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Mamm. biol. **66** (2001) 63–64
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Mammalian Biology
Zeitschrift für Säugetierkunde

Mitteilung der Gesellschaft

75. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde vom 23.–27. September 2001 in Berlin

Einladung

Die 75. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde wird von Sonntag, dem 23. September bis Donnerstag, dem 27. September 2001 in Museum für Naturkunde und im Zoologischen Garten zu Berlin ausgerichtet.

Vorläufiges Programm

Sonntag, 23. September	Anreise ab 16.00 Uhr: Vorstandssitzung der DGS ab 19.00 Uhr: zwangloser Begrüßungsabend
Montag, 24. September:	09.00 Uhr: Begrüßungen 09.30 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt: „Tiergartenbiologie“ 14.00 Uhr: Posterdemonstration 15.00 Uhr: Kurzvorträge 16.00 Uhr: Mitgliederversammlung der DGS 20.00 Uhr: Öffentlicher Abendvortrag
Dienstag, 25. September:	09.00 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Ökomorphologie“. 14.00 Uhr: Posterdemonstration 15.00 Uhr: Kurzvorträge 16.30 Uhr: Führung durch den Zoologischen Garten 19.00 Uhr: Geselliger Abend im Zoologischen Garten
Mittwoch, 26. September:	09.00 Uhr: Vorträge zu freien Themen 14.00 Uhr: Posterdemonstration 15.00 Uhr: Kurzvorträge 18.00 Uhr: Posterprämierung
Donnerstag, 27. September:	Wissenschaftliche Exkursion, wahlweise a) Deutsch-Polnischer Nationalpark „Unteres Odertal“ (in Privatwagen oder Kleinbussen) b) Führung durch den Tierpark Berlin-Friedrichsfelde

1616-5047/01/66/01-063 $ 15.00/0.

Alle Interessenten, Mitglieder und Nichtmitglieder, sind zu dieser Jahrestagung herzlich nach Berlin eingeladen. 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 an den 1. Vorsitzenden der Deutschen Gesellschaft für Säugetierkunde, Prof. Dr. R. Schröpfer, Universität Osnabrück, FB Biologie/Chemie: Ethologie, Barbarastr. 11, 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).

Wir bitten um die Anmeldung von Kurzvorträgen (15 min + 5 min Diskussion) und Posterdemonstration 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. G. B. Hartl, Institut für Haustierkunde, Universität Kiel, Olshausenstr. 40–60, D-24118 Kiel an. Der Anmeldung ist eine informative Kurzfassung beizufügen. Aus ihr sollen die Fragestellung, Methoden, Ergebnisse und die daraus gezogenen Schlußfolgerungen hervorgehen. Alle angenommenen Kurzfassungen werden in einem Sonderheft von „Mammalian Biology" publiziert.

Die Kurzfassungen sollen nach folgendem Schema abgefaßt werden:

Maximal einseitig bei 1,5-zeiliger Schrift!

Deutscher Titel

– Leerzeile –

englischer Untertitel (Im Titel mit Kleinbuchstaben schreiben. Beispiel: Lingual and biting responses …; bitte ggf. einen „native speaker" konsultieren!)

– Leerzeile –

Autorenname/n (Großbuchstaben) mit Adresse (Beispiel: M. MÜLLER und H. WEBER, Institut für Zoologie, Universität …)

– Leerzeile –

Text.

Die Kurzfassung bitte unbedingt ausgedruckt zusenden. Zusätzlich eine Diskette (3,5″, IBM-kompatibler DOS-PC) mit der Kurzfassung in Form eines Word-Dokuments, Word Perfect- oder ASCII-Files beifügen. (Bitte diese Datei nicht formatieren.)

Die Maße für die Poster werden im Rundbrief 2/2000 bekanntgeben.

Mit Fragen zum Tagungsort und zur Organisation wenden Sie sich bitte an den Geschäftsführer der DGS, Prof. Dr. G. B. Hartl, Institut für Haustierkunde, Universität Kiel, Olshausenstr. 40–60, D-24118 Kiel, Tel. +49-(0)4 31/8 80 45 07, Fax +49-(0)4 31/8 80 13 89, e-mail: ghartl@ifh.uni-kiel.de.

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Mammalian Biology

Zeitschrift für Säugetierkunde

URBAN & FISCHER Verlag
Jena/Germany

ISSN 1616-5047
Mamm. biol. · 66(2001)1 · 1-64

Contents

Abstracted/Indexed in

Animal Breeding Abstracts/Biological Abstracts/Biological Environmental Sciences/BIOSIS database/Current Advances in Ecological and Environmental Sciences/Current Contents - Agriculture, Biology & Environmental Sciences/Dairy Science Abstracts/Fisheries Review/Helminthological Abstracts/Index Veterinarius/Key Word Index to Wildlife Research/South Pacific Periodicals Index/Veterinary Bulletin/Wild Review (Fort Collins)/Zoological Record

Mammalian Biology

Zeitschrift für Säugetierkunde

2·2001

URBAN & FISCHER

ISSN 1616-5047
Mamm. biol. · 66(2001)2 · 65-128
www.urbanfischer.de/journals/mammbiol

Mammalian Biology

Zeitschrift für Säugetierkunde

IMPRESSUM
Publisher: Urban & Fischer Verlag GmbH & Co. KG, Branch Office Jena, P.O. Box 100537, D-07705 Jena, Germany; Phone: ++49(0)3641/626-3, Fax: ++49(0)3641/62 65 00, E-mail: journals@urbanfischer.de
Advertisement bookings: Enquiries should be directed to Urban & Fischer Verlag, Advertising Manager: Sabine Schröter, P.O. Box 100 537, D-07705 Jena, Germany;
Phone: ++49(0)3641/62 64 45, Fax: ++49(0)3641/62 64 21.
Advertising rates: The price list from January 1, 2001 is effective at present. **Distribution and subscription agency:**
For customers in the German speaking countries: Please turn to your bookshop or to Urban & Fischer Verlag, Aboservice und Vertrieb: Barbara Dressler, Löbdergraben 14a, D-07743 Jena, Germany; Phone: ++49(0)3641/62 64 44, Fax: ++49(0)3641/62 64 43, E-mail: k.ernst@urbanfischer.de
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Terms of delivery (2001): 1 volume consisting of 6 issues.
Subscription rate (2001): DM 498.00*/GBP 200.00. Preference price for personal subscribers: DM 150.00*/GBP 60.00. All prices quoted above are exclusive postage. *Suggested list price. Price are subject to change without notice. Personal subscription orders must be addressed directly to the publisher Urban & Fischer in Jena resp. to The Nature Publishing Group. Subscriptions at a personal rate must include the recipient's name and mailing address. An institutional or business address is only accepted, if the institute or firm has a subscription as well. Personal subscribers can pay by personal cheque or credit cardmentioned below. US dollar prices are converted at the current exchange rate.
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Subscription information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting and printing, binding: druckhaus köthen GmbH

∞ As of vol. 61, number 1 (1996) the paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Printed in Germany

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Mamm. biol. **66** (2001) 65–83
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Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Comparison of the social behaviour of captive sympatric peccary species (genus *Tayassu*); correlations with their ecological characteristics

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Receipt of Ms. 03. 01. 2000
Acceptance of Ms. 10. 08. 2000

Abstract

Comparison was made of the social behaviour of two congeneric peccary species, the white-lipped (*Tayassu pecari*) and the collared peccary (*T. tajacu*), coexisting in South American rain forests and observed in captivity. In the former species, herd cohesion is strong, and strangers generally are violently attacked. White-lipped peccaries have 2–3 times more contacts with partners of their herd than collared peccaries. In many social behavioural situations, the dominant female is the most active individual in the white-lipped peccary herd, whereas the dominant male is the focal member of the social unit in the collared peccary. Subordinate and subadult males participate in all social behaviour, including sexual, and are very well integrated into the white-lipped peccary herd. In contrast, subordinate collared peccary males are more or less neutral and peripheral individuals. Unlike the latter species, aggressiveness is noticeable in most behaviour of the white-lipped peccary; the dominant male is the main effector of these agonistic contacts, which are frequent and intense. In this species, both sexes belong to only one hierarchic order, with males always superior to females. Conversely, in the collared peccary, there are two distinct monosexual hierarchic orders, and the females dominate the males. These interspecific differences, as well as the total lack of ground marking in the white-lipped peccary, fit well the ecological characteristics of both species: the white-lipped peccary lives in wandering, large multiple-male herds, and the collared peccary in small stable and locally resident troops.

Key words: *Tayassu*, social behaviour, peccaries

Introduction

Unlike species in open habitats, terrestrial mammals of tropical forests are generally encountered alone or in small social units. While there are very few exceptions to this ecological rule, the Bovids (Estes 1974) and the Suiforms (Frädrich 1974; Barrette 1986; Caldecott et al. 1993) each have one or more gregarious forest species on every continent. There has been no specific study to date to examine the behavioural mechanisms underlying the formation of permanent social groups in closed terrestrial habitats.
Two peccary species (Tayassuidae), the white-lipped peccary (*Tayassu pecari* or

1616-5047/01/66/02-065 $ 15.00/0.

WLP) and the collared peccary (*T. tajacu* or CP), coexist in Central and South American rain forests. Both belong to the same genus and share many morphological and physiological characteristics; their basic behaviour can therefore be considered broadly similar. Both species live all year long in mixed social groups. This fact probably distinguishes the peccaries from most other Suiforms (Bigourdan 1948; Gundlach 1968; Frädrich 1974; Beuerle 1975; Caldecott et al. 1993).

In reality, the two peccary species differ markedly in the size and composition of social units, and in range utilization. White-lipped peccaries are generally encountered in large and apparently nomadic herds, while collared peccaries live in small permanent troops. The study of their general behaviour permits greater qualitative and quantitative understanding of this divergence in terms of life style parameters and social structure.

Until now, the collared peccary has mainly been studied from animals originating in the semi-desert southwestern portions of the U. S. A. Nevertheless, there is some information about this species in its forest environment (Kiltie and Terborgh 1976, 1983; Robinson and Eisenberg 1985; Bodmer 1989; Hernandez et al. 1995; Peres 1996). Much of the biology of the white-lipped peccary remains to be described.

Given that much of the behaviour of Artiodactyls, even social, is of an innate nature and appears among captive animals as well as in the wild, captive studies, at least in adequate enclosures, can provide a detailed yet accurate view of the context of each behaviour in the repertoire and how it is used. Apart from the increase in the knowledge of the biological characteristics of these peccaries, such a study permits a comparative analysis of their behaviour, which will help us to understand how these two closely related species could coexist in the same forest habitats. The study also has practical value in that captive peccaries are bred in many parts of the world to replace stocks lost to hunting. Knowledge of their natural behaviour facilitates the husbandry for this endeavour.

Material and methods

The behavioural data are derived almost exclusively from observations of semi-captive animals held at the field station of the Institut National de la Recherche Agronomique (I. N. R. A.), near Kourou, French Guiana. Each social group was maintained in a 1,000-m^2 enclosure established under an existing forest canopy, surrounded by a 2m-high wire electric fence, and equipped with 4 food tubs and 2 drinking troughs permitting bathing.

Initial social units were comprised of young animals (5 CP, 4 WLP) captured by local hunters, most often at an age of several days, and hand-reared in groups until weaning. Subsequently, each group was allowed to evolve by itself (including births and growth of the young), apart from a single daily supply of food, and occasional cleaning. From 1992 to 1994, the CP group increased steadily from 7 (2 adult males, 3 adult females, 2 juvenile males) to 16 individuals (4 adult males, 3 adult females, 1 subadult male, 4 subadult females, 2 juvenile males, 2 juvenile females). The WLP group almost tripled during the same period, progressing from 4 animals (1 adult male, 3 adult females) to 11 (2 adult males, 3 adult females, 1 subadult male, 1 juvenile male, 4 juvenile females). All individuals were identified by ear-tags or coded ear-notches.

Observations were made in both the main rainy (January to June) and dry seasons (July to December). Sampling was undertaken when animals were most active, i. e. in early morning and late afternoon. The observer stood at a distance from which all of the animals could be viewed simultaneously without any interference with their behaviour. Data were collected by observing each troop member in turn as a focal animal during 30 consecutive minutes. Excluding data on newborn infants, a total of 1,101 individual-hour units of CP observations and 1,136 individual-hour units of WLP were recorded.

The different behaviour of each species has been described elsewhere (Dubost 1997). The social behaviour included here is only that involving an approach or physical contact between 2 individuals for peaceful interactions, agonistic or sexual purposes. Given that the whole group was almost always gathered in a small area, it was easy to observe and count all interactions occurring between two individuals. During agonistic contacts, the relative ranking of one individual relative to another was determined, according to the behaviour displayed by both partners. Cases of equality were defined as occasions where encounters finished with neither individual clearly dominant

over the other. Most social behaviour involved only two individuals at the same time. Nevertheless, for resting, all individuals composing the group rejoined by an animal were taken into account without any further distinction. Data on behaviour involving no partner, but still playing a social role, are taken from Dubost (1997). These included long-range communication and olfactory marking. Field data on these species have been collected during many expeditions to French Guiana between 1965 and 1996.

Comparisons were made using X^2, Student t test, or non-parametric Mann-Whitney U test. Correlations were examined non-parametrically using Spearman rank coefficient rs.

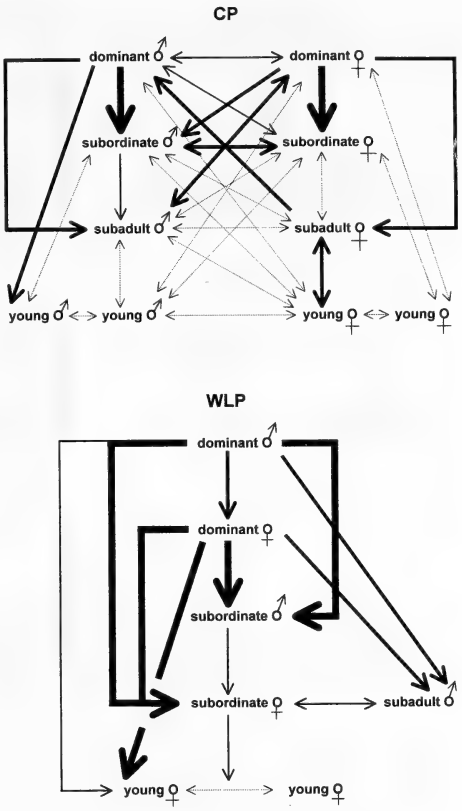


Fig. 1. Schema of the hierarchical organization of collared (CP) and white-lipped peccaries (WLP), according to the relative importance of agonistic behaviours performed by one individual towards another (arrows). Dominant and subordinate: > 2 years; subadult: > 1 year; young: < 1 year.

Results

Social organization

Hierarchical relations within the group

Here I consider both direct agonistic interactions, which indicate if one animal is dominant or subordinate to another, and situations where one individual avoids an interaction by modifying its initial direction or position to make way for another (e. g. standing up and leaving its resting place). As shown in figure 1, the dominance hierarchies are quite different for the two species.

There is a clear dominance hierarchy within males and females in the CP. Dominance rank is inversely proportional to age. However, the dominance hierarchy was less evident in females than males (4 of equal rank out of 39 cases for females vs 0/24 for males). There were no cases where two adult males were apparently equal to each other during encounters. In contrast, younger males show a high rate of equal rankings (Tab. 1). Between adults of different sexes, cases of equality are frequent (45.6% of encounters), as they are between a juvenile male and an adult or a juvenile female (41.7–60%), or between two juvenile males or females (44.4–45.5% of cases). On the whole, cases of equality are far more frequent between partners of different sexes than within the same sex.

Agonistic interactions between females are the most frequent (1.26 times the expected frequency computed using the ratio of female partners to the total number of potential partners for this behaviour). Those between a male and a female are the least common and occur approximately at the expected frequency. Females could be slightly dominant over males: adult females dominated 64.5% of the 31 contacts observed with adult males ($X^2 = 0.80$; df = 1; not significant), and 78.6% of their 14 interactions with one juvenile male ($X^2 = 1.80$; df = 1; not significant); one juvenile female dominated one adult male in 2/4 cases.

In the WLP, in contrast, all individuals of any age or either sex are subject to a single precise hierarchical system, in which dominance

Table 1. Percentage of agonistic encounters during which the two individuals are equal to each other. (CP – collared peccary; WLP – white-lipped peccary).

	CP	WLP
Male-male interactions		
adult male-adult male	0.0%	0.0%
adult male-juvenile male	20.0%	0.0%
juvenile male-juvenile male	44.4%	0/0
Total	(9/58) 15.5%	(0/101) 0.0%
Female-female interactions		
adult female-adult female	10.3%	0.0%
adult female-juvenile female	20.0%	0.0%
juvenile female-juvenile female	45.5%	1/1
Total	(11/60) 18.3%	(1/129) 0.8%
Male-female interactions		
adult male-adult female	45.6%	3.2%
adult male-juvenile female	0/4	0/0
juvenile male-juvenile female	60.0%	?
adult female-juvenile male	41.7%	0.0%
Total	(42/95) 44.2%	(5/207) 2.4%

interactions are marked and frequent, even between individuals of very different ranks (Fig. 1). Agonistic interactions between two individuals generally reveal a clear dominance of one of them. Cases of equalities are non-existent or very rare within each sex (0/101 among males, 1/129 among females), as well as between adults of different sexes (5/154 = 3.2%; Tab. 1). There are therefore no or very few events where the relative status of each individual is not respected. Thus, contrasts in frequencies of equalities between the two species are always evident in each age or sex category.

In contrast to the CP, the most frequent agonistic interactions in WLP occur between males (1.39 times the frequency expected) and the least frequent between females (0.86 times the frequency expected). Adult males dominate females in 72.7% of the 154 cases observed ($X^2 = 15.84$; df = 1; $P < 0.001$). As expected, status differences are less evident between juvenile or subadult males and adult females, appearing in only 60.4% of the 53 encounters ($X^2 = 0.76$; df = 1; not significant).

In both peccary species, all 4 subordinate adult females were elevated to the top of the hierarchy immediately after giving birth. They subsequently became equal to the dominant CP female, and to the dominant WLP male.

Comparative role of different individuals within the group

Rates at which naso-body contacts, chin-layings, and mountings are seen in each social category (in average number per animal, per hour of observation and per potential partner) are similar in the two peccary species (respectively, rs = 1.0, 0.95 and 0.90; $P < 0.01$ and < 0.05; n = 6). These behaviours are most frequent in adults: generally, rates are highest in the dominant male, next highest in females, third highest in subordinate males (Fig. 2).

For mounts occurring outside oestrus, the hierarchical order is respected among CP males. The dominant male is implicated in such behaviour 3 times more often than subordinate males: a rate of 0.027 vs 0.009 (U = 0; $P = 0.005$; $n_1 = 4$; $n_2 = 6$), and juveniles never. In the WLP, on the contrary, subordinates are involved as often or even more often than the dominant male: respectively 0.077 vs 0.067 (U = 1; $P < 0.05$; $n_1 = 3$; $n_2 = 5$) and the juveniles also participate in this behaviour (0.018). Thus, mounting has a lower hierarchical value in WLP than in CP.

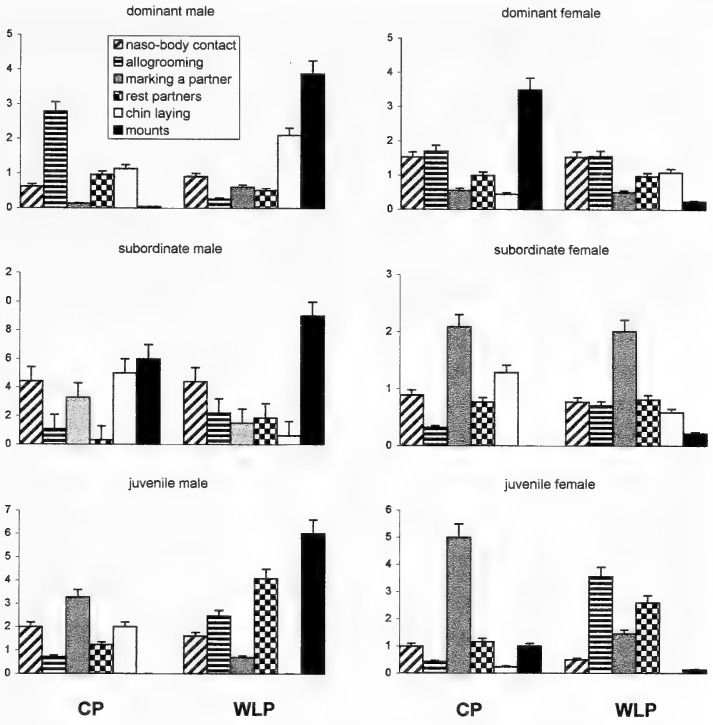


Fig. 2. Number of social behaviours or rest partners recorded in the collared peccary (CP) and white-lipped peccary (WLP) for each member of the troop per animal, per hour of observation and per potential partner (mean ± standard error).

The relative frequencies of other behaviour vary among the different social categories from one species to the other, but without any correlation (rs varying from 0.1 to 0.8; n = 6; not significant). Nevertheless, some specific features appear, as shown in figure 2.

Allogrooming and marking a partner are particularly indicative of the role played by an individual in group cohesion. The major role is held by the dominant male in the CP (respectively, 0.399 vs 0.041–0.238 and 0.558 vs 0.049–0.326 in the other animals: $U = 8$; $P < 0.01$; $n_1 = 4$; $n_2 = 20$) and by the adult males and females in the WLP (respectively, 0.481–0.760 vs 0.152–0.217 and 0.468–0.802 vs 0.091–0.142 in the other animals: $U = 6$; $P < 0.01$; $n_1 = 5$; $n_2 = 14$).

CP females show an increased frequency of social play and number of rest partners compared to males: respectively, 0.030–0.033 vs 0.008–0.029, and 0.220–0.251 vs 0.080–0.193 ($U = 0$; $P < 0.001$; $n_1 = 11$; $n_2 = 13$). In the WLP, subordinate males and juvenile females are more involved in these behaviours than are other individuals: respectively, 0.076–0.102 vs 0.047–0.084 ($U = 22$; $P < 0.025$; $n_1 = 9$; $n_2 = 12$), and 0.392–0.414 vs 0.211–0.341 ($U = 0$; $P < 0.001$; $n_1 = 9$; $n_2 = 12$).

Agonistic behaviour is mainly performed by adults. Adult males and females are nearly equivalent in the CP: 0.073–0.081 vs 0.076 ($U = 32$; not significant; $n_1 = 8$; $n_2 = 12$). In the WLP, however, the dominant male is far more involved in such behaviour than the other adults: 0.288 vs 0.122–0.153 ($U = 0$; $P < 0.01$; $n_1 = 3$; $n_2 = 11$). In this species, the level of aggressiveness of each individual corresponds to its hierarchical rank.

As shown in figure 2, subordinate CP males have a limited social role, often restricted to

play or agonistic contact. They do not seem to have many partners for allogrooming, marking, resting or mounting. They live more or less as satellites to the troop. In contrast, subordinate WLP males are more involved in the various social behaviours than are the juvenile males ($U = 13$; $P = 0.025$; $n_1 = n_2 = 8$). Among the WLP males, they show the most intense contacts with the different partners of their social group, especially for allogrooming, play, resting and mounting, and they are very well integrated socially.

Performer and receiver of social behaviour

In both species, naso-body contacts are made mainly by the dominant male, the dominant female and the subordinate male; the dominant male is also the main receiver (46.1–54.5% of all behaviour performed). Thus, both species appear quite similar to each other ($rs = 0.77$; $P \sim 0.05$; $n = 6$).

Social category and marking of partners also show similar associations in the two species ($rs = 0.77$; $P \sim 0.05$; $n = 6$). This behaviour is frequently performed by the second ranking female, the dominant of both sexes being the principal receiver (66.5–77.4% of all behaviour performed).

The initiation of allogrooming shows an opposite association with social categories in the two species ($rs = -0.83$; $P < 0.05$; $n = 6$). In the WLP, such initiations are common in the dominant female and the subordinate male, and the main receivers are the dominant male (26.0%) and the adult females (an average of 18.3% each). In the CP, on the contrary, initiations are chiefly performed by the dominant animals of both sexes, especially the dominant male, without any particular receiver.

There are no noticeable differences between CP individuals in rest partners, the dominant individual of each sex being both the principal donor and receiver. On the contrary in the WLP, subordinate adult males and juvenile females often join the other animals, particularly the dominant male (25.5%). Thus, the same individuals do not play the same social role in the two species, as shown by the lack of correlation between them ($rs = 0.60$; $n = 6$; not significant).

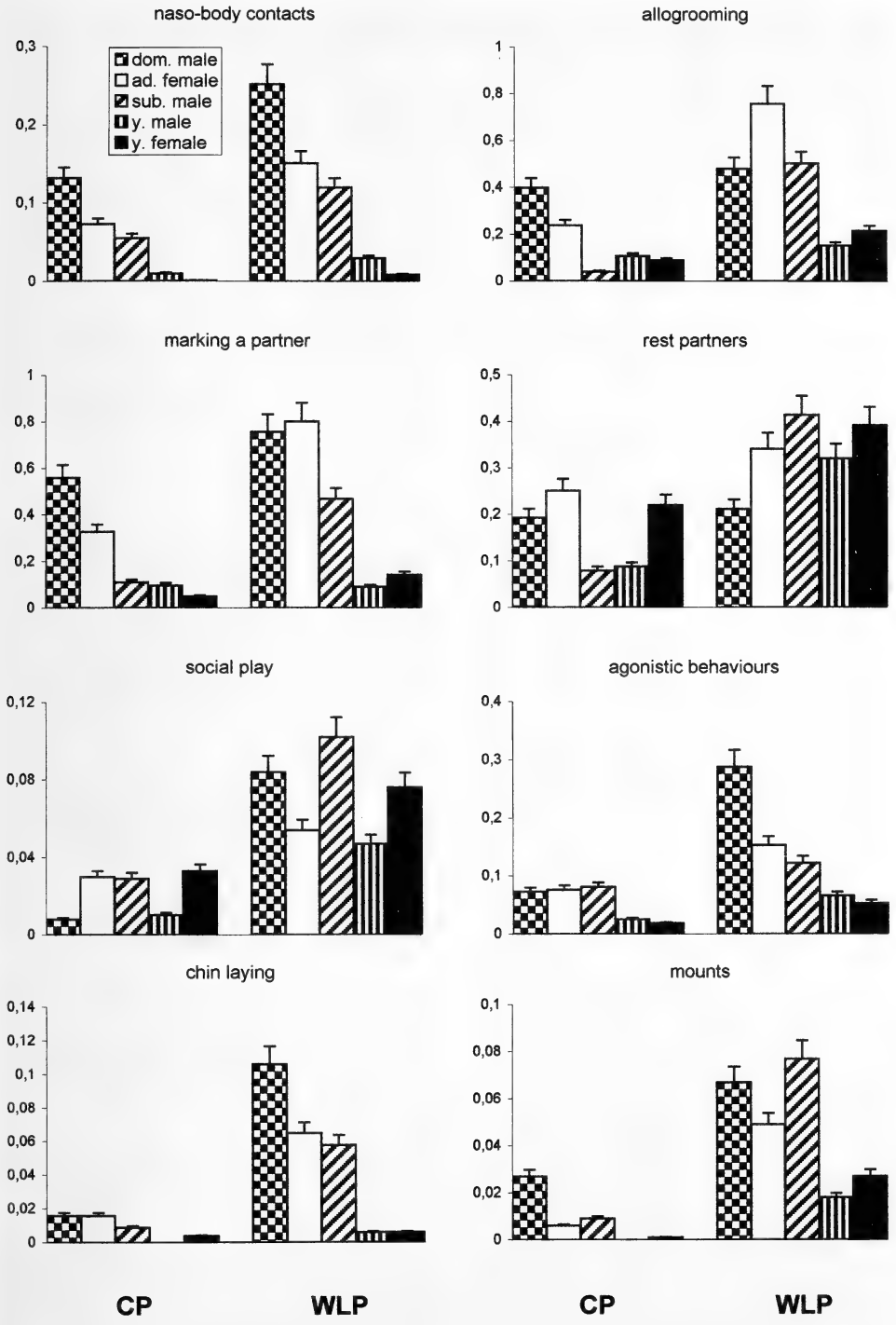
The dominant male and the second ranking female are the chief performers of chin-laying in the CP, the behaviour being mainly directed to the dominant female. In the WLP, this role is played by the dominant male and female, both also being the main receivers of such behaviour. Nevertheless, there is globally no similarity in the roles played by different individuals in the two species ($rs = -0.01$; $n = 6$; not significant).

Mounts outside oestrus are usually performed by the subordinate male and by the dominant female in the CP, the dominant male being, curiously, a great receiver of such behaviour. In contrast, mounting is the prerogative of any male in the WLP, all the females being receiver animals. Thus, again, individuals behave differently in the two species and without any link between them ($rs = 0.04$; $n = 6$; not significant).

Taking into account all these behaviours, there are many differences between the two species concerning the role played by different individuals within their social group. This is evident for the juvenile males, whose involvements in the different behaviours are almost opposite in the two species ($rs = -0.81$; $P \sim 0.05$; $n = 6$). The major exception is the similarity in the social functions of subordinate females ($rs = 0.83$; $P < 0.05$; $n = 6$). Nevertheless, some other features seem shared between both species.

By calculating the ratio of the number of behaviours performed by an individual and the number received, it is possible to determine if an individual is significantly a donor or receiver of a given behaviour (Fig. 3). On the whole, the dominant CP male is a re-

Fig. 3. Ratio of the number of behaviours performed to the number received by different individuals of the troop (mean ± standard error) in the collared peccary (CP) and the white-lipped peccary (WLP). Ratio > 1: the animal is chiefly a performer of the behaviour; ratio < 1: the individual is a receiver.


naso-body contacts
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CP
WLP

ceiver of partner marking (24/174: $X^2 = 64.58$; df = 1; $P < 0.001$) and of mounting (1/20: $X^2 = 8.64$; df = 1; $P < 0.01$), but a donor of allogrooming (267/96: $X^2 = 41.64$; df = 1; $P < 0.001$). Conversely, the dominant WLP male is a receiver of allogrooming (72/267: $X^2 = 59.90$; df = 1; $P < 0.001$) and a donor of mounting (31/8: $X^2 = 6.18$; df = 1; $P < 0.02$). The dominant CP female is neither receiver nor donor of any behaviour, whereas its WLP equivalent is a receiver of mounting (5/21: $X^2 = 4.16$; df = 1; $P < 0.05$) and of partner marking (118/233: $X^2 = 19.30$; df = 1; $P < 0.001$). Thus, the social role of the dominant animal of both sexes differs greatly between the species.

The subordinate males of both species are more often donors than receivers. In the CP, they are donors of naso-body contacts (31/7: $X^2 = 7.08$; df = 1; $P < 0.01$) and of partner marking (33/10: $X^2 = 5.52$; df = 1; $P < 0.02$), but receivers of resting partners (8/26: $X^2 = 4.04$; df = 1; $P < 0.05$). In the WLP, they are donors of naso-body contacts (66/15: $X^2 = 16.46$; df = 1; $P < 0.001$), allogroomings (252/114: $X^2 = 24.18$; df = 1; $P < 0.001$), and mounts (45/5: $X^2 = 17.20$; df =1; $P < 0.001$), but never receivers. The same is true for the juvenile males which are, in the CP, only donors of partner marking (36/11: $X^2 = 6.06$; df = 1; $P < 0.02$), but, in the WLP, only donors of allogrooming (69/28: $X^2 = 8.22$; df = 1; $P < 0.01$) and of resting partners (53/13: $X^2 = 12.04$; df = 1; $P < 0.001$).

The subordinate females are as often receivers as donors of behaviours in both species. In the CP, they are receivers of allogrooming (45/140: $X^2 = 25.02$; df = 1; $P < 0.001$) and donors of partner marking (71/34: $X^2 = 6.02$; df = 1; $P < 0.02$); in the WLP, they are receivers of mounting (9/41: $X^2 = 10.02$; df = 1; $P < 0.01$) and donors of partner marking (239/119: $X^2 = 20.00$; df = 1; $P < 0.001$). The juvenile females are also both receivers and donors. In the CP, they receive allogrooming (31/72: $X^2 = 7.68$; df = 1; $P < 0.01$) but carry out partner marking (35/7: $X^2 = 9.06$; df = 1; $P < 0.01$); in the WLP, they receive mounts (3/22: $X^2 = 10.66$; df = 1; $P < 0.01$), but are effectors of allogrooming (192/54: $X^2 = 40.80$; df = 1; $P < 0.001$) and resting partners (135/52: $X^2 = 18.46$; df = 1; $P < 0.001$).

Except for mounts in both sexes of the WLP, there are no cases where both the dominant and the subordinates or juveniles of the same sex are both performers or receivers of the same behaviour, and many similarities exist between subordinate and juvenile individuals in both species. In contrast, the subordinate adult males tend to seek contact with more troop members in the WLP than do their equivalents in CP ($U = 2$; $P = 0.057$; $n_1 = n_2 = 4$). The same difference exists in partner choice for social play.

Partner choice

Twelve different pairings were identified in each species according to sex, age and social status of the individuals. For each behaviour, the mean number of observations made on each pair was calculated. The most active pairs (number of observations ≥ 50% that of the best pair) are particularly distinguished in table 2.

Looking at all pairs, there are detectable differences between the species in choice of partners for playing, allogrooming or resting. The differences are principally due to the fact that the dominant male and the adult females have more frequent contacts with juveniles of both sexes for allogrooming and rest in the CP than in the WLP ($U = 1$; $P = 0.029$; $n_1 = n_2 = 4$). In contrast, the subordinate WLP adult males tend to seek contact with more troop members than do their CP equivalents ($U = 2$; $P = 0.057$; $n_1 = n_2 = 4$). The same difference exists in partner choice for social play.

As a rule, young of both sexes are preferred play partners in both species. Nevertheless, the dominant CP male never plays with a juvenile female.

Allogrooming is more frequent between adults than with or between juveniles in the WLP ($U = 0$; $P = 0.002$; $n_1 = 4$; $n_2 = 8$), in contrast to the CP.

Table 2. Mean number of behaviours performed by each pair of partners, according to different social categories. *: number of observations equal to or greater than 50% that of the best pair. CP: collared peccary; WLP: white-lipped peccary.

Pairs of partners	Behaviour	CP	WLP
MALE-MALE INTERACTIONS			
dominant male-subordinate male			
	naso-body contacts	4.17*	8.00*
	allogrooming	0.33	27.02*
	marking a partner	4.50	26.80*
	rest partners	0.33	12.60*
	social play	0.00	4.20
	agonistic behaviours	4.00*	12.80*
	chin-laying	0.00	4.00*
	mounts	1.00*	0.80
dominant male-juvenile male			
	naso-body contacts	1.00	2.00
	allogrooming	14.67*	4.00
	marking a partner	8.00	7.33
	rest partners	9.67*	2.33
	social play	0.67*	1.33
	agonistic behaviours	2.67*	1.00
	chin-laying	0.00	0.00
	mounts	0.00	0.00
subordinate male-juvenile male			
	naso-body contacts	1.33	1.33
	allogrooming	0.67	3.33
	marking a partner	1.67	0.67
	rest partners	3.33	9.00*
	social play	0.00	7.00*
	agonistic behaviours	2.00*	0.00
	chin-laying	0.00	0.00
	mounts	0.00	0.00
FEMALE-FEMALE INTERACTIONS			
adult female-adult female			
	naso-body contacts	0.89	2.06
	allogrooming	3.22	26.86*
	marking a partner	7.28	28.42*
	rest partners	4.63	12.40*
	social play	0.11	0.86
	agonistic behaviours	2.17*	2.07
	chin-laying	1.06*	1.17
	mounts	0.00	0.38
adult female-juvenile female			
	naso-body contacts	0.08	0.17
	allogrooming	1.89	7.67
	marking a partner	0.34	5.27
	rest partners	6.94*	9.11*
	social play	0.48	0.45
	agonistic behaviours	0.50	1.06
	chin-laying	0.00	0.00
	mounts	0.00	0.00
juvenile female-juvenile female			
	naso-body contacts	0.00	0.00
	allogrooming	0.00	5.33

Table 2. (Continued).

Pairs of partners	Behaviour	CP	WLP
	marking a partner	0.33	0.66
	rest partners	11.00*	11.67*
	social play	1.00*	13.67*
	agonistic behaviours	0.00	0.00
	chin-laying	0.00	0.00
	mounts	0.00	0.00
MALE-FEMALE INTERACTIONS			
dominant male-adult female			
	naso-body contacts	3.31*	2.20
	allogrooming	15.53*	9.50
	marking a partner	20.34*	19.95*
	rest partners	6.39*	4.13
	social play	0.17	2.00
	agonistic behaviours	1.20	6.77*
	chin-laying	0.89*	2.12*
	mounts	0.47	1.19
subordinate male-adult female			
	naso-body contacts	0.61	2.50
	allogrooming	1.09	14.93*
	marking a partner	1.39	11.40
	rest partners	1.17	11.27
	social play	0.22	2.70
	agonistic behaviours	2.31*	1.73
	chin-laying	0.22	0.83
	mounts	0.06	2.83*
juvenile male-adult female			
	naso-body contacts	0.00	0.33
	allogrooming	3.83	6.33
	marking a partner	4.50	2.78
	rest partners	8.50*	7.45*
	social play	0.00	0.45
	agonistic behaviours	1.50	0.33
	chin-laying	0.00	0.33
	mounts	0.00	0.33
dominant male-juvenile female			
	naso-body contacts	0.00	0.50
	allogrooming	4.17	5.17
	marking a partner	5.50	5.83
	rest partners	3.13	8.50*
	social play	0.00	2.17
	agonistic behaviours	0.00	0.50
	chin-laying	0.33	0.78
	mounts	0.25	2.83*
subordinate male-juvenile female			
	naso-body contacts	0.00	0.00
	allogrooming	0.67	5.17
	marking a partner	0.66	1.17
	rest partners	1.25	10.33*
	social play	0.44	7.33*
	agonistic behaviours	0.08	0.00
	chin-laying	0.00	0.17
	mounts	0.00	0.67

Table 2. (Continued).

Pairs of partners	Behaviour	CP	WLP
juvenile male-juvenile female			
	naso-body contacts	0.00	0.00
	allogrooming	0.89	3.00
	marking a partner	3.94	0.34
	rest partners	7.17*	9.33*
	social play	0.08	6.67
	agonistic behaviours	0.78	0.00
	chin-laying	0.22	0.00
	mounts	0.00	0.67

In the CP, but not in the WLP, resting groups including juveniles tend to be more frequent than those comprising only adults ($U = 6$; $P = 0.055$; $n_1 = 4$; $n_2 = 8$). Thus, an adult CP female generally lies with her juveniles of different litters. The dominant male may take part in such groups, in contrast to the WLP, where the dominant male rarely lies near a juvenile male or an adult female.

In other behaviours both species show comparable partner choices. Thus, significant similarities exist between CP and WLP for marking, chin-laying and agonistic behaviour ($rs = 0.6$; $P < 0.05$; $n = 12$) as well as for naso-body contact and mounting ($rs = 0.8$; $P < 0.01$; $n = 12$).

In both species, naso-body contacts are more frequent between adults than with or between juveniles ($U = 4$; $P = 0.024$; $n_1 = 4$; $n_2 = 8$ in the CP; $U = 0$; $P = 0.002$; $n_1 = 4$; $n_2 = 8$ in the WLP) and are chiefly performed by the subordinate males on the dominant, or by the dominant and subordinate males on adult females. Contacts between adults are also or tend to be more frequent in both species for agonistic behaviour ($U = 5$; $P = 0.036$; $n_1 = 4$; $n_2 = 8$ in CP; $U = 0$; $P = 0.002$; $n_1 = 4$; $n_2 = 8$ in WLP), and for mounting ($U = 5$; $P = 0.036$; $n = 4$; $n_2 = 8$ in CP; $U = 6$; $P = 0.055$; $n_1 = 4$; $n_2 = 8$ in WLP).

Marking a partner and chin-laying are also more frequent among adults in the WLP ($U = 0$; $P = 0.002$; $n_1 = 4$; $n_2 = 8$), but not in the PC. Partner marking occurs chiefly between adults of the same sex in the WLP (dominant male with subordinates, adult females with adult females), and between adults of different sexes (dominant male with females) in the CP. Apart from the dominant male-adult female pair in both species, chin-laying often occurs between adult females in the CP, and conversely between adult males (dominant-subordinate) in the WLP.

The most frequent agonistic contacts in the CP take place between males, or between a given adult female and another adult except the dominant male. In the WLP, most behaviour results from the dominant male performing agonistic acts towards subordinate males or adult females.

An important difference between both species therefore resides in the fact that in the WLP the subordinate male is a favoured partner of the dominant male for many behaviours, whereas in the CP the same role is held by the adult females.

However, these specific preferences are inverted for mounts occurring outside oestrus, 56.5% of them involving two males in the CP (the subordinate males mounting very often the dominant one), whereas, in contrast, 87.8% of the mounts in the WLP occur between partners of different sexes (48.1% between a subordinate male and an adult female). Thus, in both species mounts play a social role that differs from the other behaviours.

Frequency of interindividual contacts within the group

Frequency of social behaviours

Taking into account the average number of pooled social behaviour involving one given individual (per hour and per potential partner), it appears that each WLP has generally 2 to 3 times more social contacts with its partners than an equivalent CP (Tab. 3). On the other hand, both species are very similar in the relative frequencies of individual social behaviour ($rs = 0.94$; $P = 0.01$; $n = 6$), although sexual behaviour is more frequent in the WLP. In both species, marking a partner and allogrooming are the two most frequent social behaviours.

Compared to the CP, this greater degree of social contact within a WLP group is also noticeable during rest periods. Each individual rests on the average with 0.35 partners/hour (number of rest partners observed/number of potential partners), compared with 0.20 in the CP. Thus, group sizes during resting periods are significantly 1.75 times larger in the WLP than in the CP ($t = 6.02$; $df = 85$; $P < 0.001$). This is the case despite the smaller number of individuals in the WLP groups (4–11 animals in WLP vs 7–16 in CP).

Table 3. Average number of social behaviours recorded for each individual, per hour and per potential partner. CP: collared peccary; WLP: white-lipped peccary.

	CP	WLP	WLP/CP
Marking a partner	0.23	0.57	2.48
Allogrooming	0.17	0.52	3.06
Agonistic behaviours	0.06	0.16	2.67
Naso-body contact	0.05	0.13	2.60
Social play	0.03	0.06	2.00
Sexual behaviours	0.02	0.10	5.00
Total	0.56	1.54	2.75

Group cohesion

The degree of grouping of individuals during activities is indicative of the cohesion level of each group. In this respect, several differences between the two species are apparent.

In the CP, one or more individuals frequently remain apart from the group in a portion of the enclosure distant from the group's location. These individuals are neither socially expelled nor actively chased out. At feeding time, they approach the food long after the others. In contrast, all the WLP individuals come together in a very homogeneous unit.

During diurnal activities, the grouping of individuals is lower in CP than in WLP: in the former, only 3% of the individuals being separated from the group, compared to 4.5% in the latter ($X^2 = 4.7$; $df = 1$; $P < 0.05$). In the CP, this trend is more apparent during the afternoon than in the morning (1.6% isolated individuals against 4.4%: $X^2 = 14.94$; $df = 1$; $P < 0.001$), in contrast to the WLP whose percentages are quite similar for both periods (respectively 4.0% and 5.0%: $X^2 = 0.47$; $df = 1$; not significant). This could mean that there are qualitative changes in the CP behaviour throughout the day: more movements and foraging in the morning, and frequent social interactions in the afternoon.

On the whole, CP shows also a weaker allomimetic behaviour than WLP: individuals perform a behaviour different from that of the rest of the group in 19.6% of the cases in the former, against 16.0% for the latter species ($X^2 = 64.5$; $df = 1$; $P < 0.001$). Unlike WLP, CP copy each other less during the morning than in the afternoon: respectively, 23.2% and 15.8% of the animals perform activities different from the rest of the troop ($X^2 = 19.39$; $df = 1$; $P < 0.001$).

During resting periods, the dominant male and female of both species are encountered more often alone than the juveniles: respectively 28.4–48.6% cases against 3.2–11.1% ($X^2 = 28.6$ to 52.5; $df = 1$; $P < 0.001$). Subordinate adult males usually rest more often alone in the CP than in the WLP (70.8% vs 30.9%: $X^2 = 31.7$; $df = 1$; $P < 0.001$). The same is true for subadult males (20–22 months old): CPs rest alone 4 times more often than the WLPs (30.8% vs 7.6%:

$X^2 = 11.8$; df = 1; $P < 0.001$). On the other hand, subordinate WLP adult females rest alone more often than the CPs (43.9% vs 26.0%: $X^2 = 6.95$; df = 1; $P < 0.01$).

Integration of new members into the group

During tests of sexual receptivity with penned animals, it was always possible to present a female to a new male without any risk in the CP. The opposite often occurs in the WLP: on several occasions under enclosure conditions, a male attacked a "new" female so violently that we had to urgently remove the female and abandon the test.

Discussion

The behavioural repertoires of these two forest peccary species are broadly similar to each other with few exceptions (Dubost 1997). Contrary to many other suiforms which live either in permanent pairs or in unisex social units outside the reproductive period (Bigourdan 1948; Gundlach 1968; Frädrich 1974; Beuerle 1975; Kiltie and Terborgh 1983), mixed groups are the basis of the peccary social system. This fact is favoured by the persistence of sexual activity throughout the year. There is never any sexual segregation, even before or after birth. The two species mainly diverge in the frequency or mode of appearance of behaviours rather than in any real inequality in behavioural repertoire. However, some qualitative or quantitative differences, especially concerning social interactions, are sometimes significant enough to reveal a true divergence in their biology. These follow directly from specific etho-ecological characteristics of each species.

Behavioural differences between both species

In both species, young or subordinate animals of both sexes frequently mark partners. This observation, also made by Schmidt (1976) for the CP, contradicts the assertion of Sowls (1974) that dominant animals are the main effector of such behaviour. Likewise, allogrooming in the WLP is commonly initiated by juveniles of both sexes and subordinate males, and to a lesser degree by dominant females. In the CP, on the contrary, this behaviour is chiefly performed by the dominant animals of both sexes, especially the dominant male. This fact, also noted by Schmidt (1976), distinguishes the CP from most other mammals where dominants are generally groomed by subordinates, e. g. *Papio hamadryas* (Kummer 1968), *Bos taurus* (Walther 1979).

Contrary to evidence on several ruminants (Walther 1979), mounts in peccaries do not have any aggressive significance; they do not play the same role in both species. In male CPs they occur in accordance with hierarchical order, but not so in the WLP. This means that mounting has a different social role and a lower hierarchical value in WLPs than in CPs.

As previously noted by Sowls (1974) and Schmidt (1976), female CPs are slightly dominant to males, but in the WLP, males dominate females, as in several suids (Frädrich 1965) as well as in ruminants living in mixed herds – e. g. *Taurotragus*, *Bison*, *Syncerus* (Estes 1974; Walther 1979). However, in both peccary species, subordinate females are elevated immediately after giving birth to the top of the hierarchy, a fact also observed by Schweinsburg and Sowls (1972) in the CP.

In the CP, but not in the WLP, resting groups often include an adult female with her juveniles of different litters, which led Schmidt (1976) to use the term "clan". Furthermore, according to Lochmiller and Grant (1982), groups of CP are highly bonded units, whose members are intolerant of strangers of the same sex. As reported by Schmidt (1976) and Byers and Bekoff (1981), individuals which were temporarily separated from the group lost their former social status and were never completely reintegrated. However, this exclusion does not seem to exist between sexes,

because it was always possible to present a CP female to a new male without any risk, contrary to the WLP. We do not know if the intolerance observed in the latter species is triggered by the odour of the stranger and corresponds to a type of group defence, but it fits well with the high level of natural agressiveness observed in this species (Dubost 1997).

Social behaviour in relation to group size

WLP live in large herds, comprising generally from 30 to 200 animals, and including many adult males, females, and juveniles of all ages (Kiltie and Terborgh 1976, 1983; Sowls 1984; Mayer and Wetzel 1987; Benirschke et al. 1989; Hernandez et al. 1995; Peres 1996; Fragoso 2000; Judas pers. comm.; pers. data). Such social structure appears relatively unique among the artiodactyls, permanent aggregations of so many mature individuals of both sexes being only known seasonally in several migratory, open country ruminants, such as *Antilope cervicapra* (Mungall 1978), *Connochaetes taurinus* (Estes 1969) and others (Walther 1979), but exceptionally also among some forest suids, like *Sus barbatus* (Pfeffer 1959; Frädrich 1974; Caldecott et al. 1993).

Conversely, the social unit of the CP is generally composed of a limited number of individuals: 1–2 adult males and 1–3 adult females, with several young of different ages. Such small groups are found in French Guiana (Judas pers. comm.) as in other forest regions (Kiltie and Terborgh 1976, 1983; Robinson and Eisenberg 1985; Bodmer et al. 1988; Peres 1996).

When individual WLPs search for food, they are frequently at a distance from each other, the whole herd being spread out over several tens or hundreds of meters. Because the physical forest environment is largely obstructed at ground level, individuals need mechanisms for intercommunicating efficiently at short and medium distances to ensure herd cohesion. In contrast to CP, visual, acoustic or olfactory signals are particularly well developed in WLP, both in expression and in intensity: spectacularly bristled hairs; prolonged yawning as intimidation, loud blowing, grunts, teeth snaps or cries of the young (Kiltie and Terborgh 1976, 1983; Sowls 1984; Mayer and Wetzel 1987; Hernandez et al. 1995; Dubost 1997); strong odor (Benirschke et al. 1989; Dubost 1997).

The WLP is heavier than the CP: a mean of 37.1 kg for the adult males and 35.7 kg for the adult females in French Guiana, versus, respectively, 22.1 kg and 19.5 kg (Dubost 1997). Unlike the CP, the large body size of individual WLPs belonging to a well-populated and powerful herd provides protection against potential predators and dispenses with the need for cryptic behaviour. This species has the reputation of attacking jaguars en masse (Kiltie and Terborgh 1983).

Herd cohesion of the WLP must also be facilitated by the behaviours themselves. The results of this study indicate that social behaviours are from 2.5 to 6.4 times more frequent in this species than in CP. Likewise, during resting periods, the grouping of individuals at the same spot is almost twice as high in the former than in the latter. Furthermore, in comparison with the CP, the WLP shows a generalization of some behaviours, which are performed by most members of the herd, rather than just by one or several individuals. Such behaviours include collective fear, body rubbing on the ground in all individuals, play often being contagious, penis trembling and mount by all males. Several other behaviours occur in a very demonstrative manner, including strong reactions to anxiety situations, urinary marking on the standing female, play with objects, marked body displays in threat or submission situations, frequent and strong attacks (Dubost 1997).

In the WLP, the involvement of most individuals of the same herd in different social behaviours is also noticeable in sexual behaviour. In this species, all the numerous adult or subadult males are reproductive and may copulate with the females, regard-

less of their relative hierarchical position (pers. obs.), as described in some other mammals (Smuts 1987).

On the contrary, only the dominant male is reproductive in the CP. It is the only one to court and copulate with the few reproductive females of the group (Bissonette 1976; Schmidt 1976; pers. obs.). All the other males show much lower sexual hormone levels (Hellgren, in Hannon et al. 1991; pers. data); they avoid the proximity of the receptive females. Unlike most other artiodactyls and many mammals, they were never observed to be pushed away by the dominant male, as also noted by Sowls (1974), Schmidt (1976), and Byers and Bekoff (1981). Furthermore, they do not leave the social unit to live alone or grouped together in a bachelor herd, like *Sus scrofa* and *Phacochoerus* (Bigourdan 1948; Frädrich 1974; Beuerle 1975; Barrette 1986), the tylopods and many ruminants (Koford 1961; David 1973; Estes 1974; Franklin 1974; Gosling 1974; Joubert 1974; Spinage 1974; Mungall 1978), and several *Equus* species (Klingel 1974). The fact that these surplus adult males can stay inside the social unit is perhaps due to their sexual inactivity, provided they behave submissively, as in *Hippopotamus* (Klingel, in Eltringham 1993) or *Hylochoerus* (d'Huart 1993).

The life within a rather considerable herd does not allow individual WLPs to establish such an elaborate and fine contact with each other as in the CP, whose groups function as very well coordinated and stable units. In the WLP, there are, indeed, frequent encounters between animals with little knowledge of each other, each individual having to define its own place in relation to its partner. One can understand why, contrary to the CP, most interindividual contacts, even sexual ones, are of a very aggressive nature in the WLP, as noted also by Frädrich (1986) and Benirschke et al. (1989). In contrast, there are pronounced displays for appeasement and submission purposes (Dubost 1997). Likewise, this species shows a rather strict social organization, where all individuals of both sexes are included in the same linear hierarchy. Finally, since social units need to remain distinctive within a complex herd, its members are forced to stay close to each other. This would function to strengthen the bonds uniting them and to guarantee their relative isolation within the herd, when necessary, as displayed by the female WLP with her young (Dubost 1997).

Thus, the WLP herd can be considered as a multi-male society, whereas the social unit of CP corresponds more to a harem or pseudo-harem. Moreover, some intermediate situations between these specific social organizations have been observed. Indeed, the formation of a harem in the CP seems directly dependent on the group size. Sowls (1974), Byers and Bekoff (1981), Packard et al. (1991) observed, both in captivity and in nature, instances of sexual promiscuity within large groups.

Differences of social life between wandering and locally fixed groups

Another main difference between both species lies in the fact that herds of WLP travel more or less constantly throughout a huge area. In the absence of precise biological data, this species was considered nomadic and capable of travelling great distances (Kiltie and Terborgh 1983; Sowls 1984; Hernandez et al. 1995; Peres 1996). But recently, Fragoso (2000) produced data indicating that herds of WLP can live for a long time on vast home ranges of 22–110 km^2, where they move over long distances but do not migrate. Quite the contrary, each group of CP is permanently attached to a well-defined terrain, covering an average area of only 190 ha in French Guiana (Judas pers. comm.). One finds here the classical link uniting the social behaviour of a species with the characteristics of its environment, as noted in many other artiodactyls.

Life in a moving herd does not require to deposite marks on the ground. Thus, the WLP does not show the behaviours that allow the CP, especially the dominant male,

to assert its presence in the area where the group resides. Indeed, the WLP shows no sign or behaviour indicating any direct bond with the ground occupied, like defecation site or glandular marking. The home range of a WLP herd studied by Fragoso (2000) was almost completely encompassed by that of another, and the two herds were found together several times at the same site. The WLP sociality is thus nearly exclusively dependent on the exchanges existing between the individuals themselves; inter-individual contacts are particularly frequent in this species. It is also significant that WLP males never urinate on a female lying on the ground, as do CP males, but only on standing or moving females (Dubost 1997).

Finally, the more or less continuous travelling of a WLP herd demands that individuals be well synchronized during their activities. This is achieved by mass effects and allomimetic behaviour. In counterpart, the great social cohesion, as observed also by Fragoso (2000) in the wild, engenders a marked intolerance towards strangers.

On the other hand in the CP, each home range is generally distinct and belongs to only one social group, even if neighbouring home ranges overlap greatly. Each home range has several rest places (Hernandez et al. 1995; Judas pers. comm.) and defecation sites (Hernandez et al. 1995; pers. obs.). According to Bissonette (1976), the home range is regularly marked by the locally resident adult male which asserts both his status and presence by many behaviours, including surveillance, defence of the group in case of danger, display with bristled hairs and ceremonial gait, continuous olfactory control of all partners, emission of urine when walking, scraping and glandular marking of the ground and dropping of faeces on distinctive places (Dubost 1997). The behaviour of the CP appears therefore comparable to that found in many ruminants, and perhaps also in hippopotamuses and several suids (Frädrich 1974).

The harem or pseudo-harem of the CP differs from those of many ruminants by including several subordinate adult males (David 1973; Estes 1974; Gosling 1974; Joubert 1974; Spinage 1974; Mungall 1978). The fact that it stays constantly with the same dominant male within one locally fixed home range differs also from the ruminant harem, but resembles what is known in *Vicugna* (Koford 1961; Franklin 1974). Nevertheless, this similarity is only apparent, because the harem of *Vicugna* lives on two small territories separated from each other by neutral ground.

Most behavioural differences between both peccary species thus appear to be the direct result of the way of life adopted by each. In this context, it is reasonable to suppose that the Chacoan peccary, *Catagonus wagneri*, shows a social organization similar to that of the collared peccary, owing to the great resemblances of these species in both behaviour and group composition (Mayer and Brandt 1982; Mayer and Wetzel 1986).

Similar variations in social behaviour could exist in Old-World primates. Indeed, between primate species living in multi-male troops and those forming harems, obvious differences exist in the size of the social units, level of sociality, marking, function of the dominant male as the nucleus of the group, nature of the male-female relations, and hierarchical system (Rowell 1988).

Acknowledgements

This study was totally dependent on the facilities provided by the Institut National de la Recherche Agronomique. Many thanks to Dr P. Planquette for having facilitated this research, to C. Dutertre, P. Laventure, F. Periacarpin, and D. Torvic for having assured the success of this peccary breeding, to J. Judas for providing unpublished field observations, and to Drs J. Bradbury, R. Day, C.-A. Gautier, O. Henry, R. Mauget, J. J. Mayer, K. Pack, M. Schlee and an anonymous reviewer for their helpful comments and corrections of the manuscript.

Zusammenfassung

Vergleiche des Sozialverhaltens zweier sympatrischer Pekariarten (Genus *Tayassu*) in Menschenobhut; Beziehungen mit ihren ökologischen Merkmalen

Die Vergleiche des Sozialverhaltens wurden zwischen dem Weißbart-Pekari (*Tayassu pecari*) und dem Halsband-Pekari (*Tayassu tajacu*) in Menschenobhut durchgeführt, die beide im südamerikanischen Regenwald leben. Beim Weißbart-Pekari gibt es einen engen Rudelzusammenhalt und Gruppenfremde werden im allgemeinen heftig angegriffen. Die Individuen haben zwei- bis dreimal mehr Sozialkontakt mit Gruppenmitgliedern als die Halsband-Pekaris. In vielen sozialen Verhaltensweisen ist beim Weißbart-Pekari das dominante Weibchen das aktivste Individuum, während beim Halsband-Pekari das ranghöchste Männchen das meistbeachtete Mitglied der Sozialeinheit ist. Randniedere und subadulte Männchen beteiligen sich bei allen sozialen Interaktionen und sind bestens in das Rudel integriert. Beim Halsband-Pekari dagegen leben rangniedere Männchen mehr oder weniger als neutrale und periphäre Individuen. Völlig verschieden verhält sich das Weißbart-Pekari mit beträchtlicher Aggressivität in der Mehrzahl der Auseinandersetzungen, wobei das ranghohe Männchen der Hauptinitiator der häufigen und intensiven agonistischen Interaktionen ist. Bei dieser Art unterliegen beide Geschlechter einer einzigen, alle Rudelmitglieder einschließenden Rangordnung, in der die Männchen den Weibchen stets überlegen sind. Beim Halsband-Pekari dagegen gibt es zwei getrennte, geschlechtsspezifische Rangordnungen und beim zwischengeschlechtlichen Kontakt dominieren die Weibchen über die Männchen. Diese zwischenartlichen Unterschiede und das völlige Fehlen einer Bodenmarkierung beim Weißbart-Pekari verdeutlichen die ökologischen Merkmale beider Arten. Während das Weißbart-Pekari in großen Mehrmännchen-Rudeln umherzieht, lebt das Halsband-Pekari in kleinen stabilen und lokal seßhaften Rotten.

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Mamm. biol. **66** (2001) 84–89

http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Biochemical identification of three sympatric *Apodemus* species by protein electrophoresis of blood samples

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Receipt of Ms. 28. 02. 2000
Acceptance of Ms. 20. 09. 2000

Abstract

The allelic pattern of seralbumine and general protein 1 of the three sympatric *Apodemus* species *Apodemus sylvaticus*, *A. flavicollis*, and *A. alpicola*, were studied using electrophoretic analysis of blood samples. This method appears to be a sensitive tool for distinguishing the three *Apodemus* species in the Alps. Their identification on the basis of external characteristics in the field is sometimes extremely difficult, even more so for juvenile specimens. Compared to previously described methods the electrophoretic analysis does not require killing animals and can be used on juveniles.

Key words: *Apodemus*, rodents, protein electrophoresis, biochemical identification

Introduction

The determination of the two common mouse species in western Europe, *Apodemus sylvaticus* (Linnaeus, 1758), and *A. flavicollis* (Melchior, 1834), is not always easy because their morphological characters strongly overlap. Some individuals or populations suggested hybridisation or introgression (Engel et al. 1973), but allozymatic studies did not reveal any hybrids (Engel et al. 1973; Debrot and Mermod 1977; Niethammer and Krapp 1978; Gemmeke 1980; Benmehdi et al. 1980; Nascetti et al. 1980; Csaikl et al. 1980; Gemmeke and Niethammer 1981; Fraguedakis-Tsolis et al. 1983; Nascetti and Filippucci 1984; Gebczynski et al. 1986).

Since the recognition of a third sympatric species, *A. alpicola* Heinrich, 1952, by Storch and Lütt (1989) with intermediate morphological traits, the discrimination became even more problematic. A better accuracy of species identification was obtained by a discriminant function developed from a limited number of skull measurements (Reutter et al. 1999). Six cranial characters are sufficient to differentiate between the three *Apodemus* species with a correct classification above 97%. While, this technique is indeed a good tool for reclassifying museum material, it does not overcome the determination problem of young animals and of living individuals during field studies.

A discrimination independent of morphology should be based on genetic markers, e. g. specific allozyme pattern. The analysis

1616-5047/01/66/02-084 $ 15.00/0.

of allozyme variation by starch gel electrophoresis has frequently been used in genetic and systematic investigations of the genus *Apodemus* (Engel et al. 1973; Behnmehdi et al. 1980; Csaikl et al. 1980; Gemmeke 1980; Fraguedakis-Tsolis et al. 1983; Gemmeke 1983; Korpimäki and Norrdahl 1987; Filippucci et al. 1989; Fernandes et al. 1991; Britton-Davidian et al. 1991; Vapa et al. 1995). Vogel et al. (1991) and Filippucci (1992, 1996) included *A. alpicola* in their allozyme analysis and confirmed the specific status of this species. Debrot and Mermod (1977) found that the seralbumine pattern obtained by polyacrylamide gel electrophoresis is very distinctive for *A. sylvaticus* and *A. flavicollis*.

The aim of this study is to develop a technique applicable to all age cohorts of the three sympatric *Apodemus* species, *A. sylvaticus*, *A. flavicollis*, and *A. alpicola*, based on blood samples without need to sacrifice animals, in analogy with the techniques used for sibling species of shrews (Hausser and Zuber 1983; Brünner 1988; Neet 1989; Neet and Hausser 1989, 1990, 1991; Brünner and Neet 1991; Turni and Schönherr 1994).

Material and methods

Electrophoretic analysis was carried out on 41 individuals of the three species *Apodemus sylvaticus* (n = 15), *A. flavicollis* (n = 18), and *A. alpicola* (n = 8) from 11 localities in Switzerland and neighbouring Italy. Localities and collection numbers (IZEA: Institut de Zoologie et Ecologie Animale) of animals investigated are presented in the following list:

Apodemus sylvaticus Linnaeus, 1758. Switzerland: Bern: Haslital: (IZEA, 7381, 7382, 7383); Valais: Ayer: (7379); Monnaz: (4887, 4888); Vaud: Aclens (7380); Echichens: (4880, 4884); Morges: (4886); Renens: (7363, 7366); St. Saphorin: (4883, 4885). Italy: Domodossola: (7384).

Apodemus flavicollis Melchior, 1834. Switzerland: Bern: Haslital: (7389, 7390, 7392, 7393); Valais: Monnaz: (4894, 4895); Vaud: Aclens (7401); Le Brassus: (7395, 7396, 7397, 7398); Echichens: (4890); Morges: (4891); Renens: (7364); St. Saphorin: (4881, 4882, 4889, 4892).

Apodemus alpicola Heinrich, 1952. Switzerland: Valais: Sanetsch: (7337, 7338, 7339, 7345, 7346, 7347, 7348, 7361).

From every individual a blood sample of about 2 µl was taken from the base of the tail of the animals with heparinized Micro-Hematocrit tubes. The incision of the caudal vein with a razor blade (or another sharp blade) to get blood samples (maximum 0.1 ml) is recommended for mice by the Swiss Federal Office of Veterinary. By being transferred into an Eppendorf tube, the blood could be kept for more than 10 hours at ambient temperature (20 °C) or a week at a cool place (4 °C), and at least one year and even longer at –20 °C. This circumstance allows the use of animals for the electorphoretic analysis that were frozen a few hours after death.

Blood samples were diluted in a solution (1 : 5) of saccharose (40%) and 0.075 M Tris/HCl buffer, pH 8.9 with a trace of bromophenol blue. The added amount of the saccharose-buffer solution depended on the volume of the blood sample. For example, to a 2 µl blood sample 8 µl saccharose and 50 µl buffer solution were added. The samples were then run in a Polyacrylamid-disc-electrophoresis (resolution gel: 8%, 0.325 M Tris/HCl, pH 8.9; concentration gel: 3%, 0.056 M Tris/HCl, pH 6.9; running buffer: 0.05 M Tris/HCl, 0.38 M glycerine) with a constant power of 4 W during migration in the concentration gel and 12 W in the resolution gel (gel size: 180 × 155 × 15 mm; power supplies: Bio Rad 3000/300 and 1000/500; gel support: Zabona AG, Basel). Proteins migrated from cathode to anode during 4–5 h (band of bromophenol blue at 1 cm from lower gel border). Proteins were non-differentially stained with Coomassie blue (0.025% Coomassie blue R250, Sigma; 50% methanol; 3.5% glacial acetic acid) for 1 h and destained afterwards (50% methanol; 3.5% glacial acetic acid). The method is slightly modified according to Hausser and Zuber (1983).

Relative migrating distances of the proteins in relation to the bromophenol blue dye front were calculated to identify clearly the different protein bands.

All skulls of the examined specimens were prepared, measured, and assigned to one *Apodemus* species by using a discriminant function analysis (Reutter et al. 1999).

To test our results we included 58 unknown *Apodemus* specimens from the Bündner Natur-Museum Chur. All these animals came from the eastern part of the Swiss Alps (Graubünden). Blood samples were taken with heparinized Micro-Hematocrit tubes from the defrosted bodies.

Results

The results of the electrophoretic analysis (Fig. 1) are best understood when considering the different allelic pattern of the albumin and an unknown general protein 1 (GP 1). These two proteins are represented on the gel by three different bands which are labelled from cathode to anode as A, B, and C. *Apodemus flavicollis* and *A. alpicola* are characterised by the slower migrating albumin allele (band A), whereas the faster migrating albumin allele (band B) is present only in *A. sylvaticus*. Moreover, *A. flavicollis* shows an additional protein band C (GP 1), which migrated further than either A and B. Nothing is known about the identity of GP 1, its possible polymorphism and the position of other allelic bands in *A. alpicola* and *A. sylvaticus*. However, the presence of the characteristic GP 1 band in *A. flavicollis* allows the distinction between this species and *A. alpicola*.

When the migration distance of band A is taken as 100%, the relative distances are for band B 101.6% (101.3–102.0) and for band C 107% (105.2–108.5) (Tab. 1). In that way 100% of all examined specimens could be determined unequivocally.

All 58 test specimens from Graubünden could be identified according to the protein electrophoresis of blood samples. 52 individuals were assigned to *A. sylvaticus*, five to *A. flavicollis* and only one to *A. alpicola*. Skull measurements using a discriminant function (REUTTER et al. 1999) confirmed this determination.

Table 1. Protein markers and bands (Alb and GP 1) of the three species *A. sylvaticus* (B), *A. flavicollis* (A, C) and *A. Alpicola* (A).

marker	band	*A. sylvaticus*	*A. flavicollis*	*A. alpicola*
Alb_{100}	A		x	x
$Alb_{101.6}$	B	x		
GP 1_{107}	C		x	

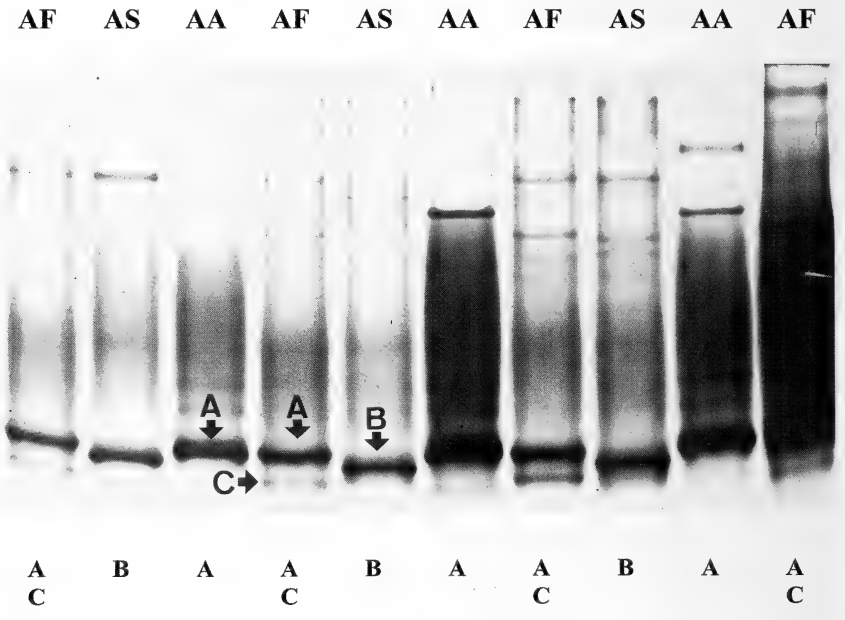

Fig. 1. The serum albumin and general protein (GP 1) patterns obtained by protein electrophoresis on polyacrylamide gels for *A. sylvaticus* (B), *A. flavicollis* (A, C) and *A. alpicola* (A). Symbols: AF = *A. flavicollis*, AS = *A. sylvaticus*, AA = *A. alpicola*.

Discussion

The determination of the three morphologically similar species *A. sylvaticus*, *A. flavicollis*, and *A. alpicola* remains sometimes difficult. *A. sylvaticus* and *A. flavicollis*, are easily distinguishable in northern Europe by morphological characteristics and by the ecological parameters of their habitats. *A. flavicollis* is larger, with a complete collar of yellow-reddish or wide spot on the breast, and inhabits forest. *A. sylvaticus* is smaller and an eurytopic species with an elongated pectoral spot never forming a collar or without any spot at all. These two species converge morphologically in southern Europe, due to clinal variation in body size and pelage colour following opposite trends (*Engel* et al. 1973).

Hence, convergence and overlapping in external characters do not always allow a correct specific assignment of specimens, especially in areas where the two sibling species are distributed sympatrically, and when juvenile individuals are concerned. The recognition of *A. alpicola* further complicated this determination problem in certain regions. The alpine mouse resembles the wood mouse in pelage colour while in body size it resembles the yellow-necked mouse.

The present results clearly show that the three species *A. sylvaticus*, *A. flavicollis*, and *A. alpicola* can be 100% distinguished biochemically by their albumin and general protein 1 (GP 1) patterns. The electrophoretic patterns of the albumin and the GP 1 of *A. sylvaticus* and *A. flavicollis* in the present study correspond to those of Debrot and Mermod (1977), who also analysed animals from Switzerland using the same technique. Darviche et al. (1979) reported two specific albumin alleles for *A. sylvaticus* and *A. flavicollis* from France, Corsica, Spain, and Italy, and suggested that these differences are good criteria for differentiation between the two species. Moreover, it has been shown that *A. alpicola* has an intermediate position between *A. sylvaticus* and *A. flavicollis* with regard to allozyme allele frequencies (Vogel et al. 1991; Filippucci 1992). For the albumin locus, the species *A. alpicola* and *A. flavicollis* share the same allele.

In all analysed individuals of the present study (including the test animals from Graubünden) no heterozygotes were found. These findings support the hypotheses that there is no gene flow between these taxa.

The fact that the two alleles do not show a very pronounced difference in gel migration may lead to problems in the case of a monospecific sample of *A. sylvaticus* and *A. alpicola* or a mixture between these species. Therefore, we recommend to load reference samples of the two more common species *A. sylvaticus* and *A. flavicollis* on every gel.

For ecological studies the electrophoretic analysis of blood samples offers not only the advantage that the animal need not be sacrificed as well as the identification of juvenile individuals, what was impossible with previously described methods. Moreover, the blood samples can be taken from living, freshly killed (even after several hours), as well as frozen animals and can be stored for months at –20 °C. The application of the technique is simple (duration of the whole laboratory procedure about 5 hours). All these advantages allow an application for ecological and long-term studies in the field.

Acknowledgements

We would like to thank Nelly Di Marco, who performed most of the electrophoreses. We are also very grateful to Jürg Paul Müller from the Bündner Natur-Museum Chur (Switzerland), and to Etienne Bertouille who provided us with a lot of wood mice and to Tiziano Maddalena and Manuel Ruedi, who gave us a lot of precious technical advices. Last, but not least, we thank Karen Parker who corrected the English manuscript.

Zusammenfassung

Biochemische Bestimmung dreier sympatrisch vorkommender *Apodemus*-Arten mittels Elektrophorese von Blutproteinen

Mittels Elektrophorese von Blutproteinen wurde das Allelbandenmuster von Albumin und eines „General Protein 1" der drei in den Alpen sympatrisch vorkommenden Waldmausarten *Apodemus sylvaticus, A. flavicollis* und *A. alpicola* untersucht. Die Methode erwies sich als ein zuverlässiges Werkzeug zur Unterscheidung der drei Arten. Ihre Bestimmung anhand äußerer morphologischer Merkmale ist nicht immer einfach, vor allem, wenn es sich um juvenile Tiere handelt. Mit dieser Methode können lebende Individuen aller Altersklassen bestimmt werden, was eine Anwendung in ökologisch ausgerichteten Felduntersuchungen erlaubt.

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Mamm. biol. **66** (2001) 90–101
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Diversity of mammals in the Bladen Nature Reserve, Belize, and factors affecting their trapping success

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Receipt of Ms. 12. 11. 1999
Acceptance of Ms. 20. 04. 2000

Abstract

The presence of 33 non-volant mammal species was recorded in the Bladen Nature Reserve, an area of subtropical wet forest in south central Belize, as determined from walking transects and using Sherman and Tomahawk traps to capture mammals. Using trapgrids over 6 075 trapnights, the effects of trap design, bait, moon phase, logging, elevation, and proximity to a river on three measures of trapping success were examined systematically. Open wire mesh traps yielded somewhat higher trapping success than Sherman traps; oats and molasses produced higher trapping success than other kinds of bait; and trapping success was higher in selectively logged than in unlogged forest, and marginally higher at lower elevations and close to a river. Moon phase had no effect on trapping success. These results provide baseline data on mammal diversity in a relatively unexploited area of central America and, though preliminary, indicate which aspects of trapping technique need to be standardized when comparing species diversity and abundance across neotropical sites.

Key words: Mammals, trappability, diversity, Bladen, Belize

Introduction

Most ecological studies of neotropical mammals require data on species diversity and abundance. For example, questions about population dynamics (e. g., O'Connell 1989), population demography (e. g., Torres-Contrera et al. 1997), community structure (e. g., Asquith et al. 1997), and regions of mammal abundance (e. g., Mares 1992) all require information on the number of mammal species or their relative abundance in an area. Conservation studies similarly require data on diversity and abundance in order to understand the effects of habitat fragmentation (Lynam 1997; Malcolm 1997), loss of top predators (Wright et al. 1994; Terborgh et al. 1997), and mammal exploitation (Dirzo and Miranda 1991; Glanz 1991; Wright et al. 2000) on communities of mammals. In the neotropics data on mammal communities are growing (Voss and Emmons 1996) but they still come from only a handful of locations, the most notable of which are La Selva in Costa Rica (Timm 1994 a), Los Tuxlas, Mexico (Estrada et al. 1994), Barro Colorado Island, Panama (Glanz 1990), Cosha Cashu, Peru (Janson and Emmons 1990) and near Manaus, Brazil (Malcolm 1990)

1616-5047/01/66/02-090 $ 15.00/0.

which limits our ability to make generalizations about how mammalian communities are organized.

As studies of mammals in the neotropics increase, and comparisons between areas become more feasible, researchers must standardize their techniques for estimating mammal abundance, or at least be aware of the biases inherent in different methods of mammal estimation (Wilson et al. 1996). We therefore investigated six different factors that influence trapping success outside the neotropics and might therefore be of importance elsewhere. Two of these were methodological factors (type of small mammal trap and characteristics of the bait) and four were ecological factors (phase of the moon, selective logging, elevation, and proximity to rivers).

Trap design can influence trapping success substantially in temperate regions (Sealander and James 1958) and this problem has been identified in at least one neotropical site (Woodman et al. 1996). We therefore compared measures of trapping success using hand-made wire mesh small mammal traps which could be seen through with standard Sherman traps which obscure visibility. It is also well known that baits can affect trapping success in temperate zones (e. g., Buchalczyk and Olszewski 1971). Although far less work has been carried out on this problem in the neotropics, preliminary evidence suggests that bait is not an important factor in mammal trapping (Woodman et al. 1996). Increased moonlight lowers trapping success in open habitats in temperate regions (Brown et al. 1988) because small mammals often show changes in activity in accordance with a reduction of predation risk from visually hunting aerial and terrestrial predators (Clarke 1983). Although moonlight is known to influence activity patterns of some tropical mammals (Fenton et al. 1977; Emmons 1987; Alkon and Saltz 1988), it has received little systematic attention in small neotropical mammal trapping studies. Selective logging has many influences on mammal community structure in tropical environments with arboreal mammal densities being lower (Eisenberg et al. 1979) and small mammal abundance being higher in logged sites (Kasenene 1984; Isabiyre-Basuta and Kasenene 1987; Malcolm 1995). Increased elevation has been found to change species diversity in some areas of the tropics (Rickart et al. 1991) while proximity to seasonally flooded areas close to rivers may alter species diversity and abundance in complex ways (Janson and Emmons 1990). Therefore the aim of this study is to investigate the diversity of species at a new site in the neotropics and to analyse factors affecting trapping success in this environment.

Material and methods

The study was conducted in and adjacent to the Bladen Nature Reserve in the Maya Mountains, Toledo District, Belize (Fig. 1). The reserve encompasses 350 km^2 of the watershed of the Bladen River between latitudes 16° 36′ 18″ and 16° 24′ 34″ N and longitudes 88° 42′ 16″ and 89° 04′ 51″ W. Elevation ranges from 50 to 1 000 m. Rainfall averages around 3 000 mm per annum or more; January to April are the driest months with rain starting from June onwards through November. Mean monthly temperatures range from 16 ° to 33 °C in Belize. Much of the reserve is composed of Coban formation limestone and volcanic rock. The reserve contains subtropical wet forest (Hartshorn et al. 1984) with the lowest parts, along the main flow of the river where we worked, supporting alluvial soils and tall broad-leaved forest. Most of the Bladen Nature Reserve is unlogged; selective logging has been practiced immediately outside its eastern border, however. The reserve is subject to unknown hunting pressure by local people for game meat.

The study was conducted during four periods of fieldwork: June and July 1994, June through August 1995, March 1997 and July 1998. Some rain fell in each of these periods but trapping was suspended under extremely wet conditions because we were concerned about hypothermia of captured individuals. All the work was conducted adjacent to the eastern entrance of the reserve, 1–3 km inside, and 0.5 km outside it.

Mammal diversity was assessed in three ways: through night and daytime walks in which observations and calls of mammals were noted, by in-

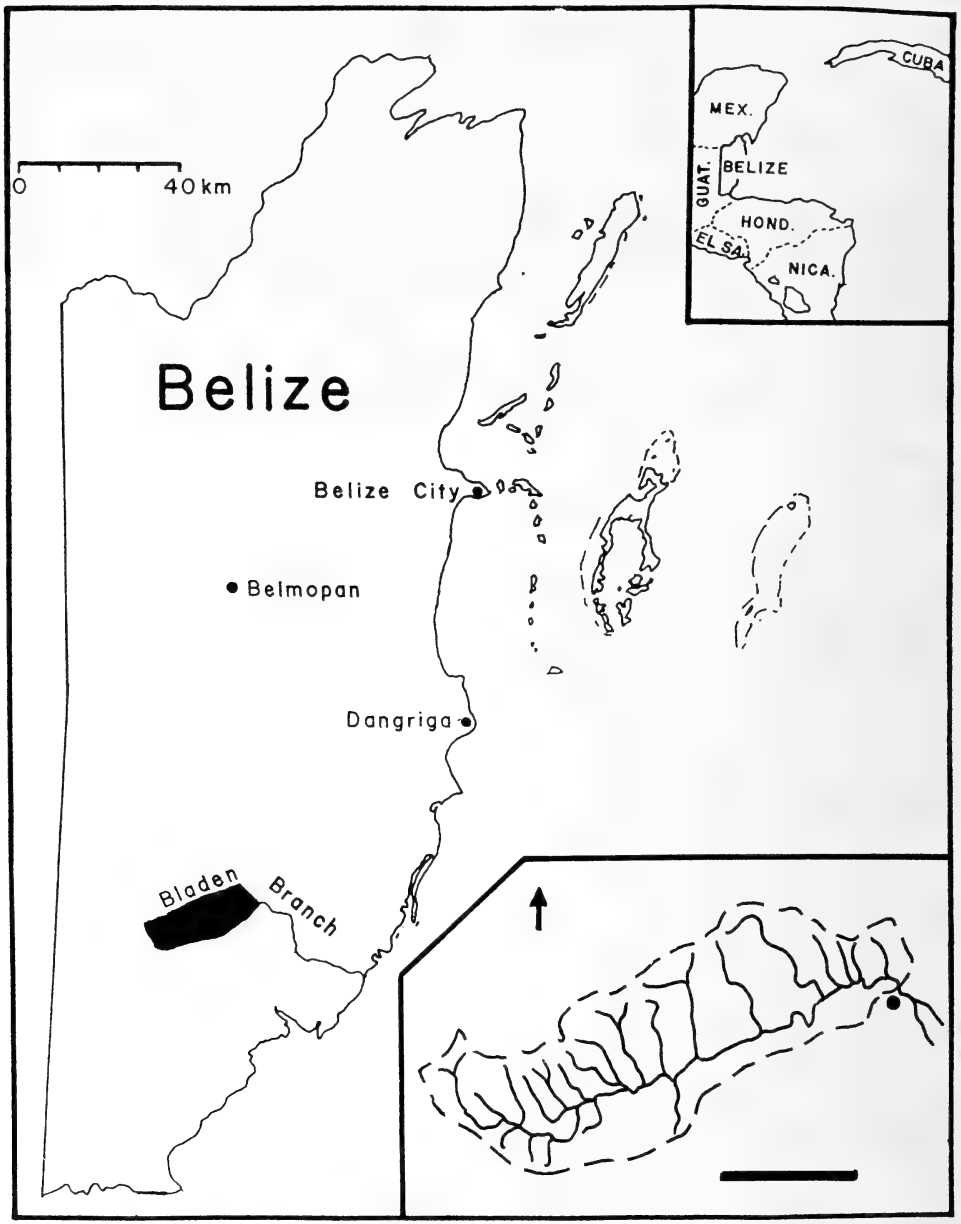

Fig. 1. Belize and the location of Bladen Nature Reserve (in black) in the country. Top right inset shows location of Belize in central America. Bottom right inset shows the boundary of Bladen Nature Reserve (dashed line) and the Bladen Branch River and its tributaries (solid lines). The entrance to the reserve is at Forest Hill shown as a black dot. Three 2 km transects were located (i) just inside the reserve boundary running south west to north east terminating at Forest Hill; (ii) between Forest Hill and the Richardson Creek (fifth tributary upstream from the entrance) confluence south and parallel to the Bladen River; (iii) and outside the reserve from and due north east of Forest Hill. All trapgrids within the reserve were set south of the Bladen River between Forest Hill and the second tributary upstream from the entrance. Trapgrids outside the reserve were set within 500 m of the reserve entrance. Black bar denotes 10 km; arrow shows north (adapted from Hartshorn et al. 1994).

terpreting mammal tracks in the mud, and through live trapping. Abundances of certain mammal species were estimated through repeat trapping using standard Sherman, custom-made small mammal traps, and three sizes of Tomahawk traps. We used the field guide of Emmons (1990) to identify mammals in the field. Two previous mammal surveys had been conducted in the Bladen (Brokaw and Lloyd-Evans 1987; The Nature Conservancy 1993).

We set up three 2 km transects that were walked at a pace of 1 km/hour. One was located within the reserve and followed an abandoned logging track that serves as the main road into the reserve; the second was further inside the reserve on the south side and parallel to the Bladen River; the third was located adjacent to but outside the Reserve in a selectively logged area. Night walks (N = 18) were conducted between 18.30 and 21.00 h and animals were spotted using flashlights; day walks (N = 28) took place between 05.30 and 07.30 h. Tracks of mammals were examined opportunistically and in specially prepared flats of mud, at the center at which was placed a commercial carnivore olfactory lure.

Small mammals were trapped using standard Sherman traps (23×8×8 cm), or traps of the same dimensions custom-made entirely out of galvanized wire mesh (by the late R. Schwab) save for a galvanized aluminum plate door that was part of the floor until the door swung upwards on closure (see also Emmons 1984). Traps were usually set in an 8×8 or 7×7 grid with traps 10 m apart; infrequently they were set along a transect precluding calculation of density. Grids of small mammal traps were baited either with a mixture of oats and molasses, with peanut butter, with green or ripe bananas, or with a medley of fruit consisting of apple, banana, and coconut mixed together. Ripe and green bananas were lumped together in bait analyses because green bananas quickly ripened in traps making it difficult to distinguish between the two. Traps were usually set on the flat valley floor of the reserve approximately 20–200 m from the Bladen River bank. In another protocol, trapgrids were set at higher elevations on the steep limestone slope bordering the floodplain approximately 50 and 100 m above the valley floor and 200–250 m from the river.

We set two types of Tomahawk traps (40×13×13 cm and 40×17×17 cm) which we termed middle-sized traps. These were usually set in a 6×8 grid with traps 50 m apart. Traps were baited either with oats and molasses, with green or ripe bananas, raisins, or a fruit found on the forest floor, Warre Cohune palm, *Astrocarynm mexicanum*. These traps were set approximately 50–450 m from the river. In one set of tests these traps were placed at a height of 1–2.5 m in trees and baited with oats and molasses in order to estimate squirrel abundance.

We also set large Tomahawk traps (65×22.5×22.5 cm) in a 6×8 grid with traps set 50 m apart. These were baited with either green or ripe bananas, *Astrocarynm mexicanum* fruit, commercial cat food or fresh fish; these latter two baits were combined in bait analyses since they both contained animal protein and smelled similar. In none of the trapping protocols were different baits run at the same time on either the same or different grids.

Traps were usually set for 5 consecutive nights although a small minority was set for fewer or more nights (range 1–7). Traps were set either in unlogged forest with a tall thick canopy and relatively open understory inside Bladen Nature Reserve, or in the area east of the reserve where selective logging allowed light to penetrate, producing a thicker understory of vegetation. Traps were opened and baited between 16.00 and 17.00 h and checked next morning between 06.00 and 09.00 h. Captured animals were individually marked by cutting small patches of fur since we were only interested in recaptures over a maximum of 7 days. Quarter of the moon was noted during each sequence of trapping; in some analyses traps set during the first and last quarter spanning the new moon, and then the second and third quarters spanning the full moon were combined.

We recorded number of species caught, percentage capture success, individual mammals caught/100 trapnights, and densities when traps were set in a grid square. Percentage capture success was the number of captures divided by the number of trapnights (i.e., number of traps multiplied by the number of nights on which they were set); individual mammals caught per 100 trapnights was the number of different individuals captured divided by the number of trapnights × 100; and densities were calculated by dividing the number of individuals captured by the area covered by the grid expressed as number of individuals/km^2. We took this area to be the dimensions of the grid plus 5 m either side (i.e., 70 m×70 m or 4 900 m^2 in a 7×7 grid) because paucity of captures made it difficult to calculate maximum distance between captures of known individuals. We did not use mark-recapture techniques to estimate density because recapture rates were so low.

Data were analysed by comparing trapgrids although the number of trapnights that these represented is also presented for clarity. Non-parametric statistics were used as number of species was an ordinal measure, and captures/trapnight and individual mammals caught/100 trapnights produced too many zeroes (no captures) to justify normalizing the data required for parametric statistics. The use of non-parametric statistics made it difficult to control for confounding variables; instead we conducted a series of carefully controlled comparisons among grids by excluding variables that were found to be important in previous analyses even though these resulted in a reduction in sample sizes. α was set at 0.05; nevertheless p values lying between 0.1 and 0.05 are noted and discussed with appropriate caution.

Results

Captures

In this study, twenty eight species of non-volant mammals were identified inside and outside but within 0.5 km of the Bladen Nature Reserve, although two of these were equivocal identifications (Tab. 1). In our study all of these species except five, *Philander opossum*, *Urocyon cinereoargenteus*, *Conepatus semistriatus*, *Leopardus* sp., and *Panthera onca* were found inside the reserve; in a previous study conducted by the Rapid Ecological Assessment Team in 1993 a jaguar and a small felid had been identified inside Bladen (The Nature Conservancy 1993). Our results, combined with those of the two earlier surveys (Tab. 1), show that the Bladen area holds a minimum of 33 non-volant species including large predators such as *Felis concolor* and *Panthera onca*.

Employing small mammal traps, we captured five non-volant species, *Heteromys desmarestianus*, *Ototylomys phyllotis*, *Tylomys nudicaudus*, *Marmosa robinsoni*, *Oryzomys couesi* and an unknown species of bat with an average percentage capture success of 6.5% (sd ± 5.9), or 5.6 individuals/100 trapnights (sd ± 5.6) (n = 26 grids; 4 236 trapnights). These traps yielded respective densities of 6 836/km^2, 270/km^2, 183/km^2, 925/km^2 and 2 127/km^2 for the five non-volant species (n = 18 grids; 3 521 trapnights). With the middle-sized Tomahawk traps, we caught only two species, *Ototylomys phyllotis* and *Tylomys nudicaudas*. Trap success was low at 0.7% (sd ± 1.0), or 0.6 individuals/100 trapnights (sd ± 0.8) (n = 9 grids; 1 354 trapnights). Density of these two species was 2/km^2 and 10/km^2, respectively (n = 5 grids; 1 200 trapnights). With the large Tomahawk traps, we caught *Didelphis marsupialis*, *Didelphis virginianus*, *Dasypus novemcintus* and a *Tylomys nudicaudus* giving an average percentage trap success of 4.3% (sd ± 4.3), or 3.9 individuals/100 trapnights (sd ± 3.9) (n = 9 grids; 1 218 trapnights). Density of these species was 28/km^2, 8/km^2, 2/km^2, and 2/km^2, respectively (n = 5 grids; 1 152 trapnights). Excluding bats, we calculated a Shannon-Wiener index of 2.021.

Factors affecting trapping success

Type of trap: Compared to standard Sherman traps, custom-made wire mesh traps of the same dimensions caught marginally more terrestrial mammal species (n = 6; 20 grids, respectively; 618, 3 618 trapnights, Means ($\overline{X}$s) = 1.0 (sd ± 0.9), 2.1 (sd ± 1.4) species, Mann-Whitney U test, z = –1.763, P = 0.078), demonstrated marginally higher percentage capture success ($\overline{X}$s = 2.2% (sd ± 3.0), 7.7% (sd ± 6.1) respectively, z = –1.951, P = 0.051), and caught a marginally greater number of individuals per trapnight ($\overline{X}$s = 2 (sd ± 3), 7 (sd ± 6) individuals/100 trapnights respectively, z = –1.830, P = 0.067).

Type of bait: For small mammal traps, there were significant differences in the number of species caught (n = 26 grids; 4 236 trapnights, Kruskal-Wallis test, H = 11.444, P = 0.01), percentage trap success (H = 8.464, P = 0.037), and individuals captured/100 trapnights (H = 7.888, P = 0.048) depending upon the type of bait offered. On each measure, oats and molasses were most successful followed by green and ripe bananas combined, and then the fruit medley (Tab. 2). There were no significant differences between baits on measures of density,

Table 1. List of species of mammals in and immediately adjacent to Bladen Nature Reserve.
1994–1998 this study: Tp: trapped; O: observed; Tr: tracks; H: heard; I/O: inside or outside Bladen Nature Reserve. 1. refers to species noted by the 1993 Rapid Ecological Assessment Team (The Nature Conservancy 1993); 2. refers to species noted by the 1987 Manomet survey (Brokaw and Lloyd-Evans 1987). * species may have been *Marmosa mexicana*; + species may have been *Leopardus wiedii* (Margay).

Scientific name	Common name	Tp	O	Tr	H	I/O
Marsupilia						
Didelphis marsupialis	Common opossum	X				I
Didelphis virginianus 2	Virginia opossum	X				I
Philander opossum	Common gray four-eyed opossum		X			O
Chironectes minimus 1	Water opossum		X			I
Micoureus alstoni 1	Alston's wolly mouse opossum					
*Marmosa robinsoni**	Robinson's mouse opossum	X				I/O
Xenarthra						
Tamandua mexicana	Northern tamandua		X			I
Dasypus novemcinctus	Nine-banded long-nosed armadillo	X				I/O
Chiroptera						
Balaniopteryx io 1	Least sac-winged bat					
Noctilio leporinus	Greater fishing bat		X			I
?	Unidentified species	X				I
Primates						
Alouatta pigra 1	Mexican black howler monkey				X	I/O
Ateles geoffroyi 1, 2	Central American spider monkey		X			I
Carnivora						
Urocyon cinereoargenteus	Gray fox		X			O
Nasua narica 1	White-nosed coati				X	I
Potos flavus	Kinkajou		X			I
Mustela frenata 1	Long-tailed weasel					
Eira barbara 2	Tayra		X			I
Conepatus semistriatus	Striped hog-nosed skunk		X			O
Lontra longicaudus 2	Neotropical otter		X			I
Leopardus pardalis + 1	Ocelot			X		O
Puma concolor 2	Puma			X		I/O
Panthera onca 1	Jaguar			X		O
Perissodactyla						
Tapirus bairdii 1, 2	Baird's tapir			X		I/O
Artiodactyla						
Tayassu tajacu 1	Collared peccary					
Tayassu pecari 1, 2	White-lipped peccary				X	I/O
Mazama americana 1, 2	Red brocked deer		X			I/O
Odocoileus virginianus 1, 2	White-tailed deer					
Rodentia						
Sciurus yucatanensis	Yucatan squirrel	X				I
Sciurus deppei 1, 2	Deppe's squirrel		X			I
Heteromys desmarestianus	Forest spiny pocket mouse	X				I/O
Oryzomys couesi	Coues' rice rat	X				I/O
Tylomys nudicaudus 1	Naked-tailed climbing rat	X				I/O
Ototylomys phyllotis	Big-eared climbing rat	X				I/O
Agouti paca 1, 2	Paca			X		I/O
Dasyprocta punctata 1, 2	Central American agouti					

Table 2. Mean ($\bar{X}$) and standard deviation (sd) measures of trapping success in all small mammal traps separated by type of bait; round brackets refer to numbers of trapgrids or traplines, square brackets to the number of trapnights.

		Oats and molasses	Peanut butter	Bananas	Fruit medley
		(7) [1 973]	(3) [502]	(14) [1 461]	(2) [300]
Number of species	$\bar{X}$	3.1	0.7	1.6	1.0
	sd	0.9	0.6	1.2	1.4
Percentage trap success	$\bar{X}$	10.3	0.6	6.6	1.0
	sd	1.0	0.6	6.8	1.4
Individuals/100 trapnights	$\bar{X}$	7.5	0.6	6.5	0.4
	sd	1.3	0.6	6.8	0.6
		(7) [1 973]	(1) [245]	(10) [1 303]	
Individuals/km^2	$\bar{X}$	8 600	6 100	12 200	-*
	sd	14 300	0	12 400	

* traps were set in a line, rather than grid, so estimates of density are unavailable.

however. When analyses were restricted only to small mammal wire mesh traps, the number of species captured still differed significantly by type of bait (n = 20 grids; 3 618 trapnights, H = 7.792, P = 0.02) although this was no longer the case for measures of percentage trap success and individuals/100 trapnights. There were no effects of bait for any measure in the medium-sized or large traps.

Moon phase: Considering either small, medium-sized or large traps, there was no effect of moon phase on number of species captured, percentage capture success, number of individuals caught/100 trapnights, or density either when quarters were analyzed separately or when quarters respectively spanning the new and full moons were combined.

Selective logging: Somewhat more individual mammals were captured in logged forest than in unlogged forest using small mammal traps (n = 11,15 grids, respectively; 956, 3 280 trapnights, n = 8 (sd ± 7), 4 (sd ± 4) per 100 trapnights, Mann-Whitney U test, z = 1,664, P = 0.096) but there were no significant differences on the three other measures. Restricting analyses to the custom-made traps that were somewhat more effective in catching small mammals, we found that percentage capture success and individuals/trapnight were significantly greater in logged forest outside Bladen than in unlogged forest inside (n = 7,13 grids, respectively; 741, 2 877 trapnights, $\bar{X}$s = 12.2% (sd ± 5.4), 5.3% (sd ± 5.1), z = 2.260, P = 0.024; $\bar{X}$s = 12 (sd ± 4), 4/100 trapnights (sd ± 6), z = 2.539, P = 0.011). In the Tomahawk traps, a slightly greater number of species was captured in the unlogged than in the logged forest in the medium-sized (n = 7,2 grids, respectively; 1 312, 42 trapnights, $\bar{X}$s = 0.7 (sd ± 0.5), 0 (sd ± 0) species, z = 1.690, P = 0.091) and in the large traps (n = 7,2 grids, respectively; 1 200, 18 trapnights, $\bar{X}$s = 2.0 (sd ± 1.0), 0.5 (sd ± 0.7) species, z = 1.869, P = 0.062).

Elevation: We obtained a marginally greater number of species, percentage capture success and number of individuals/100 trapnights on the valley floor than at higher elevations on the slope above the Bladen River (n = 24,2 grids, respectively; 3 876, 360 trapnights, $\bar{X}$s = 2.0 (sd ± 1.3), 0.5 (sd ± 0.7) species, Mann-Whitney U test, z = 1.642, P = 0.1; $\bar{X}$s = 0.7% (sd ± 0.6), 0.3% (sd ± 0.4), z = 1.832, P = 0.067; $\bar{X}$s = 6.1 (sd ± 5.6), 0.3 (sd ± 0.4), z = 1.832, P = 0.067). Two of these three results still held after analyses were restricted to custom-

made small mammal traps placed in unlogged areas only (n = 11 low and 2 higher elevation grids; 3 258, 360 trapnights, $\overline{X}$s = 2.4 (sd ± 1.6), 0.5 (sd ± 0.7) species respectively, z = 1.610, P = 0.107; $\overline{X}$s = 6.3% (sd ± 5.0), 0.3% (sd ± 0.4) respectively, z = 1.781, P = 0.075; $\overline{X}$s = 4.7 (sd ± 3.5), 0.3/100 trapnights (sd ± 0.4) respectively, z = 1.781, P = 0.075). Tomahawk traps were not placed above the valley floor.

Proximity to the river: Finally, we compared traps Set within < 50 m of the river bank with those placed further away (50–200 m). Results showed that the number of species captured was marginally higher close to the river than further away from it (n = 11,11 grids, respectively; 2 239, 1 349 trapnights, $\overline{X}$s = 2.4 (sd ± 1.6), 1.2 (sd ± 0.9) species, Mann-Whitney U test, z = 1.793, P = 0.073) but there was no effect on percentage trap success or individuals/100 trapnights. When analyses were restricted to custom-made traps set on the valley floor in unlogged areas, however, proximity to the river resulted in greater numbers of mammals caught on all three measures (n = 8,3 grids next to and away from the river, respectively; 2 103, 414 trapnights, $\overline{X}$s = 2.9 (sd ± 1.5), 1.0 (sd ± 1.0) species, z = 1.763, P = 0.078; $\overline{X}$s = 7.9% (sd ± 4.6), 1.9% (sd ± 2.8) trap success respectively, z = 2.041, P = 0.041; $\overline{X}$s = 5.7 (sd ± 3.2), 1.9 individuals/100 trapnights (sd ± 2.8) respectively, z = 1.837, P = 0.066).

Discussion

Captures

Bladen Nature Reserve and land immediately adjacent to it held a minimum of 33 species of non-volant mammals which is comparable to other central American sites. Rabinowitz and Nottingham (1989) documented 39 species of non-volant mammals in the Cockscomb basin which is almost adjacent to the Bladen; Medellin (1994) reported 48 species in Selva Lacondona, Chiapas, Mexico but these were compiled over 10 years as opposed to our 6 month total period; Timm (1994 b) documented 50 species for La Selva in Costa Rica over 20 years; and Glanz (1990) reported 39 species on Barro Colorado Island, Panama, which had been studied for 13 years at the time.

Small mammal trapping success in Bladen (6.5%) was comparable to that in other neotropical wet forests such as Cockscomb. For example, trapping success in the Gigante Peninsula, Panama was 4.2% for the wet and 7.3% for the dry season (McClearn et al. 1994). In contrast to measures of mammal diversity, it is difficult to make many direct comparisons of species' densities with other sites as data for many of the same species are unavailable. *Didelphis* and *Dasypus* densities appeared low compared to Barro Colorado Island and south American sites (Glanz 1990), whereas *Marmosa* densities were higher than either at Barro Colorado or even Guatopo, Venezuela (Eisenberg et al. 1979). *Oryzyomys* densities were extremely high in comparison to Barro Colorado, Guatopo, Cosha Cashu and Cabassou, French Guiana (Charles-Dominique et al. 1981; Glanz 1990) possibly because some traps were set in selectively logged habitats.

Factors affecting trapping success

There is a substantial literature on the effects of trap type on trapping success in temperate regions (e. g., Sealander and James 1958; Slade et al. 1993). The few studies that have been conducted in the neotropics have compared live traps to snap traps and found the latter to catch more species and individuals (Pizzimenti 1979; Woodman et al. 1996). The only studies to compare wire mesh and Sherman traps were conducted in temperate climates (Holdenreid 1954; O'Farrell et al. 1994). In both cases a greater proportion of captures was made using wire mesh traps and heteromyid rodents in particular were captured in mesh traps. O'Farrell et al. (1994) found that custom-made wire mesh traps captured two to three times more individuals than Sherman traps. Our results from the neotropics replicated

these findings in that they showed marginally greater percentage success and individuals caught/100 trapnights in mesh traps. Clearly, comparisons of small mammal densities in the neotropics must take into account of whether traps are of mesh or box design.

There is also a considerable literature on the effects of baits on trap success but again mostly from temperate regions (e. g., Beer 1964; Slade et al. 1993; but see Laurance 1992) and it is well known that rolled oats and peanut butter is a very effective bait in capturing terrestrial mammals in this part of the world. Although very few comparisons have been reported for the neotropics, Woodman et al. (1996) found no differences in captures using suet or peanut butter in tropical forest in south-eastern Peru. In contrast, we found that oats and molasses caught more species, generated greater trap success, and captured more individuals/100 trapnights than other baits, with peanut butter producing poorest results. In addition, there are many other baits that include animal protein that we did not use. It therefore appears premature to suggest that bait has little influence on trapping in the neotropics.

In contrast to many studies in deserts of North America (e. g., Price et al. 1984), phase of the moon had no effect on measures of trapping in this study. Possibly, the thick canopy obscured the moon to such an extent that little light penetrated to the forest floor.

It is well documented that small mammal abundance is greater in selectively logged habitats in temperate regions (e. g., Monthey and Southiere 1995) as well as in the tropics (Delany 1971; Struhsaker 1997). For example, Malcolm (1995) showed that terrestrial mammal abundance, richness and diversity were all greater in pasture and young secondary forest than in continuous forest north of Manaus. Our results are consistent with his findings in that percentage success and number of individuals captured was greater in areas that had been logged outside the reserve than inside it. In addition, we caught a greater variety of species, principally marsupials, outside the reserve. There may be many reasons for these associations including a more abundant and predictable insect prey base (Malcolm 1995), increased seed abundance stemming from increased vertical vegetation density (Monadjem 1997), or even reduced threat of predation (da Fonesca and Robinson 1990) but these were not investigated.

Studies that have looked into the effects of elevation on small mammals have often found different results. For example, abundance increased with elevation in a tropical rainforest in the Philippines but species richness did not change (Heaney et al. 1989). In contrast, in a temperate rainforest in Chile, number of species, number of individuals, and species diversity all declined with increased elevation (Patterson et al. 1989). We found a marginally reduced number of species, trapping success, and number of individuals at higher elevations although trapping effort was relatively low off the valley floor. In addition, we caught a somewhat greater number of species, had somewhat greater success, and captured somewhat more individuals per trapnight near the river than farther from it. Taking these two results together, there appeared to be a gradient of decreasing small mammal diversity and abundance as one progressed away from the Bladen River and up the slope. Whether these findings reflect differences in humidity, soil drainage or type, or habitat structure remains unresolved.

Our findings are necessarily preliminary because we chose to examine a large number of factors which reduced our sample size. Nevertheless, they highlight the importance of carefully selecting the type of trap and type of bait in trapping studies of neotropical mammals. They also point to the differences that may be expected in estimating mammal abundance and diversity in areas with different logging regimes, elevations and proximity to rivers in neotropical habitats. As such, they reinforce the necessity of standardizing techniques when comparing species abundance and diversity across neotropical sites.

Acknowledgements

We thank The Forestry Department and Belize Audubon Society for permission to work in the Bladen Nature Reserve and Raphael Manzanero and John Pinello for important assistance. We thank Jake and Kelly Marlin for permission to work in the Belize Foundation for Research and Environmental Education (BFREE). This work was supported by two University of California faculty research grants and a President's undergraduate fellowship as well as funding from San Francisco State University. Work was conducted under UC Davis Animal Care and Use Protocols. We thank Deirdre Doherty, Dave Drouillard, Chris Gregory, Beth Johnstone, Tom McNamara, Jeremy Mull, Megan Templeton, and Susan Woofsy for logistical help in the field; Ron Cole, Jake and Kelly Marlin, and Dirk Van Vuren for loaning and storing equipment; Steven Brewer, Doug Kelt, Marcel Rejmanek, and Dirk Van Vuren for discussions; and Sabine Schmid-Holmes for translating the summary into German.

Zusammenfassung

Diversität von Säugern im Bladen Naturreservat, Belize, und Faktoren, die einen Fangerfolg beeinflussen

Im Bladen Naturreservat, einem subtropischen Feuchtwaldgebiet, wurde durch Zählungen an Transekten und unter Einsatz von Sherman- und Tomahawk-Lebendfallen das Vorkommen von 33 Säugetierarten festgestellt. In insgesamt 6 075 Fallennächten wurden Einfluß von Fallendesign, Köder, Mondphase, Holzeinschlag, Höhenlage und Nähe eines Flusses auf Fangerfolg systematisch untersucht. Drahtgitterfallen hatten etwas größeren Fangerfolg als Sherman-Fallen, Haferflocken und Molasse erzielten größeren Fangerfolg als andere Köder, Fangerfolg in Wald mit selektivem Holzeinschlag war größer als in Wald ohne Einschlag und er war etwas größer in höher gelegenen Gebieten und näher an einem Fluß. Die Mondphase hatte keinen Einfluß auf Fangerfolg. Die Resultate liefern Basisdaten über die Säugetiervielfalt in einem relativ unerforschten Gebiet Zentralamerikas und geben an, wenn auch nur vorläufig, welche Aspekte im Fangdesign standardisiert werden sollten, um einen Vergleich der Artenvielfalt zwischen verschiedenen neotropischen Studiengebieten zu ermöglichen.

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Mamm. biol. **66** (2001) 102–110
© Urban & Fischer Verlag
http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Welche quantitativen Beziehungen bestehen bei Säugetieren zwischen Schädelkapazität und Hirnvolumen?

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Receipt of Ms. 20. 03. 2000
Acceptance of Ms. 10. 09. 2000

Abstract

How is cranial capacity related to brain volume in mammals?

The measurement of cranial capacity is often used to obtain information about the brain volume in mammals. Brain volume and cranial capacity are of the same size only in small mammals. For 17 mammalian species (451 individuals) we could show that cranial capacity often is larger than brain volume, and the differences in size are not equal in the 17 species. The relation cranial capacity % brain volume ranges from 102.45% to 116.97%. Therefore, assuming that cranial capacity = brain volume can lead to remarkable errors.
The intraspecific allometric relation of cranial capacity to brain volume may be isometric or positive allometric, the interspecific relation is positive allometric. Thus, if the allometric relations are known, it is possible to estimate unknown brain volumes on the basis of known cranial capacity.

Key words: Allometry, cranial capacity, brain size, mouse-to-elephant-line

Einleitung

Ein intra- bzw. interspezifischer Vergleich von Hirngrößen ist ein erster und einfacher Schritt die funktionelle Bedeutung des Gehirns bei verschiedenen Arten zu schätzen. Das beste Maß für die Hirngröße ist das Frischhirngewicht (HG) bzw. das Frischhirnvolumen (HV = HG/1,036). Die Hirngröße hängt ab von verschiedenen Faktoren: Körpergröße, Evolutionshöhe und Spezialisation. Bevor dieser Einfluß auf die Hirngröße verschiedener Arten bewertet werden kann, muß die Bedeutung der Körpergröße für dieses Organ festgestellt werden. Ein geeignetes Maß für die Körpergröße ist das Bruttokörpergewicht (BKG). Die Ermittlung des Einflusses des BKG auf das HG ist möglich mit der Allometrieformel: log Organgewicht = log b + a · log Körpergewicht. Der Wert für a sagt aus, ob der relative Anteil der Hirngröße am Körpergewicht von kleinen zu großen Tieren abnimmt, gleich bleibt oder zunimmt, der Wert b enthält Faktoren, welche zudem das HG beeinflussen.
Die Bestimmung von a für den interspezifischen Bereich ist möglich bei unterschied-

1616-5047/01/66/02-102 $ 15.00/0.

lich großen Arten naher Verwandtschaft, die sich außer der Körpergröße in anderen Merkmalen nur gering unterscheiden. Ist a bekannt, dann können Unterschiede in b als quantitativer Ausdruck von Verschiedenheiten in der Cephalisationshöhe (Evolutionshöhe, Spezialisation) angesehen werden (Stephan et al. 1986; Röhrs 1986; Röhrs et al. 1989).

Die Beschaffung von Daten über Hirn- und Körpergewicht von möglichst vielen Säugetierarten ist schwierig, daher sind zur Erweiterung der Datenbasis andere Verfahren als die direkte Messung von HG und BKG versucht worden. In den zoologischen und paläontologischen Museen lagern viele Schädel von fossilen und rezenten Säugetierarten. Als Ersatzmaß für die tatsächliche Hirngröße sind bei diesem Material häufig Messungen der Hirnschädelkapazität (HSK) möglich; aber stimmen HSK und HV wirklich überein? Diese Frage soll hier untersucht werden. Auf das Problem der Schätzung des BKG nach Schädel- und Skelettmaßen wird in dieser Arbeit nicht eingegangen.

Messungen der HSK zur Gewinnung von Informationen über die tatsächliche Hirngröße sind eine alte Methode (Darwin 1868; Klatt 1912), und bis heute ist dieses Verfahren noch üblich. Jerison (1973) bestimmte die HSK bei fossilen und rezenten Säugetierarten, um Änderungen der Hirngröße in der Geschichte der Säugetiere zu erforschen. Jerison (1973) setzt dabei voraus, daß HSK und HV übereinstimmen; auch Radinsky (1978), Gittleman (1986), Towe und Mann (1992) und Martin (1990) nehmen für die von ihnen untersuchten Säugetierarten Übereinstimmung von HSK und HV an. Jerison (1973) weist aber darauf hin, daß bei Walen die HSK beträchtlich größer sein kann als das HV. Martin (1990) bemerkt, daß es angebracht sei, die Beziehungen HSK–HV zu erforschen, bevor Schlüsse aus der HSK auf die tatsächliche Hirngröße gezogen werden können.

Eingehende Untersuchungen über die Beziehung von HSK zu HV fehlen bis heute. Nach Daten von Röhrs und Ebinger (1998) beträgt die Hirnschädelkapazität bei 14 Zoo-Przewalskipferden durchschnittlich 116% des Hirnvolumens, wobei die mittlere HSK ein Volumen von 649 cm^3 und das HV einen Mittelwert von 558 cm^3 haben; die allometrische Beziehung HSK–HV ist hierbei isometrisch. Bei *Nasua rufa* (n = 12) beträgt die mittlere HSK 105% des mittleren Hirnvolumens; die intraspezifisch allometrische Beziehung HSK–HV ist positiv (a = 1,19). Der prozentuale Anteil der HSK am HV nimmt von 100,5 beim kleinsten HV bis auf 109,5 beim größten HV zu (Röhrs et al. 1989).

Diese Beispiele zeigen, daß HSK und HV beträchtliche Größenunterschiede aufweisen können, und daß die Beziehung HSK – HV im intraspezifischen Bereich auch positiv allometrisch sein kann. Wird die HSK ohne Berücksichtigung solcher Tatsachen mit dem HV gleich gesetzt, kann es zu Fehlbeurteilungen der Hirngröße kommen. Wir haben daher an einem umfangreichen Datenmaterial untersucht, welche Beziehungen im intraspezifischen und interspezifischen Bereich zwischen HSK und HV bestehen können, und ob es Möglichkeiten gibt, das HV (damit auch das HG) nach der HSK zu schätzen.

Material und Methode

Bei 451 Individuen von 17 Säugetierarten erfolgte die Bestimmung des Frischhirngewichts durch Wiegen nachdem das Schädeldach aufgesägt, das Rückenmark durchtrennt und das Gehirn entnommen wurde. Durch Division mit dem Faktor 1,036 – dem spezifischen Gewicht für Hirnmasse – wurde das Hirnvolumen aus dem HG errechnet. Nach der Mazeration des Schädels und Schließen des Schädeldachs konnte die Hirnschädelkapazität durch Auffüllen des Hirnschädelhohlraums mit Schrot oder Glaskugeln gemessen werden. Bei allen Individuen wurde auch das Bruttokörpergewicht festgestellt. So kennen wir bei 451 Tieren jeweils HSK, HV, HG und BKG. Das Material stammt von Forschungsreisen (Herre und Röhrs, Südamerika 1956/57, 1962; Galapagos 1971) sowie aus Sammlungen von Herre, Röhrs und Ebinger.

Für 12 Arten konnten die intraspezifischen Allometriegeraden (Ellipsenhauptachsen) HSK–HV

berechnet werden. Weiterhin haben wir für insgesamt 17 Arten jeweils den mittleren prozentualen Anteil der Hirnschädelkapazität am Hirnvolumen bestimmt (HSK%HV). Bei Arten mit positiver Allometrie für die Beziehung HSK zu HV wurden entsprechend den Allometriegleichungen die Werte HSK%HV für das kleinste und größte HV errechnet. Darüber hinaus haben wir die interspezifischen Allometriegeraden HSK–HV für Myrmecophagidae, Mustelinae, Canidae sowie für alle untersuchten 17 Arten ermittelt.

Ergebnisse und Diskussion

Intraspezifische Allometrien HSK–HV

Ist nur die Hirnschädelkapazität bekannt, so können intraspezifisch allometrische Beziehungen HSK zu HV geeignet sein, das HV von Individuen einer Art zu schätzen. Dies kann wichtig sein für Vergleiche der Hirngrößen innerhalb von Arten, so z. B. zwischen Unterarten, Geschlechtern sowie Wild- und Haustieren (Kruska 1980; Röhrs und Ebinger 1983, 1998).

In Tabelle 1 sind die intraspezifischen Allometriegleichungen HSK–HV für 12 Säugetierarten aufgeführt. Bei *Mustela nivalis, Mustela, erminea,* und *Martes foina* ist diese Beziehung etwa isometrisch (Abb. 1). Eine solche Isometrie haben wir bei Zoo-Przewalskipferden bereits 1998 nachgewiesen (Röhrs und Ebinger 1998). Bei den übrigen 8 von den 12 Arten ist die Beziehung HSK–HV positiv allometrisch, und die a-Werte reichen von 1,05 bei *Dusicyon gymnocercus* bis zu 1,25 bei Hausziegen (Abb. 2). Es gibt also keinen einheitlichen intraspezifischen a-Wert für die Beziehung HSK–HV bei allen Säugetierarten.

Bei den von uns untersuchten Spezies ist

Tabelle 1. Intraspezifische allometrische Beziehungen Hirnschädelkapazität zu Hirnvolumen (log HSK = log b + a · log HV) bei 12 Säugetierarten.

Spezies	log HSK	log b	a	log HV
Oryctolagus cuniculus (n = 35, r = 0,9727)	1,0191	−0,0713	1,0812	1,0085
Mustela nivalis (n = 78, r = 0,9916)	0,3628	−0,0224	0,9916	0,3432
Mustela erminea (n = 29, r = 0,9812)	0,7320	−0,0230	0,9873	0,7182
Martes foina (n = 19, r = 0,9763)	1,3512	0,0720	0,9913	1,3154
Dusicyon gymnocercus (n = 56, r = 0,9864)	1,6229	−0,0627	1,0505	1,6046
Dusicyon culpaeus (n = 15, r = 0,9840)	1,7581	−0,1672	1,1079	1,7377
Canis aureus (n = 32, r = 0,9160)	1,8423	−0,0578	1,0567	1,7982
Canis latrans (n = 32, r = 0,9149)	1,9709	−0,1268	1,0833	1,9365
Canis lupus (n = 65, r = 0,7791)	2,1730	−0,2860	1,1584	2,1226
Lama guanacoe (n = 20, r = 0,9663)	2,4427	−0,0735	1,0449	2,4081
Hausziegen (n = 36, r = 0,9484)	2,1298	−0,4423	1,2456	2,0650
Zooprzewalskipferde (n = 14, r = 0,9550)	2,8126	0,0656	1,0000	2,7469

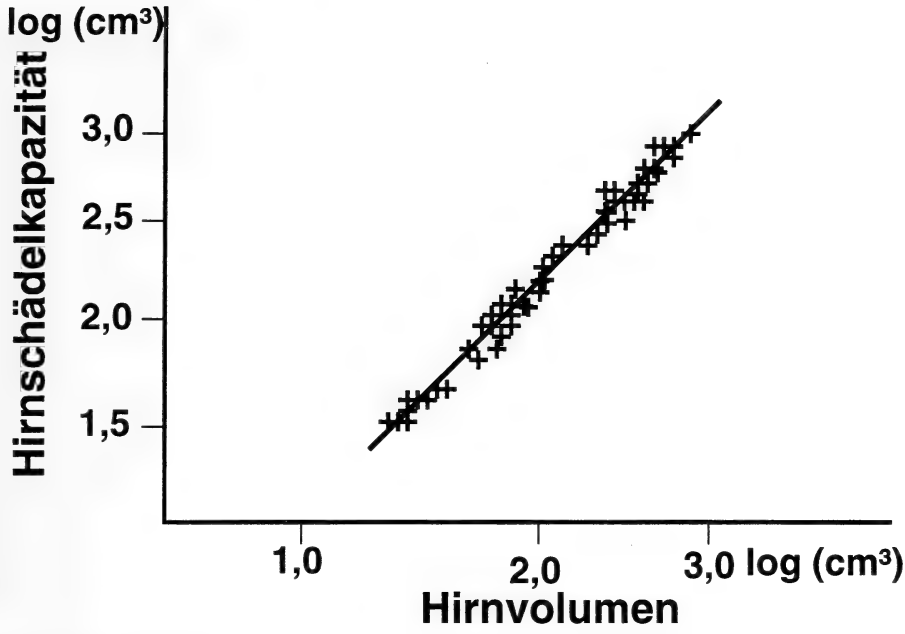

Abb. 1. Intraspezifische allometrische Beziehung HSK–HV bei *Mustela nivalis*, a_{EHA} = 0,9916 (Standardfehler: x = 0,0093, y = 0,0093).

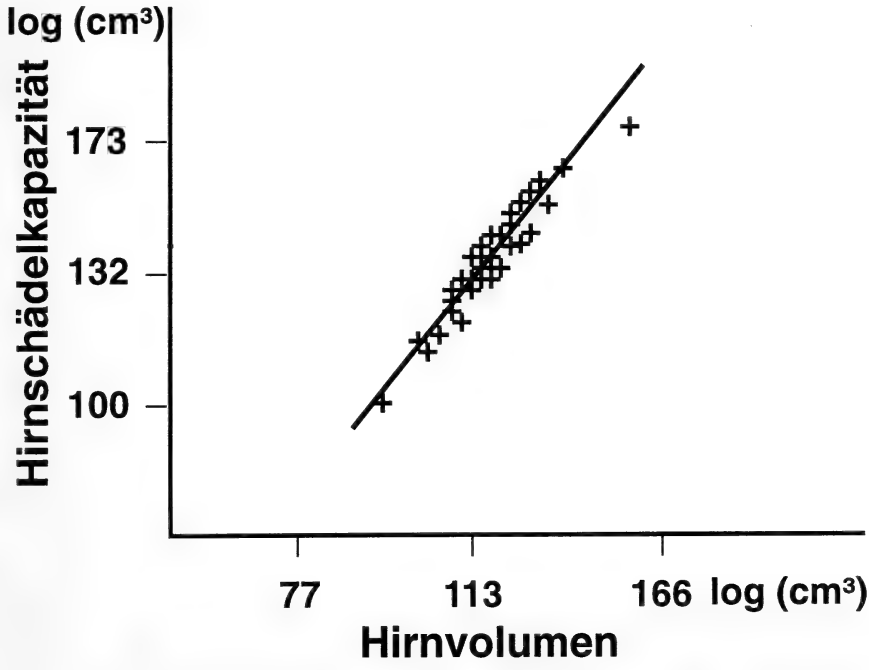

Abb. 2. Intraspezifische allometrische Beziehung HSK–HV bei Hausziegen, a_{EHA} = 1,2456 (Standardfehler: x = 0,0066, y = 0,0082).

Tabelle 2. Mittelwerte von HSK (cm^3), HV (cm^3) und HSK%HV bei 17 Säugetierarten

Spezies	HSK	HV	HSK%HV	Min – Max	N
Oryctolagus cuniculus	10,45	10,20	102,45	101,15–104,00	35
Mustela nivalis	2,3056	2,2039	104,62	Isometrie	78
Mustela erminea	5,3951	5,2264	103,23	Isometrie	29
Martes foina	22,45	20,67	108,61	Isometrie	19
Eira barbara	50,35	46,39	108,35		3
Dusicyon sechure	33,46	32,63	102,54	–	4
Dusicyon gymnocercus	41,97	40,23	104,33	103,08–105,57	56
Cerdocyon thous	50,65	46,57	108,76	–	7
Dusicyon culpaeus	57,29	54,66	104,80	103,31–106,69	15
Canis aureus	69,55	62,83	110,70	109,88–111,71	32
Canis latrans	93,52	86,40	108,24	107,32–109,76	32
Canis lupus	148,94	132,62	112,31	108,53–115,34	65
Lama guanacoe	277,14	255,92	108,29	107,70–109,07	20
Hausziege	134,83	116,14	116,09	110,32–124,81	36
Tamandua tetradactyla	28,32	26,23	107,95	–	3
Myrmecophaga tridactyla	96,58	82,53	116,97	–	3
Zooprzewalskipferd	649,46	558,39	116,31	116,31–116,31	14

die mittlere HSK immer größer als das HV. Der Größenunterschied ist aber bei den einzelnen Arten nicht gleich. Der Wert HSK%HV reicht von 102% bei *Oryctolagus cuniculus* bis zu 117% bei *Myrmecophaga tridactyla* (Tab. 2). Bei Isometrie der intraspezifischen Beziehung HSK–HV ist der Wert HSK%HV auf allen Größenstufen des Gehirns etwa gleich; so bei *Mustela nivalis*, *Mustela erminea*, *Martes foina* und Zoo-Przewalskipferden (Tab. 2). Bei positiver Allometrie steigt der Wert HSK%HV von den kleinen zu den großen Gehirnen an; bei Hausziegen von 110% bis 125% an. Bei diesem Maximum beträgt das HV 156 cm^3 und die HSK 195 cm^3; das ist eine Differenz von 39 cm^3. Weitere Beispiele sind in Tabelle 2 aufgeführt.

Eine Übereinstimmung von HSK und HV kann besonders bei kleinen Säugetieren vorkommen. MANN et al. (1988) nehmen bei Muridae und Cricetidae die Gleichheit von HSK und HV an. Eine solche Konformität ist aber für Säugetiere nicht allgemein gültig und unsere Ergebnisse machen für den intraspezifischen Bereich deutlich, daß eine Gleichsetzung von HSK und HV zu erheblichen Überschätzungen der Hirngröße führen kann.

Interspezifische Beziehungen HSK–HV

Mittelwerte der Frischhirnvolumina (oder des Hirngewichts) und der Bruttokörpergewichte von Arten sind die Basis für interspezifische Vergleiche von Hirngrößen. Interspezifische Allometrien HSK–HV könnten die Möglichkeit bieten, Mittelwerte der Hirnvolumina von Arten nach der Hirnschädelkapazität abzuschätzen. Dazu folgen drei Beispiele.

Für *Tamandua tetradactyla* und *Myrmecophaga tridactyla* lautet die interspezifische Allometriegerade HSK–HV: 1,7100 = 0,0778 + 1,0763 · 1,6677 (r = 0,9981), für vier Arten der Mustelinae: 1,0367 = 0,0097 + 1,0163 · 1,0108 (r = 0,9999) und für sieben Canidenarten (Abb. 3): 1,7995 = –0,0724 + 1,0583 · 1,7687 (r = 0,9993).

Nach der interspezifischen Allometriegleichung HSK–HV bei Mustelinae wurde für die vier untersuchten Arten das jeweils nach der Hirnschädelkapazität zu erwartende Hirnvolumen („HV“) errechnet. In Tabelle 3 sind die Mittelwerte HSK%HV den Mittelwerten „HV“%HV gegenübergestellt. Das gleiche Verfahren wurde für sieben Canidenarten durchgeführt (Tab. 4). In allen Fällen weicht der Wert „HV“%HV

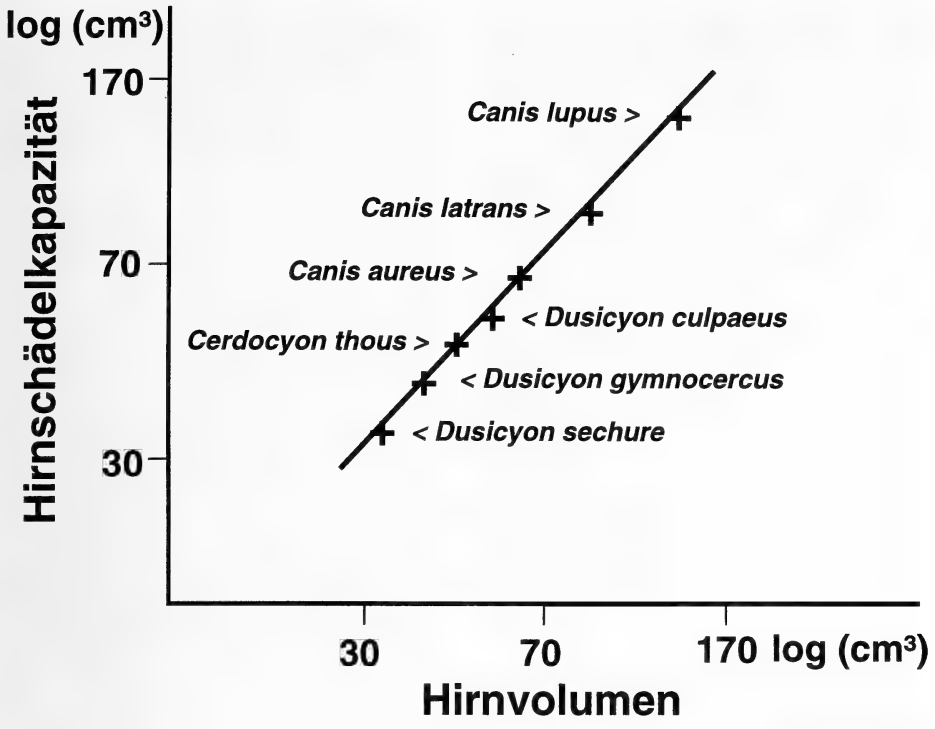

Abb 3. Interspezifische allometrische Beziehung HSK–HV bei 7 Canidenarten, a_{EHA} = 1,0583 (Standardfehler: x = 0,0783, y = 0,0825).

Tabelle 3. Vergleich HSK%HV mit „HV"% HV. „HV" errechnet nach der interspezifischen Allometriegeraden HSK–HV bei Mustelinae.

Spezies	HSK%HV	„HV"%HV
Mustela nivalis	104,62	100,98
Mustela erminea	103,23	98,29
Martes foina	108,61	101,08
Eira barbara	108,35	99,71

Tabelle 4. Vergleich HSK%HV mit „HV"%HV. „HV" errechnet nach der interspezifischen Allometriegeraden HSK–HV bei Canidae.

Spezies	HSK%HV	„HV"%HV
Dusicyon sechure	102,54	98,93
Dusicyon gymnocercus	104,33	99,00
Cerdocyon thous	108,76	102,36
Dusicyon culpaeus	104,80	98,17
Canis aureus	110,70	103,32
Canis latrans	108,24	98,68
Canis lupus	112,31	99,79

geringer von 100% ab als der Wert HSK%HV. Je größer das Hirnvolumen, um so mehr Unterschied besteht zwischen Hirnvolumen und Hirnschädelkapazität; so ist beim Wolf die mittlere HSK gegenüber dem HV um 16,3 cm^3 oder 112% größer, beim erheblich kleineren *Dusicyon sechure* beträgt die Differenz aber nur 0,83 cm^3 oder 103% (Tab. 2, 4).

Wir sind der Ansicht, daß auch für weitere Arten der Mustelinae und Canidae mit unbekanntem Hirnvolumen die genannten interspezifischen Gleichungen HSK–HV gültig sind. Damit ist es möglich (bei ausreichendem Schädelmaterial), das mittlere HV nach der mittleren HSK abzuschätzen. Für umfangreiche Studien müßten allerdings zunächst bei weiteren Familien die interspezifischen allometrischen Beziehungen HSK zu HV untersucht werden. Es ist aber schwierig, ausreichendes Datenmaterial zu erlangen. Vielleicht ist es machbar, eine Al-

lometriegleichung HSK–HV für alle Säugetiere einzusetzen, die zwar nur näherungsweise Schätzungen des HV nach der HSK erlaubt, die aber bessere Werte liefert als die Gleichsetzung von HSK und HV.

Bei Säugetieren sind viele Untersuchungen über allometrische Beziehungen zwischen Organgrößen (auch Stoffwechselgrößen) und Körpergrößen durchgeführt worden. Dabei stößt man immer wieder auf das Bemühen, jeweils einen a-Wert zu finden, der für alle Säugetiere (mouse to elephant line) Gültigkeit hat. Solche Fälle sind aber selten, was sicher mit besonderen Anpassungen und Spezialisationen zu tun hat. Evolutionshöhe und Spezialisationen haben aber wohl kaum eine Auswirkung auf das Verhältnis HSK–HV. Möglich ist jedoch – wie schon gezeigt – der Einfluß der Hirngröße. Martin (1990) hat für 33 Primatenarten die Beziehung HSK–HG berechnet und nennt als Ergebnis: $HSK = 0{,}94 \cdot HG^{1{,}02}$. Die Datenpaare stammen allerdings nicht von den selben Individuen. Martin (1990) nennt die Beziehung isometrisch und sagt weiter, daß man bei den untersuchten Primaten HSK und HG gleichsetzen könne, und daß dies auch bei anderen Säugern mit gleichem Größenbereich möglich sei. Ist diese Annahme richtig?

Nehmen wir an, bei einem HV von 1 cm^3 ist die HSK ebenfalls 1 cm^3 und rechnen dann mit dem a-Wert von 1,02 die HSK bei 10 cm^3 HV aus, so beträgt diese 10,5 cm^3. Bei 100 cm^3 HV ergibt sich eine HSK von 110 cm^3, und bei 1000 cm^3 HV beläuft sie sich auf 1158 cm^3. Ein Pottwal mit 6080 cm^3 HV würde nach dieser Gleichung eine HSK von 7237 cm^3 haben, damit wären wir bei dem von Jerison (1973) erwähnten großen Unterschied zwischen HSK und HV bei Walen. Es ist also nicht angebracht, für die Beziehung HSK–HV auch im interspezifischen Bereich für alle Säugetierarten Isometrie anzunehmen, und es ist hier ebensowenig angebracht HSK und HV gleichzusetzen.

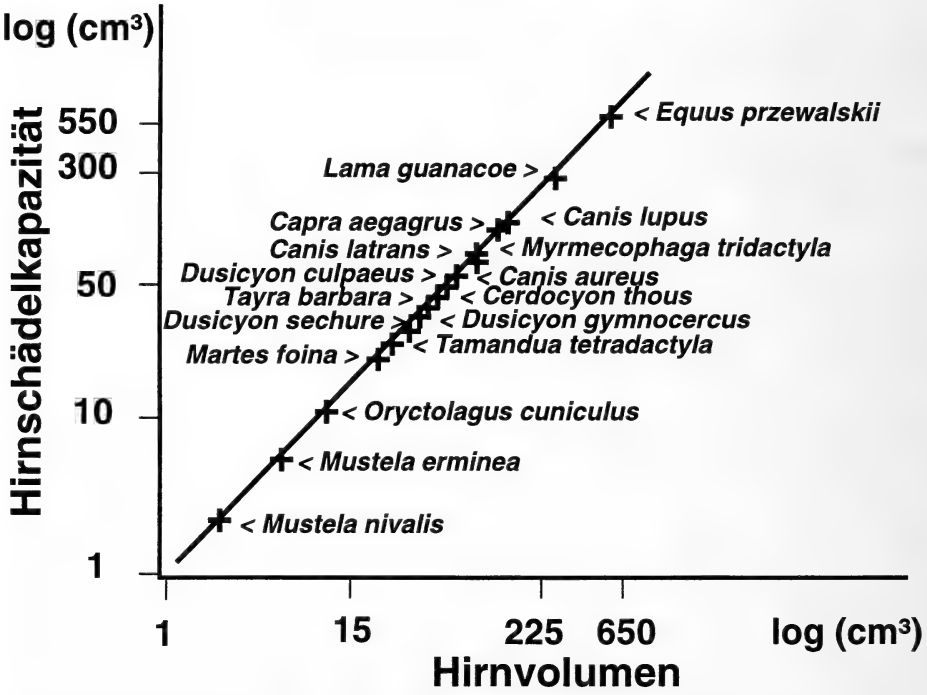

Abb 4. Interspezifische allometrische Beziehung HSK–HV bei 17 Säugetierarten, $a_{EHA} = 1{,}0222$ (Standardfehler: x = 0,1426, y = 0,1458),

Wir haben nun für 17 Säugetierarten (Tab. 2, Abb. 4) aus verschiedenen systematischen Einheiten die interspezifische Allometriegerade berechnet, sie lautet: log HSK = –0,0015 + 1,02 · log HV (r = 0,0997). Die Beziehung ist positiv allometrisch und stimmt fast mit der von MARTIN (1990) ermittelten überein. Der Wert HSK%HV nimmt von kleinen bis zu großen Gehirnen zu, und zwar von 102% bis zu 116% (Tab. 2, 5). Das heißt, besonders bei größeren Gehirnen kann die Differenz zwischen HSK und HV ein beträchtliches Ausmaß erreichen. Diese höhere Differenz könnte auch durch Zunahme der Volumina der Subarachnoidalräume und der Dicke der Dura mater bedingt sein. Quantitative Daten über die Größen dieser Strukturen liegen nicht vor.

In Tabelle 5 sind die Mittelwerte HSK%HV für die 17 untersuchten Arten aufgeführt und mit denen nach der o. a. interspezifischen Allometriegleichung ermittelten Werte „HV"%HV verglichen. Es ist eindeutig, daß die Schätzung des HV nach der Allometriegleichung HSK–HV weit bessere Werte liefert als die Gleichsetzung von HSK und HV. Wir schlagen daher vor, die von uns errechnete Allometriegerade HSK–HV von 17 Säugetierarten zu verwenden, wenn für Säuger das Hirnvolumen nach der Hirnschädelkapazität geschätzt werden soll. Wünschenswert sind weitere Datenpaare von HSK und HV, um die Zuverlässigkeit der Geraden zu verbessern.

Tabelle 5. Vergleich HSK%HV mit „HV"%HV. „HV" berechnet nach der interspezifischen Allometriegeraden HSK–HV für 17 Säugetierarten

Spezies	HSK%HV	„HV"%HV
Oryctolagus cuniculus	102,45	97,73
Mustela nivalis	104,62	103,02
Mustela erminea	103,23	99,89
Martes foina	108,61	101,92
Eira barbara	108,35	100,09
Dusicyon sechure	102,54	95,90
Dusicyon gymnocercus	104,33	96,59
Cerdocyon thous	108,76	100,28
Dusicyon culpaeus	104,80	96,39
Canis aureus	110,70	101,38
Canis latrans	108,24	98,50
Canis lupus	112,31	101,18
Lama guanacoe	108,29	96,27
Hausziege	116,09	104,82
Tamandua tetradactyla	107,95	100,78
Myrmecophaga tridactyla	116,97	106,42
Zooprzewalskipferd	116,31	101,52

Zusammenfassung

Zur Ermittlung der Größe des Hirnvolumens von Säugetieren wird häufig die Messung der Hirnschädelkapazität eingesetzt. Hirnvolumen und Hirnschädelkapazität stimmen aber nur bei kleinen Säugetieren überein. Für 17 Säugetierarten (451 Individuen) konnten wir nachweisen, daß die Hirnschädelkapazität größer ist als das Hirnvolumen. Die Größenunterschiede sind bei den einzelnen Arten nicht gleich. Der Mittelwert Hirnschädelkapazität % Hirnvolumen reicht von 102,45% bis 116,97%. Die Bewertung der Größe der Hirnschädelkapazität als Maß für das Hirnvolumen kann zu beträchtlichen Fehleinschätzungen der Hirngröße führen.

Die intraspezifische allometrische Beziehung Hirnschädelkapazität – Hirnvolumen kann isometrisch oder positiv allometrisch sein, die interspezifische ist positiv allometrisch. Sind solche Allometrien bekannt, dann kann man für Individuen von Arten mit unbekanntem Hirnvolumen, aber bekannter Hirnschädelkapazität die Hirngröße abschätzen. Entsprechendes gilt für Arten im interspezifischen Bereich.

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Mamm. biol. **66** (2001) 111–115
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Reproductive ecology of the endangered monogamous Malagasy giant jumping rat, *Hypogeomys antimena*

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Receipt of Ms. 11. 05. 2000
Acceptance of Ms. 06. 10. 2000

Key words: *Hypogeomys antimena*, reproductive ecology, Madagascar

Hypogeomys antimena, the Malagasy giant jumping rat, is the largest extant endemic rodent of Madagascar. Both sexes are ca. 30 cm long and weigh ca. 1.2 kg. It is considered to be one of the most endangered mammalian species of Madagascar. The distribution of this rodent has greatly diminished during the past two millennia. The last remaining population is restricted to patches of dry deciduous forest with a total extension of 20 km × 40 km situated north of the town Morondava, along the western coast of Madagascar. The whole area is subject to slash and burn agriculture and commercial logging (Genini 1996; Goodman and Rakotondravony 1996). Until recently, the information on *H. antimena* was limited to anecdotal information (Petter 1972; Starck 1974) and preliminary data from a nine-week field study by Cook et al. (1991). *H. antimena* was reported to be strictly nocturnal, to live in long deep burrows and to move by jumping and running. It was suggested that the rodent lives in social units, probably consisting of a pair plus their offspring. The most surprising information for a rodent species was that it produces only a single offspring per year. Most rodent species are characterised by large litter sizes, short birth intervals and sexual maturation at an early age (Hasler 1975).

In order to increase our very limited knowledge of the biology, ecology, and behaviour of *H. antimena* and for conservation purposes long-term field studies were initiated in 1992. It turned out that *H. antimena* has some very unusual life characteristics for a rodent species such as an obligate monogamous social and mating system. Pairbonds apparently last until one mate dies. Mates defend an exclusive territory throughout the year (for more details see Sommer 1996; 1997; 1998; 2000; Sommer and Tichy 1999). One critical component to understand the population dynamics of an endangered species is its reproductive ecology (for reviews on the behaviour-conservation interface see Sutherland 1998; Caro 1999). The aim of this study therefore was to investigate length of the reproductive period, reproductive rate, and offspring growth of the endangered *H. antimena* in its natural habitat.

Field studies were carried out in the 12 500 ha forestry concession of the Centre de Formation Professionnelle Forestière de Morondava (C.F.P.F.) in the Kirindy Forest (20°03′ S 44°39′ E) at the research station

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of the German Primate Center (DPZ, Göttingen, Germany). A detailed description of the area is given in GANZHORN and SORG (1996). Field work took place between October 1992 and January 1993, February and April 1994, April and June 1995, November and December 1995 and April and June 1996. In a 100 ha study area, all existing burrow systems were known and were regularly monitored and classified as active or inactive. Capture/recapture studies were carried at least once during each field period. Tomahawk live traps (51×19×19 cm, Tomahawk, Wisconsin) were set in front of the burrow holes before the nocturnal activity period of the rats started and checked at least once every hour after sunset until the animals entered the traps. Captured animals were anaesthetised for 10–15 min the next morning with an intramuscular injection of 0.1 to 0.25 ml ketamine hydrochloride (100 mg/ml), sexed, weighed, and measured. 157 animals from 30 active burrows have been marked individually with a passive integrated transponder (Trovan, Römerberg, Germany) since the beginning of the field studies in October 1992. The rats were released during their normal activity period in the evening in front of their burrows. The statistical tests were performed with SPSS (1997).

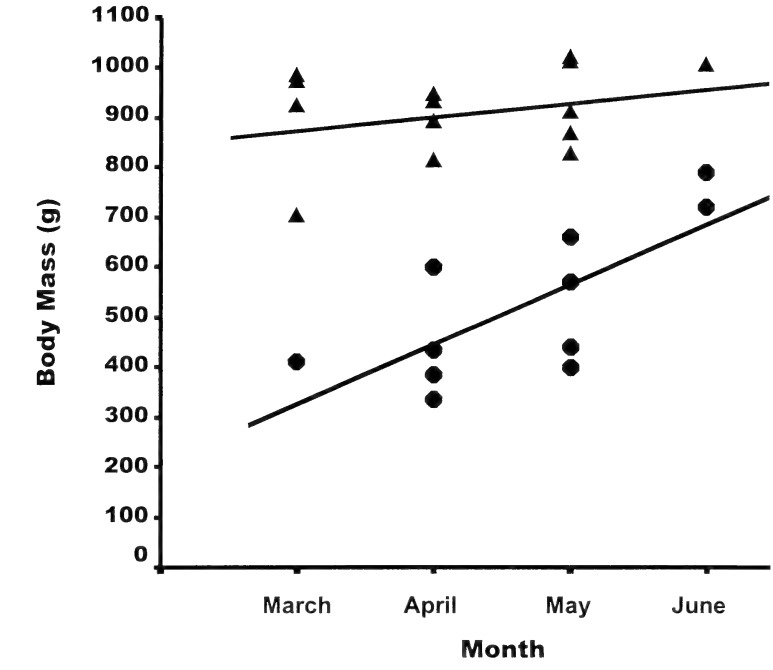
The study indicated that the reproduction of *H. antimena* is seasonal and takes place during the rainy season (Dec–March). The smallest, early born offspring was observed at the beginning of December (8th Dec) with a body mass of about 200 g and the smallest, late born offspring was observed at end of March (24th March) with a body mass of around 250 g.

In contrast to the anecdotal information on the reproductive rate, the capture/recapture studies indicated that not always a male and female couple was accompanied by a single offspring. One single offspring was present in 60 cases out of 78 investigated family units but in 11 cases two offspring of the present reproductive period lived together in a burrow system with their assumed parents. The sex ratio of offspring was balanced.

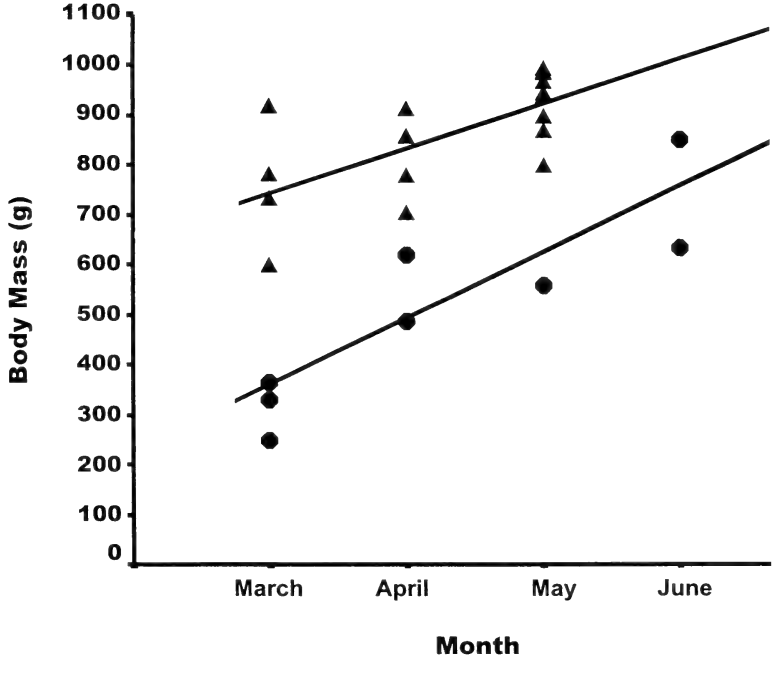
To answer the question whether this can be explained by the birth of twins or by two consecutive litters per reproductive period, the body mass of offspring which were born during one reproductive period in the same burrow were compared (Table 1). Only data were included in this analysis where all offspring of a pair could be weighed within two days. The mean difference in body mass of offspring trapped in the same burrow was 368 ± 89 g (n = 6). In one case (Dec 1992, Tab. 1) two offspring of about the same body mass (370 g, 395 g) were trapped at the same time which were assumed to be born in the same litter. The data suggest that *H. antimena* can have two single offspring born consecutively during one reproductive period but also twins might occur in natural populations. The reproductive rate per couple was calculated from trapping results after the reproductive period and was 1.5 offspring in 1994, 1.5 in 1995 and 1.1 in 1996. The average number of marked offspring per pair and year was 1.4. This might be an underestimation as

Table 1. Body mass (g) of offspring which were born during one reproductive period in the same burrow

Trapping date	1. Offspring	2. Offspring	Difference	Conclusion
10. 12. 92	395	370	25	twins
24. 03. 94	780	330	450	consecutive litters
25. 03. 94	980	730	250	consecutive litters
27. 03. 94	595	250	345	consecutive litters
27.–28. 03. 94	1175	700	475	consecutive litters
01.–02. 06. 95	1040	850	290	consecutive litters
06. 05. 95	795	400	395	consecutive litters



a)



b)

Fig. 1. Body mass of all offspring trapped between March and June. Early born offspring are symbolised by triangles, late born offspring by circles. a: male offspring, b: female offspring. Details on the linear regression lines are given in the text.

offspring spend the first 4–6 weeks of their life in the burrow and regularly leave it and can be trapped after another 4 weeks. The reason that to date *Hypogeomys* was reported to have only one single offspring per year (PETTER 1972; STARCK 1974; COOK et al. 1991), might be due to a high offspring mortality rate. Radiotracking and capture/recapture studies revealed a mean offspring mortality of more than 50% (SOMMER 2000).

In order to investigate the body mass development of early and late born offspring of consecutive litters born during one reproductive period and possible sex specific differences, the body mass of all offspring trapped between March and June were analysed (Fig. 1). The body mass development of early and late born female offspring and late born male offspring can be described by a significant linear regression (female offspring: early born: $R^2 = 0.46$, $p = 0.002$, late born: $R^2 = 0.74$, $p = 0.003$; male offspring: early born: $R^2 = 0.09$, n. s., late born: $R^2 = 0.53$, $p = 0.01$). The present data do not indicate that male and female offspring differ in the development of their body mass (ANOVA: early born: $F_{1,28} = 2.7$, n. s., late born: $F_{1,20} = 0.75$, n. s.). The difference of body mass of early and late born offspring during one reproductive period decreases with increasing age in their first year of life. At the end of the dry season (Nov/Dec), female offspring weighed 866 ± 177 g ($n = 11$) and male offspring 863 ± 99 g ($n = 5$) (t-test: n. s.). Also the analyses of other body measurements (body-, tail-, ear-, hindfoot-, head length, and head width) did not show any age-dependent differences in male and female offspring (SOMMER 1998).

Although the study indicated that *H. antimena* can have more offspring per couple and year than suggested previously, the reproductive rate is still very low. The survival prospects of this endangered species is critical due to changing environmental and ecological conditions as a consequence of the increasing human impact on the remaining habitat (SOMMER and HOMMEN 2000).

Acknowledgements

The studies are supported by the "Commission Tripartite" of the Malagasy Government, the Laboratoire de Primatologie et des Vertebrés de l'Université d'Antananarivo, the Ministère pour la Production Animale et des Eaux et Forêts, the Centre de Formation Professionnelle Forestière de Morondava, J. GANZHORN, B. RAKOTOSAMIMANANA, R. RASOLOARISON, L. RAZAFIMANANTSOA, WWF International, WWF Madagascar, and the German Research Foundation (So, 428/1-1).

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Mamm. biol. **66** (2001) 116–120
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Mating behavior during the estrus cycle in female Mongolian gerbils (*Meriones unguiculatus*)

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Receipt of Ms. 21. 06. 2000
Acceptance of Ms. 15. 10. 2000

Key words: Mongolian gerbils, estrus cycle, mating behavior, vaginal smears

Mongolian gerbils (*Meriones unguiculatus*) are common socially living rodents in the Steppe and semi-desert regions of Mongolia and Mandchuria (Gromov 1990). In their natural habitat, families, grouped around a founder pair, are strictly territorial (Ågren et al. 1989). Male behavior has been shown to be influenced by females (Probst and Lorenz 1987). Since the current literature on the female estrus cycle is limited and ambiguous (Marston and Chang 1965; Nishino and Totsukawa 1996), a redescription appears to be necessary. The aim of the present study was to obtain detailed data on the four stages of the estrus cycle in the Mongolian gerbil.

Adult Mongolian gerbils (*Meriones unguiculatus*) of both sexes from different litters aged 12–28 weeks were selected for this study. They were derived from our own laboratory stock (Zoh : CRW) and were kept in climatised windowless rooms under a photoperiod of LD = 14 : 10 (lights on at 0500 h CET; 200–300 lx during the light phase, approximately 5 lx during the dark phase). The room temperature was 23 ± 2° C and the relative humidity varied between 65 and 70%. The animals were housed in plastic cages (55 × 33 × 20 cm) with a wire mesh top. Tap-water and food pellets (Altromin® 7024, Altromin GmbH, Lage) were provided ad libitum. The animal bedding (Allspan®, NL) was renewed every two weeks.

Initially, the four different stages of the estrus cycle were defined in adult females (n = 18) by taking vaginal smears daily between two to four hours after lights on, over a period of two months. The stained smears were microscopically analysed (Leica®, Type DMRBE, ×200).

In figure 1 the respective pattern of the four stages of the estrus cycle is depicted. Some females remained in diestrus for up to 14 days, i. e., the cycle became irregular or was arrested for that period of time. However, it was always followed by the proestrus and the estrus cycle proceeded regularly.

Mating tests were performed during the four different stages of the estrus cycle of the gerbils. To prevent gravidity, adult but sexually unexperienced males were sterilized by vasectomy. Two weeks after surgery they were taken to perform mating tests. Vaginal smears were taken from all 24 females to evaluate their stage of estrus cycle two hours before the start of the mat-

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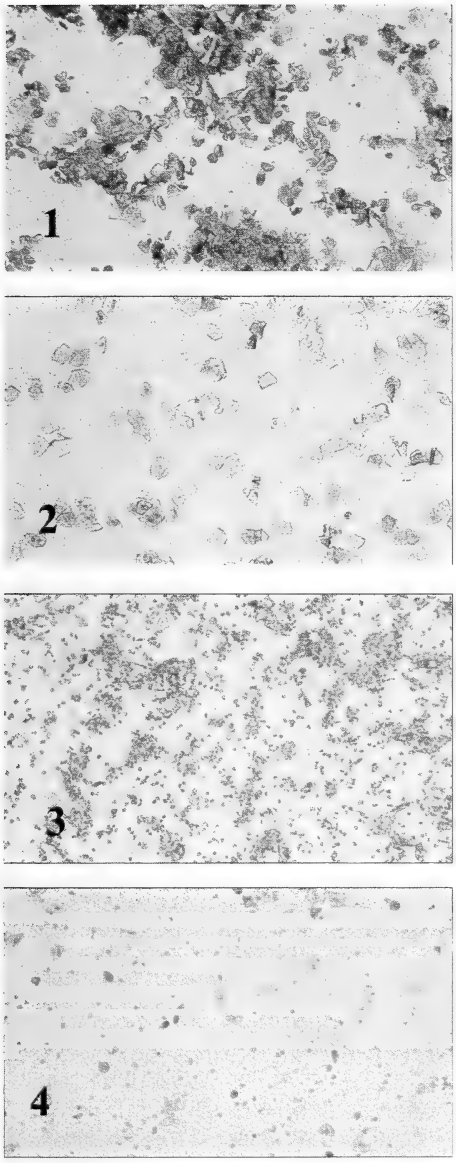

Fig. 1. Vaginal smears during the estrus cycle. Photographed under microscope (×200).
1. Preestrus: high number of squamous epithelial cells, absence of leukocytes and almost no cornified epithelial cells; 2. Estrus: low number of squamous epithelial cells, high number of dispersed cornified epithelial cells and no leukocytes; 3. Metestrus: mainly leukocytes, isolated squamous epithelial cells and/or cornified epithelial cells; 4. Diestrus: low number of leukocytes, no or only a few squamous epithelial cells and/or cornified epithelial cells.

ing tests (20–30 minutes after lights off). The lowest number of females, to which a stage could be unambiguously assigned, counted 11. In the following, always 11 out of 24 females were randomly chosen before every mating test. For each stage the animals were tested in a clean cage with new animal bedding. Ten minutes before the female was introduced, a vasectomized male was put into the cage. Each test lasted for ten minutes and the frequency of the following activities of the females was registered: copulation [c]: female is mounted by the male combined with friction movements; copulation trials [ct]: female presses tail to bottom and prevents the male, which tries to mount the female; lordosis [l]: female remains in front of the male with bent hind paws and lifted tail; copulation avoidance behavior [cab]: female poses head towards the male, vocalizes and/or avoids the male, genitals and tail are directed away. Kruskal-Wallis analysis of variance and subsequent two-tailed Mann-Whitney U-test (Winstat V 3.1) were used to assess differences in the mating tests. Since multiple tests were run on the same basic dataset, the resulting p-values were corrected by the standard Bonferroni procedure. Differences were accepted as significant at $p < 0.05$ (* in Fig. 2).

Figure 2 shows the results of the mating tests. The copulation behavior occurred exclusively in estrus (Kruskal-Wallis H-test: H-value = 20.23, $n = 11$, $p < 0.05$; Mann-Whitney U-Test estrus vs. preestrus, metestrus and diestrus: in all cases $U = 27.5$, $p = 0.0346$). The number of copulation trials was highest during the preestrus and lowest at diestrus. This difference was significant (Kruskal-Wallis H-test: H-value = 10.86, $n = 11$, $p < 0.05$; Mann-Whitney U-Test preestrus vs. estrus: $U = 31$, n. s.; preestrus vs. metestrus: $U = 26.5$, n. s.; preestrus vs. diestrus: $U = 16$, $p = 0.0188$; estrus vs. metestrus: $U = 48$, n. s.; estrus vs. diestrus: $U = 35.5$, n. s.; metestrus vs. diestrus: $U = 50.5$, n. s.). The lordotic behavior was mainly shown in the estrus (Kruskal-Wallis H-test: H-value = 18.37, $n = 11$, $p < 0.05$; Mann-Whitney U-Test preestrus vs. estrus:

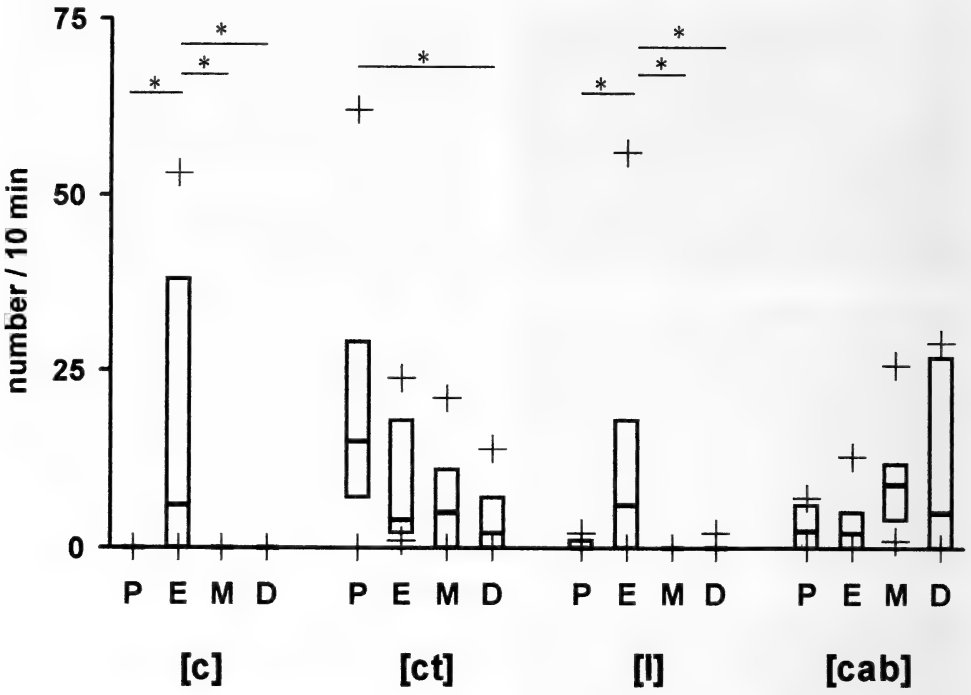

Fig. 2. Frequency of behavioral parameters during the mating tests. Females (n = 11) were tested during preestrus (P), estrus (E), metestrus (M) and diestrus (D).
[c] = copulation; [ct] = copulation trials; [l] = lordosis; [cab] = copulation avoidance behavior. Median values and the interquartils are shown, differences are significant at $p < 0.05$ and given as asterisks in the graph.

U = 21.5, p = 0.0369; preestrus vs. metestrus: U = 44, n. s.; preestrus vs. diestrus: U = 57, n. s.; estrus vs. metestrus: U = 16.5, p = 0.0048; estrus vs. diestrus: U = 20.5, p = 0.0244; metestrus vs. diestrus: U = 12.5, n. s.). There were no significant differences concerning copulation avoidance behavior towards the males during the estrus cycle (Kruskal-Wallis H-test: H-value = 7.21, n = 11, n. s.). The morning after the females were tested in estrus, 7 of the 24 tested females developed a vaginal plug.

In various rodents the uterus and the vagina as targets of ovarian hormones show cycle-dependent proliferation and apoptosis of luminal and glandular epithelium (Sato et al. 1997). The periodical increase and decrease of squamous epithelial cells, leukocytes and cornified epithelial cells in vaginal smears is a consequence of these changes and has already been described for rats (Otha 1995) or golden hamsters (Sandow et al. 1979; Gattermann et al. 1985) and reliably indicates the estrus. In gerbils, the preestrus used to be characterized by an increased number of squamous epithelial cells and the absence of leukocytes (Nishino and Totsukawa 1996). The aggressiveness of the females was low and they displayed only minor copulation avoidance behavior towards the males. This belongs to precopulatory behavior which may have a proceptive function (Holman et al. 1985). The estrus stage is a period of characteristic behavior including sexual receptivity (lordotic posture) in confrontation with males and the related vaginal smear pattern has already been described (Barfield and Beemann 1968; Adams and Norris 1973; Vick and Banks 1969). A further indicator for the re-

ceptivity in ***Meriones unguiculatus*** is a vaginal plug (Marston and Chang 1965; Norris and Adams 1981). Due to the receptive stage, the interactions initiated by the females were not aggressive during the mating tests. The typical cellular pattern of metestrus was in some cases preceded by clustered cornified cells and isolated leukocytes. This has already been described in a previous study and classified as "estrus II" (Nishino and Totsukawa 1996). Our data do not confirm this suggestion, because our vaginal smear alike was always connected to metestrus behavior. A possible explanation for these contradictory results may be found in the diverging procedure, i. e., in the cited investigation the animals were injected with pregnant mare serum gonadotropin and human chorionic gonadotropin. The elevated level of gonadotropin might have extended the estrus without affecting the vaginal epithelium. In the present study the females displayed no sexual behavior in that stage. The diestrus is generally defined as a "state of rest" between met- and preestrus, when the female was not fertilized. As described in an earlier study (Ågren and Meyerson 1977) the behavior of the females is agonistic and biased towards avoidance. Our analysis of the estrus cycle revealed characteristic changes in mating behavior of female gerbils.

Acknowledgements

We wish to thank Dr. Peter Fritzsche and Dr. Karsten Neumann for their valuable comments on the manuscript, Birgit Gebhardt for the fine technical assistance and Kate Williams for revising the English. We are grateful to Professor Gerald Moritz for supplying the facilities for the photo documentation. This study was supported by the Deutsche Forschungsgemeinschaft (Ga 437/1–2).

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Mamm. biol. **66** (2001) 121–126
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

The Bolivian bamboo rat, *Dactylomys boliviensis* (Rodentia: Echimyidae), a new record for chromosome number in a mammal

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Receipt of Ms. 20. 09. 2000
Acceptance of Ms. 30. 10. 2000

Key words: *Dactylomys boliviensis*, Rodentia, Bolivia, new record

The family Echimyidae, a highly diverse group of rodents, occurs throughout most of Central and South America. There are 16 recent genera and about 70 living species (Woods 1993), however, new taxa continue to be described (e. g., Da Silva 1998; Patton et al. 2000). To date no comprehensive phylogenetic analysis is available for the group although great advances have been forthcoming (e. g., Lara et al. 1996; Patton et al. 2000). The group is highly diversified ecologically and has had a long evolutionary history in South America (Patterson and Pascual 1972; Woods 1982). Karyologically, less than half of the species have been analyzed but it is known that there is considerable variation in diploid (from 2n = 14 to 2n = 96) and fundamental numbers (from FNa = 18 to FNa = 144) (Tab. 1). One of the most specialized groups within the Echimyidae is the subfamily of bamboo rats (Dactylomyinae). Woods (1993) placed three genera in the subfamily Dactylomyinae; *Dactyloms*, *Kannabateomys*, and *Olallamys*. The biology and evolutionary relationships of the Dactylomyinae are poorly known, likely due to their rarity to collectors and subsequent scarcity in museum collections. What is known is well summarized in Patton et al. (2000). Until recently (Aniskin 1993) no information on the chromosomal complement of any member of this group was available.

As part of a long-term survey of the mammals of Bolivia, many new and important records for the country were collected (Anderson 1997). In July of 1992 and May of 1996, we took a total of five specimens of *Dactylomys boliviensis* (Bolivian bamboo rat) from a locality in the Yungas of La Paz (Salazar et al. 1994). Here we report the karyotype of this species, the highest chromosomal number known in a mammal.

The individuals were located and collected at night in a dense stand of bamboo and secondary growth within the village of La Reserva (Departamento La Paz, Nor Yungas, La Reserva, elev. 840 m, 15° 44′ S, 67° 31′ W) by following their distinctive calls and eye shine. The village of La Reserva lies along Rio La Reserva, a small tributary of the Caranavi River. The village is at the bottom of a valley in the subtropical montane forest that covers most of the eastern Andean slopes between 15° and 17° S latitude in the Cordillera Oriental of Bolivia. The foothills at this elevation are cov-

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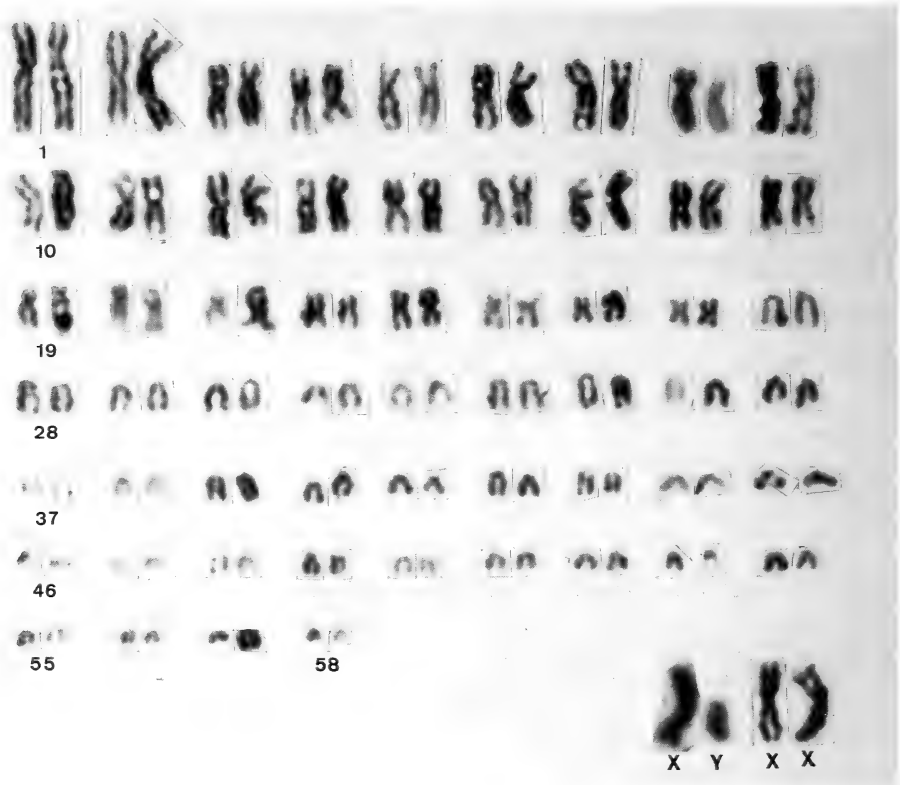

Fig. 1. Standard karyotype of *Dactylomys boliviensis*.

ered with semi-deciduous vegetation intermingled with columnar cacti and bromeliads. The forest is drier and sparser than at higher elevations. Compared to forests at higher and lower elevations, the trees are smaller, more highly branched, and most grow in open sun. The east facing slope above the river is steep, with much vegetation, some secondary growth, and banana and tangerine cultivation. Palms and tree ferns are absent (Salazar et al. 1994).

Chromosomal preparations were obtained using the technique described in Anderson et al. (1987). Metaphase cells were photographed and scored to determine the diploid (2n) and fundamental numbers (FNa). One of us (JLD) scored 5 slides per animal and over 20 spreads per slide to determine chromosome numbers. The analysis of the morphology of the chromosomes was based on 10 metaphase plates from three individuals. Nomenclature for chromosome morphology and fundamental number follows Patton (1967).

Chromosome slides, tissue samples, and cell suspensions are deposited in the Division of Biological Materials, Museum of Southwestern Biology (MSB). Voucher specimens are deposited at MSB (MSB 68547, MSB 85627, NK 40537), the American Museum of Natural History (AMNH 264887, 264884), and the Colección Boliviana de Fauna (CBF 2608), in La Paz, Bolivia.

The standard karyotype of *Dactylomys boliviensis* is highly asymmetrical, composed of 26 pairs of metacentric or sub-metacentric autosomes and 32 pairs of acrocentric autosomes. The X chromosome is a large sub-metacentric and the Y chromosome is a medium sub-metacentric. The resulting karyotype has a diploid count of 2n = 118 and FNa of 168 (Fig. 1). Chromo-

Table 1. Diploid (2n) and fundamental number (FN) for members of the family Echimyidae.

Taxon	2n	FN	Reference
Dactylomys boliviensis	118	168	this report
Dactylomys dactylinus	94	144	Aniskin (1993)
Echimys blainvillei	50	94	Reig (1989)
Echimys dasythrix	96	102	Lima et al. (1998)
Echimys semivillosus	94	134	Aguilera et al. (1998)
Echimys sp.	90	108	Lima et al. (1998)
Echimys sp.	90	110	Aniskin (1993)
Echimys sp.	90	112	Reig (1989)
Isothrix bistriata	60	116	Patton et al. (2000)
Isothrix bistriata	60	120	Lima et al. (1998)
Isothrix pagurus	22	38	Patton and Emmons (1985)
Isothrix sinnamariensis	28	42	Vie et al. (1996)
Makalata armata	70	120	Lima et al. (1998)
Makalata didelphoides	66	106	Lima et al. (1998)
Clyomys laticeps	34	60	Reig (1989)
Euryzygomatomys guiara	46	82	Aniskin (1993)
Euryzygomatomys spinosus	46	92	Reig (1989)
Hoplomys gymnurus	46		Aniskin (1993)
Lonchothrix emiliae	60	116	Aniskin (1993)
Mesomys hispidus	60	120	Lima et al. (1998)
Mesomys hispidus	60	116	Patton et al. (2000)
Mesomys occultus	42	54	Patton et al. (2000)
Proechimys albispinus	60	116	Leal-Mesquita et al. (1992)
Proechimys amphicoricus	26	44	Reig (1989)
Proechimys brevicauda	28–30	48–50	Gardner and Emmons (1984)
Proechimys canicollis	24	44	Gardner and Emmons (1984)
Proechimys cuvieri	28	46	Maia and Langguth (1993)
Proechimys decumanus	30	54	Gardner and Emmons (1984)
Proechimys echinothrix	32	69	Patton et al. (2000)
Proechimys gardneri	40	56	Patton et al. (2000)
Proechimys goeldii	24	44	Patton et al. (2000)
Proechimys guiarae	44–50	72–76	Gardner and Emmons (1984)
Proechimys gularis	30	48	Gardner and Emmons (1984)
Proechimys guyannensis	40	54–56	Gardner and Emmons (1984)
Proechimys iheringi	62–65	117–124	Reig (1989)
Proechimys kulinae	34	52	Patton et al. (2000)
Proechimys mincae	48	68	Gardner and Emmons (1984)
Proechimys oconnelli	32	52	Gardner and Emmons (1984)
Proechimys oris	30	52–56	Gardner and Emmons (1984)
Proechimys pattoni	40	56	Patton et al. (2000)
Proechimys poliopus	42	76	Gardner and Emmons (1984)
Proechimys quadruplicatus	28	44	Gardner and Emmons (1984)
Proechimys semispinosus	30	50–54	Gardner and Emmons (1984)
Proechimys simonsi	32	58	Gardner and Emmons (1984)
Proechimys steerei	24	42	Gardner and Emmons (1984)
Proechimys trinitatus	62	80	Gardner and Emmons (1984)
Proechimys urichi	62	88	Gardner and Emmons (1984)
Proechimys yonenagae	54	104	Leal-Mesquita et al. (1992), Rocha (1995)
Proechimys sp.	34	56	Aniskin (1993)
Proechimys sp.	14–16	18	Reig (1989)
Proechimys sp. (Balta)	40	56	Reig (1989)
Proechimys sp. (Barinas)	62	74	Gardner and Emmons (1984)
Thricomys aperoides	26	48	Leal-Mesquita et al. (1993)
Thricomys aperoides	30	54	Reig (1989)
Thricomys aperoides	30	50	Aniskin (1993)

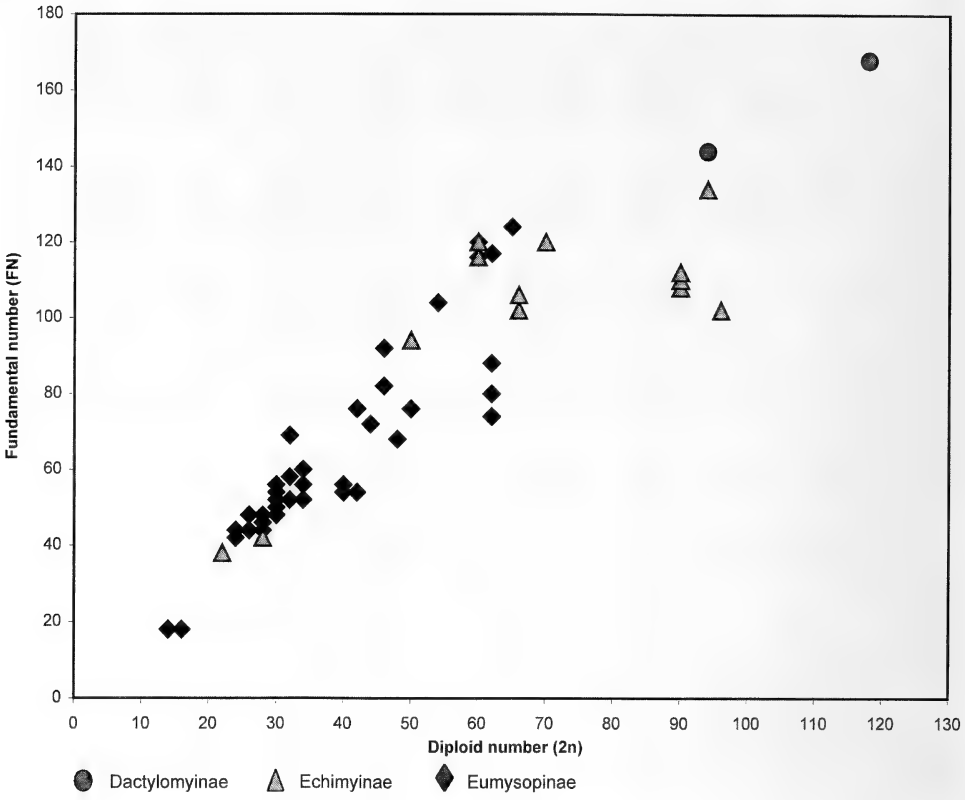

Fig. 2. Karyogram of known echimyid karyotypes.

some pair nine exhibits the characteristic satellite chromosome found in other echimyid rodents.

No chromosomal information is available for *Kannabateomys*, *Olallamys*, or *D. peruanus*. Aniskin (1993) described the karyotype of *D. dactylinus* (2n = 94, Fn = 144) from the Loreto Department in Peru. The karyotype of *D. boliviensis* differs from that of *D. dactylinus* by the presence of one additional set of meta or sub-metacentric pairs, and 10 pairs of acrocentric chromosomes although comparisons are difficult due to the fact that Aniskin (1993) did not identify sex chromosomes. At least 14 Robertsonian rearrangements would be necessary to transform the karyotype of one species into the other.

We compiled a list of all species of echimyid rodents for which data were available (Tab. 1) and created a karyograph (Iami and Crozier 1980) based on chromosomal and fundamental numbers (Fig. 2). A definite pattern of subfamily grouping is clear where two species of *Dactylomys* assume the highest positions on the plot and the echimyine rodents (*Echimys*, *Makalata*, *Isothrix*) are positioned at an intermediate level (with the exception of *I. pagurus* and *I. sinnamariensis*). The most speciose and karyologically studied group is the Eumysopinae (represented in this sample by *Proechimys*, *Clyomys*, *Euryzygomatomys*, *Hoplomys*, *Lonchothrix*, *Mesomys*, and *Trichomys*). For the most part these fall at the lower end of (Fig. 2). To date, no eumysopids have been found with a $2n > 65$.

Lima et al. (1998) proposed that Robertsonian rearrangements were more important in the evolution of the karyotype of arbo-

real echimyids than other chromosomal rearrangements because karyotypes of this group appeared to show higher levels of variation in diploid numbers than in fundamental numbers. Our data do not support Lima et al. (1998). We found statistically significant differences in the levels of variation between diploid and fundamental number for the arboreal echimyids (Kruskal-Wallis; $P < 0.004$), terrestrial echimyids (One-way ANOVA; $\alpha = 0.05$; $P < 0.004$), and for the entire echimyid radiation (Kruskal-Wallis; $P < 0.001$). However, in all cases the fundamental number varied more than the diploid number, suggesting that pericentric inversions may be more common. None the less it is quite likely that several processes may have influenced the evolution of the karyotype in this group.

Prior to our results, the highest chromosome number reported for a mammal was $2n = 102$ in *Tympanoctomys barrerae* (Contreras et al 1990). These authors also suggested that the family Octodontidae presented the greatest chromosomal diversity. While this remains true for Fundamental number, the Echimyidae now represent the family with the greatest diversity in diploid number ($2n = 14$ to $2n = 118$).

Although *Tympanoctomys* and *Dactylomys* represent terminal branches in two different families of South American hystricognath rodents with a long history on this continent, they also share another characteristic: both occupy restricted ecological niches and posses highly specialized life history traits. We concur with Contreras et al. (1990) in suggesting that the high chromosomal count appears to be a derived character.

Acknowledgements

This work was supported by grants from the National Science Foundation and a Research Experience for Undergraduates supplement. We would like to thank the 1992 and 1996 members of the joint CBF-MNK-AMNH-MSB field expeditions for their exceptional work. Mike Bogan, Jerry Dragoo, and William Gannon reviewed earlier drafts. Special thanks to Suzy and Somiya. Collecting and exportation permits were facilitated by the Coleccion Boliviana de Fauna.

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Mamm. biol. **66** (2001) 127–128
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Book reviews

Denzau, Gertrud; Denzau, H.: **Wildesel.** Stuttgart: Jan Thorbecke Verlag 1999. 221 pp., zahlreiche farbige Abbildungen und Karten. DM 79,–. ISBN 3-7995-9081-1.

Eine der frühesten Erinnerungen, welche der Rezensent aus seinen Studententagen an den früheren Vorsitzenden unserer Gesellschaft, Herrn Professor Dr. Dr. Wolf Herre, hat, bezieht sich auf dessen Ankündigung, nach der Emeritierung ein Buch über die Domestikation und Kulturgeschichte des Esels schreiben zu wollen. Leider verstarb Prof. Herre am 12. November 1997 ohne ein entsprechendes Werk hinterlassen zu haben. Es ist aber sehr wahrscheinlich, daß er von dem hier vorzustellenden Band von Gertrud und Helmut Denzau sehr beeindruckt und erfreut gewesen wäre, haben doch die Autoren mit einem klaren und informativen Text die Natur- und auch die Kulturgeschichte der Wildesel dargestellt und ihre Darstellung mit beeindruckenden, häufig sogar hinreißenden, Farbphotos illustriert.
Im vorliegenden Buch wird unterschieden zwischen dem Afrikanischen Wildesel (*Equus africanus* mit drei Unterarten, von denen eine – *E. a. atlanticus* – ausgestorben ist) und den beiden Asiatischen Wildeseln (*Equus hemionus* mit sechs Unterarten, davon eine – *E. h. hemippus* – ausgestorben, und *Equus kiang* mit drei Unterarten). Zunächst wird in einem kurzen Kapitel die Stammesgeschichte der Equiden mit besonderer Betonung der Esel besprochen, dann folgen in einem Kapitel mit dem irreführenden Titel „Wissenschaftsgeschichte" Darstellungen der taxonomischen, osteologischen, genetischen und ethologischen Charakteristika der Esel, ferner Bemerkungen zu Zoobeobachtungen und zu – weitgehend erfolglosen – Zähmungsversuchen. Ein sehr instruktives, mit anschaulichen, meist farbigen, Karten illustriertes Kapitel stellt die Lebensräume von Khur, Kulan, Onager und Dschiggetai (vier Unterarten von *E. hemionus*), sowie von Kiang (*E. kiang*) und Somali-Wildesel (*E. africanus somaliensis*) vor. Das folgende ausführliche Kapitel bietet nicht nur Angaben zur Entdeckung, Beschreibung und Erforschung dieser Arten, sondern auch zum ausgestorbenen Syrischen Halbesel (*E. hemionus hemippus*). Es enthält auch Auszüge von Beobachtungsprotokollen, welche die Autoren auf ihren Expeditionen anfertigten.
Die Kulturgeschichte der wilden Esel wird von der Vor- und Frühgeschichte her aufgerollt und mit Berichten aus verschiedenen Kulturkreisen und Epochen – mit dem Gilgamesch-Epos beginnend – illustriert. Die Fragen zur Domestikation des Afrikanischen Wildesels (*E. africanus*), die vermutlich im 5. oder 4. Jahrtausend v. Chr. in Nordafrika oder Westasien stattgefunden hat, sowie zu Zähmungs- und Kreuzungsversuchen mit Halbeseln, „sind keineswegs endgültig geklärt".
Eine Schilderung der gegenwärtigen Lebensbedingungen wilder Esel unter Berücksichtigung von Wiedereinbürgerungsversuchen und der Einflüsse des Tourismus auf die Lebensräume der Wildesel, sowie ein Ausblick auf mögliche zukünftige Entwicklungen schließen den Textteil dieses für den Spezialisten und den Laien höchst reizvollen Buches ab. Es folgt ein Anhang, in dem u. a. ein ausführliches Literaturverzeichnis (8 eng bedruckte Seiten), ein Personenregister und ein Index geboten werden.

P. Langer, Gießen

Flade, J. E.: **Die Esel, Haus- und Wildesel, *Equus asinus*.** Hohenwarsleben: Westarp Wissenschaften 2000. Die Neue Brehm-Bücherei Bd. 638. 126 pp., 5 Farbtafeln, 41 sw Abb., 21 Tab. DM 39,90/ öS 292,–/sFr 39,90. ISBN 3-89432-887-8.

Am Ende des vorliegenden Bandes finden sich Informationen der „Interessengemeinschaft für Eselfreunde in Deutschland e. V.". Dieser Anhang darf nicht zur Vermutung verleiten, daß es sich bei dem Buch nur um eine emotionsgeladene „Liebeserklärung" für das Grautier handelt; der Text bietet vielmehr Informationen zu Stammesgeschichte und Systematik, sowie zur Verbreitung der Wildesel, auch widmet sich ein Kapitel der Geschichte der Domestikation des Esels, sowie ein weiteres seiner Verbreitung und Kulturgeschichte. Im Text, der durch zahlreiche Tabellen ergänzt wird, bietet der Autor diverse äußere Körpermaße verschiedener Eselrassen und schildert das Verhalten und die Sinnesleistungen, sowie die Haltung von Hauseseln. Ein klares, durch viele Tabellen ergänztes Kapitel beschreibt die verschiedenen Populationen des Hausesels in der Mittelmeerregion, Afrika, Europa, sowie in Mittel- und Südamerika. Die Nutzung von Eseln zur Maultierproduktion in vielen Teilen der Welt wird ebenfalls behandelt.
Die Fülle der im vorliegenden Band gebotenen Informationen ist bemerkenswert. Es werden vergleichende „Seitenblicke" auf das Hauspferd, insbesondere auf Ponies, geworfen werden. Der

1616-5047/01/66/02-127 $ 15.00/0.

Autor, der seine Sympathie für die behandelte Säugetierart nicht verleugnet, verfaßte einen Band, der sich würdig in die bewährte Reihe der Bände der „Neuen Brehm-Bücherei" eingliedert.

P. Langer, Gießen

Feldhamer, G. A.; Drickamer, L. C.; Vessey, S. H.; Merritt, J. F.: **Mammalogy. Adaptation, Diversity, and Ecology.** New York: McGraw Hill 1999. 576 pp.; numerous figs. and tabs. DM: 160,–. ISBN 0-697-16733-X

This new textbook on mammalogy, written by internationally known and experienced authors, covers a broad range of zoological disciplines and briefly summarizes today's knowledge on this animal group under diverse points of view. It is intended to serve in undergraduate and graduate courses at North American universities and is addressed primarily to students with a basic background in vertebrate biology but to teachers as well. Content and length are calculated to cover a one-semester course.

The text is arranged in 5 parts with 29 chapters, where of part I (chapters 1–4) deals with mammalogy as a special science, with its history, with methods and techniques of investigations to reach various aims, and with the emergence of modern mammals in an adaptive evolutionary process from synapsid reptilian roots through mesozoic radiation. Part II (5–9) is devoted to an overview on structure and function. Here, the following features are focused: integument and derivatives, basic skeleton and muscular arrangement, modes of locomotion, intestines, modes of feeding and foraging, sensory organs, central nervous system, endocrine system, biological rhythms, temperature regulations, water balance, reproductive systems, gestation, parturition, and lactation. Part III (10–19) on adaptive radiation and diversity describes morphological and anatomical peculiarities and fossil history of the mammalian orders. The aim of Part IV (20–26) is on overview on behaviour, ecology, and biogeography with chapters on communication, aggression and spatial relations, sexual selection, parental care, and mating systems, social behaviour, dispersal, habitat selection, migration, and homing, as well as populations and life history, community ecology, and zoogeopraphy. Finally, Part V (27–29) is rather short but attributed to special topics such as parasites and diseases, domestication and domesticated mammals, and conservation. Each of the chapters closes with a brief summary, some special questions and suggested readings. At the end of the book a glossary is given, a list of references as well as subject and species indices.

The text is clearly written and corroborated with many instructive drawings, pictures, other figures, and tables. Thus, the book reads fluently and describes main biological phenomena and special adaptations in convergent and divergent phylogenetic lineages. However, Part V deserves special attention since it covers important themes, usually not dealt with in comparable books. This is in general praiseworthy but unfortunately the mode of treatment and presentation are not satisfying. There are several points of severe criticism, especially concerning domestication. This chapter is presented rather confusingly and not according to the current state of knowledge. The authors do not seem to be well informed about this matter and the text does not indicate any general reflection on this special field of zoology. Some of the descriptions and statements are strictly false, contradictory or at least incorrect. Domestication research on mammals was not only accomplished to answer archaeozoological questions, to achieve culture-historical results or to describe efforts of animal-husbandry as is mainly mentioned here. A more strongly zoological point of view and appropriate evaluations are missing. In this sense, domestication was and still is the longest and greatest experiment of man with animals generally demonstrating an enormous variability and changeability of the organism at the species level with several convergent adaptations in diverse lineages. Some of these changes are doubtlessly intended through breeding, many more are not. However, the potential for all these must have been present in the ancestral gene pool but remained latent under natural selection. Thus, in principal, domestication can serve as a model for ideas on phenomena of transspecific evolutionary processes in nature although not occurring in domestication and leading to other directions through evolution. The origin of new species must have started at the species level from certain preadapted ancestors. There are numerous zoological studies since Darwin, mainly from European countries, that compare individuals of wild ancestral species with domesticated derivatives concerning quantitative anatomy, physiology, ethology and genetics. Accordingly, concluding treatises are available but not mentioned in this book. Although some of these studies were not published in English, they are not less important. However, altogether this book is an important source and suited to support mammalogy also at European universities, but corrections of the queries seem appropriate in future editions.

D. Kruska, Kiel

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Instructions to authors

Submission and acceptance of manuscripts: Manuscripts for publication should be sent to the managing editor, Prof. Dr. D. Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40-60, D-24118 Kiel, Germany (e-mail: dkruska@ifh.uni-kiel.de). Acceptance of the manuscript follows the bylaws of the German Society for Mammalogy (Deutsche Gesellschaft für Säugetierkunde). Receipt of the manuscript will be confirmed immediately by normal mail or e-mail, and as soon as the peer reviews are received the authors will be informed concerning any decision. All correspondence dealing with details of production should be sent to: Mammalian Biology, Urban & Fischer Verlag, Löbdergraben 14a, D-07743 Jena, Germany (e-mail: e.czauderna@urbanfischer.de

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Mammalian Biology

Zeitschrift für Säugetierkunde

URBAN & FISCHER Verlag
Jena/Germany

ISSN 1616-5047
Mamm. biol. · 66(2001)2 · 65-128

Contents

Abstracted/Indexed in
Animal Breeding Abstracts/Biological Abstracts/Biological Environmental Sciences/BIOSIS database/Current Advances in Ecological and Environmental Sciences/Current Contents - Agriculture, Biology & Environmental Sciences/Dairy Science Abstracts/Fisheries Review/Helminthological Abstracts/Index Veterinarius/Key Word Index to Wildlife Research/South Pacific Periodicals Index/Veterinary Bulletin/Wild Review (Fort Collins)/Zoological Record

Mammalian Biology

Zeitschrift für Säugetierkunde

3·2001

URBAN & FISCHER

ISSN 1616-5047
Mamm. biol. · 66(2001)3 · 129-192
www.urbanfischer.de/journals/mammbiol

Mammalian Biology

Zeitschrift für Säugetierkunde

IMPRESSUM
Publisher: Urban & Fischer Verlag GmbH & Co. KG, Branch Office Jena, P.O. Box 100537, D-07705 Jena, Germany; Phone: ++49(0)3641/626-3, Fax: ++49(0)3641/62 65 00, E-mail: journals@urbanfischer.de
Advertisement bookings: Enquiries should be directed to Urban & Fischer Verlag, Advertising Manager: Sabine Schröter, P.O. Box 100 537, D-07705 Jena, Germany;
Phone: ++49(0)3641/62 64 45, Fax: ++49(0)3641/62 64 21.
Advertising rates: The price list from January 1, 2001 is effective at present. **Distribution and subscription agency:**
For customers in the German speaking countries: Please turn to your bookshop or to Urban & Fischer Verlag, Aboservice und Vertrieb: Barbara Dressler, Löbdergraben 14a, D-07743 Jena, Germany; Phone: ++49(0)3641/62 64 44, Fax: ++49(0)3641/62 64 43, E-mail: k.ernst@urbanfischer.de
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Subscribers in the **USA** can call toll free on ++1 800 747 3187.
Terms of delivery (2001): 1 volume consisting of 6 issues.
Subscription rate (2001): DM 498.00*/GBP 200.00. Preference price for personal subscribers: DM 150.00*/GBP 60.00. All prices quoted above are exclusive postage. *Suggested list price. Price are subject to change without notice. Personal subscription orders must be addressed directly to the publisher Urban & Fischer in Jena resp. to The Nature Publishing Group. Subscriptions at a personal rate must include the recipient's name and mailing address. An institutional or business address is only accepted, if the institute or firm has a subscription as well. Personal subscribers can pay by personal cheque or credit cardmentioned below. US dollar prices are converted at the current exchange rate.
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Subscription information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting and printing, binding: druckhaus köthen GmbH

(∞) As of vol. 61, number 1 (1996) the paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Printed in Germany

For detailed journal information see our home page: http://www.urbanfischer.de/journals/mammbiol

Mamm. biol. **66** (2001) 129–134
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Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Small mammal exploitation of upper vegetation strata in non-forest, mixed farmland habitats

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Receipt of Ms. 31. 01. 2000
Acceptance of Ms. 20. 10. 2000

Abstract

In September 1998, activity of small mammals in upper herbal and shrub vegetation strata was examined and quantified in a standardized field experiment using a paired upper stratum (height = 0.5 m) vs. ground stratum trapping design. Trapping took place across a range of different biotope types in a typical Danish mixed farmland within the Kolindsund area, Djursland, Denmark.

Seven small mammal species were encountered among the 409 catches during 776 trapnights. Upper vegetation stratum activity was considerable in *Micromys minutus* and *Apodemus flavicollis*. *Clethrionomys glareolus*, *Sorex minutus* and *Sorex araneus* also exploited upper vegetation strata but only to a lesser extent. *Microtus agrestis* and *Apodemus sylvaticus* were only caught in ground stratum traps.

Our results show that, at low to moderate densities, some small mammal species, such as *M. minutus*, may be greatly underestimated or entirely missed by a traditional ground trapping grid. Therefore, the potential upper vegetation stratum activity in some small mammal species should generally be considered in studies performed in areas or seasons with vigorous herbal or shrub vegetation suitable for climbing.

Key words: rodents, shrews, arboreal activity, vertical movement

Introduction

In general, it is well known that some rodent species are capable of climbing trees, shrubs etc. In Europe, this is mainly reported for some species of *Apodemus*, *Clethrionomys* and *Micromys* and is usually described as 'arboreal activity'. However, the issue has only rarely been subjected to systematic and quantitative studies.

In unmanaged old forests, Olszewski (1968) found that *Apodemus flavicollis* is frequently exploited uprooted trees as arboreal runways, while *Clethrionomys glareolus* never did. In spruce-oak woodland, Holisova (1969) demonstrated considerable arboreal activity in both *A. flavicollis* (43%) and *C. glareolus* (17%) and further listed a *Sorex minutus* specimen caught at a height of 3 m as the first published report of arboreal activity in European shrews. In deciduous woodland, Montgomery (1980)

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found extensive arboreality in *A. flavicollis*, *A. sylvaticus* and *C. glareolus*, although less so in *C. glareolus*, while in the same habitat type, in the absence of *A. flavicollis*, Tattersall and Whitebread (1994) found arboreality in both *C. glareolus* (14%) and *A. sylvaticus* (20%).

As a part of performing a larger conventional small mammal ground trapping programme across a range of uncultivated farmland biotope types, we wanted to estimate species biases when trapping only on the ground. Using a paired ground and upper vegetation stratum trapping design, the present study analyses vertical activity in seven small mammal species across various non-forest biotopes with tall herbal or shrubby vegetation.

Material and methods

The study was conducted in September 1998 within a 1×2 km study area in a typical Danish intensive mixed farmland landscape situated in the reclaimed former fiord Kolindsund, Djursland, Denmark. Six trap lines were established at one side of each of six existing trapping grids and each comprised from 10 to 28 trap points (total no. = 97) with each trap point 10 m apart. Trap lines ran through woody, shrubby or tall herbal vegetation, viz. along ditches, fringes of wood fragments, short rotation coppiced (SRC) biomass willow plantations, hedgerow bottoms and grass banks and into uncut perennial set-aside areas. Within and between trap lines, the environment of trap points varied with respect to vegetation type. However, we assumed the trap lines, in total, to be fairly representative of main non-field biotope types – in the study area and in Danish farmland in general.

Each trap point consisted of two Ugglan-live traps. One trap was placed on a wooden platform nailed to a stake 0.5 m above ground level, and the other below it on the ground. In all cases, the immediate trap environment was a dense vegetation composed of grasses, reed, mugworts, nettles, bramble of varying height (0.5–2 m), and all platform traps were set in a way allowing small mammals to gain access to the trap by climbing the vegetation.

Traps were baited with oatmeal and apple slices, supplied with dry bedding and were checked daily in four-day series. Trap lines were run one at a time and only once and hence, the total material comprised 776 trap nights. Captives were sexed, weighed, aged and all rodents individually marked and identified using PIT's (Passive-Integrated-Transponders) and PIT-scanner, and then released at the capture site. Visiting traps once per day, trap mortality was considerable in shrews, while it was negligible in rodents.

For each species, we performed a trap point based pairwise comparison of upper vegetation stratum vs. ground stratum catches across all six trap lines using the non-parametric "Wilcoxon Matched-Pairs Signed-Ranks Test" (Siegel and Castellan, 1988). The null-hypothesis ,"no differences between levels" was tested two-sided.

Maximizing the exploitation of the dataset and the statistical power of the analysis may often conflict with test assumptions of independence between observations in frequency data. Violations of the independence criterion may depend on determent of other species, on attraction to conspecifics in the traps (Kalinowska 1971; Montgomery 1979; Andrzejewski et al. 1997) or on trap addiction (Tanton 1965). Accordingly, we produced a hierarchy of progressively reduced datasets and thus progressively conservative tests 1–4 (cf. Tab. 1).

1. Dataset 1 included all captures. 2. Dataset 2 comprised Dataset 1 minus cases with simultaneous captures in both traps at one trap point to avoid a possible determent effect (second individual more likely to enter trap 2 because trap 1 is occupied). 3. Dataset 3 comprised Dataset 2 minus cases when more than one individual was caught simultaneously in a trap (excluding determent but also attraction effects). 4. Dataset 4 comprised Dataset 3, but only included the first catch of an individual in a specific trap (avoiding individual trap addiction).

Results

The total material comprised 409 catches and seven small mammal species corresponding to a gross mean of 53 small mammal catches per 100 trap nights (including captures, dead and recaptures). Within each species, the total number of catches at the upper and ground stratum, respectively, is presented in table 1. All seven species significantly responded to trap stratum in Dataset 1: two species, *Micromys minutus* and *A. flavicollis*, occurred more frequently in upper vegetation stratum traps, while the

Table 1. Total individual numbers (N : N) in trap catches of small mammals in paired traps, i. e. upper vegetation stratum (0.5 m) vs. ground stratum (0 m) levels, listing also P-values from Wilcoxon Matched-Pairs Signed-Ranks Test (two-sided; null-hypothesis assuming no difference between levels). Species are sorted by proportion of upper stratum activity (descending). For non-significant results and large N, exact P-values are given in (), while, for small N, only 'NS' is given as tables only yield critical values. For very small samples, the power of the test is insufficient to detect significance ('nt': no test performed).
(***, P < 0.0001; **, P < 0.01 and *, P < 0.05)

Datasets	*M. minutus*	*A. flavicollis*	*C. glareolus*	*S. minutus*	*S. araneus*	*M. agrestis*	*A. sylvaticus*
Dataset 1							
Above ground vs. Ground	13 : 3	97 : 39	36 : 139	5 : 18	2 : 29	0 : 19	0 : 9
P	*	***	***	*	***	***	**
Dataset 2							
Above ground vs. Ground	7 : 0	35 : 22	23 : 86	2 : 10	2 : 23	0 : 16	0 : 9
P	*	*NS (0,17)*	***	*	**	***	**
Dataset 3							
Above ground vs. Ground	5 : 0	21 : 13	17 : 53	2 : 8	2 : 21	0 : 16	0 : 9
P	*NS (nt)*	*NS (0.23)*	***	*NS*	**	***	**
Dataset 4							
Above ground vs. Ground	4 : 0	18 : 12	12 : 45	2 : 8	2 : 21	0 : 11	0 : 7
P	*NS (nt)*	*NS (0.34)*	***	*NS*	**	**	*

other five species occurred more frequently (or even exclusively) in ground stratum traps.

M. minutus showed a consistent and strong tendency to higher catches in upper stratum within all four datasets, but differences were only significant in Dataset 1 and 2. However, non-significance in Datasets 3 and 4 were entirely due to the sample size reduced below the critical size of the test.

A. flavicollis exhibited considerably higher catches (c. 2.5 ×) in upper stratum in Dataset 1. In the progressively reduced Datasets 2–4, the tendency for higher catches in upper stratum remained but seemed less pronounced (c. 1.6 ×) which, along with the reduction in sample size, resulted in non-significance. This change in proportions of upper and ground level catches was the largest observed between datasets, and was slightly significant (Testing proportions in Dataset 2 against proportions in material discarded from Dataset 1 to produce Dataset 2; Chi-test; $\chi^2 = 3.92$; df = 1; P < 0.05).

C. glareolus was caught most often on the ground in all four datasets. Still, in all datasets, more than 20% of catches occurred in upper stratum traps. *Sorex minutus* and *S. araneus*, the two shrew species, occurred most often in the traps on the ground (with similar but non-significant pattern in *S. minutus* in Datasets 3–4). In both species, however, specimens were occasionally caught at upper stratum. *Microtus agrestis* and *A. sylvaticus* were not caught in upper stratum traps in our material of 19 and 9 catches, respectively.

Discussion

Our results show that two rodent species, *M. minutus* and *A. flavicollis*, may have a high proportion of activity in vegetation strata considerably above the soil surface. In our trapping design within non-forest vegetation types, we actually observed more catches at the 0.5 m level than at the soil surface. Also, our results showed that most small mammal species may visit upper vegetation strata, at least occasionally. For that reason, the influence of upper vegetation stratum activity of small mammals should be considered in most kinds of tall

vegetation when studying population size and density, home range, intra- and interspecific competition and food energetics.

Three-dimensional use of the habitat space might be an integral component of several behaviours such as escape from predators, exploration, fouraging and intra- and interspecific competition (Holbrook 1979). As a consequence, differential changes in food availability between ground and upper vegetation strata may lead to seasonal changes in arboreality (Montgomery 1980). Our study was performed in September when upper vegetation level has a high coverage and offers an abundance of food to frugivorous, granivorous, and insectivorous small mammals. Thus, activity at this stratum could be different and possibly lower during other seasons.

We trust our results not to be an artefact of our experimental setup, i. e., small mammals gaining access to upper levels by climbing our platform stakes. Using a design similar to ours, Meserve (1977) demonstrated that such direct stake climbing only accounted for 4% of all upper level records.

It is a common experience that catchability of *M. minutus* is reduced during the summer months (e. g. Trout 1978), probably because the species exploits upper vegetation strata in the search for food and nest sites. Analysing a large material of nests, Feldmann (1997) showed that in moist habitats, most nests were placed high (mean $H > 0.5$ m) in tall grasses, mainly *Phalaris arundinacea* and *Phragmites australis*, with some nests also occurring at lower levels (mean $H = 0.35$ m) in grass tussocks (such as *Dactylis glomerata* and *Molinia coerulea*). Our results confirm the findings of Warner and Batt (1976) that catches can be improved by mounting traps on stakes, and demonstrate, that *M. minutus* utilizes the vertical space intensively. Consequently, the chance of recording *M. minutus* from a site, using only conventional ground trapping methods, may be rather low, unless densities are high and/or trapping is intensive.

Further, we found considerable vertical movements in other small mammal species indicating that such species regularly explore and/or exploit upper vegetation strata, and, in particular, we showed that this applies to non-woody vegetations, e. g., tall herbs and grasses. For this reason, we do not use the phrase 'arboreal' and, in general, believe it to be a too narrow and somewhat misleading term for describing the biology of the species in question.

We found *A. flavicollis* to have a high proportion of upper level catches, 60–71% in Dataset 4 and 1, respectively, which is roughly similar to the arboreality reported for this species by Holisova (1969) and Montgomery (1980), viz. 43% and 47–63%, respectively. In *C. glareolus* we had more catches at the ground than at the upper level, with the latter comprising 20–24%. Similarly, Montgomery (1980), Olszewski (1968), Holisova (1969), and Tattersall and Whitebread (1994) all reported mean estimates below 50%, viz. 42, 35, 17 and 14%, respectively. The two shrew species, *S. araneus* and *S. minutus* were both most often caught in ground traps, but it is worth noting that, across both species, 7 out of 47 catches (15%) occurred at the upper level.

Considering the morphology and feeding biology of *M. agrestis*, it is not surprising that we caught this species exclusively in ground traps. *M. agrestis* is heavy and has short limbs and tail, which do not facilitate climbing, and its diet is almost exclusively composed of grasses. Climbing does not seem to occur in this species.

Regarding climbing in *A. sylvaticus*, the literature offers different viewpoints. Hoffmeyer (1973) and Corke (1974, cited from Montgomery 1980) suggested that coexistence of *A. flavicollis* and *A. sylvaticus* relied on vertical separation, with *A. flavicollis* being more arboreal than *A. sylvaticus*, whereas Montgomery (1980) and Tattersall and Whitebread (1994) found considerable arboreal activity in the species, ca. 50% and 20%, respectively. Our scarce data on *A. sylvanicus* favours the idea of vertical separation, but must, significant or not, be viewed at with considerable caution. In general, arboreal activity in this species cannot a priori be excluded.

Our study in a unique way tested successively reduced datasets 1–4 in a systematic attempt to avoid various biases which might impair statistical assumptions of independence. However, with the exception of *A. flavicollis* (between Dataset 1 and 2), our results did not change considerably in this process which may indicate that such analyses are rather robust against well-known potential biases such as trap addiction, determent, attraction, etc. At any rate, we suggest that this type of approach may be explored in further detail, analysing the effects of various biases to small mammal trapping data.

In conclusion, our results show that, at least temporarily, a few small mammal species utilize the vertical space considerably or even entirely and that most species do it at least occassionally, and that this also applies to other than woody habitats. Especially *M. minutus* and *A. flavicollis* catches may, in many situations, be greatly enhanced by trapping at above soil surface levels.

Acknowledgements

The present work formed a part of a study of the habitat potential for wildlife of SRC-willow biomass plantations within mixed farmland landscapes, which was financed by the Danish Ministry of Environment and Energy. Supplementary finance from University of Aarhus, Department of Zoology, is likewise gratefully acknowledged. Farmer Claus Wistoft kindly allowed access to his estate.

Zusammenfassung

Ausnutzung höherer Vegetationsstrata durch Kleinsäuger in gemischten Ackerland-Habitaten

Im September 1998 wurde die Ausnutzung höherer Vegetationsstrata durch Kleinsäuger in Kraut- und Strauchvegetation in einem standardisierten Feldexperiment untersucht und quantifiziert. Das Experiment wurde mit Hilfe von paarweise kombinierten Fallen am Boden und in der Höhe von 0,5 m in einem typischen dänischen Ackerland in Kolindsund, Jütland, durchgeführt. In 776 Fallennächten wurden bei 409 Fängen sieben Kleinsäugerarten in den Fallen gefangen. Aktivität in der Höhe von 0,5 m war bei *Micromys minutus* und *Apodemus flavicollis* erheblich, während *Clethrionomys glareolus*, *Sorex minutus* und *Sorex araneus* die oberen Vegetationsschichten in geringerem Ausmaß nutzten. *Microtus agrestis* und *Apodemus sylvaticus* wurden nur in den Bodenfallen gefangen. Unsere Ergebnisse zeigen, daß bei niedrigen und mäßigen Dichten das Vorkommen von z. B. *M. minutus* von einem gewöhnlichen Bodenfallengitter unterschätzt oder vollkommen übersehen werden kann. Daher muß man auch bei Studien der meisten anderen Kleinsäugerarten diese Aktivität in oberen Schichten berücksichtigten.

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Mamm. biol. **66** (2001) 135–143
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Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Description, taxonomy, and distribution of *Talpa davidiana*

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Receipt of Ms. 27. 10. 2000
Acceptance of Ms. 04. 01. 2001

Abstract

The type of *Talpa streeti* is shown to be cranially very close to and thus probably conspecific with *Scaptochirus davidianus*, a little known mole described from the border between "Syria and Asia Minor". The pelvis of *T. davidiana* is of caecoidal type, thus disproving any relationship between this species and *Scaptochirus moschatus* from China. This species is known from two localities in Iran (Kurdistan) and from three regions in Turkey: vicinity of Meydanekbez, Hakkari and Tatvan. Around Tatvan, *T. davidiana* is sympatric with *T. levantis*. Specimens of *T. davidiana* from Iran and Hakkari have a complete dental complement of 44 teeth. Due to the absence of lower incisors and the peglike premolars, this number is reduced to 38 in three moles from Tatvan and to 39 (asymmetry) in the type of *S. davidianus*.

Key words: *Scaptochirus davidianus*, *Talpa streeti*, taxonomy, nomenclature, distribution

Introduction

Milne-Edwards (1884) named and described *Scaptochirus davidianus* from a specimen collected in the environs of Akbès at the border between "Syria and Asia Minor". This taxon remains as one of the least known among mammals of the Western Palaearctic fauna. Ellerman and Morrison-Scott (1966) consider it as a synonym of *Talpa caeca* Savi, 1822, a statement accepted by Doğramaci (1988, 1989 a) and, with reservations, by Corbet (1978). Similarly, Demirsoy (1996) reported on it as *T. levantis davidianus*, giving Gaziantep as the type locality.

In 1965 Lay described a new mole *Talpa streeti* from Kurdistan province, north-western Iran. This mole is cranially so well characterised that its specific status was never questioned (Corbet 1978; Corbet and Hill 1980, 1986, 1991; Honacki et al. 1982; Hutterer 1993). Known at first only from its type locality (Lay 1967), *T. streeti* was later also reported for Turkey (Doğramaci 1989 a). Spitzenberger (in Felten et al. 1973) stated that *Scaptochirus davidianus* is a member of the genus *Talpa* and might be either a species on its own or the oldest name for *T. streeti*. Assuming that reports of *T. caeca* for Saqqez by Misonne (1959) and for Tatvan by Osborn (1964) actually refer to *T. davidiana* this would, together with the type locality of *T. streeti*,

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form a plausible distribution area (SPITZENBERGER, in FELTEN et al. 1973). GUREEV (1979) and HUTTERER (1993) gave their opinions about the conspecificity of *T. davidiana* and *T. streeti*, but did not formally synonymise them. STROGANOV (1948) and GRULICH (1982) argued, in contrast, that *S. davidianus* is not a member of the genus *Talpa*, but is closely related to east Asian *S. moschatus* of MILNE-EDWARDS (1867). If this is the case, it would mean that the genus of *Scaptochirus* is disjunct in distribution, with the east Asian species being separated from *S. davidianus* in the Middle East by 5 500 km. Further information on the exact identities of *T. streeti* and *S. davidianus* is thus of importance also from a zoogeographical point of view. Therefore, the aim of this study is to elucidate relations within these little-known moles, to define their geographic range and the extent of cranial and dental variation.

Material and methods

We examined 14 specimens of *T. davidiana*, including the types of *Scaptochirus davidianus* and *Talpa streeti*. For comparative purposes we also included in the analysis 26 museum specimens of *Talpa levantis* Thomas, 1906 from Turkey and Iran, three *T. romana* from Italy and 32 *T. stankovici* from Federal Republic of Yugoslavia and from Macedonia. Specimens were mainly skins and skulls, but in some cases also hip bones.

Specimens examined (14). – Iran: Kurdistan, Hezar Darreh (FMNH 96424, type of *Talpa streeti*; FMNH 96421, 96423, 96425); Kurdistan, 1 mile south of Divandarreh (FMNH 111007). Turkey: Bitlis, Tatvan, Kurtikan (FMNH 82136, 82137); Tatvan (OMU 167); Hakkari, Mergan Zoma in Cilo-Sat-Mts. (NMW 20326, 20327); Hakkari, Megabuti yaylası (OMU 231); Hakkari, Otluca köyü (OMU 166, 232); Meydanekbez (MNHN 1883-469; type of *Scaptochirus davidianus*).

Material examined from other species. – *Talpa levantis* (26) Iran: Ghilan, 12 km W Chalus (FMNH 96416, 96417, 96418, 96419). Turkey: Trabzon, Çosandere (BMNH 6.5.1.1, 6.5.1.2, 6.5.1.3, 6.5.1.4); Trabzon, Euthey (BMNH 6.3.6.6); Trabzon, Meryemana (BMNH 6.3.6.4; NMNH 327252, 327253); Trabzon, Altindere (BMNH 25.11.1991, the type *Talpa caeca levantis*); Giresun, Bicik, Yavuz-Kemal (NMW 19859); Ordu, Ulubey (NMW 19858); Samsun, Kürtler (PMS 10299); Tamdere, Giresun Dağları, Şehitlor Geçidi (PMS 11372); Bitlis, Tatvan (OMU 233, 234, 236, 237, 238, 239, 240, 241, 242). *Talpa romana* (3) Italy: Napoli, Roccarainola (PMS 6710, 6711); Quindici, Avellino (PMS 6712). *Talpa stankovici* (32) Macedonia: Mt. Bistra (PMS 2441, 9211, 9532, 7497); Mt. Pelister (PMS 9541); Bitola (PMS 7490); Prilep (PMS 7486, 7488, 7521); Resen (PMS 7522, 7505, 7506, 7508); Mt. Šara (PMS 7496); Struga (PMS 7494, 7495); Mt. Galičica (PMS 7492, 7493, 7502). Federal Republic of Yugoslavia: Ulcinj (PMS 3202-3204, 8834-8839, 7500, 7501).

Seven linear measurements were taken from each skull with a vernier calliper (accurate to the nearest 0.1 mm). Their abbreviations are: CbL – condylobasal length, MxT – maxillary tooth-row length (C – M3), BcB – braincase breadth, BcH – braincase height (without bullae), RoC – breadth of rostrum over canines, RoM – breadth of rostrum over molars, MdL – length of mandible. External measurements were deduced from specimen labels: H & B – head and body length, TL – tail length, HF – hind foot length, W – weight. All measurements are in mm, weight in grams. Overall cranial similarity was assessed by Principal Components Analysis (PCA) of the correlation matrix of log transformed measurements. Factor loadings were subjected to Varimax rotation. Statistical analyses were performed using STATISTICA analysis system (Release 5.5 '99).

Types of teeth are indicated by letters; capitals indicate upper teeth and small letters indicate lower teeth: I/i – incisors, C/c – canines, P/p – premolars, M/m – molars. The number denotes the position of a particular tooth in the tooth row.

The following abbreviations were used for collections: FMNH – Field Museum of Natural History, Chicago; MHNP – Muséum National d'Histoire Naturelle, Paris; NMW – Naturhistorisches Museum Wien, Vienna; OMU – Zoological collection of the Ondokuz Mayis University, Samsun; BMNH – Natural History Museum London; PMS – Slovenian Museum of Natural History, Ljubljana.

Results and discussion

Craniometrics

T. davidiana is well defined amongst the moles of the Western Palaearctic region by its robust rostrum, a feature best expressed by the breadth across canines (Fig. 1). The

type of *S. davidianus* certainly has nothing in common with the small blind moles of Turkey, traditionally reported on as *T. caeca* (Osborn 1964; Doğramaci 1989 a), but actually representing an independent species, *T. levantis* (Kefelioğlu and Gençoğlu 1996). Lay (1965) considered two specimens from Tatvan, Turkey (FMNH 82136 and 82137) to be *T. caeca.* In spite of their small size (see Tab. 1) and somewhat aberrant dentition, they resemble the type of *S. davidianus* in all other respects. Doğramaci (1988) reported *Talpa caeca* davidianus for Tatvan, however, later on (Doğramaci 1989 a) reported *T. caeca* for Tatvan and *T. streeti* for Hakkari, south-eastern Turkey. It is therefore not exactly clear what Doğramaci (1988) understood as *T. caeca davidianus.* As is clear from the available material (Fig. 1), the Tatvan area is inhabited by two moles: *T. levantis* and *T. davidiana.* In the subsequent text, when we refer to Tatvan moles, we have in mind those having the cranial morphology of *T. davidiana* and not of *T. levantis.* Moles from the Hakkari region are indistinguishable from the type and topotypes of *T. streeti*; they also resemble the type of *S. davidianus*, but are of larger size.

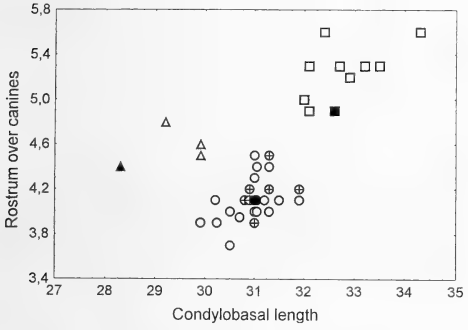

Fig. 1. Plot of rostral breadth over canines against condylobasal length of skull in *T. streeti* from Iran and Hakkari (diamonds), moles from Tatvan (empty triangles), type of *S. davidianus* (closed triangle) and *T. levantis* (circles). Types are indicated by closed symbols. *T. levantis* from Tatvan is indicated by crosses.

Projection of specimens onto the first two Principal Components (85.7% of the variance explained) clustered groups according to their previous taxonomic assignment and geographic origin (Fig. 2). Principal Component 1 (PC1) with high character loadings for CbL, MxT, and MdL, was evidently a factor of general size, which is a common phenomenon in mammalian morphometrics (Lemen 1983) – of more interest was the grouping along Principal Component 2 (high loadings for RoC and RoM). Therefore, the close cranial similarity of *S. davidianus* and *T. streeti* is beyond doubt. Again, moles from Tatvan were placed within the *T. davidiana* cluster. Interlocality variation in size was more strongly ex-

Table 1. External and cranial dimensions in *T. davidiana* from Turkey and Iran. See list of specimens for their geographic origin.

Coll. & No.	Sex	H & B	TL	HF	W	CbL	MxT	BcB	BcH	RoC	RoM	MdL
FMNH 96424	Male					32.6	12.6	16.4	9.5	4.9	9.6	22.2
FMNH 96421	Male					32.0	12.8	16.7	8.8	5.0	10.1	21.4
FMNH 96423	Male					33.2	12.9	16.9	9.5	5.3	10.4	22.3
FMNH 96425	?					32.1	12.1	16.6	9.0	4.9	10.0	21.8
FMNH 111007	Male					34.3	13.2	18.0	9.8	5.6	10.8	22.8
FMNH 82136	Female	128	18	18		29.9	11.3		8.6	4.5	8.9	19.7
FMNH 82137	Female	129	20	18		29.9	11.3	14.9	8.6	4.6	9.0	19.7
OMU 166	Male			21	76	32.4	12.5	16.3	8.8	5.6	10.7	21.6
OMU 167	Female					29.2	10.8	15.3	9.0	4.8	9.7	19.9
OMU 231	Male	130	29	20	80	32.1	12.3	16.6	9.4	5.3	9.9	21.5
OMU 232	Female	134	30	20	79	32.9	13.0	16.0	9.5	5.2	9.8	22.2
NMW 20326	Male	127	27	18	75	33.5	13.2	17.1	9.4	5.3	9.8	22.5
NMW 20327	Female	130	25	17.8	61.5	32.7	12.0	16.3	9.1	5.3	9.9	22.1
MNHN 1883-469	Male	120	20			28.3	10.6	14.0	8.0	4.4	8.1	19.3

Table 2. Variation in number of teeth in *T. davidiana* from Turkey and Iran. First row gives complete dental set in *Talpa*. (N) – number of specimens examined. See text for explanation of abbreviations.

* One specimen with three premolars on the right side.

	(N)	I	C	P	M	i	c	p	m	Total
Talpa		3	1	4	3	3	1	4	3	44
Iran	(4)	3	1	4	3	3	1	4	3	44
Hakkari	(5)	3	1	4	3	3	1	4*	3	44
Tatvan	(3)	3	1	3	3	2	1	3	3	38
Meydanekbes	(1)	3	1	3	3	2/3	1	3	3	39

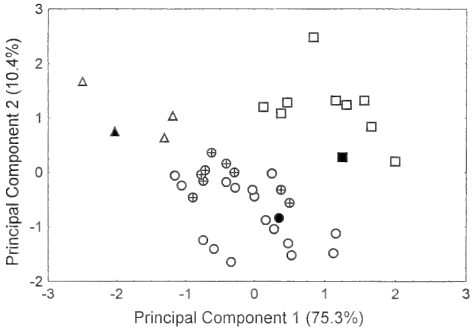

Fig. 2. Projection of specimens onto the first two principal components (percentage of variance in parentheses). For symbols see Fig. 1.

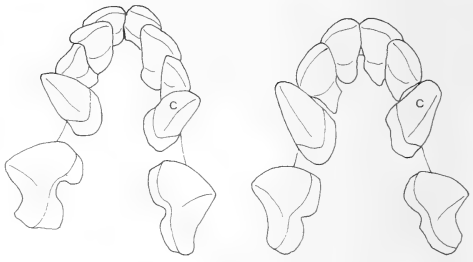

Fig. 3. Variability in the number of lower incisors in *T. davidiana*. Left – complete set with crowded incisors in a mole from Hakkari (NMW 20326); right – only two incisors on each side in a mole from Tatvan (FMNH 82137). c – lower canine. Not to same scale.

pressed in *T. streeti* than in *T. levantis*, although the latter originated from a much wider geographical range.

Dentition

As mentioned by LAY (1965), the type of *T. streeti* displays the complete dental set of the genus *Talpa* (i. e. 44 teeth) but this number is reduced to 38 in the three moles from Tatvan (Tab. 2). Reduction affects both the upper and lower premolars, a condition also found in the type of *S. davidianus*. In the type and topotypes of *T. streeti*, sub-equal and peglike P2 and P3 are smaller than P1. Moles from Tatvan and the type *S. davidianus* had lost one small premolar; the two remaining premolars between the upper canine and P4 are peglike and of approximately the same size. Between the caniniform p1 and large p4, *T. streeti* has two sub-equal peglike premolars; again, one of them is lost in the moles from Tatvan, and in the type *S. davidianus*, which result in an increase in the size of the remaining premolar. ZIEGLER (1971) stated that in *Talpa* s. l. the first peglike premolar lost from a row is the anterior one. Consequently, the moles from Tatvan and the type of *S. davidianus* most likely lack both the p2 and P2.

All three specimens from Tatvan are unique in having only two lower incisors. The lower incisors are evidently crowded in *T. davidiana* from Hakkari and in the topotypes of *T. streeti*, a condition which possibly resulted in the loss of i3 (Fig. 3). The type specimen *S. davidianus* has 39 teeth with three incisors in the left mandible and two in the right.

Pelvis

GRULICH (1971) reported on a mogerid hip bone (with the 5th sacral foramen closed posteriorly by a bony bridge) in *S. moschatus* and presumed such a condition also existed in *S. davidianus* (GRULICH 1982).

However, Doğramaci (1989 b) demonstrated that *T. streeti* from Hakkari lacks a bony bridge posterior to the 5th sacral foramen, having also the 4th sacral foramen opened posteriorly (caecoidal pelvis). Furthermore, we examined five hip bones from *T. davidiana* (Iran – 1, Tatvan – 1, Hakkari – 3) and all were of caecoidal morphology. Thus, according to the morphology of the pelvis, *T. davidiana* is close to the genus *Talpa* from the western Palaearctic, having nothing in common with *Scaptochirus moschatus*.

Taxonomy

Milne-Edwards (1884) based his description of *S. davidianus* on the reduced number of teeth: 3/3, 1/1, 3/3, 3/3 = 40, although a higher number was mentioned in the original description of *S. moschatus*: "Inc. 3/4 can. 1/1 prem. 2/2 mol. 4/4" i. e. 42 teeth (Milne-Edwards 1867). Fourty teeth have been cited as diagnostic of the genus *Scaptochirus* by most subsequent authors (Stroganov 1948; Stein 1960; Gureev 1979; Grulich 1982; Niethammer and Krapp 1990). The usefulness of dental formulas in generic diagnostics within the Talpinae, and particularly in the *Talpa* group, continues to be a matter of debate. Schwarz (1948) considered that the number of genera based on dental formulas is grossly exaggerated, an opinion shared by Ellerman and Morrison-Scott (1951) and Corbet (1978). Corbet (1978) also concluded that genera based on dental formulas may cut across other cranial differences.

Oligodonties are fairly common within *Talpa* s. l. (as defined by Schwartz 1948). The following teeth are prone to reduction or complete loss: i3, p2, p3, P2, and P3 (Ziegler 1971). Oligodonties appear to increase in frequency across the Western Palaearctic (oligodonties rare) into the Oriental region (oligodonties frequent; see Ziegler 1971). The reduction or complete loss of i3 is present in *Euroscaptor micrura*, *E. longirostris*, and *Parascaptor leucura* (generic assignments are by Hutterer 1993). It is evident from Stroganov (1948) that i3 is also missing in *Mogera robusta*; Gureev (1979) however, explained this as a missing canine. An extreme loss of the premolars is seen in *Euroscaptor*, which lacks all four peglike premolars (i. e. p2, p3, P2, P3; Ziegler 1971).

Among *Talpa* s. str. from the Western Palaearctic with 44 teeth, i. e., with the conservative dental formula of the primitive extant eutherians (Ziegler 1971), oligodonties are not as common. In 8184 *T. europaea* skulls examined by Stein (1963) only 0.3% lacked at least one peglike premolar in the upper, and 0.6% in the lower jaws. In a smaller sample (N = 464) from the Netherlands, Niethammer (1990 a) found 5.6% of the specimens were missing one or more premolars. Loss of premolars was also recorded in *T. occidentalis* (incidence 3.3%; Niethammer 1990 b), but not in *T. caeca* (Niethammer 1990 c) and *T. stankovici* (Niethammer 1990 d; specimens in PMS). A high share of oligodonties was reported in *T. romana* (Capolongo and Panasci 1978): 36.5% of moles lacked between one and four upper premolars (N = 255); in three geographic samples, the share of oligodontic moles varied between 14% and 51%. Loss of the two peglike premolars was common in *T. romana*, and found in 21.5% of moles on average. Ziegler (1971) also recorded a reduction of i3 in *T. romana*, in addition to missing of P2. Assuming that electrophoretic divergences reflect actual evolutionary relations amongst European moles (Filippucci et al. 1987) one would not expect any phylogenetic background to oligodonties. Moreover, Miller (1940) expressed surprise that teeth of such a small size and apparent mechanical unimportance as the peglike premolars are so constant in most moles.

Stein (1963) showed that oligodonties in *T. europaea* are more likely to occur in smaller skulls. In our case, a complete dental set was recorded only in the largest moles. Thus, 38 teeth, as observed in moles from Tatvan, are possibly just a case of extreme oligodonty and a by-product of size reduction in marginal populations of *T. davidiana*. Although this feature is unique within *Talpa* s. str., it is supposedly of no taxonomic significance; the asymmetry in

the number of lower incisors (as seen in the type of *S. davidianus*) demonstrates that the presence of the small incisor is not stable.
In conclusion, the most parsimonious taxonomy is recognition of a single, although highly variable species *T. davidiana*, with *T. streeti* as its junior synonym. Furthermore, the caecoidal pelvis suggests their inclusion in the genus *Talpa* not *Scaptochirus*. The latter is thus a monotypic genus, in distribution restricted to east Asia.

Talpa davidiana

1884. *Scaptochirus davidianus* Milne-Edwards, Compt. Rend. Acad. Sci., Paris, 99: 1141, December 29. Type locality – vicinity of Akbès on the border between Syria and Asia Minor ("environs d'Akbès, sur les confins de la Syrie et de l'Asie Mineure") = Meydanekbez (also Meydanı Akbes or Meydān Ikbis), southwest of Gaziantep, Turkey (see SPITZENBERGER in FELTEN et al. 1973).
1965. *Talpa streeti* Lay, Fieldiana Zool., 24: 227, 22 October. Type locality – Hezar Darreh, Kurdistan, Iran.
1967. *Talpa streetorum* Lay, Fieldiana Zool., 54: 131, October 1967. Unjustified emendation of *T. streeti* (see CORBET 1978).

Amended diagnosis: A mole with a caecoidal pelvis. Rostrum is broader and heavier than in any other *Talpa* species (*T. romana* and *T. stankovici*) with the broadest rostrum of the European moles (Fig. 4). Rostrum remains robust also across canines while it is slim in this region in other west Palearctic *Talpa*. Tail is shorter than in any other west Palaearctic mole (Fig. 5). *T. davidiana* is more inclined towards oligodonties than any other species of the genus *Talpa* s. str. Comparison of this species (under

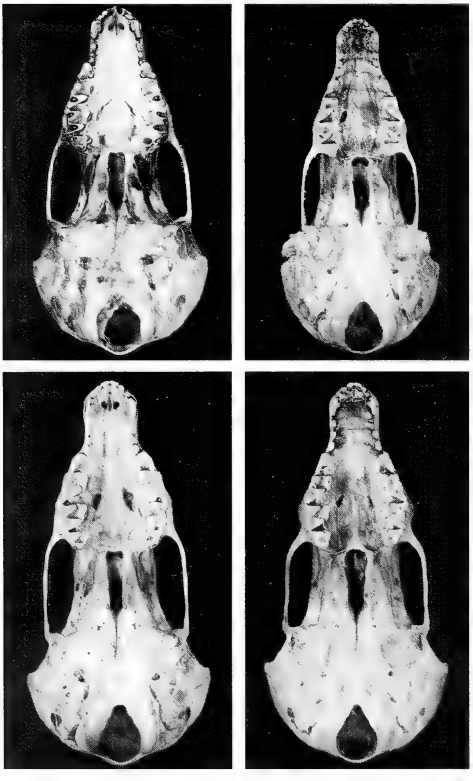

Fig. 4. Ventral side of skull in (top left) *T. davidiana* (OMU 267), (top right) *T. levantis* (PMS 10299), (bottom left) *T. romana* (PMS 6710), and (bottom right) *T. stankovici* (PMS 2441).

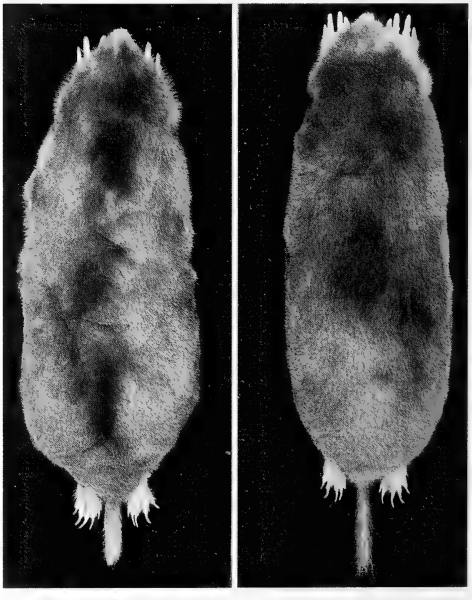

Fig. 5. Skins of *T. davidiana* (left) and *T. levantis* (right), both from Tatvan; note the shorter tail in *T. davidiana*.

the name *T. streeti*) with other moles was provided by Lay (1965).

Homonymy: The binomen *Scaptochirus davidianus* was used for the first time by Swinhoe (1870 a) in his list of Chinese mammals. As already pointed out by Ellerman and Morrison-Scott (1951) this is evidently a case of accidental renaming of *S. moschatus*. Although Swinhoe (1870 a) used the name *S. davidianus*, he simultaneously refers to the original description of *S. moschatus*: "(Annales des Sciences Nat. 5e série, t. 7), anteà, p. 450." and also credits Milne-Edwards with authorship. From one of his earlier publications in the same volume of the Proceedings of the Zoological Society (Swinhoe 1870 b) it is also clear that Swinhoe was familiar with the description of *S. moschatus* by Milne-Edwards. The introduction of *S. davidianus* by Swinhoe was simply an error which, however, coincided with the name proposed by Milne-Edwards (1884) – fourteen years after Swinhoe's study was published. If one considers *S. davidianus* Swinhoe, 1870 and *S. davidianus* Milne-Edwards, 1884 as homonyms, then the former is a nomen oblitum as it has never been used as a valid name (International Commission of Zoological Nomenclature 1999, Article 23.9).

Distribution: Range is summarised in figure 6. The largest distance between extreme localities is >800 km in a west – east direction and up to 400 km in a north – south direction. This range is comparable in size with those of some of the blind *Talpa* species with caecoidal pelvis: *T. occidentalis*, *T. romana*, *T. stankovici* (Mitchell Jones et al. 1999) and *T. caucasica* (Sokolov and Tembotov 1989). All the records are from the southern margin of the Anatolian – Iranian high plateau.

Specimens were apparently always collected at high altitudes (around 2000 m a. s. l.), however, very few facts are available. Habitat is little known; two specimens from Tatvan were collected from burrows in a hayfield, whilst those from Mergan Zoma are from alpine meadows at 2400 m a. s. l. (for a photograph of the habitat see Spitzenberger 1976).

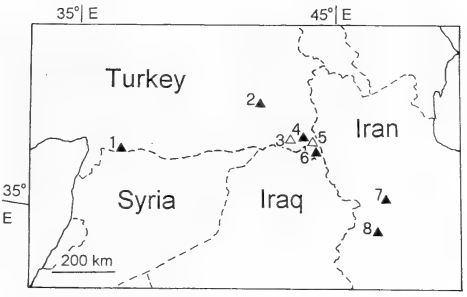

Fig. 6. Distributional records of *T. davidiana*. Turkey: 1 – Meydanekbes; 2 – Tatvan; 3 – Hakkari, Mezralar (1800 m a. s. l.); Megabuti yaylası (3700 m a. s. l.); 4 – Mergan Zoma in Cilo-Sat-Mts. (2400 m a. s. l.); 5 – Hakkari, Otluca köyü (2000 m a. s. l.); 6 – Yüksekova. Iran: 7 – l mi south of Divandarreh; 8 – Hezar Darreh. Localities 3 and 5 are based on Doğramaci (1989 a).

Meydanekbes seems anomalous from the point of view of both altitude and habitat, and we doubt whether the environs of the town of Meydanekbes are a suitable habitat for the burrowing mole. This specimen might originate from the mountains, either to the north (e. g. Engizek Dağı with the peak of 2814 m a. s. l.; ca. 80 km away) or to the west of Meydanekbes (Bozdağ, highest peak 2240 m; ca. 90 km away).

Sympatry: *T. davidiana* is the southemmost member of its genus, being allopatric throughout the major part of its little known range. The only known incidence of sympatry is from Tatvan. where *T. levantis* was also collected.

Acknowledgements

For the access to specimens under their care we thank W. Stanley (FMNH), Linda Gordon (NMNH), and Paula Jenkins (BMNH). R. Hutterer (Bonn) helped with the loan of FMNH specimens to Europe and L. Granjon (MNHN) provided photographs of the type of *Scaptochirus davidianus*. Special thanks go to K. Bauer (Vienna) for critical comments and help with literature. H. I. Griffiths (Hull) improved the English text and C. Mlinar (Ljubljana) prepared figures 4 and 5.

Zusammenfassung

Beschreibung, Taxonomie und Verbreitung von *Talpa davidiana*

Wegen großer morphologischer Ähnlichkeit der Schädel des Typus von *Talpa streeti* mit *Scaptochirus davidianus* wird auf Konspezifität der beiden Taxa geschlossen. Das Becken von *Talpa davidiana* ist caecoidal, so daß eine Verwandtschaft mit *Scaptochirus moschatus* aus China ausgeschlossen werden kann. *T. davidiana* wurde aus dem Grenzgebiet von Syrien und Kleinasien beschrieben und ist bisher von drei Fundorten (Umgebung von Meydanekbez, Hakkari und Tatvan) bekannt. Bei Tatvan lebt die Art sympatrisch mit *Talpa levantis*. Individuen von *T. davidiana* aus Iran und Hakkari haben eine Gesamtzahl von 44 Zähnen. Als Folge des Fehlens der unteren Incisivi und der stiftförmiger Prämolaren ist die Zahnzahl bei drei Maulwürfen aus Tatvan auf 38 und beim Typus von *S. davidianus* auf 39 (Asymmetrie) reduziert.

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Mamm. biol. **66** (2001) 144–154

http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Bats in the Bavarian Alps: species composition and utilization of higher altitudes in summer

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Receipt of Ms. 10. 03. 2000
Acceptance of Ms. 20. 09. 2000

Abstract

Habitat use and species composition of bats in the higher altitudes of the Bavarian Alps were studied from May to September 1997. Five hundred buildings at altitudes between 800 and 1 800 m above sea level were surveyed; traces of bats or roosting animals were found in 189 of these. Bat occupation of buildings decreased at elevations higher than 1 300 m above sea level, and also decreased with increasing distance of buildings to the surrounding forest. 203 solitary roosting animals and 14 nursery colonies (indicated with*) of the following species were found: *Myotis myotis, M. emarginatus, M. mystacinus*, M. brandti, Pipistrellus pipistrellus*, Pipistrellus nathusii, Eptesicus nilssonii*, Plecotus auritus,* and *Vespertilio murinus*. Relative to adjacent lower regions where *Myotis myotis* is the most abundant species, *M. mystacinus* and *M. brandti* together make up an average of 70% of all reliably determined animals at higher altitudes. Within all occurring species, higher regions are mainly inhabited by adult males. They might thus avoid competition with nursery colonies in the lowlands.

Key words: Bats, altitudinal distribution, Bavarian Alps, species composition

Introduction

The Bavarian Alps are likely to provide good habitats for bats in summer with extensively developed pastures and large areas of natural forests. However, lower temperatures and shorter vegetation periods relative to lowlands (REISIGL and KELLER 1987) might be rather disadvantageous for these aerial insectivores.

Studies from neighbouring mountainous countries like Austria and Switzerland show that higher altitudes are in fact inhabited by bats (SPITZENBERGER 1993 a, b; ARLETTAZ et al. 1997; GÜTTINGER 1994). However, certain aspects in the life cycle such as reproduction seem to be concentrated at lower altitudes (SPITZENBERGER 1993 a, b), possibly because juvenile growth is favoured by warm conditions in many bat species (TUTTLE and STEVENSON 1982; ZAHN 1999). Also, the composition of species is influenced by altitude (SPITZENBERGER 1993 a; ARLETTAZ et al. 1997; GÜTTINGER 1994). This effect may depend both on climatic circumstances and on the availability of suitable roosts.

1616-5047/01/66/03-144 $ 15.00/0.

In the "lowland areas" adjacent to the Bavarian Alps, the bat fauna is well known (Richarz 1986; Richarz et al. 1989; Zahn and Krüger-Barvels 1996; Zahn and Maier 1997). At least 10 of 16 lowland species, which could potentially occur also at higher altitudes, are known to prefer various anthropogenic structures as day roosts (Richarz 1986). In this study we therefore focussed on bats roosting in buildings. Buildings exist in relatively large numbers even at higher altitudes in the Bavarian Alps and are well suited for a systematic investigation of the bat fauna. Moreover, buildings are readily accessible and of better comparability than natural roosts such as rock crevices or tree holes. Of special interest were the following questions: (i) Which building dwelling species of bats occur over 800 m above sea level in the Bavarian Alps? (ii) Does a species-specific altitudinal distribution exist? (iii) How are roosts in buildings at different altitudes used by bats? (iv) What types of roosts are preferred?

Material and methods

The study area ranges from Garmisch-Partenkirchen (11°06′ O, 47°29′ N) in the west to Berchtesgaden (13°0′ O, 47°37′ N) in the east and includes altitudes from approximately 800 m to 2 963 m above sea level (Zugspitze). About 50% of the area is covered with forest (mostly *Fagus sylvatica*, mixed with *Picea abies*, *Abies alba* and *Acer pseudoplatanus*). The remaining area consists of extensively used mountain pastures and, over about 1 800 m above sea level, of unused alpine meadows, dwarfpines and rocky outcrops.

Five hundred buildings (from small wooden mountain cabins to hotel-sized stone houses) at altitudes between 800 m and 1 800 m were surveyed between May and September 1997. Of these, 451 provided potential roosts for bats. As potential roosts we regarded all kinds of crevices if they were dry, narrow (< 5 cm wide), dark and without a strong airflow (< 15 cm deep). As described below, these crevices were roughly divided into five categories. Shutters, which are frequently used by bats (Richarz 1986) in spite of that fact that they offer less shelter from wind and rain than the other types, were also included. Large accessible attics, which are common roost sites for bats in the lowlands, were rarely present in the investigated buildings and are therefore not included in the list of potential roosts.

Faeces and dead or living animals were taken as evidence for site use. Substantial accumulation of faeces was taken as evidence for colonies. Site use inferred from faeces' presence is referred to as "indirect proof", whereas alive animals were taken as "direct proof". When possible, living animals were caught for species identification. With the exception of *Myotis myotis* whose droppings reliably could be identified through size and structure, no species identification was attempted using faeces. During the study we did not distinguish between *Pipistrellus pipistrellus* and the "new species" *Pipistrellus "pygmaeus/mediterraneus"* (Häussler et al. 2000).

For comparison with the lowland bat population, data of the ASK Bavaria (database "Arten- und Biotopschutzkartierung" of the Bavarian State Office of Environmental Protection) were called upon. These data were obtained as well by systematic controls of churches, castles and other buildings that offer suitable attics as by roost controls conducted after house owners informed the relevant authorities about bat presence. These roost controls (visits of attics, inspection of crevices) were conducted in the same way as in the present study.

Results

Species composition and abundance of roosting bats

At 189 (41.9%) of the 451 potentially suitable buildings evidence of site use by bats was obtained. In 100 of these cases, the animals' presence was indicated by faeces alone. A total of 203 roosting animals (excluding nursery colonies) was found. Of these, 110 were identified to the following nine species: Greater mouse eared bat (*Myotis myotis*, 4%), Geoffroy's bat (*M. emarginatus*, 1%), whiskered bat (*M. mystacinus*, 50%), Brandt's bat (*M. brandti*, 13%), common pipistrelle (*Pipistrellus pipistrellus*, 13%), Nathusius' pipistrelle (*Pipistrellus nathusii*, 1%), northern bat (*Eptesicus nilssonii*, 13%), common long eared bat (*Plecotus auritus*, 5%) and parti-coloured bat (*Vespertilio murinus*, 2%). With 29 animals, no reliable differen-

tiation between *M. mystacinus* and *M. brandti* could be made. We assumed that the relative fraction of the two species was the same as that determined reliably, i. e. *M. mystacinus* about 80%, *M. brandti* about 20%. In the following, these two species are mostly combined and referred to as *M. my./br.* 64 animals remained unidentified but certainly belonged to smaller species (i. e. larger species like *M. myotis*, *Eptesicus spec.*, *V. murinus* or *Plecotus spec.* could be excluded). Species dwelling in buildings which occur in adjacent areas but were not found in buildings at higher altitudes included barbastelle (*Barbastella barbastellus*), noctule bat (*Nyctalus noctula*), serotine bat (*Eptesicus serotinus*) and lesser horseshoe bat (*Rhinolophus hipposideros*).

Altitudinal distribution

Bats preferred roosts in buildings at lower altitudes. Figure 1 shows that the percentage of buildings with traces of bats – either alive animals or faeces – decreased significantly at altitudes higher than 1 300 m above sea level ($X^2 = 26.6$, $p < 0.01$).

Species composition did not change significantly with altitude. At all altitudes, *M. my./br.* were by far the most abundant species (Fig. 2). Together they made up 70.5% of all reliably identified individuals. Assuming a relation of 20% *M. brandti* in all *M. my./br.* individuals, also Brandt's bat was more abundant than any other species except the whiskered bat. It is also apparent that, within the studied range of altitude, no species showed any preference for particular elevations. The only exception was *M. myotis*, which was found exclusively below 1 200 m. However, with *M. brandti* and *E. nilsonii* two species were present which are only rarely found in the adjacent lowland areas.

The highest site where roosting bats were found was at 1 670 m in a group of cabins near Königssee (Berchtesgaden). In five different cabins, a total of 10 animals, including *M. mystacinus*, *Pl. auritus* and *V. murinus* was found.

A total of 14 nursery colonies was found. Nine colonies were indicated through faeces and could thus not be reliably identified on species level. However, concerning pellet size they most likely belonged to *Pipistrellus* spec. or *M. my./br.* The other colonies consisted of *M. mystacinus* (n = 2), *P. pipistrellus* (n = 2) and *E. nilssonii* (n = 1). While solitary animals reached altitudes up to 1670 m, the highest nursery colony was recognized at 1400 m. Ten of the

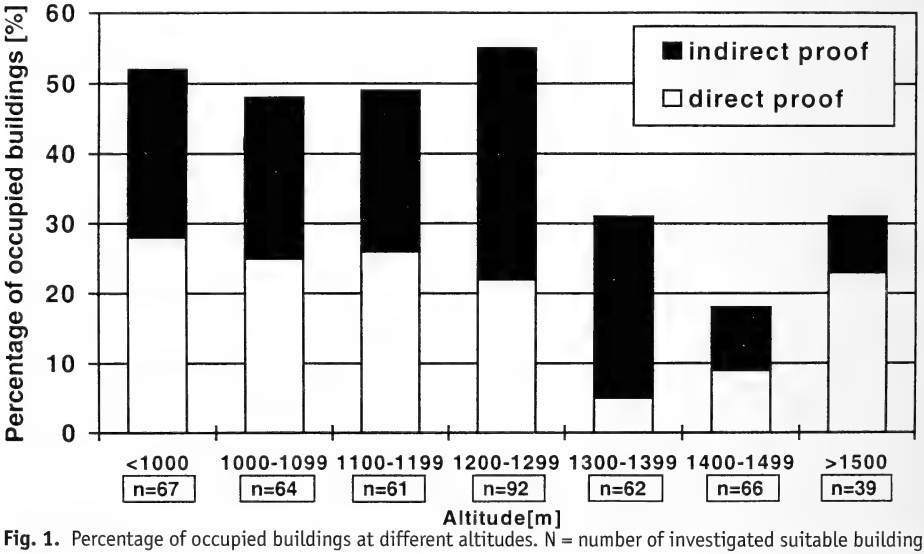

Fig. 1. Percentage of occupied buildings at different altitudes. N = number of investigated suitable buildings.

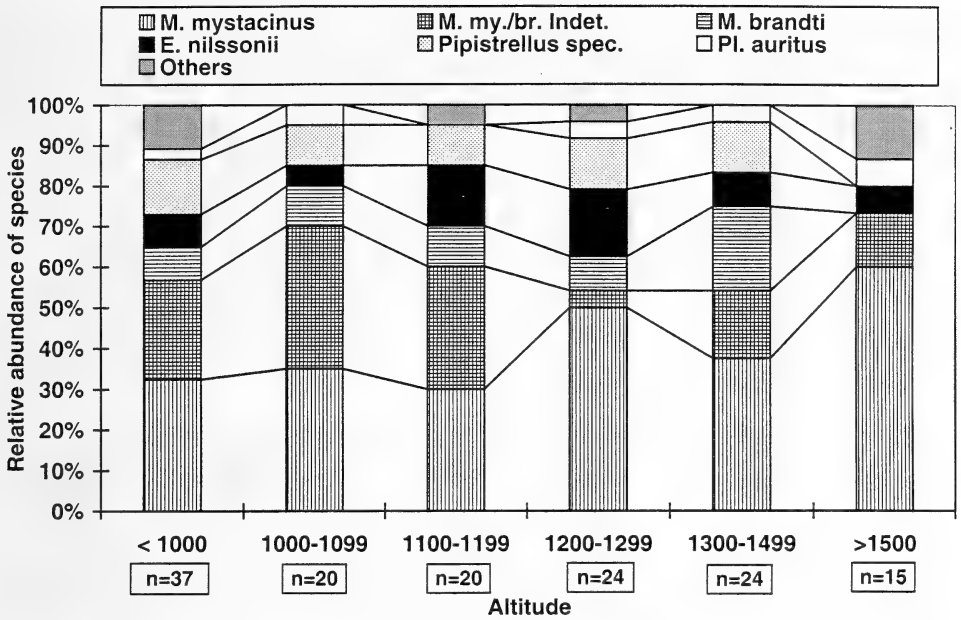

Fig. 2. Relative abundance and altitudinal distribution of reliably identified species. N = number of bats. The altitudes 1 300 m–1 499 m are drawn together because of only two direct observations between 1 300 m and 1 399 m.

Table 1: Altitudinal distribution of nursery colonies

	M. myst.	*E. nilssonii*	*P. pipistrellus*	indicated through faeces	Total
< 1 000 m	1	–	1	5	7
1 000 m–1 099 m	–	1	1	1	3
1 100 m–1 199 m	–	–	–	–	–
1 200 m–1 299 m	–	–	–	3	3
1 300 m–1 399 m	1	–	–	–	1
Total	2	1	2	9	14

fourteen colonies occurred below 1 100 m (Tab. 1).

Age structure and composition of sexes

In all species, the great majority of solitary animals consisted of adult males. Only 16 females (14.5%) were found outside nursery colonies, the first one on July 23rd. They belonged to *M. mystacinus* (n = 9), *M. brandti* (n = 2), *M. myst./brandti* indet. (3), *E. nilssonii* (n = 1) and *P. pipistrellus* (n = 1).
Three mating communities of *M. mystacinus* were found, one consisting of three animals (2 females, one male), the others of one male and one female each. Two subadults of *M. brandti* (one male, one female) were found outside colony sites at the beginning of September.

Preference of roosts and surrounding

The occupation of each type of roost by bats deviates significantly from the distribution of existing roosting possibilities (X^2-Test,

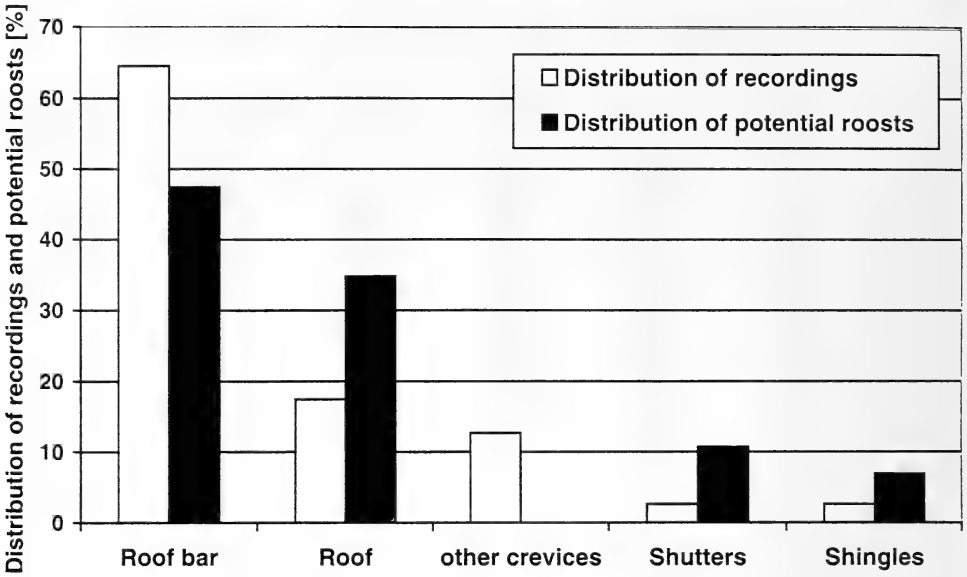

Fig. 3. Distribution of recordings compared to the distribution of potential roosts. As the number of "other crevices" can hardly be estimated, no value is given for this category.

$X^2 = 17.7$, $p < 0.01$, Fig. 3), which can be roughly divided into the following categories. The most frequently used type of building roost (174 of 268 recordings, including direct and indirect evidence) was the crevice behind the board at the ridge of the roof, which was present at almost every surveyed building. It was followed in preference by crevices in the roof itself between tin roof covering and underlying roof beams (used by 47 animals) which are characteristic especially for smaller, traditionally built wooden cabins. In many buildings also spaces behind shingles (7 records), open shutters (7 records) and other crevice-like structures (34 records) were used by bats. Figure 4 shows a typical mountain cabin with the most common types of roosting possibilities. Also, bats significantly favoured buildings closer to forests. While 45.6% of the roost sites in buildings less than 100 m away from a forest edge were occupied by bats ($n = 375$), only 24% ($n = 76$) of all suitable buildings farther than 100 m away were used ($X^2 = 15.4$, $p < 0.01$).

Concerning the compass bearings of the roosts, no absolute preference for roosts, openings towards one distinct orientation could be shown. However, when only roosts at cabins built with one distinct orientation (i. e. for example all buildings facing in North/South-direction) were considered, southern and south-western exposed roosts were clearly preferred to northern and north-eastern ones ($X^2 = 4.3$, $p < 0.05$).

Influence of seasons

Significantly more buildings were occupied by bats as the summer progressed. The percentage of buildings with evidence of bats rose from 7.6% ($n = 13$) in May to 40.1% ($n = 332$) in June/July, and 51.8% ($n = 106$) in August/September ($X^2 = 0.42$, $p < 0.05$). With the exception of *E. nilssonii*, which was found only after the end of July, the occurrence of all species was evenly distributed over the summer.

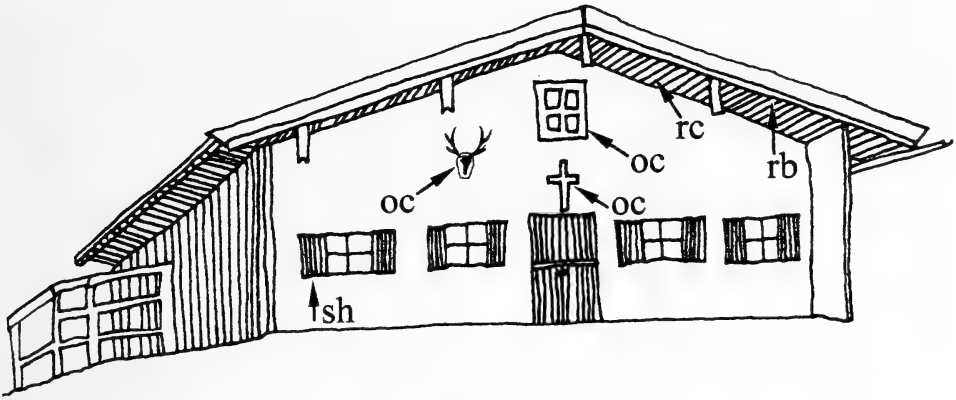

Fig. 4. Typical Bavarian mountain cabin with various roosting possibilities. rb = crevice behind ridge board, rc = roof crevice (i. e. crevices between tin covering and underlying roof bars), sh = crevice behind shutter, oc = other crevices.

Comparison between higher altitudes and lowlands

Species composition at higher altitudes demonstrates some striking differences relative to the conditions in the contiguous lowland areas. In the latter, the following species were found by Richarz (1986), Richarz et. al (1989), Zahn and Krüger-Barvels (1996) and Zahn and Maier (1997) (species where nursery colonies are known are marked with*): Lesser horseshoe bat (*Rhinolophus hipposideros*)*, greater mouse eared bat*, Bechstein's bat (*M. bechsteini*), Daubenton's bat (*M. daubentoni*)*, Brandt's bat*, whiskered bat*, Geoffroy's bat*, Natterer's bat (*M. nattereri*)*, common long eared bat*, barbastelle*, serotine bat, noctule bat (*Nyctalus noctula*), common pipistrelle*, Nathusius' bat and particoloured bat.

Seven of these species were absent at buildings in the study area, viz. *R. hipposideros*, *B. barbastellus*, *M. nattereri*, *M. daubentoni*, *M. bechsteini*, *N. noctula* and *E. serotinus*. *E. nilssonii* was found at montane sites but was virtually absent in the lowland roosts.

Apart from these absent species, a comparison between the database ASK and the present study shows that a complete shift in the relative dominance of the different species is apparent between the lowlands and higher altitudes.

In lower regions, *Myotis myotis* dominates species' abundance with about 62% of all solitary animals (n = 277). A total of 27 nursery colonies is known in the adjacent rural districts. Also *Plecotus auritus* occurs quite often (17%).

On the other hand, at higher altitudes there is a strong dominance of the two "moustached" bat species, Brandt's bat and whiskered bat.

At higher elevations, such roost sites as large church attics were not found. When species that normally roost in these sites in the lowlands are excluded (*M. myotis*, *Pl. auritus*, *R. hipposideros*), the moustached bats represent 54% of the solitary animals in the mountainous study areas, but only 22% in the lowlands (Fig. 5). *P. pipistrellus*, which reached a frequency of only 14% at higher altitudes, made up 28% of all species in the lowlands. Also *M. emarginatus* and *V. murinus* are more abundant in lower regions.

Discussion

Roosts

In general, higher altitudes in the Alps are inhabited by bats, although there are some restrictions.

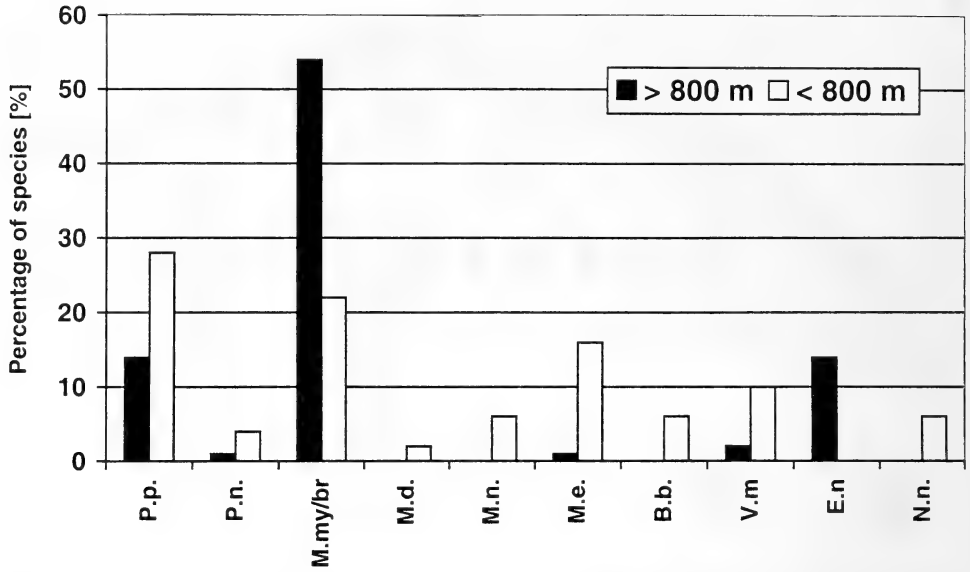

Fig. 5. Comparison of the species composition in solitary roosting bats at high (> 800 m, n = 101) and low (< 800 m, n = 50) altitudes. *M. myotis, Pl. auritus* and *R. hipposideros*, which probably find only few suitable buildings in higher regions, are excluded. P. p. = *Pipistrellus pipistrellus*; P. n. = *P. nathusii*, M. d. = *Myotis daubentoni*, M. n. = *M. nattereri*, M. e. = *M. emarginatus*, B. b. = *Barbastella barbastellus*, V. m. = *Vespertilio murinus*, E. n. = *Eptesicus nilsonii*, N. n. = *Nyctalus noctula*.

The number of occupied roosts in buildings decreases significantly over 1 300 m above sea level. This is probably due to adverse climatic conditions at higher elevations. The average temperature for July, for example, is 17 °C at 600 m but only 13 °C at 1 200 m (REISIGL and KELLER 1987). Furthermore, buildings at these altitudes are often at sites exposed to wind, precipitation and cold temperatures, factors which might thus diminish their suitability as roosts. The importance of warmer roosts is also supported by the fact that, given the opportunity, bats tend to choose southern and south-western roosting possibilities at the buildings. A reduced exposure to wind could also explain the observed preference for houses in or near forests. Additionally, forests offer a sheltered flight path between roost and foraging area. Many bat species avoid crossing open land without structures such as hedges or tree lines (LIMPENS and KAPTEYN 1991). This may additionally lower the value as bat roosts of houses located far from forests.

The special climatic conditions in the Alps may also be the reason for the low number of bats roosting behind shutters, which are often used by whiskered bats, pipistrelles and barbastelles in other areas (SPITZENBERGER 1993 a, b). Probably, their exposure to all sides affects their suitability as a roost in the adverse weather conditions of higher altitudes stronger than it does in lower regions. However, the strong preference for crevices behind roof bars that was observed in this study may partially be due to a methodological artefact, since this roost type is very easy to investigate. Other potential bat roosts, such as crevices in the roof itself, which offer warm shelters too, are probably occupied more often than is apparent, since bats may roost very hidden at these sites and are easily overlooked.

Species composition

Some of the species absent in higher areas, such as Natterer's bat, Bechstein's bat and

Daubenton's bat, are known to roost preferentially in natural structures like tree holes (Richarz 1986), so it is not amazing that they were not found in the surveyed buildings. However, mistnetting at several caves in the Bavarian Alps shows that these species actually do occur at higher altitudes also in summer: *M. bechsteini* was caught several times at a cave near Frasdorf (1 200 m) (Meschede pers. comm.); *M. daubentoni*, occurred at a cave near Kochel in great numbers and could regularly be seen foraging at ponds up to 1 100 m; *M. nattereri* even occurred at a cave 1 800 m high in August and September 1997.

Nyctalus noctula, which tends to roost in trees and buildings, was neither found in buildings in the study area nor was it ever seen hunting or identified acoustically in occasional bat-detector surveys. The absence of roosting noctules in study buildings might be due to a lack of suitable roosts, as these bats prefer large crevices in high buildings (Zahn et al. 1999).

Barbastella barbastellus, on the other hand, is known to live at higher altitudes in Switzerland and Austria, and to preferably use roosts of the type that mainly occur in the surveyed buildings: crevices behind ridgebars and open shutters (Spitzenberger 1993 b). It is thus a species almost predestined to occur in buildings in the study area. Several animals caught while mistnetting at caves near Kochel, Frasdorf, and Bichlersee in 1997 show that barbastelles actually do occur in the Bavarian Alps (Meschede and Rudolph pers. comm.). Nevertheless, whereas it is not very numerous but widely spread in Austria (Spitzenberger 1993 b), it is one of the rarest species in Germany with only five recordings of nursery colonies in southern Bavaria and very few recordings of solitary animals (Rudolph et al. 2001). We might have failed to find their roosts in buildings simply due to the low population density of this species. It is also possible that they use natural roosts more frequently than is now realised, since radiotracked individuals favoured roosts behind patches of loose tree bark (Steinhauser 2001).

M. myotis, *R. hipposideros*, and *P. auritus*, which were rare or absent in the higher regions, depend strongly on large attics for roosting which are much more abundant in lower regions. Moreover, *M. myotis*, which was the dominant species in the lowlands, is known to be strongly thermophilous (Spitzenberger 1988; Güttinger 1994; Rudolph and Liegl 1990). In Switzerland and Austria, their complete live cycle is concentrated in relatively low areas. Solitary animals range up to an average of 531 m in Austria, whereas nursery colonies are found only up to 439 m (Spitzenberger 1988). Also most colonies in Switzerland occur lower than 600 m (Haffner and Moeschler 1995). More or less the same is true for the lesser horseshoe bat, which mainly occurs between 600 m and 900 m in Austria (Spitzenberger 1995). It is also one of the rarest bat species in Bavaria with only two known nursery colonies (Zahn and Schlapp 1997). Thus, they could not be expected to occur in the studied buildings.

Particularly solitary animals of *Plecotus auritus* are also known to use tree holes and bird- or bat-boxes as roosts, which were not investigated in this study. They might therefore be more numerous in the Alps than is apparent from this investigation.

The whiskered bat is the only species of this study for which every aspect of the life cycle (breeding, mating, hunting, hibernating) was observed to take place at higher altitudes. The distribution of whiskered bat and Brandt's bat in other countries show that they are indeed sturdy species in adverse climates: in Scandinavia they reach 64° of latitude (Schober and Grimmberger 1987), and in Switzerland nursery colonies of *M. mystacinus* occur up to 1 670 m (Zingg and Burkhard 1995). In a recent investigation of the National Park Hohe Tauern in Austria *M. my./br.* also make up almost two-thirds of the species composition at higher altitudes (Hüttmeir and Reiter 1999). *P. pipistrellus*, on the other hand, has quite similar habitat demands and roost preferences but reaches only 61° of latitude in Scandinavia (Schober and Grimmberger 1987) and seems to prefer the lower altitudes. In Canton Wallis (Swit-

zerland), the number of roosts decreases continually over 400 m above sea level (ARLETTAZ et al. 1997).

It seems that the great flexibility especially of *M. mystacinus* (TAAKE 1984), its cold-hardiness, and its preference for crevice-like roosts which are so common in the Alps, lead to the strong dominance of this species in the study area.

It is still not quite clear whether a true preference for higher altitudes exists for *M. brandti*, although the virtual absence of this species in lowland areas and multiple records in the study area above 800 m encourage this suggestion. The low population density in the lowlands could partially be an artefact due to the difficulties in differentiating between *M. mystacinus* and *M. brandti*, especially concerning the females. It might well be that some *M. brandti* colonies in the lowlands have been mistaken for *M. mystacinus*. Still, its abundant occurrence at higher altitudes, especially of males, is apparent. Results from Canton Wallis in Switzerland, where *M. brandti* was found exclusively over 1 200 m above sea level (ARLETTAZ et al. 1997), also support that *M. brandti* is indeed well adapted to the conditions in the mountains.

Also the northern bat seems to prefer the higher altitudes. While 14 solitary animals plus one nursery colony were found at the higher altitudes, neither solitary roosting animals nor nursery colonies are known from adjacent areas in the last 10 years. Also in Switzerland, the majority of *E. nilssonii* was found between 1 200 m and 2 000 m above sea level (ARLETTAZ et al. 1997).

However, SKIBA (1995), using a bat detector, recorded up to 80 animals per night in some regions below 800 m in the study area. It is possible that roosting and hunting habitats differ for this species, so that foraging of high elevation roosting animals takes place in lower regions. However, hunting activity in the higher regions of the study area was never investigated systematically and there is no apparent reason why this species should not use higher altitudes for foraging as well.

Male dominance

One of the most apparent features of this study is the strong dominance of solitary males in all occurring species. Whereas in adjacent lower regions almost one-third of all bat roosts recorded in the database ASK are nursery colonies, such colonies only provide 7.4% of all animals in the study area. The reason for this is not a lack of suitable roosts. Especially for two frequently found species, *M. mystacinus* and *P. pipistrellus*, most nursery colonies in lower altitudes are known from sites also most abundant in this study: crevices behind roof bars and open shutters. One explanation for the high percentage of colonies in the lowlands may be the sampling method: While in the mountains all buildings were controlled systematically, many lowland collections of data were made after owners had informed bat conservationists of bat presence in their houses. Since the presence of a colony may be more obvious than that of a solitary bat, the numbers of males may be underrepresented in these data. However, the dominance of males in the Alps could be also due to climatic factors. Females in nursery colonies depend on relatively high temperatures during gestation and lactation for optimising foetal growth (AUDET 1992; RACEY 1969; TUTTLE and STEVENSON 1982; ZAHN 1999). This may underlie the fact that nursery colonies are found more often in lower and therefore warmer regions. Males, which have a lower energy demand and should thus be able to live in harsher conditions (BARCLAY 1991), are able to utilise higher altitudes as day roosts. They may also avoid foraging competition with nursery colonies (KUNZ 1974) in the lowland areas by evading into the Alps. Such avoidance of food competition has been inferred for other bat species (KUNZ 1974). Moreover, males may even save energy by falling into torpor more often due to lower air temperatures (BARCLAY 1991). However, comparative behavioural and physiological studies of both males and females settling at different altitudes are needed to verify these possible reasons for the prevalence of male bats in the Alps.

Climatic chance and altitudinal distribution

Climatic conditions appear to be a key factor influencing species composition and population structure of bats in the Alps. A long term monitoring of populations at different altitudes and a comparison of the nursery colonies in respect of roost selection, roost climate, timing of reproduction, growth and mortality of juveniles would offer the opportunity to increase our knowledge concerning the influence of climate on the population biology of bats. This could allow predictions about possible reactions of bat populations to the current deviations in climatic patterns which may be altering the present scenario of altitudinal distribution.

Acknowledgements

We thank PD Dr. Roland Melzer for critical comments on the manuscript and valuable help with the drawing of the cabin. Thanks to Prof. Robert Dudley and Dr. Les Williams for improving the English. We are indebted to the Bavarian State Office for Environmental Protection for the permission to analyse the data of the ASK.

Zusammenfassung

Fledermäuse in den Bayerischen Alpen: Artenspektrum und Nutzung von höheren Lagen im Sommer

Von Mai bis September 1997 wurde das Artenspektrum von Fledermäusen sowie ihre Habitatnutzung in den höheren Lagen der Bayerischen Alpen untersucht. Von 500 kontrollierten Gebäuden zwischen 800 und 1 800 m über Seehöhe wiesen 189 Spuren von Fledermäusen oder lebendige Tiere auf. Der Anteil an besetzten Gebäuden nahm oberhalb von 1 300 m und mit wachsender Distanz zum Wald signifkant ab. Es wurden 203 Einzeltiere und 14 Wochenstuben (mit * gekennzeichnet) folgender Arten nachgewiesen: *Myotis myotis, M. emarginatus, M. mystacinus*, M. brandti, Pipistrellus pipistrellus*, Pipistrellus nathusii, Eptesicus nilssonii*, Plecotus auritus, Vespertilio murinus*. Im Gegensatz zum angrenzenden Flachland, wo *Myotis myotis* die häufigste Art ist, stellen in höheren Lagen Bartfledermäuse (*M. mytacinus* und *M. brandti*) etwa 70% aller sicher bestimmten Tiere. Bei allen Arten werden die höheren Lagen in erster Linie von adulten Männchen bewohnt. Diese vermeiden dadurch möglicherweise Konkurrenz mit Wochenstubentieren im Tal.

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Mamm. biol. **66** (2001) 155–164
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

The rise of urban fox populations in Switzerland

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Receipt of Ms. 12. 04. 2000
Acceptance of Ms. 15. 10. 2000

Abstract

Since 1985 increasingly more foxes have been recorded from cities in Switzerland. The inquiry of town officials showed that foxes are observed in 28 out of the 30 largest Swiss cities today and breeding dens are known in 20 of these cities. Urban foxes are observed more often than one would expect in larger cities than in smaller towns. In Zürich, the largest city in Switzerland, urban foxes were very scarce until the early 1980s. According to the hunting statistics, from 1985 onwards, there was a drastic increase in the urban fox population. In the adjacent rural areas, there was also a clear but less extreme increase in the fox population from 1984 onwards due to successful vaccination campaigns against rabies. As an explanation for the presence of foxes in human settlements we suggest two alternative hypotheses, which focus either on the population pressure in the rural areas or on the behavioural adaptations of urban foxes. The presence of foxes in urban areas influences behaviour and attitudes of people towards urban wildlife and it has a consequences for the management of foxes and the treatment of zoonoses such as rabies and the alveolar echinococcosis.

Key words: *Vulpes vulpes*, urban habitat, invasion, adaptation

Introduction

Since 1985 fox populations have experienced a drastic increase in Switzerland (Breitenmoser et al. 2000). Apart from this development in rural areas, increasingly more foxes have been recorded from large Swiss conurbations and cities such as Zurich and Geneva. Game wardens and wildlife biologists have observed foxes in urban areas; people having noticed foxes in their gardens turned to local officials for information; pictures and articles about foxes in the middle of residential areas have been published. Are these records just occasional observations or do they indicate the colonisation of a new habitat by the red fox?

Red foxes living in urban areas are known from Great Britain where urban foxes have been observed in cities such as London since the 1930s (Teagle 1967; Beames 1969, 1972; Page 1981). In the 1970s and 1980s, fox populations in British cities reached densities of up to five fox family groups per km^2 (representing 12 adults on average), densities which had never been

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observed so far (HARRIS 1981 a; HARRIS and RAYNER 1986 a). Similar fox population densities were nowhere recorded in urban areas outside of Great Britain, either on the European continent or in other parts of the distribution areas of the red fox. Therefore, urban foxes were thought to be a British phenomenon (HARRIS 1977; MACDONALD and NEWDICK 1982).

In the 1970s and 1980s, the fox population on the European continent experienced a heavy rabies epizootic, which reached Switzerland in 1967 (STECK et al. 1980; MÜLLER et al. 2000). Fox densities decreased drastically, and, as seen from the Swiss hunting record, reached a low in 1984 (BREITENMOSER et al. 2000). After the success of oral vaccination campaigns against rabies, started in Switzerland in 1978 (WANDELER et al. 1988), the fox population recovered again from 1985 onwards (KAPPELER 1991; BREITENMOSER et al. 2000). At that same time, foxes were increasingly observed in human settlements.

Our objectives in this study are to investigate the present situation in large Swiss settlements, to evaluate the recent development of the fox population in Zurich, the largest conurbation of Switzerland, and to compare it with the trend in surrounding rural areas.

Material and methods

Study area

Switzerland is a diverse and mountainous country. 24% of its total area of 40 000 km^2 (excluding lakes), are above 2 000 meters in elevation where fox population density is low. The remaining 76% of the country forms heterogeneous and mostly good quality habitat for the red fox.

In Switzerland there are 30 cities with more than 20 000 inhabitants, where 19% of the 6.9 million inhabitants live. The largest conurbation of Switzerland is the area of Zurich with some 1 000 000 inhabitants. However, only 352 200 of them live in the actual "city", the political community of Zurich. The political community of Zurich (92 km^2) – which we refer to when we are talking about the "city of Zurich" in the following report – consists of 53% urban area, 24% forest, 17% agricultural areas and 6% water (FEDERAL OFFICE OF STATISTICS 1998). Forest and agricultural areas surround the urban area and are referred to as the rural area of the city in the following. As far as hunting is concerned, the city of Zurich is organised as a game sanctuary. The city of Zurich belongs to the canton of Zurich, one of the most densely populated cantons of Switzerland (area 1 661 km^2, 683 inhabitants per km^2).

The present distribution of urban foxes in Switzerland

During a television series about urban foxes in spring 1997, the public was called to report fox sightings in Swiss cities. The sightings were recorded personally by collaborators of the Integrated Fox Project. Only fox sightings within human settlements were recorded. As the call on TV was biased towards the German speaking part of Switzerland, the scanty information from the French and Italian speaking regions of the country were excluded from further analyses. The program actus (ESTABROOK and ESTABROOK 1989) was used for the statistical test, which performs randomised contingency tables and gives probabilities for deviations from expected values.

In spring 1999 we carried out a phone inquiry with people or institutions in charge of wildlife management in all 30 Swiss cities (communities) with more than 20 000 inhabitants (FEDERAL OFFICE OF STATISTICS 1998). The experts were asked about occurrence and abundance of urban foxes, evidence of breeding dens in the urban area, the year of the first urban fox sightings and the current trend in the urban fox population. In cities with official game wardens (18 out of 30), they were interviewed, in all other cities we questioned non-professional hunters and the nature conservation officials. In the conurbation of Geneva (three communities with >20 000 inhabitants) our contacts were wildlife biologists running an urban fox project; in Zurich we knew the situation from our own project.

Development of the urban fox population in the city and the canton of Zurich

There are no direct figures on the red fox population available. Therefore its development has to be shown indirectly through the hunting record and other recorded causes of death. Longtime figures for an urban area are available for the city of Zurich, because it has been a game sanctuary since 1929. All wildlife management tasks in the city are exclusively performed by official game

wardens, therefore the hunting result is recorded and the locations of dead foxes (shot or found dead) are known.

For comparison of the data from the canton and the city of Zurich, we used the HIPD (hunting indicator of population density; Bögel et al. 1974). We defined the HIPD as the annual number of foxes hunted per km^2 excluding lakes and areas above 2000 meters. We did not include data on foxes with other causes of death than hunting because generally these data have only been available since 1968.

To compare data from urban and adjacent rural areas within the city of Zurich, we used a total number of foxes shot or found dead (available from 1960 to 1997), and additionally numbers of the two mortality factors "shot" and "found dead" (mostly road casualties; for the whole city available since 1960, for urban and adjacent rural areas separately available since 1984). To analyse the development of the fox population in the city of Zurich we performed simple linear regressions because the fit of regression of the two mortality factors on the years 1984 to 1997 did not improve by exponential or logistic functions.

Results

The present occurrence of urban foxes in Switzerland

After the call for urban fox sightings on Swiss Television in spring 1997, 194 sightings from 78 different towns and villages of the German-speaking part of Switzerland were reported. 138 sightings came from towns with more than 10000 inhabitants (Tab. 1). Of those, more sightings than expected concerned cities with more than 50000 inhabitants (randomisation test, $p < 0.01$), and less sightings than expected from towns with 10000 – 20000 inhabitants ($p < 0.05$; Tab. 1).

According to our inquiry among institutions in charge of wildlife management in 8 out of 9 cities with > 50000 inhabitants, and in 18 of the 19 cities with 20000 – 50000 inhabitants, foxes were occasionally found or common (Fig. 1, Tab. 2). Foxes seem not to

Table 1. Reported sightings of foxes in urban areas from the German-speaking part of Switzerland (randomisation test).

Size of township	Accumulated number of inhabitants	Number of fox reports	Expected number of fox reports according to numbers of inhabitants	Significance
> 50000	958746	97	60	higher ($p < 0.01$)
20000–50000	335192	10	21	ns
10000–20000	897430	31	57	lower ($p < 0.05$)
Total	2191368	138	138	

Table 2. Occurrence and trend of urban fox populations in 30 Swiss cities, according to an inquiry among people/institutions in charge of wildlife management. The two cities where no urban foxes were observed (Bern, Lugano) are excluded.

Questions	Answers	Cities with many urban foxes (n = 13)	Cities with few urban foxes (n = 15)
1. Where are the urban foxes observed?	(a) whole of the city	13	4
	(b) outskirts only	0	11
2. Are there any urban breeding dens?	(a) yes	13	7
	(b) no	0	8
3. Since when have urban foxes been present?	(a) 1985–1999	10	7
	(b) < 1985	3	3
	(c) not known	0	5
4. How do you judge the trend of the fox population?	(a) increasing	8	5
	(b) stable	2	10
	(c) decreasing	3	0

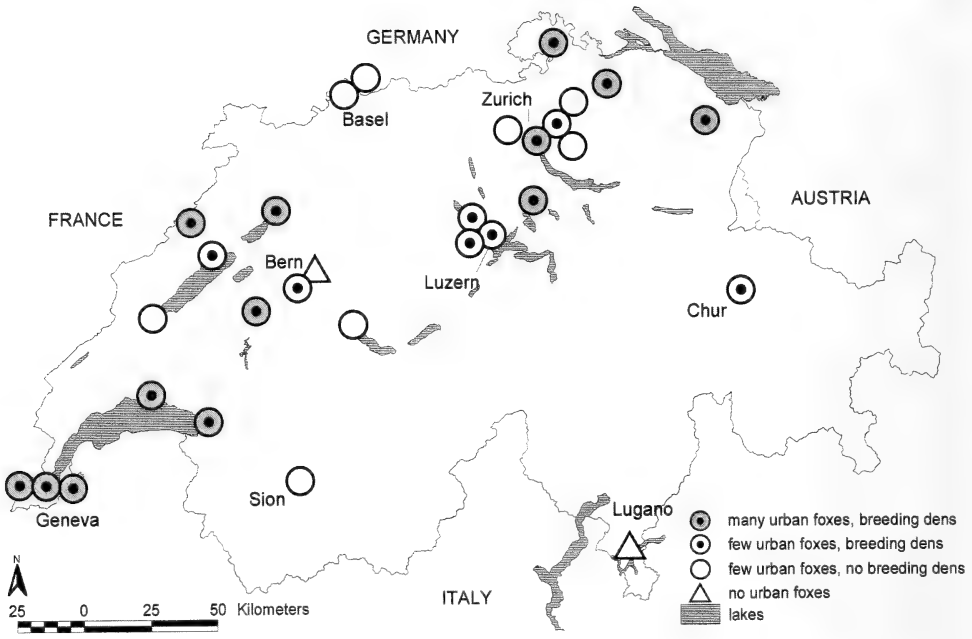

Fig. 1. Distribution of urban foxes in 30 cities with more than 20 000 inhabitants according to local wildlife management experts. Circles of adjacent cities are shifted to avoid overlapping.

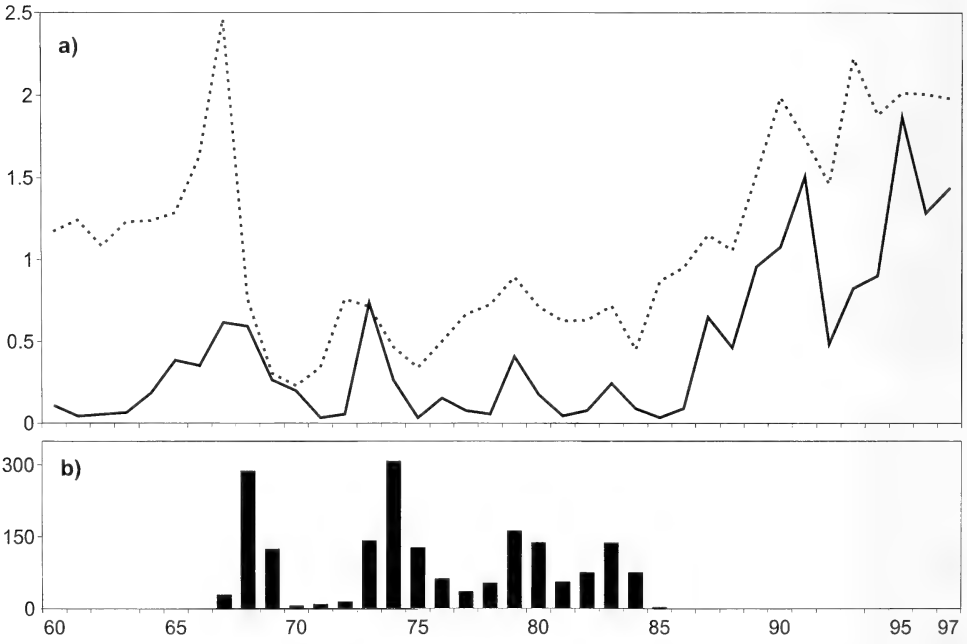

Fig. 2. a) Hunting indicator of population density (HIPD) for the city of Zurich (straight line) and the canton of Zurich (dotted line) from 1960 to 1997. **b)** Rabies cases in the canton of Zurich from 1960 to 1997.

be present in two towns only: in Bern, situated on the Swiss Plateau, and in Lugano, a city in the southern Alps.
In all 13 towns where foxes were reported to be common, they were observed throughout the urban area, (including the centre), and they were breeding in the urban area also (Tab. 2). In 4 cities with more than 50 000 inhabitants (Zurich, St. Gallen, Luzern, Biel), breeding dens are known even in the very city centre. In most cities (17 out of 28), urban foxes have been perceived as a recent phenomenon since 1985. No geographical trend can be recognised as far as the beginning of settlement in different cities is concerned.
Only in the conurbation of Geneva, with three cities (communities) with > 20 000 inhabitants (Geneva, Lancy, Vernier; Tab. 2) the population is said to decrease because of an outbreak of sarcoptic mange in 1996 (C. Fischer, pers. comm.).

Development of the urban fox population in the city of Zurich

The HIPD of the canton of Zurich and the city of Zurich correlate significantly (Spearman, $r = 0.66$, $p < 0.001$; Fig. 2 a), the HIPD in the canton always being higher than in the city. Additionally, the HIPD of canton and city are strongly influenced by rabies trends between 1967, the year when rabies reached Switzerland, and 1985, the year with the last cases of rabies found on foxes in the canton of Zurich (Fig. 2 a, b).
According to the HIPD, the fox population in the city of Zurich and in the whole area of the canton of Zurich seems to have developed in parallel at least since the beginning of the 1970s. Both HIPDs are higher after the rabies epizootic than before. The average of the HIPD from 1993 to 1997 compared to the average of the HIPD from 1960 to 1964 is by 1.7 times higher (2.02 vs. 1.19) in the canton and 13.7 times higher (126 vs. 0.09) in the city of Zurich, indicating a stronger population increase in the city than in the canton. The increase of the HIPD started in the canton in 1984 and in the city in 1985, respectively.
However, the development of the fox population in the whole city of Zurich (with urban as well as adjacent rural areas) is not the same as the development of the population within the urban area. The first peak of the HIPD in 1967 (Fig. 2) only occurred in the records of foxes from the rural part of the city (Fig. 3), whereas in the urban part of the city fox numbers remained low during the 1960s and 1970s. The trend to an increasing urban fox population in fact just started from 1985 onwards.
Before 1985, most of the few foxes of the urban area were only recorded at the border of the city, apart from two foxes, one young fox near the city centre in August 1964 and one young fox in the fairly central railway station Enge in June 1967.
Rabies cases were recorded in and near the city of Zurich from 1967 to 1983 (Fig. 3). The prophylactic culling of foxes was carried out as intensively as possible from 1965 to 1995. The numbers of foxes found dead and shot, analysed separately for the whole city correlate significantly (Spearman, $r = 0.73$, $p < 0.001$). According to these numbers, the population remained low for almost 20 years after the rabies outbreak, and only in 1985, two years after the last rabies cases were recorded in the area, the fox population started to increase, both in the urban and in the adjacent rural part of the city. From 1985 to 1997 the number of foxes shot or found dead in the whole city increased by 20 times from 11 to 223. This trend is true for both mortality factors "shot" and "found dead" and examined separately for urban and adjacent rural areas (Tab. 3). Yet the increase in the number of foxes found dead was stronger in the urban than in the rural area (difference of coefficients, $t_{24} = 4.11$, $p < 0.001$).

Discussion

Today, urban foxes are recorded in almost all cities of Switzerland. The presence of breeding dens in urban areas up to the city centres indicates that foxes really live in the cities and are not just occasional roamers from the vicinity. We ascribe differences

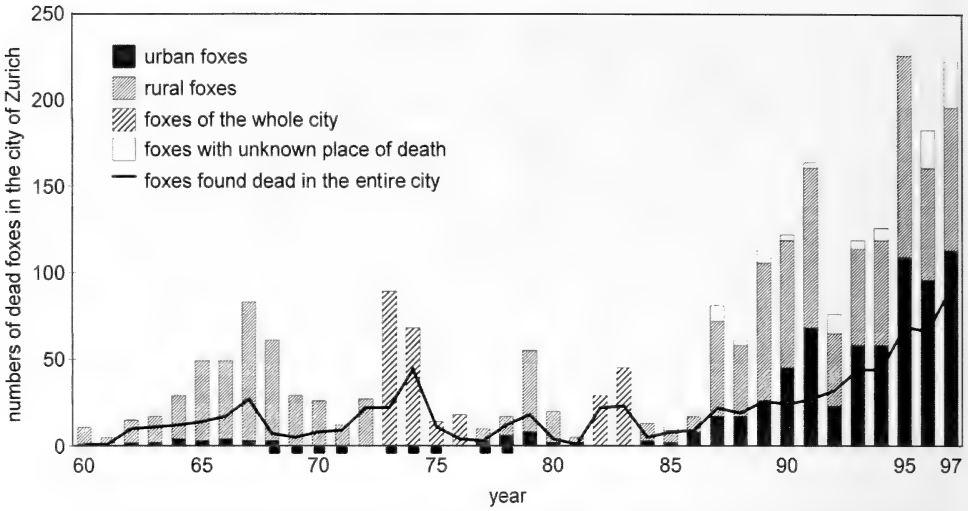

Fig. 3. Fox mortality (animals shot or found dead) in urban and rural areas in the city of Zurich from 1960 to 1997. From the years 1973–1976 and 1982–1983 there are only total numbers of dead city foxes available (widely hatched bars). No precise locations of death are available for some recorded foxes from 1984 onwards (white bars). The years with rabies cases within 5 km of the city centre (Kappeler 1991) are marked with black bars.

Table 3. The increase of numbers of recorded dead foxes within the city bordes of Zurich, described by the linear regression of the two mortality factors "shot" and "found dead" (mostly road casualties) from 1984 to 1997.

Foxes of urban areas			
Mortality factor	Coefficient	R^2	p <=
Shot	5.215	0.78	0.001
Found dead	3.310	0.85	0.001
Foxes of adjacent rural areas			
Mortality factor	Coefficient	R^2	p <=
Shot	4.842	0.46	0.01
Found dead	0.831	0.74	0.001

in fox population densities in Swiss cities of today mainly to the fact that urban foxes have been a recent phenomenon and the development is still going on.

Our call for fox sightings on Swiss television revealed that more foxes are recorded from larger towns than from smaller ones, a relation that was also observed by MACDONALD and NEWDICK (1982) in Great Britain. This could be because larger towns may have a higher proportion of suburban habitat, where the highest fox densities are found (HARRIS and RAYNER 1986 b).

Although red foxes generally avoid the direct presence of humans, some foxes have lived in the neighbourhood of humans settlements for a long time, shown, e. g., by the naturalist SCHINZ (in INEICHEN 1997), who noted in 1842, that red foxes had always lived in the moats surrounding the city of Zurich. The hunting statistics of the city of Zurich show that foxes have been present in the urban area since the early 1960s, but such observations remained isolated cases.

In 1985 the situation began to change. Due

to successful oral vaccination campaigns against rabies, the fox population in Switzerland started to recover (Breitenmoser et al. 2000), which is recorded in other European countries, as well (e. g. Vos 1993; Artois et al. 1997). It was parallel to this general trend, when the urban fox population in the city of Zurich and in most other Swiss cities showed a drastic increase.

However, hunting statistics have to be interpreted cautiously, because they do not only correlate with the real fox populations but are also influenced by other factors such as the preferences of the hunters (Macdonald and Voigt 1985; Goszczynski 1989) or outbreaks of zoonoses (Kappeler and Wandeler 2000). A high hunting pressure most probably lasted during the whole period of rabies from 1967 until at least to the end of the 1980s. Therefore, the low HIPD during this period presumedly reflects low densities of fox populations. With the decrease of rabies the motivation to hunt foxes probably decreased drastically. The HIPD, on the other hand, was still increasing during the 1990s. We therefore suggest that the real trend of fox populations is underestimated by hunting statistics. The fox population in the canton of Zurich with its high degree of urbanisation must be even more underestimated by the HIPD, because foxes are hardly ever shot in most urban areas, where hunting generally is not permitted.

The game sanctuary of the city of Zurich is an exception, where a constant hunting regime is maintained by official game wardens. The significant correlation of the development of foxes "shot" and "found dead" within the city confirms, that the increasing numbers of dead foxes are not only the result of an increased shooting effort.

A similar development of urban foxes as in Switzerland recently took place in other parts of the distribution area of the red fox which is shown by reports, e. g., from Oslo, Norway (Christensen 1985), Arhus, Denmark (Moller Nielsen 1990), Stuttgart, Germany (T. Romig, pers. comm.), Toronto, Canada (Adkins and Stott 1998) and Sapporo, Japan (K. Uraguchi, pers. comm.). The questions arises why the invasion of urban habitat started and which factors caused this new development.

According to Harris and Rayner (1986 c), the colonisation of British towns already started in the 1930s. During these years there was a boom of private house construction resulting in large districts of middle-class suburbs with low-density housing, and medium-sized gardens. This is the type of habitat which Harris and Rayner (1986 b) found to be favoured by foxes. Once established in these residential suburbs, foxes moved further into the city and also colonised less favoured habitats. Harris and Rayner (1986 b) found urban foxes to be less common in areas consisting of council-rented housing, in city centres, and around industrial areas.

The colonisation of Swiss cities by foxes resulted in a similar phenomenon as known from Great Britain. However, the underlying cause for the rise of the urban fox populations seems to be different, because the development of Swiss cities in the past thirty years was unlike British cities in the 1930s. We propose two hypothetical explanations for the presence of urban foxes: The population pressure hypothesis (PPH) and, as an alternative, the urban island hypothesis (UIH).

The population pressure hypothesis PPH postulates that urban foxes are simply intruders from the adjacent rural areas. These foxes invade in human settlements because of a high population density in rural areas. According to the PPH, urban areas would provide suboptimal habitats for foxes, the dynamics of an urban fox population would closely correlate with the trend of the fox population in the adjacent rural areas, and the urban fox population would genetically not be different from the adjacent rural population (Rousset 1999).

The alternative urban island hypothesis UIH postulates that urban foxes have adapted to specific urban conditions such as high density of human population. Therefore, urban foxes would be able to use specific urban resources such as scavenged food items or special hiding places during daytime. The dynamics of such an

urban fox population would be independent from the trend in the adjacent rural areas. The colonisation of urban areas could have been initiated by the behavioural adaptations of a few foxes that gave them access to exploit human settlements as a free niche. As only a few individuals founded the new urban population, we would expect it to be genetically isolated from the population in the rural surroundings.

The simultaneous emerging of urban foxes throughout Switzerland along with the increasing fox population indicates that the high population pressure has at least initiated the immigration of the founder individuals into the cities. MACDONALD and NEWDICK (1982) suggested that there was no strict division between rural and urban foxes in Oxford, because they had radiotracked foxes which regularly commuted between urban and rural areas. Nevertheless, living in the city requires special adaptations, and many anecdotal observations reveal that foxes indeed have adapted to this exceptional environment. Further research on resource exploitation and genetic structure of the urban fox population will allow to compare the two hypotheses.

The presence of foxes in human settlements raises the question of the impact of human behaviour and human attitudes on the urban fox population (BONTADINA et al. 2000). HARRIS (1981 b) and DONCASTER et al. (1990) showed, that food directly or indirectly provided by humans can make up a major part of the diet of urban foxes. People feel ambivalent about urban foxes, being either fascinated by this wild carnivore in their neighbourhood or afraid of it because of zoonoses (Bontadina et al. 2000).

In fact, foxes in close vicinity to humans and pets could indicate new zoonotic risks (HOFER et al. 2000). The red fox is the main vector of rabies in Europe. Up to now urban areas were considered to be barriers to the spread of rabies (STECK et al. 1980), therefore the increase of urban fox populations calls for additional strategies in case of a new outbreak of rabies (MACDONALD and VOIGT 1985; HARRIS et al. 1988).

Furthermore, the zoonosis alveolar echinococcosis (AE), caused by the small fox tapeworm *Echinococcus multilocularis*, could become more important through the increase of urban fox populations. In Switzerland, the incidence rate of human AE has not significantly changed over the past 36 years, suggesting a stable epidemiological situation (ECKERT and DEPLAZES 1999), but regarding the long incubation period of AE of 5–15 years, it would be advisable to study this zoonosis further, especially in urban areas. Results of such studies could have an important impact on the management of urban fox populations.

Acknowledgements

The authors thank all collaborators involved in the Integrated Fox Project. We especially thank CLAUDE FISCHER, who conducted the inquiry of game officials in the French part of Switzerland and provided useful information on the urban fox population of Geneva, and CHRISTIAN STAUFFER for his generous collaboration and for providing access to the data of the game sanctuary of Zurich. We thank ALEXANDER MATHIS, CLAUDE FISCHER, CHRISTIAN STAUFFER, and JEAN-MARC WEBER for comments on an earlier draft. We also thank the game wardens and people in charge of wildlife management in the 30 large cities of Switzerland. The study was supported by the Swiss National Science Foundation (grant no. 31-47031.96), the Fonds zur Förderung des akademischen Nachwuchses FAN of the Zürcher Hochschul-Verein and the Swiss Federal Offce for Education and Science (EU FAIR Projekt CT97-3515/BBW Nr. 97.0586).

Zusammenfassung

Die Entstehung urbaner Fuchspopulationen in der Schweiz

Seit Mitte der 1980er Jahre werden zunehmend Füchse inmitten von Schweizer Städten beobachtet. Die Befragung der zuständigen Behörden ergab, daß heute in 28 der 30 größten Schweizer Städte

Füchse registriert werden. In 20 dieser Städte sind Fuchsbaue mit Jungenaufzucht im Siedlungsraum bekannt. Dabei werden Stadtfüchse überproportional häufger in größeren Städten als in kleineren Ortschaften beobachtet. In Zürich, der größten Schweizer Stadt, waren gemäß der Jagdstatistik bis zu Beginn der 1980er Jahre Stadtfüchse sehr selten. Erst ab 1985 begann die städtische Fuchspopulation markant anzusteigen. Auch die umliegenden ländlichen Gebiete verzeichnen ab 1984 eine deutliche, allerdings weniger starke Zunahme der Fuchsbestände, die u.a. mit der erfolgreichen Tollwutbekämpfung zusammenhängt. Als Erklärung der Präsenz von Füchsen im Siedlungsraum, einem bisher vor allem aus Großbritannien bekannten Phänomen, schlagen wir zwei alternative Hypothesen vor, welche einerseits den Populationsdruck in ländlichen Gebieten, andererseits stadtspezifsche Verhaltensanpassungen der Füchse ins Zentrum stellen. Fuchspopulationen im Siedlungsraum beeinflussen das Verhalten und die Einstellung der Bevölkerung gegenüber Wildtieren und haben Konsequenzen für das Fuchsmanagement und den Umgang mit Zoonosen, wie Tollwut und alveoläre Echinokokkose.

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Mamm. biol. **66** (2001) 165–173
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Feeding selectivity and food preference of *Ctenomys talarum* (tuco-tuco)

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Receipt of Ms. 02. 06. 1999
Acceptance of Ms. 17. 10. 2000

Abstract

We tested feeding selectivity and food preference of *Ctenomys talarum* (tuco-tuco). To test feeding selectivity, above ground and below ground plant biomass from the field was determined and botanical composition of the diet was estimated in stomach contents using microhistological techniques. Feeding preferences were studied carrying out laboratory cafeteria experiments. *Ctenomys talarum* behave as generalist and opportunistic herbivores consuming the greater part of species present in the grassland. The above ground portion was preferred over the subterranean one. Grasses constituted 94% of the above ground vegetative fraction consumed and were generally selected. Preference trials also showed that *C. talarum* prefer above ground parts of grasses to other choices.

Key words: *Ctenomys talarum* diet, feeding selectivity, food preference

Introduction

Rodents of the genus *Ctenomys* (tuco-tucos) are subterranean herbivores whose populations are distributed in a discontinuous pattern throughout Argentina, Paraguay, Bolivia, Uruguay, Perú, Chile, and southern Brazil (Woods 1984). Most herbivores inhabit a biotope in which the food plants are more or less continuously distributed in space and time, and whose accessibility is restricted by the structural and chemical properties of the vegetation (Illius and Gordon 1993). They select food items according to their preference, and availability in the field. Preference is the predilection of a consumer for a particular class of food, and it is the result of how well the consumer "likes" this food relative to other ones, when all are equally available (Norbury 1992). Diet selection in herbivores may be explained by models where the rate of intake is maximized with nutrient constraints, toxins are avoided or their intake is minimized (Stephens and Krebs 1986). A foraging herbivore maximizes its nutrient intake when greater nutrient intake converts directly into greater survival and reproduction (nutrient maximization; Belovsky and Schmitz 1994).

Food resources have been implicated as important to both burrow location and burrow

1616-5047/01/66/03-165 $ 15.00/0.

system size, suggesting that foraging is a critical component of ecology of subterranean rodents (BUSCH et al. 2000). In terms of nutritional value, below ground plant tissues may represent a more variable resource than above ground tissue (ANDERSEN 1987). This fact and the high energetic costs of digging may influence food selectivity. HETH et al. (1989) proposed that subterranean herbivores cannot afford to be selective feeders since search costs would exceed the benefits of being selective, therefore they should utilize all food that they encounter. Furthermore, subterranean rodents are expected to consume a great proportion of below ground vegetation (VLECK 1979).

Diet selection by herbivores is important in determining their effects on plant communities. Empirical evidence and theoretical models suggest that generalist herbivores may have more widespread effects on plant communities than specialist herbivores, since they can greatly reduce, or even eliminate, some plant species while persisting on the remaining species. Much remains to be learned regarding the foraging ecology of subterranean rodents. Cafeteria-style test of food preference would help to determine the nature and extent of dietary specialization. In addition, field studies of foraging behavior would allow to test optimal foraging models (STEPHENS and KREBS, 1986) under the condition faced by free-living animals.

This study assesses different aspects of the feeding behavior of individuals of a *Ctenomys talarum* population inhabiting a coastal dune grassland in the southeastern Buenos Aires province, Argentina. Specifically assessed are: 1) *C. talarum* feeding selectivity in the field, and 2) food preferences of *C. talarum* in cafeteria test.

Material and methods

Two studies were conducted. One was carried out in the field to evaluate *C. talarum* feeding selectivity. The other was a cafeteria test developed to determine if food quality (fiber/protein) determines their feeding preference.

Feeding selectivity (field data)

The study was conducted on coastal dunes at Mar de Cobo (Buenos Aires Province, Argentina), in a natural grassland with the predominance of perennial grasses (COMPARATORE et al. 1991).

Vegetation and animals were sampled in autumn, winter, spring, and summer. Fifty seven animals were kill-trapped and their stomachs removed. Because above ground foraging occurred near the burrow opening, for each animal captured, four vegetation samples were collected from around the opening (30 cm diameter and 30 cm depth). Above ground and below ground samples were separated and dry plant biomass was estimated and expressed as percentage of total biomass. In addition, the percentage of the above ground fraction of each species was computed.

The botanical composition of *Ctenomys talarum* diet was estimated using microhistological techniques. Stomach contents were processed individually according to WILLIAMS (1969), and the botanical composition of the diet was quantified according to SPARKS and MALECHEK (1968). The subterranean, above ground and reproductive fractions were quantified. In addition, the species percentages in the vegetative fraction were determined, since it is the only one in which fragments could be differentiated to species level.

The seasonal percentages of the components of *Ctenomys* diets were compared using a Kruskal-Wallis test ($P = 0.05$). Diet and grassland botanical composition were contrasted, establishing animal selectivity for total above ground and subterranean fractions. Reproductive fraction selectivity could not be established because its percentage was not determined in the grassland. In addition, selectivity for the above ground vegetative fraction of the species in the diet was computed.

The following index (KRUEGER 1972) was used to determine relative species selectivity:

$$SI = \% Di \times fdi / \% Pi \times fpi,$$

where % Di and fdi are the seasonal mean percentage and the frequency of component i in the diets, and % Pi and fpi are the seasonal mean percentage and the frequency of the component i in the grassland. Chi square with 95% confidence was used to determine if the seasonal SI for each component was significantly different from 1. Kulcyznski's similarity index (HOLECHEK et al. 1984) was used to evaluate the similarity of diets and pasture. The species considered in the analysis were those whose seasonal mean percentage by the frequency, in the diets and/or in the grassland, were over 2%. Results are shown as mean ± SD (standard deviation).

Feeding preference (cafeteria test)

Animals for the experiments were live-trapped in the coastal dunes of Necochea (Buenos Aires province). Food preference was investigated in the laboratory by the amount of plant matter consumed during feeding trials (Phillipson et al. 1983). To conduct the trials, animals were set in a feeding apparatus (42×42×6 cm) which consisted of a central nest box with an opening in each of four feeding arenas. The gridded floors of the feeding arenas allowed food remains and faeces to drop into a collecting tray without being moistened with urine.

Leaves and stems of plant species for the experiment were collected at the same site where the animals were trapped. Potatoes and carrots, which have low fiber percentages, were also used as choices. Standard cafeteria trials were conducted performing three different tests. In each one the same wet weight of four different kinds of food was offered simultaneously. Each test lasted for four days with 10 repetitions using different individual tuco-tucos (5 adult females and 5 adult males). Every day equal wet weight of each plant choice was offered. Intake was calculated on both a fresh-mass and a dry-mass basis. The residual plant material was sorted and weighed on succeeding days and the difference recorded. Then, it was dried at 70–80 °C to invariable weight. Conversions of fresh mass to dry mass were calculated from samples of plant material that was maintained in empty cages during the trials.

Each choice of food was weighed to the nearest 0.01 g and offered in different compartments of the feeding apparatus. The position of the foods varied at random. Species chosen for the cafeteria test are present in the natural diet of *Ctenomys talarum* in Necochea, except for *Ipomea batatae* and *Daucus carota*.

To test if dietary preference correlates with some particular portion of the plant we offered different parts of two species of grasses that appeared in the field diet: *Cynodon dactylon* stem, *C. dactylon* leaf, *Bromus unioloides* stem, *B. unioloides* leaf. To test if the preference has a relation with the fiber content of the choice *C. dactylon* stem, *B. unioloides* stem and *Ipomea batatae* tuber and *Dacus carota* root (fiber content: 17% and 13%, respectively) were offered. We also tested the preference for forbs or grasses and different parts of them, offering two species from the field diet: *Hydrocotile bonariensis* (forb) above ground portion *H. bonariensis* below ground portion, *Panicum racemosum* (grass) above ground portion, *P. racemosum* below ground portion.

Protein content was determined by the microbiuret method (Gornall et al. 1949) and fiber content was determined by the Goering and van Soest (1970) technique. Results are shown as mean ± S. D. A non-parametric multiple comparison test (Zar 1984) was used to ascertain the significance of the preferences observed. Chi square with 95% confidence was used to test whether the proportions of food consumed were equal to expected frequencies, based on the relative dry weight of food offered.

Results

Feeding selectivity

Comparison of botanical composition of grassland and diet

Proportion of subterranean biomass was not significantly different from the above ground ($P > 0.05$; Fig. 1 a). Perennial grasses dominate the grassland biomass (79% of total above ground available biomass). The proportion of perennial monocotyledoneans decreased in spring, while annual monocotyledoneans increased; annual forbs decreased in autumn and perennials in winter (Fig. 2 a). Monocotyledonean composition was dominated by *Panicum racemosum*, which constituted 25% of the annual biomass.

Analysis of the contents of 57 stomachs revealed that tuco-tucos exploited at least 16 species of plants annually. The above ground vegetative portion of plants predominated (84.5%) in the annual diet, whereas subterranean and reproductive portions constituted only 11% and 4.5%, respectively (Fig. 1 b). Grasses comprised the highest proportion of the annual diet. Its average annual occurrence was 94% of the annual above ground vegetative fraction (Fig. 2 b). *Bromus unioloides* (46%), *Panicum racemosum* (16%), and *Poa bonariensis* (10%) were consumed more intensively, as they constituted 72% of the dry weight of the annual diet.

Seasonal changes in diet

Although perennial grasses comprised the highest proportion of the diet year round (Fig. 2 b), consumption preference of differ-

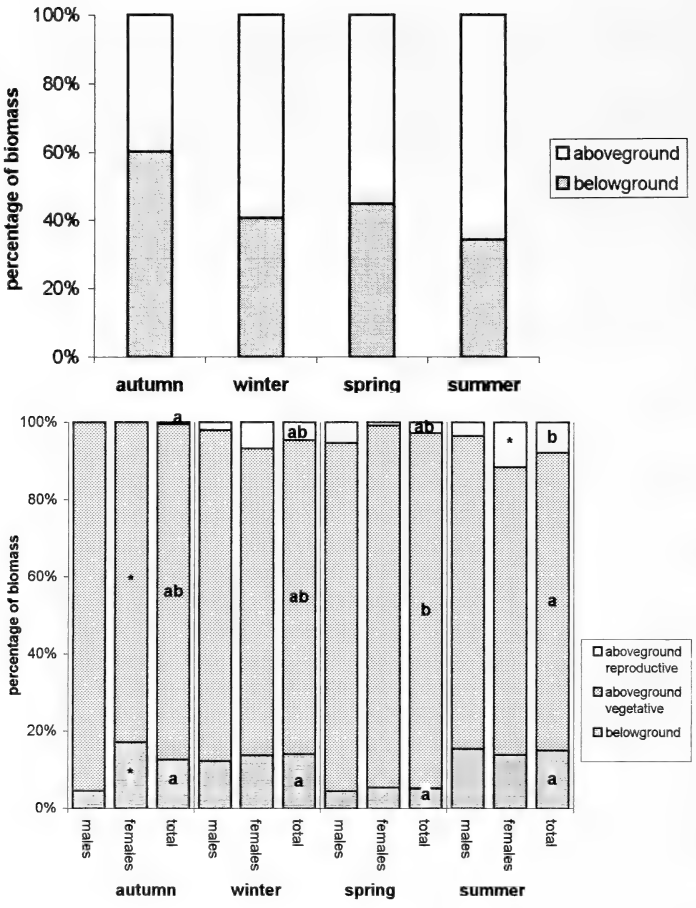

Fig. 1. Percentages of biomass in the grassland and in the diet of tuco-tuco: a) Above ground and subterranean percentage of plant biomass in the natural grassland at Mar de Cobo where *Ctenomys talarum* was trapped; b) Above ground, reproductive and below ground percentage of plant biomass in the stomach of *Ctenomys talarum* trapped in a natural grassland at Mar de Cobo.
Different letters indicate significant differences between seasons; * indicates significant differences between sexes in each season.

ent species varied. Thus, the analysis of the seasonal diet of the tuco-tucos revealed that *Bromus unioloides* was an important source of nutriment almost year round, but it was consumed less during the autumn season. On the other hand, only during spring *Panicum racemosum* ceased to be an important component of the tuco-tuco's diet. *Poa bonariensis* was consumed more in autumn, spring, and summer and less in winter. The perennial forb *Adesmia incana* became an important component in the spring diet (10%). Although there were no significant differences between the average of the below ground fraction consumed in each season ($P > 0.05$); the mean consumption (5.3 ± 4) in spring was lower than in the other seasons (Fig. 1 b).

Effect of sex on diet

Males seem to be more selective than females (male and female diets show a 58% and 66% similarity with the grassland, respectively; Kulcyznski's index). Differences were noticed in winter and in summer when male and female diets exhibited statistical differences in the proportion of *Bromus unioloides* ($P < 0.02$). Moreover, plant fractions were consumed differentially (Fig. 1 b). Whereas males consumed the subterranean and vegetative fractions of plants in the same proportions year round, females did not ($P < 0.02$). Furthermore, in autumn females consumed a higher proportion of the subterranean fraction ($P = 0.006$) and smaller proportion of the above ground vegetative ($P = 0.004$) than males, and during sum-

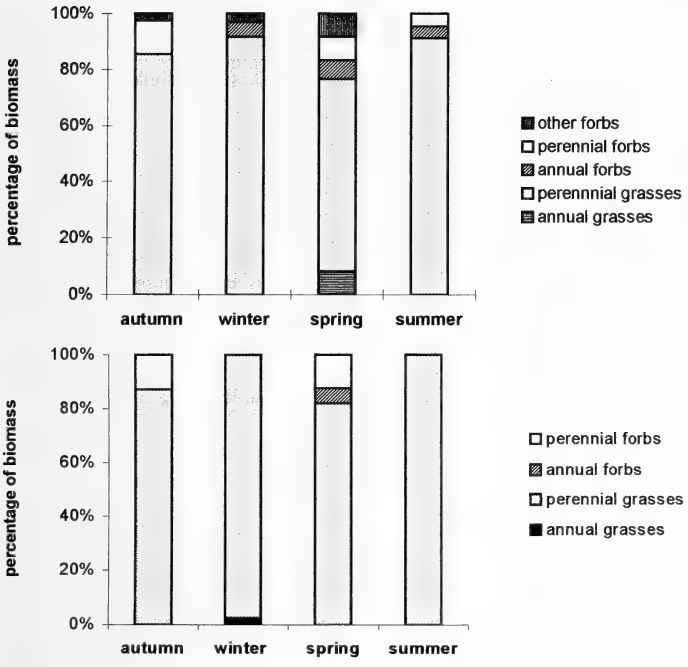

Fig. 2. Botanical composition of the grassland and of the diet of tuco-tuco: a) Percentage of biomass of above ground available vegetation on a natural grassland at Mar de Cobo; b) Percentage of biomass of different types of above ground vegetation in stomachs of *Ctenomys talarum*.

Table 1. Seasonal values of selectivity index (SI) for each above ground vegetative food item and for the subterranean fraction. (*) denotes statistically significant difference from 1 (SI ≠ 1) Chi-square test (P = 0.05)

	AUTUMN N = 15	WINTER N = 15	SPRING N = 12	SUMMER N = 15
Above ground fraction				
Annual grasses	–	–	0	–
Perennial grasses	1.01	1.06	1.19	1.09
Annual forbs	–	0	0.84	0
Perennial forbs	1.07	–	1.46	0
Subterranean fraction	0.32*	0.35*	0.12*	0.44*

mer they consumed a significantly higher proportion of reproductive structures than males (P = 0.028; Fig. 1 b).

Relative plant selectivity

Tuco-tuco ingested perennial monocots and dicots in proportion to their mass (Tab. 1), and thus according to the probability of encountering them. Nevertheless, tuco-tucos are capable of selective foraging, since the above ground fraction of the plant was not selected by individuals of both sexes in all seasons (P < 0.05). In addition, the analysis of the stomachs showed that tuco-tucos select some monocots species with preference changing seasonally; the grass *Bromus* was selected in winter, spring, and summer but was indifferent in autumn, whereas *Poa* was selected in autumn, spring, and summer but not in winter. *Panicum* was preferred in autumn and avoided in other seasons (P = 0.05). Furthermore, males and females showed different feeding selectivity for *Bromus unioloides*, thus, it was selected in winter and summer by males, but not by females (P = 0.05).

Feeding preference

Tuco-tucos consumed 200 ± 57 g ind^{-1} d^{-1} of food, and 8 ± 3 g protein and 26 ± 53 kcal per day. The experiments demostrate that *C. talarum* is able to discriminate among the plant species tested, and harvested grasses selectively. Although some species and/or part of the plant were consumed more than others (Tab. 2), tuco-tucos consumed all plants offered in the test and consumption of choices other than the preferred ones make an important contribution to total ingested nutrient (7–44% protein). Results indicate preference for above ground portions of grasses over other choices tested. Furthermore, plant portions with a low fiber/protein ratio were less preferred than those with a high fiber/protein ratio. When offered as above ground samples, significant quantities of all grasses were consumed by the tuco-tucos and no preference for stems or leaves was detected, but as noted above a preference for low quality food was noticed, thus the *B. unioloides* leaf, which has the lowest fiber/protein ratio, was eaten to a lesser proportion than the other choices (Tab. 2 a). When offered monocots (*B. unioloides*, *C. dactylon* or *P. racemosum*) and other choices, grasses represented 70–90% of the total consumption and grass stems were preferred to other choices tested (Tab. 2 b, c). This preference was independent of the nutritional quality of the other choice, thus the stems of grasses with a higher fiber/protein ratio were preferred to *I. batatae*, *D. carota* or to *Hydrocotyle bonaroensis* above ground proportion (Tab. 2 b, c).

Discussion

Feeding selectivity

Ctenomys talarum behave as a generalist and opportunistic herbivore since it consumes the greatest part of the species present in the grassland, and changes its diet in relation to food availability. Similar food habits were reported for other *Ctenomys* species (*C. australis*, COMPARATORE et al. 1995 and *C. mendocinus*, MADOERY 1993) and other subterranean rodents such as

Table 2. Dry weight consumption and fiber/protein ratio of food items for three different cafeteria tests. (a) First cafeteria test compared the consumption between different portions of two species of grasses; (b) second cafeteria test compared the consumption between items with high and low fiber/protein ratio; (c) third cafeteria test compared between subterranean and above ground fraction of forbs and grasses. Non parametric multiple comparisons test to differentiate among preference fractions (small letters) (P = 0.05).

SPECIES	QUANTITY EATEN g/day ± SD	FIBER/PROTEIN RATIO
(a)		
B. unioloides leaf	11.29 ± 4.79 a	2.42
B. unioloides stem	24.93 ± 11.61 b	7.41
C. dactylon leaf	23.63 ± 12.26 ab	2.44
C. dactylon stem	28.87 ± 12.69 b	5.56
(b)		
B. unioloides stem	32.35 ± 16.3 a	7.41
C. dactylon stem	31.55 ± 14.21 a	5.56
I. batatae	4.65 ± 2.18 b	3.50
D. carota	2.87 ± 1.72 b	1.57
(c)		
H. bonariensis above ground	8.6 ± 2.26 a	2.27
H. bonariensis subterranean	15.42 ± 12.21 ab	11.06
P. racemosum subterranean	17.23 ± 4.07 bc	14.89
P. racemosum above ground	39.33 ± 25.57 c	8.11

Thomomys talpoides (Stuebe and Andersen 1985), *Geomys attwateri* (Williams and Cameron 1986), *Heterocephalus glaber* (Brett 1991) and *Spalax ehrenbergi* (Nevo 1979). This behavior would be adaptive for a mammal that supports a high cost of burrowing and poor available energy (Heth et al. 1989). In general, the food habits of *C. talarum* at Mar de Cobo appear to be similar to those reported for *C. talarum* at Necochea (Comparatore et al. 1995). Individuals of both populations preferred monocotyledoneans, but tuco-tucos consumed large amounts of *Bromus* at Mar de Cobo and of Poa at Necochea (Comparatore et al. 1995), suggesting that modifications in the diet may be influenced by changes in food offered. Given the high cost of burrowing (Vleck 1979) it is not surprising that tuco-tucos shift their diet in accordance with habitat availability.

C. talarum selected the above ground fraction of plants. This may be due to the fact that tuco-tucos live in areas where plant species have different life cycles, therefore the above ground fraction would be available all year round. On the other hand, the lowest consumption of the subterranean fraction during spring is in relation with the active growth of the above ground fraction in this season. Williams and Cameron (1986) indicated that the difference in the subterranean and above ground proportion of plants in the diets of pocket gophers is related to the different behavior of the animal species. The above ground proportion would be higher in those groups that spend more time out of their burrows. In this sense although tuco-tucos forage within their tunnels, they feed mostly above ground by venturing away for their tunnels for brief periods to gather plant parts from the surface. The vegetation in the vicinity of their holes commonly shows evidence of their feeding activities (Reig 1970).

At Mar de Cobo where densities were high (65 ind./ha), reproductive structure consumption was minimal (4%), whereas at Necochea (13 ind./ha) it played an important role in *Ctenomys* diet (38% of total; Comparatore et al. 1995). This suggests that the proportion of high caloric food is higher in animals living in populations of low density. Bujalska (1983) reported a similar relationship between density and diet quality for *Clethrionomys*, a forest dwelling microtine.

The diet of tuco-tucos depends on sex, as females appeared to be less selective than males. The larger consumption of reproductive plant structures by females could respond to higher protein requirements for lactation. Differences in preference by reproductive females have been reported for other subterranean mammals like *Geomys attwateri* (Williams and Cameron 1986) and *Spalax erhenbergi* (Nevo 1991).

Feeding preference

Choice tests support the fact that *Ctenomys talarum* is a herbivorous generalist with a preference for the above ground fraction of grasses. Thus, although some items were preferred, the diet was supplemented with other choices. In this manner, a varied diet was maintained, even with the abundance of the preferred food resource and without differential foraging costs. Herbivores may select a diet that mixes different types of dietary items to balance the intake of nutrients required for proper growth or successful reproduction (Rezsutek and Cameron 1998).

If we accept 200 g fresh weight as an average daily consumption, tuco-tucos intake would amount to 2 600 g and 13 000 g fresh vegetation per ha consumed each day at Necochea and Mar de Cobo, respectively. This amounts to 996–4 680 kg per ha per year, not including vegetation stored uneaten or used to build nests. Tuco-tuco total energy intake per day was comparable to data reported for the subterranean rodent *Thomomys talpoides* by Stuebe and Andersen (1985).

In our experiments, grasses provided not only most of the daily energy and protein requirements, but also with more than 80% of the daily dietary fiber. As tuco tucos are coprophagous rodents with a large caecum (11% of the gut), they are able to optimize

the assimilation of nutrient from this dietary fiber. Thus, in a study on efficiency of food utilization MARTINO (2000) found that in spite of the high fiber/protein ratio of *B. unioloides* its apparent digestibility (NDF) was high (0.81 ± 0.04). Selection of grasses was also reported for the rodent *Lagostomus maximus* by BRANCH et al. (1994). Assuming food quality is correlated with the amount of annual forbs in the diet, these authors suggested, that grasses may provide essential dietary fiber to maintain caecum motility and the appropriate microbial environment in the hindgut.

According to optimal-foraging models, plant defenses (e. g., structural, digestive-inhibiting chemicals, toxic chemicals, and nutritional content) may be effective in reducing their intake by mammalian herbivores (BELOVSKY and SCHMITZ 1994). For example, *Hydrocotile bonairensis*, which was not preferred by *C. talarum*, belongs to a genus known to contain relatively high concentrations of phytotoxins (JUSCAFRESA 1975).

Acknowledgements

This research was granted by UNMdP subs. N° 2; Agencia Nacional de Promociones Cientificas y Tecnológicas subsidio N° 01-00000-01348, CONICET-PEI-N° 6429. We thank two anonymous reviewers for giving constructive comments on earlier versions of the manuscript.

Zusammenfassung

Auswahl und Bevorzugung von Nahrung bei *Ctenomys talarum* (Tuco-Tuco)

In der Studie wurde die Auswahl und die Bevorzugung von Futterpflanzen bei *C. talarum* untersucht. Um die Auswahl zu schätzen wurde die oberirdische Biomasse der Futterpflanzen bestimmt, und die Zusammensetzung der Nahrung im Mageninhalt mittels mikrohistologischer Technik geschätzt. Die Bevorzugung von Futterpflanzen wurde mit Cafeteria-Experimenten im Laboratorium untersucht. *C. talarum* verhielt sich als ein Generalist und Opportunist durch Nutzung der meisten Arten, ändert die Nahrungswahl aber gemäß Verfügbarkeit. Oberirdische Pflanzenteile wurden gegenüber unterirdischen Teilen oder Blüten bevorzugt. Gräser bildeten 94% der oberirdischen Teile. Die Nahrung vom Tuco-Tuco variierte zwischen den Geschlechtern. Männchen verhielten sich selektiver als Weibchen. Die Cafeteria-Experimente zeigten auch, daß *C. talarum* oberirdische Teile der Gräser gegenüber den übrigen bevorzugt.

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Mamm. biol. **66** (2001) 174–177
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Bullate stapedes in some phalangeriform marsupials

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Receipt of Ms. 06. 10. 2000
Acceptance of Ms. 12. 12. 2000

Key words: Marsupialia, possums, ossicles, stapes, ear

Stapes form varies considerably among mammals and has been a disputed topic in morphology-based mammalian systematics (Novacek and Wyss 1986; Rose and Emry 1993; Gaudin et al. 1996). One particular specialization that has received recent attention (Wilkins et al. 1999) is the bullate form of the stapes' footplate. A bullate stapes possesses 'a highly convex hollow footplate that protrudes into the vestibule of the inner ear' (Wilkins et al. 1999), instead of being flat or nearly flat like in most mammals. This situation was first reported by Hyrtl (1845) for the common ring-tailed possum *Pseudocheirus peregrinus* (= '*Phalangista cooki*', Petauridae, Marsupialia). Subsequent to this work, other authors have described this anatomical specialization in several phylogenetically distant eutherian mammals (Doran 1878; Segall 1971; Burda et al. 1992; Wilkins et al. 1999 and references therein). Contrary to the statements of Wilkins et al. (1999), *P. peregrinus* is not the only marsupial showing a bullate stapes. Segall (1971) reported (but did not illustrate) this for the feathertail glider, *Acrobates pygmaeus* (Acrobatidae, Diprotodontia).

During the course of our studies on the evolution of ear ossicles in marsupials, we examined the stapes in more than 70 specimens representing 26 species in eight 'families'. In all cases the stapedial footplate was flat and not bullate, with the following three exceptions (Fig. 1): the brush-tailed opossum, *Trichosurus vulpecula* (n = 13); the grey cuscus, *Phalanger orientalis* (n = 2); and the spotted cuscus, *Spilocuscus maculatus* (n = 1). Of these three taxa, *T. vulpecula* shows this feature most marked, followed by *S. maculatus*. In *T. vulpecula*, the depth of the footplate equals that of the crural portion of the stapes, while in the other two taxa the proportion is smaller.

Some other marsupial taxa in addition to those mentioned above have a somewhat bullate stapes. Segall (1971: 34) reported that in *Petaurus norfolcensis* 'the vestibular surface of the plate is only slightly convex.' Fleischer (1973: 142) noted in his description of the stapes of *Petaurus breviceps* that '...seine Basis ist geringfügig ins Vestibulum vorgewölbt.' The condition in these species of *Petaurus* approximates that described here for *Phalanger orientalis*, as confirmed by examination of a specimen of *Petaurus breviceps* (SM-64418). Several eutherians have a convex footplate that approximates the bullate condition, e. g. *Sus* and *Cynocephalus* (Doran 1878; Rose and Emry 1993). These cases illustrate well the fact that the definition of a bullate stapes is to some extent a matter of evaluation.

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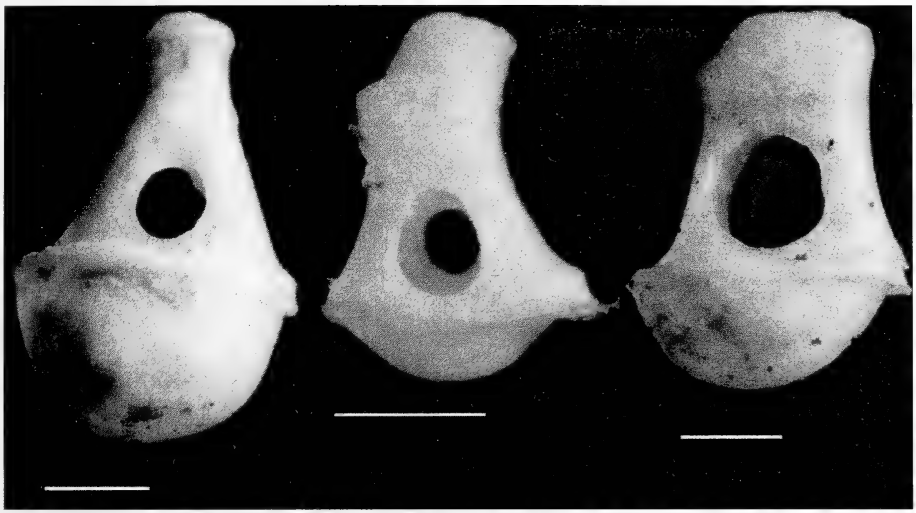

Fig. 1. Stapes of left) *Trichosurus vulpecula* (WM-pers.coll.) center) *Phalanger orientalis* (SM-54981) and right) *Spilocuscus maculatus* (SM-5610). Scale = 0.5 mm.

All the marsupial taxa for which a bullate stapes is reported here and elsewhere are phylogenetically close and taxonomically ordered within the Phalangeriformes (Kirsch et al. 1997). The stapedes of other members of this group were studied by Segall (1971), including *Pseudocheirus herbertensis*, *Petauroides volans*, and *Dactylopsila trivirgata*, and in no case did this author mention any peculiarity in their stapes. Plotting the distribution of bullate stapedes in the phylogenetic tree of Phalangeriformes based on DNA-hybridization studies by Kirsch et al. (1997), it is obvious that the bullate condition (at least in its marked form) has either evolved independently in several taxa, or has been lost independently if present in the last common ancestor of *Acrobates* and the other Phalangeriformes.

In addition to the adult macerated skulls, we examined histologically prepared specimens of several South American and Australasian marsupial taxa. Most species are represented by pouch-youngs, in some cases complete developmental series were examined (for a complete list, see Sánchez-Villagra 2001). Among the species showing bullate stapes as adults, *T. vulpecula* was represented by two specimens.

An early pouch-young of *Trichosurus vulpecula* shows already a prominently outbulging footplate of the stapes that protrudes into the inner ear (Fig. 2), a condition that persists in the adult. Of all other taxa examined, only an early pouch-young of the eastern quoll, *Dasyurus viverrinus* also shows this condition. Adults of this species, as well as other adults of the Dasyuromorpha (Archer 1976) do not show this feature. For comparison, a pouch-young of *Perameles* sp. with the plesiomorphic marsupial condition of the stapes' footplate is shown in figure 2. In the specimens illustrated, the ear ossicles are in a blastemous, pre-cartilaginous stage. Much remodeling and growth takes place in the ear ossicles between these stages and adulthood.

The eutherians showing the most pronounced bullate stapes are rodents belonging to the Heteromyidae and Geomyidae, with highly derived middle ears and specialized to low-frequency hearing. Of all marsupials possessing bullate stapedes, only for *Trichosurus vulpecula* there has been an (electrophysiological) audiogram published (Gates and Aitkin 1982). Even though *T. vulpecula* does not have similar hearing abilities to those of the desert rodents mentioned above, an interesting departure from the few other marsupials (phylogenetically

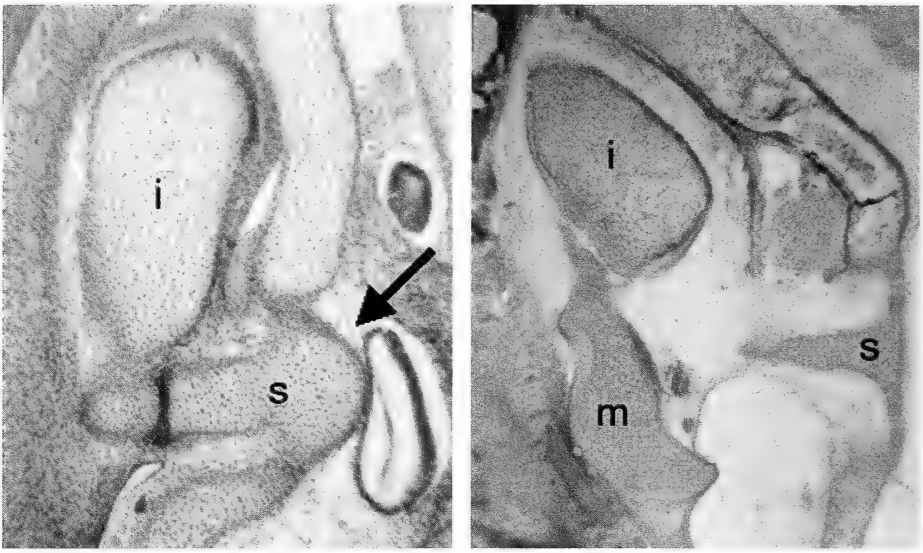

Fig. 2. Cross sections of a portion of the right middle ear of left) *Trichosurus vulpecula* (ZSH, HL = 7.5 mm) and right) *Perameles* sp. (ZSH, HL =17.5 mm). m = malleus, i = incus, s = stapes. The arrow indicates the bullate condition of the stapes. Not to scale.

and ecologically disparate) for which audiograms are available can be noticed. As pointed out by Aitkin (1995), *T. vulpecula* is more sensitive over a wide range to low frequencies than the other marsupials.

Based on the distribution of the bullate stapes among mammals, it appears that there is no obvious correlation between the possession of a bullate stapes and any particular habit or ecology. A wide size-range is represented by the marsupial species showing a bullate stapes, from the 10–17 g *Acrobates* to the much larger *Trichosurus* reaching around 4.5 kg (Nowak 1999). They include mostly arboreal species, omnivorous-herbivores and predominantly nectar-eaters (Hume 1999).

In summary, we report here the presence of a singular specialization of the stapes in three marsupial taxa. Based on the study of pouch-youngs of one of them, we observe that this feature appears relatively early in ontogeny. A bullate stapes represents either an autapomorphy of Phalangeriformes lost independently in several members of this monophylum, or characterizes several clades within this group of diprotodontian marsupials.

Acknowledgements

Osteological specimens reported in this study are deposited in the Senckenberg Museum, Frankfurt (SM) or belong to Wolfgang Maier's personal collection (WM). Histological specimens belong to the Lehrstuhl für Spezielle Zoologie, Zoologisches Institut, in Tübingen (ZSH). We thank the following persons and institutions for allowing us to examine collections under their care: G. Storch (SM), A. Forstén (Zoological Museum, Helsinki), S. B. McLaren and J. R. Wible (Carnegie Museum), J. A. W. Kirsch (University of Wisconsin), K. K. Smith and A. van Nievelt (Duke University, Durham), and W. Maier (Tübingen). We thank R. Britz for his help with photographic equipment and procedures, W. Maier (Tübingen), T. Reuter and S. Hemilä (Helsinki) for their support, and W. Maier and an anonymous reviewer for their helpful criticisms to the manuscript. Ella and Georg Ehrnrooth Foundation, and Oskar Öflund Foundation supported SN. A research travel grant from DFG supported MRSV.

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Mamm. biol. **66** (2001) 178–180
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short Communication

Twinning in the big fruit-eating bat *Artibeus lituratus* (Chiroptera: Phyllostomidae) from eastern Paraguay

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Receipt of Ms. 20. 09. 2000
Acceptance of Ms. 17. 11. 2000

Key words: *Artibeus lituratus*, twinning, reproduction, Paraguay

Although the litter size of bats is variable and ranges from one to five (Hamilton and Stalling 1972), multiple embryos in American leaf-nosed bats are rare and have been reported for only a few species. Twinning in the Phyllostomidae was first reported for *Macrotus waterhousii* by Cockrum (1955) and then by Bradshaw (1961). Barlow and Tamsitt (1968) later reported twinning in three additional species: *Glossophaga soricina*, *Erophylla sezekorni*, and *Artibeus jamaicensis*. Herein, I report twinning in *A. lituratus*.

Artibeus lituratus is widely distributed geographically, ranging from northern Mexico to northern Argentina (Koopman 1993). This species exhibits considerable geographic variation regarding color, morphology, diet, and reproductive patterns (Baker et al. 1976, 1977, 1979). Wilson (1979), based on extensive data, suggested that reproductive patterns in this species are geographically variable, ranging from monoestry at the northern limit of its range to bimodal polyestry (Thomas 1972) and acyclic breeding (Tamsitt and Valdivieso 1963, 1965; Tamsitt 1966) in Colombia. Subsequently, Willig (1985) demonstrated that *A. lituratus* exhibits seasonal bimodal polyestry in northeastern Brazil. Sazima (1989) demonstrated that the timing of reproduction is dynamic in this species and dependent on weather patterns and primary productivity. Although patterns of reproduction are well documented, no report of twinning in this species currently exists.

Of 864 female *A. lituratus* collected and necropsied in this investigation, I encountered one gravid female containing two embryos. The female was caught on 29 December 1997 at Yaguarete Forests, located approximately 40 kilometers due east of the town of Santa Rosa de Lima in the department of San Pedro in eastern Paraguay (23° 48.50′ S, 56° 07.68′ W). The twins consisted of one male and one female. Accordingly, they were likely the result of fertilization of two separate ova. They were 11.6 mm and 11.3 mm in length, respectively. Toothwear on the mother was relatively slight and she was post lactating, suggesting that she was relatively young in age but had previously produced offspring.

Several explanations have been put forth to account for the paucity of instances of twinning in the Phyllostomidae. Barlow and Tamsitt (1968) suggested that differences in litter size between vespertilionid and phyllostomid taxa exist because these groups have evolved in or radiated from areas that differ in seasonality and the length of growing seasons. They suggest

1616-5047/01/66/03-178 $ 15.00/0.

that temperate vespertilionids should have larger litters because they have a protracted period in which to produce offspring, whereas smaller litters are facilitated in tropical phyllostomids by more constant availability of resources. Moreover, phylogenetic as well as mechanical constraints likely maintain the single embryo condition in phyllostomid species. This is supported by the observation that phyllostomid fetuses attain relatively larger size than members from most other families of bats, and multiple embryos likely would cause overly great mechanical and physiological strain on the mother (Wimsatt and Trapido 1952).

Finally, Taddei (1976) suggested that mechanisms operating during ovulation limited the number of ova released from follicles of females of this species. He found that more than one oocyte per ovarian follicle (suggestive of the potential for twinning) was not uncommon yet none of the individuals examined contained more than a single embryo. These observations combine to suggest that twinning is a rare phenomenon that results from accidents during ovulation or development. Moreover, twinning in the Phyllostomidae likely is a condition that is selected against because of its deleterious effects on the mother. Finally, of the group of Phyllostomid species that exhibit twinning, no phylogenetic or ecological pattern exists regarding which species should exhibit this condition. This suggests that the phenomenon of twinning, although rare, should be expected from any large collection of phyllostomid bats.

Acknowledgements

L. Gimenez and H. Stevens provided field and laboratory assistance. Research assistantships were provided by M. Willig and Texas Tech University. I. Gammara de Fox and the National Museum of Natural History of Paraguay provided logistical assistance. Paul Mueller and Yaguarete Forests allowed field work to be conducted on their property. Celia Lopez-Gonzalez reviewed a previous version of this manuscript. I am indebted to each of these people and institutions for their contributions.

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Mamm. biol. **66** (2001) 181–184
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Questionable status of the "Taynguyen civet", *Viverra tainguensis* Sokolov, Rozhnov and Pham Trong Anh, 1997 (Mammalia: Carnivora: Viverridae)

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Receipt of Ms. 04. 12. 2000
Acceptance of Ms. 12. 01. 2001

Key words: *Viverra tainguensis*, Vietnam, systematics, morphology

Corbet and Hill (1992) recognized four species of *Viverra* Linnaeus in the Indomalayan Region. Two of these are known from Vietnam: the large Indian civet, *V. zibetha*, and the large-spotted civet, *V. megaspila* (Osgood 1932; Dang Huy Huynh et al. 1994). In 1997, Sokolov et al. described the "Taynguyen civet", *Viverra tainguensis*, from Vietnam. The description was based on characters of the holotype only, a subadult male. A paratype was designated but its characters were not used in the description. The authors state that they had examined 46 *V. zibetha* from Vietnam, four *V. zibetha* from China, two *V. megaspila* from Vietnam, and eight *V. tangalunga* from Indonesia and the Philippines. In 1999, Rozhnov and Pham Trong Anh assigned an additional five specimens to *V. tainguensis* and later contributed to another publication detailing additional morphometric parameters of two of the specimens (Sokolov et al. 1999). Although the present authors have not examined the holotype, which remains at the Zoological Museum of the Moscow State University (ZMMU), the original description of *V. tainguensis* and both subsequent publications contain a number of factual errors and questionable interpretations that cast doubt on the validity of the supposed new species. However, since V. E. Sokolov died in early 1998, it is not clear to what extent he was involved in the latter publication authored by Sokolov et al. (1999).

Pocock (1939) recognised, as full genera, *Viverra, Viverricula* and *Moschothera*. *Viverra megaspila* and *V. civettina* were placed in *Moschothera*, which was distinguished from *Viverra*, in the sense of Pocock, by the absence of sheaths of skin covering the claws of the 3rd and 4th digits of the forefeet. This feature was clearly described and well-figured by Pocock. Corbet and Hill (1992) placed *Moschothera* as a synonym of *Viverra*, but regarded the claw sheathing as an important diagnostic character for distinguishing *V. zibetha* and *V. tangalunga* from their congeners. Although the claw sheathing is present in *V. tangalunga*, this species is restricted to the Sundaic subregion and is not known from the Indochinese subregion.

In Corbet and Hill's (1992) table 138, the presence or absence of sheathing in each species of *Viverra* is indicated by a "+" or "o", respectively, for all species except for *V. tangalunga*. However, as confirmed by Corbet (pers. comm.), a typographical error has resulted in the symbols being reversed. The absence of supporting text or

1616-5047/01/66/03-181 $ 15.00/0.

illustrations prevents this error from being easily detected. The remainder of the table agrees with POCOCK's (1939) findings.

The most consequential error in the description of *V. tainguensis* by SOKOLOV et al. (1997) relates to the confusion over the sheathing of the front claws. Repeating the error of CORBET and HILL (1992), SOKOLOV et al. (1997) affirmed the presence of sheathing in *V. megaspila*, and its absence in *V. zibetha*, exactly the reverse of the situation found in nature. This error is made repeatedly; the incorrect, reversed, character are said to have been observed in specimens examined; and they are used as the first and most important diagnostic features distinguishing their *V. tainguensis* from *V. zibetha*. In order to check the status of the sheathing on *V. zibetha*, specimens from the Natural History Museum, London (BMNH), were examined. In addition, the 28 specimens at the Institute of Ecology and Biological Resources (IEBR), Hanoi, said to have been examined by SOKOLOV et al. (1997), in the course of their description of *V. tainguensis*, were re-examined (R. J. TIMMINS, pers. comm.). All specimens conformed to the situation as described by POCOCK (1939), rather than that as given by SOKOLOV et al. (1997), with respect to the sheathing. Perhaps the characters as given in table 138 by CORBET and HILL (1992) were simply accepted by SOKOLOV et al. (1997), earlier publications were not read carefully, and actual characters of specimens of *V. zibetha* were not ascertained but were merely assumed to be as given by CORBET and HILL (1992). In any event, if the animals ascribed to *V. tainguensis* have sheathed claws, then this trait would be shared between them and specimens properly identified as *V. zibetha*, rather than being one to suggest a specific distinction between the two.

The second supposedly distinguishing feature given by SOKOLOV et al. (1997) for *V. tainguensis* was body size, which was said to be less than that in *V. zibetha*. However, the holotype of *V. tainguensis* is subadult with a head-body length of 600 mm (SOKOLOV et al. 1997) and head-body lengths (of 790 and 780 mm) have been provided for only two additional specimens, both adults (ROZHNOV and PHAM TRONG ANH 1999). These measurements are well within the known range of 740–860 mm for *V. zibetha* (CORBET and HILL 1992). Although POCOCK (1939) was cited by SOKOLOV et al. (1997), they made no mention of adult specimens of *V. zibetha* that POCOCK examined from northeastern India, Nepal, and Myanmar, and which had head-body lengths of 742–863 mm. In addition, THOMAS (1927) described a subspecies of *V. zibetha* (*V. z. surdaster*) from northern Laos and central and southern-central Vietnam; the last locality being less than 50 km from the type locality of *V. tainguensis*. SOKOLOV et al. (1997) and ROZHNOV and PHAM TRONG ANH (1999) did not mention THOMAS's *V. z. surdaster*, although it was listed by CORBET and HILL (1992). THOMAS (1927) described *V. z. surdaster* as "averaging rather smaller than true Indian *zibetha*", and noted further that "among the variable races of the... Indian, civet the form may be distinguished by its comparatively small size and especially by its small bullae". The condylobasal length of the only existing adult skull of *V. tainguensis* is 132.5 mm (SOKOLOV et al. 1999), whilst that of the type of *V. z. surdaster* measures 128 mm, and specimens measured by POCOCK (1939) range from 129–135 mm for *V. z. pruinosa*. The specimens that THOMAS assigned to *V. z. surdaster* are clearly important in assessing the validity of *V. tainguensis* and it appears that *tainguensis* cannot be distinguished from *surdaster* based on measurements. Certainly the body and skull sizes given for *V. tainguensis* fall within the range of those known for *V. zibetha*, and in no way argue for the specific distinctness of the former.

The supposed third distinguishing feature of *V. tainguensis* given by SOKOLOV et al. (1997) was relative tail length. The tails of the seven specimens of *V. tainguensis*, were reported to average 52% of the head-body length, proportionately smaller than the 55–60% given for *V. zibetha*. However, the mean tail to head-body length of the adult

V. zibetha examined by Pocock (1939) was 53.5%, hardly different from that given for the *V. tainguensis*. The supposed difference becomes even less significant when one considers that the holotype of *V. tainguensis* is a subadult, that measurements of the adult paratype are not included in the description, and the only two specimens of *V. tainguensis* with accompanying morphometric data had tail to head-body length ratios of 53% and 56% (Rozhnov and Pham Trong Anh 1999). Furthermore, neither publication dealing with *V. tainguensis* gave relative tail lengths for any *V. zibetha* specimens examined. Both merely quoted the figure from Corbet and Hill, (1992). Clearly, no convincing evidence has been presented to show that relative tail length can be used to distinguish *V. zibetha* from a second species to be known as *V. tainguensis*. (It should also be noted that Sokolov et al. (1997) stated that *V. megaspila* has a tail 45–55% of the length of its head-body. They appear to mean '*V. tangalunga*', which, according to Corbet and Hill (1992), does have a tail 45–55% of its head-body length, whereas in *V. megaspila* it is 30–50%.)

A fourth supposed distinguishing feature of *V. tainguensis* was stated to involve the pelage colour pattern. Sokolov et al. (1997) cited Corbet and Hill (1992) as stating that *V. tangalunga*, *V. zibetha*, and *V. megaspila* show little variation in their pelage pattern. Later, Rozhnov and Pham Trong Anh (1999) cited the same source to support their contention that "Weak variation in external morphology is typical for all species of genus *Viverra*". These claims are incorrect. The first claim holds for *V. tangalunga*, but not for *V. megaspila* and it also involves a misinterpretation of a statement concerning *V. zibetha*. Corbet and Hill (1992) mentioned "little regional variation" in *V. zibetha*. This clearly refers to inter-regional, rather than intra-regional, variation. There is clearly a considerable degree of variation, both in pelage colouration and other characteristics in *V. zibetha*. The description of *V. z. surdaster* states "colour, as usual, variable, but with less tendency to definite markings on the flanks and hips" (Thomas 1927). Osgood (1932) stated that the species is "variable" and that "doubtless there are several recognizable races." Pocock (1939), wrote "In *V. zibetha*... the coat, colour, and pattern vary considerably... The body-pattern is strongly pronounced in summer, indistinct or even obliterated in winter; and the ground-colour varies individually, even irrespective of season, from tawny to clear, almost silvery-grey... The differences ... in colour and pattern, now known to be individual and... seasonal, account for the number of names applied to most of the local races of this civet." Examination of existing specimens from south-east Asia clearly reveals the variability of the pelage pattern of *V. zibetha*. Specifically, Sokolov et al. (1997) considered there to be three distinctive pelage features of *V. tainguensis*: the "semi-lunar" spots, the colour pattern of the fore and hind legs, and the light brown stripe running parallel to the crest. All three of these features are present separately in *V. zibetha* specimens at the Muséum National d'Histoire Naturelle (MNHN). The "semi-lunar" spots can be observed in combination with both, one or none of the other pelage characteristics claimed for *V. tainguensis* in specimens from Vietnam, and is also a characteristic of a *V. zibetha* specimen from China (CG 1962-156 at the MNHN). Another specimen from China (CG 1902-688) displays the colour pattern on its legs but lacks the distinctive spots and lateral stripes, whilst a specimen from Vietnam (CG 1929–390, paratype of *V. z. surdaster*) has highly distinctive lateral stripes but lacks the colour pattern of the legs and any spots. Semi-lunar spots can also be observed on *V. zibetha* specimens of the BMNH from across the geographic range of the species. The pelage features stated to distinguish *V. tainguensis* will not separate this nominal form from all known individuals of *V. zibetha*.

In view of all of the above, insufficient evidence has been presented to suggest that *V. tainguensis* is in any way a distinct spe-

cies. However, a proposal to synonymise *V. tainguensis* with *V. zibetha* would be premature without an examination of the holotype. Thus, we propose that all records of *V. tainguensis*, except possibly that of the holotype, be withdrawn and that a re-examination of the holotype be undertaken.

Acknowledgements

The authors would like to thank ROB TIMMINS for the examination of the paratype and other specimens held at IEBR in Vietnam, and for his observations that initiated this work. To Dr. NGUYEN XUAN DANG we are grateful for his translation of the original description of the "Taynguyen civet". We are especially indebted to Dr. WILL DUCKWORTH and Dr. RON PINE for their extensive comments and guidance on various drafts of the manuscript.

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Mamm. biol. 66 (2001) 185–189
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Response of *Apodemus flavicollis* to conditions at the altitude limit in the Western Tatra Mountains

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Receipt of Ms. 10. 05. 2000
Acceptance of Ms. 09. 11. 2000

Key words: Rodentia, population dynamics, subalpine habitat

The occurrence of a species at the distribution border exhibits a dynamic pattern which sensitively reacts to the changing conditions of the environment as well as the state of the population of the species (Begon et al. 1997). The distribution border is set by at least one environmental factor close to its limiting value. Regardless of the patchiness of suitable habitat within the distribution range, the quality of habitat changes towards the distribution border from optimal through suboptimal to pessimal. Local populations adjacent to the distribution border react to the changes of local conditions and become extinct or are recolonized (Kozakiewicz 1993; Hanski et al. 1996) causing the distribution border to expand and contract (Angelstam et al. 1987).

The distribution border of *Apodemus flavicollis* (Melchior, 1834) includes a wide range of habitats and diverse climatic conditions due to its large distribution range (Niethammer 1978; Lura et al. 1995). The local occurrence and altitude tolerance of the species seems to be affected by the requirements of a continental climate (Lura et al. 1995) and food abundance (Angelstam et al. 1987). The seed abundance appears to be a critical factor affecting the distribution and population dynamics of *A. flavicollis*. Populations are usually noncyclic but density outbursts occur in years of high seed crop (Gurnell 1985; Angelstam et al. 1987; Pucek et al. 1993; Žiak and Kocian 1994). Considering habitat, *A. flavicollis* prefers mature deciduous forests with an open ground layer (Gurnell 1985). Therefore, the altitude range stretches from sea-level (Greece, Italy) to about 2 000 m (Alps) (Niethammer 1978; Yoccoz 1992).

The aim of this study is to investigate the population response and habitat selection of *A. flavicollis* to conditions at an altitude border in an upper subalpine zone.

The research was conducted in the Western Tatra Mts., Slovakia. The locality in the National Nature Reserve Roháče Lakes (elevation of the trapping grids: 1 570–1 600 m a. s. l.) represents a transition between a subalpine and an alpine zone due to climatic conditions caused by north-western orientation of the mountain range. The habitat is characterized by scattered patches of *Pinus mugo* cover, the occurrence of wet subalpine meadows, and a talus gradient of various rock sizes partially overgrown with vegetation dominated by *Juncus trifidus*.

Small mammal live-trapping was carried out in June, August, and October 1991–99

1616-5047/01/66/03-185 $ 15.00/0.

with the exception of 1992 and 1994 when trapping was carried out twice, in July and October. In the years 1991–95 two trapping grids were established, one 1 ha in size containing 10×10 live-traps, and the other 0.5 ha containing 6×8 live-traps, both with 10 m spacing. In 1996–99 another 1 ha trapping grid was added, and the trap layout was modified in the previous two grids giving in total two 1 ha grids with 7×7 live-traps at 15 m intervals, one 1.3 ha grid containing 10×13 live-traps at 10 m intervals. The traps were baited with rolled oats, operated for 3–5 consecutive nights, and were checked twice daily. Animals were marked by toe-clipping, data on species, body weight, sex, reproductive status (scrotal testes, open vagina, gravidity, lactation), and body length were recorded.

The habitat characterization was modified from DUESER and SHUGART (1978, 1979), and M'CLOSKEY and FIELDWICK (1975). The habitat at each trap point was characterized for the years 1996–98. The habitat variables were recorded in the summer series 1996–97 in a circle (diameter 10 m, or 15 m) centered on the trap. At each point, the proportion of the area covered by rocks, by rocks smaller and greater than 50 cm in diameter was registered. The vegetation structure was estimated by the proportion of the area covered by litter, herbs, shrubs and trees (including *Pinus mugo*), and specifically by dominant plant species: *Juncus trifidus*, *Vaccinium myrtillus*, *Pinus mugo*, and grasses other than *J. trifidus*. The total number of plant species present at the sample was recorded. The vegetation density below or above 50 cm was counted as the number of touches on a stick at 20 check-points forming a cross 10 + 10 centered on the trap and expressed as percent. The heights of herb, shrub and tree layers were measured at the same intersection depending on the availability of the given layer. Finally, the distance to the nearest patch of *Pinus mugo* larger than 30 m in diameter was recorded.

Discriminant function analysis was used to explore the microhabitat preferences of *A. flavicollis*. A qualitative model was chosen where trap points used by at least one resident individual, defined by the time span between first and last capture being at least two days, were referenced against trap points not used by resident individuals.

During the research time span (7200 trap-nights) 12 species of small ground mammals were registered: *Sorex araneus, S. minutus, S. alpinus, Neomys* sp., *Apodemus flavicollis, Clethrionomys glareolus, Microtus nivalis, M. agrestis, M. tatricus, Muscardinus avellanarius, Mustela nivalis*, and *M. erminea* (ŽIAK and KOCIAN 1994; N. MARTÍNKOVÁ, D. ŽIAK, L'. KOCIAN unpubl.). *Apodemus flavicollis* has only been captured in the years 1993, 1996, and 1998 (Fig. 1). A total of 44 individuals was caught, 30 males and 14 females, a significant deviation from an expected sex ratio of 1 : 1 ($\chi^2 = 5.8$, $p = 0.016$). Except for two individuals, all animals were captured in one trapping series. The first exception was a sexually inactive female trapped in August and October 1993, and the second was a male trapped in August and October 1996, which was in breeding condition in August, but not so in October. No individuals were registered to stay the entire winter at the locality. Recaptures have also been rare with 60% of all individuals captured only one or two times, the average number of captures per individual being 2.3 and the maximum was eight (the sexually inactive female present in series VIII/93 and X/93). Individuals captured five or six times were all trapped in August 1996. No females were found demonstrating perforated vagina, or lactation, but one female may have been pregnant in August 1993. Among males, twenty-two possessed scrotal testes.

The discrimination of the preferred habitat of *A. flavicollis* was significant at $p < 0.001$. The discrimination model correctly classified 77% of unused trap points and 76% of used trap points (Tab. 1). Habitat variables that possess the highest absolute values of standardized coefficients influenced to a greater extent the position of samples on the discriminant function axes. This means that the variation of these variables best describes the differences between preferred and non-preferred habitat (LEGENDRE and LEGENDRE 1983). Variables associated with

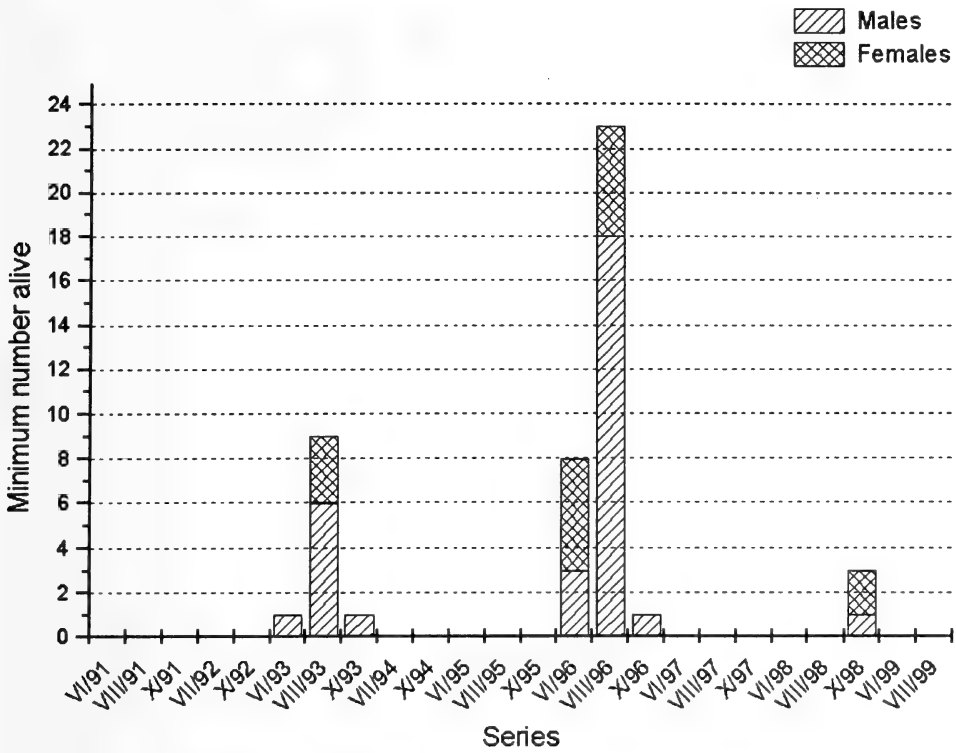

Fig. 1. Minimum number of *Apodemus flavicollis* known to be alive each season. Total number of yellow-necked mice being 44 individuals, where one individual was present in series VIII/93 and X/93, and another VIII/96 and X/96. Starting June 1996 methodology was changed so that 228 live-traps on three trapping grids were used instead of 148 on two grids.

Table 1. Discriminant function analysis coefficients characterizing habitat occupied by resident (time span between first and last capture being at least two days) individuals of *A. flavicollis* ($p < 0.001$). Habitat variables are ordered with regard to their importance in discriminating preferred and non-preferred habitat based on the absolute value of standardized coefficients.

Habitat variable	Standardized coef. of DFA	Average	Stand. Dev.
Vegetation density above 50 cm	−0,819	0,31	0,22
Distance from *Pinus mugo* patch	0,813	8,69	22,84
Pinus mugo cover	0,789	0,35	0,28
Area covered by rocks less than 100 cm in diameter	−0,417	0,06	0,14
Juncus trifidus cover	−0,399	0,07	0,17
Herb height	−0,393	35,05	15,28
Vaccinium myrtillus cover	−0,263	0,36	0,25
Grass cover	−0,246	0,43	0,31
Shrub height	−0,242	24,13	9,37
Vegetation density below 50 cm	−0,240	0,81	0,14
Area covered by rocks more than 100 cm in diameter	−0,180	0,06	0,11
Number of plant species	−0,125	8,06	2,98
Litter cover	0,071	0,09	0,16
Tree height	−0,060	148,40	61,55
Total area covered by rocks	0,031	0,12	0,22

Pinus mugo cover showed a strong indication that *Apodemus flavicollis* preferred a habitat dominated by *P. mugo*. However, the raw data show that no used trap was located within the dwarf pine cover (neither trap point had negative values of distance to the nearest *P. mugo* patch). This would characterize the habitat of occurrence of *A. flavicollis* as the edge of *P. mugo* stands. The typical habitat of *Apodemus flavicollis* is described as open mature forests, preferably deciduous with open ground level. Its occurrence at ecotones, grasslands or shrubby habitat is considered atypical (NIETHAMMER 1978; GURNELL 1985). Yet, the ecotone of dwarf pine and subalpine meadows is the habitat preferred by this species in the subalpine zone in western Tatras. Here, large seeds forming the base of *A. flavicollis* diet (NIETHAMMER 1978; SMETTAN 1996) are in short supply as well as in coniferous forests in general. These are usually considered suboptimal habitats or serving as corridors (ANGELSTAM et al. 1987; KOTZAGEORGIS and MASON 1996; ŠMAHA 1996).

Since the locality does not enable individuals to remain through the winter, but their survival is possible during the vegetation season, it could be considered a suboptimal habitat for this species (GLIWICZ 1989, 1993). However, sporadic occurrence of *A. flavicollis* at the locality indicates that the species is not a regular seasonal resident to this area. This assumption is supported also by the fact that the sexual ratio is deviant from the expected values, which occurs in dispersers (GLIWICZ 1988), i. e., most individuals were present at the locality exclusively in a single trapping series and by low number of captures per individual. In a habitat in which reproduction per individual is low, population density has a tendency to decline (GAINES et al. 1994) and the population shows a high turnover rate (MAZURKIEWICZ 1991, 1994) in this type of habitat, is referred to as a "sink" habitat. This is the case for the area investigated in the present study.

The appearance of yellow-necked mice can be explained by high population densities in altitudes below the research area. *Apodemus flavicollis* tends to occur in "nuclei" within occupied forests, which are relatively stable centers of occurrence, and spatially oscillate depending on the population density (GURNELL 1985). If we assume a positive correlation between population density in a given nucleus and the effort that the dispersers make to travel from the nucleus (distance × number of dispersers), then population density at our study plots indicates the culmination phases at lower altitudes. A crowded habitat would force subdominant individuals to seek vacant space and they will appear at our study plots. If such a situation occurs, the population probably exhibits a three year cycle.

Acknowledgements

The research in the National Nature Reserve was carried out with the permission of the Slovak Ministry of Environment. We are indepted to Mr. HALÁK and Mr. HUDÁČEK (Tatra National Park), their support is acknowledged. Financial support of the research provided by VEGA (grant number: 1/4140/97, assigned to Ľ. KOCIAN).

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Mamm. biol. **66** (2001) 190–192
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Non-invasive PCR sexing of rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*)

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Receipt of Ms. 22. 09. 2000
Acceptance of Ms. 27. 12. 2000

Key words: *Lepus europaeus*, *Oryctolagus cuniculus*, sex determination, Sry, faeces

Genetic sex verification has important implications for population studies of free-ranging animals relying on the knowledge of reproductive status and sex ratio of the animals. In the brown hare (*Lepus euroaeus*) a continuous population decline has been reported in many European countries (Flux and Angermann 1990). The reason for the decrease is under debate (McLaren et al. 1997; Panek and Kamieniarz 1999; Reynolds and Tapper 1995), and population studies of this species are therefore highly needed. The collection of blood causes stress due to trapping and handling of animals (Jessup 1993) that could affect the parameters under investigation, particularly in a highly irritable species like the brown hare. Previous studies have demonstrated the potential for faeces collected in the field as a suitable source of DNA for genotyping and sexing free-ranging mammals (Taberlet et al. 1997). Since no sex-specific DNA sequences are known for the brown hare, we initially developed a PCR test for sex determination in rabbits (*Oryctolagus cuniculus*) and adapted it for sexing hares (*Lepus europaeus*). The assay co-amplifies a part of the Y-chromosomal Sry and the autosomal rabbit transferrin gene, which is used as an internal amplification control.

Because most sex-identification methods are not species specific, some precautions have to be made to be aware of possible contamination with extraneous DNA, especially when animal remains such as hair or faeces are used as source for DNA analysis (Taberlet et al. 1997). In contrast to this universal primer approach, primers described in this report are placed in rabbit-specific sequence regions. To test the specificity of the assay, we amplified DNA from human, mouse, horse, and sheep, but none of these species amplified even under low stringency conditions (data not shown).

We first verified the accuracy of the assay by analysing genomic DNA from a total of 78 rabbits. Genomic DNA was isolated from 200 µl EDTA-blood from 24 adult males and 27 females of different rabbit breeds (Gemmell and Akiyama 1996). For 27 new born rabbits, buccal swabs sampled with Q-Tips were used for sexing in order delete to apply a minimal invasive technique. The cut cotton-wool end of the Q-tip was placed in a 1.5 ml vial containing 600 µl digestion buffer (Gemmell and Akiyama 1996) and stored at room temperature. Genomic DNA was obtained as described above by digestion of the whole swab with proteinase K (80 µg) for 2 hours at 56 °C. DNA was then extracted from the supernatant (Gemmell and Akiyama 1996). Primers (Tab. 1) amplifying a fragment from the Sry region were designed accord-

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Table 1. Specifications of duplex-PCRs for sex determination in rabbit and hare DNA sequence of rabbits Sry region in SINCLAIR et al. (1990). Rabbit transferrin (Acc. number. X58533). T_a: Annealing temperature

Species	Primer	5′-primer sequence – 3′	T_a	Primer conc.	Fragment length
Rabbit	Transferrin Exon 4/5	GACCTTCTACTATGCTGTGGC GTAGCCGAAATACGGCTGAAC	65 °C	0.5 µM	1 kb
	Sry	AATACAGGAGGAACACGTAAAGTG CAAACTGTCGCTCTTCTGTAGGAT		0.5 µM	294 bp
Hare	Transferrin Exon 6/7	GCCTTTGTCAAGCAAGAGACC CACAGCAGCTCATACTGATCC	60 °C	0.5 µM	0.5 kb
	Sry	AATACAGGAGGAACACGTAAAGTG CAAACTGTCGCTCTTCTGTAGGAT		1.0 µM	294 bp

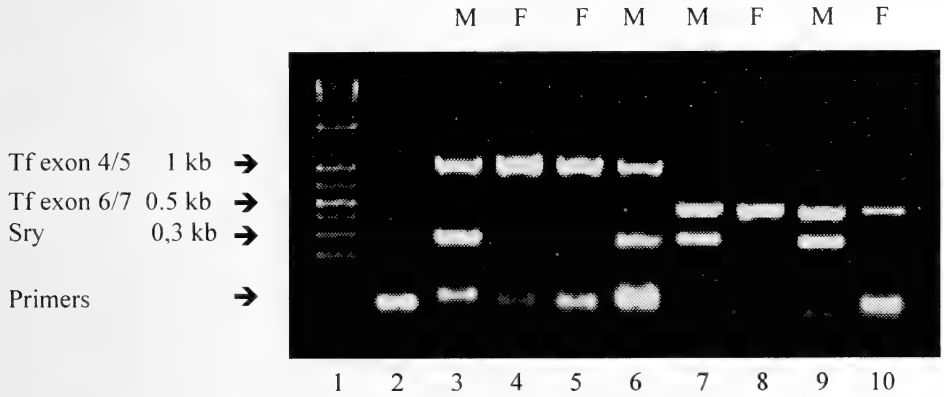

Fig. 1. Sex determination of rabbit and hares using the transferrin (Tf)/Sry duplex-PCR assay. Lane 1 Molecular size marker (Gibco); lane 2 no template control; rabbit: lane 3, 4 blood samples; lane 5, 6 buccal swabs; hare: lane 7, 8 tissue; lane 9, 10 faeces. M = male, F = female

ing to a published rabbit-human sequence alignment with their 3′-end being placed in rabbit-specific sequence regions (SINCLAIR et al. 1990). An amplicon from exons 4/5 (Tab. 1) of the rabbit transferrin gene (Tf) was used as amplification control. Duplex-PCR was carried out in a reaction mixture of 15 µl containing 20 ng template DNA, 0.5 U AmpliTaq polymerase Gold (PE Biosystems), 15 mM Tris-HCl pH 8.0, 50 mM KCl, 2 mM $MgCl_2$, 0.25 mM of each dNTP and primers as indicated in table 1. The cycling conditions on a GeneAmp 2400 Cycler (PE Biosystems) were: 10 min at 95 °C; 30 sec at 95 °C, 30 sec at 65 °C, and 60 sec at 72 °C for 35 cycles. Amplicons were separated by agarose gel electrophoresis. PCR on male samples amplifies two products (Sry and Tf), whereas from female samples only one product (Tf) is obtained (Fig. 1). The PCR result was consistent with the animals' phenotypic sex in the 51 rabbit blood samples tested. When using genomic DNA isolated from 27 buccal swabs we obtained unambiguous results in 24 cases and the assigned gender was correct. In three cases we could not amplify any fragments because of degraded DNA.

The assay was then adopted for sexing brown hares using DNA extracts of tissue samples from 12 individuals. In hares the Sry region could only be amplified under less stringent conditions (Tab. 1). Primers for Tf exons 6/7 were used as internal control. Target specificity was certified by comparing directly sequenced gel-purified PCR products with published sequences. The amplified hare Sry sequence has been sub-

mitted to the GenBank database (Acc. number AF230075). Rabbit and hare Sry sequences differed at four nucleotide positions indicating that the amplified region is not completely conserved between these species. Rabbit specific primers may not perfectly match hare target sequences and thus only amplify the respective genomic regions under reduced stringency.

DNA extracted from hare faeces can be used for sex determination, but at a higher test dropout rate. We collected fresh faecal samples from 36 individually caged hares with known sex into separate plastic tubes and froze them immediately. We extracted DNA from faeces by a silica-based purification method in order to purify DNA and to break down compounds that inhibit subsequent PCR reactions (after BOOM et al. 1990; CONSTABLE et al. 1995). PCR reactions of faeces samples contained bovine serum albumin (100 µg/ml final concentration) and were incubated for 47 cycles. Analysis of 20 out of the 36 DNA samples purified from faeces revealed the correct gender. Fifteen samples amplified no PCR product, probably because of poor DNA quality. Only one female was sexed incorrectly, possibly due to male-derived contamination of the cage.

Acknowledgements

We thank Prof. G. BREM for initiation of the project, R. SELHOFER and C. HAAS for providing samples, B. AIGNER for supplying transferrin primers and U. BRUNS for advice on DNA extraction from faeces. We gratefully acknowledge W. ARNOLD and M. MÜLLER for the provision of laboratory facilities. We are grateful to Agrobiogen GmbH and the State government of Lower Austria for financial support.

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ISSN 1616-5047
Mamm. biol. · 66(2001)3 · 129-192

Contents

Abstracted/Indexed in
Animal Breeding Abstracts/Biological Abstracts/Biological Environmental Sciences/BIOSIS database/Current Advances in Ecological and Environmental Sciences/Current Contents - Agriculture, Biology & Environmental Sciences/Dairy Science Abstracts/Fisheries Review/Helminthological Abstracts/Index Veterinarius/Key Word Index to Wildlife Research/South Pacific Periodicals Index/Veterinary Bulletin/Wild Review (Fort Collins)/Zoological Record

Mammalian Biology

Zeitschrift für Säugetierkunde

4·2001

URBAN & FISCHER

ISSN 1616-5047
Mamm. biol. · 66(2001)4 · 193-256
www.urbanfischer.de/journals/mammbiol

Mammalian Biology

Zeitschrift für Säugetierkunde

IMPRESSUM
Publisher: Urban & Fischer Verlag GmbH & Co. KG, Branch Office Jena, P.O. Box 100537, D-07705 Jena, Germany; Phone: ++49(0)3641/626-3, Fax: ++49(0)3641/62 65 00, E-mail: journals@urbanfischer.de
Advertisement bookings: Enquiries should be directed to Urban & Fischer Verlag, Advertising Manager: Sabine Schröter, P.O. Box 100 537, D-07705 Jena, Germany; Phone: ++49(0)3641/62 64 45, Fax: ++49(0)3641/62 64 21.
Advertising rates: The price list from January 1, 2001 is effective at present. **Distribution and subscription agency:**
For customers in the German speaking countries: Please turn to your bookshop or to Urban & Fischer Verlag, Aboservice und Vertrieb: Barbara Dressler, Löbdergraben 14a, D-07743 Jena, Germany; Phone: ++49(0)3641/62 64 44, Fax: ++49(0)3641/62 64 43, E-mail: k.ernst@urbanfischer.de
For customers in all other countries: Please contact your bookshop or The Nature Publishing Group, Linda Still, Brunel Road, Basingstoke, RG21 6XS, UK; Phone: ++44(0)1256/30 26 29, Fax: ++44(0)1256/46 35 70, E-mail: l.still@nature.com Subscribers in the **USA** can call toll free on ++1 800 747 3187.
Terms of delivery (2001): 1 volume consisting of 6 issues.
Subscription rate (2001): DM 498.00*/GBP 200.00. Preference price for personal subscribers: DM 150.00*/GBP 60.00. All prices quoted above are exclusive postage. *Suggested list price. Price are subject to change without notice. Personal subscription orders must be addressed directly to the publisher Urban & Fischer in Jena resp. to The Nature Publishing Group. Subscriptions at a personal rate must include the recipient's name and mailing address. An institutional or business address is only accepted, if the institute or firm has a subscription as well. Personal subscribers can pay by personal cheque or credit cardmentioned below. US dollar prices are converted at the current exchange rate.
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Subscription information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting and printing, binding: druckhaus köthen GmbH

(∞) As of vol. 61, number 1 (1996) the paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Printed in Germany

For detailed journal information see our home page: http://www.urbanfischer.de/journals/mammbiol

Mamm. biol. **66** (2001) 193–203
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Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Supernumerary molars in neotropical opossums (Didelphimorphia, Didelphidae)

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Receipt of Ms. 17. 05. 2000
Acceptance of Ms. 28. 09. 2000

Abstract

Dental abnormalities, such as the occurrence of extra teeth, are recurrently found in many groups of mammals. Supernumeray molars were found in *Didelphis aurita*, *D. albiventris*, *D. marsupialis*, *Philander andersoni*, *P. frenata*, *P. opossum*, *Chironectes minimus*, and *Caluromys philander*. Frequencies of occurrence of supernumerary teeth in these marsupial species remained within a range similar to that found in other species. Four hypotheses are proposed and discussed to explain the origin of these teeth: appearance of extra teeth due to excessive development in size of the skull, reappearance of an atavistic condition, retention of the third deciduous premolar at the eruption of the permanent premolar, or some sort of ontogenetic disturbance that lead to the duplication of a tooth germ. The first hypothesis is discarded as all individuals have normal sizes for the species. No evidence in the marsupial fossil record supports the second. The morphology of the teeth observed does not support the third, as all teeth are apparently permanent (except for one specimen). Finally it is hard to find evidence against or in favour of the fourth, as there is no information available of the development of the museum specimens observed.

Key words: Marsupials, abnormalities, dentition, Neotropics

Introduction

The study of abnormalities can be particularly interesting for those involved in developmental genetics and morphological evolution, providing useful data for medical, evolutionary, and taxonomic studies. For instance, by focusing on abnormalities one can assess the potentialities for the rise of new variant morphologies. Morphological shifts occur with the rise of such deviant morphologies and its spreading through the taxon. Thus, abnormalities, as highly deviant morphologies, could initiate such morphological shifts.

Mammal dental abnormalities have long been reported, and include teeth specific malformations (e. g. Long and Long 1965; Feldhamer and Stober 1993), size reduction or missing of teeth (e. g. Mech et al. 1970; Drehmer and Ferigolo 1996), or supernumerary teeth (e. g. Krutzsch 1953; Steele and Parama 1979; Kvam 1985; Drehmer and Ferigolo 1996). The latter corresponds to the occurrence of more teeth than those expected from the species normal dental formula. Such phenomenon

1616-5047/01/66/04-193 $ 15.00/0.

has been described for eutherian families as diverse as e. g. Mustelidae (Long and Long 1965), Otariidae (Drehmer and Ferigolo 1996), Felidae (Kvam 1985), Canidae (van Valen 1964), Cervidae (Fowle and Passmore 1948; Pekelharing 1968; Steele and Parama 1979; Mech et al. 1970), Soricidae (Hooper 1946), Dipodidae (Krutzch 1953), and Sciuridae (Goodwin 1998). Within the marsupial family Didelphidae supernumerary teeth have been reported for the genus *Didelphis* (Allen 1901; Takahashi 1974) only and recently for *Philander* (Hershkovitz 1997). The aim of this study therefore is to investigate the situation for South American marsupials in more detail.

Material and methods

The following species were investigated: *Caluromys philander* (Linnaeus, 1758), *Chironectes minimus* (Zimmermann, 1780), *Didelphis albiventris* Lund, 1840, *D. aurita* Wied-Neuwied, 1826, *D. marsupialis* Linnaeus, 1758, *Philander andersoni* (Osgood, 1913), *P. frenata* (Olfers, 1818), and *P. opossum* (Linnaeus, 1758), from specimens deposited in the following collections: Museu Nacional, Rio de Janeiro (MN); Departamento de Zoologia, Universidade Federal de Minas Gerais (DZUFMG); Museu de Zoologia, Universidade de São Paulo (MZUSP); American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); National Museum of Natural History (NMNH); and Laboratório de Vertebrados, Universidade Federal do Rio de Janeiro (MC). Collection numbers, sexes and localities for specimens found with supernumerary molars are listed in table 1.

Unless otherwise specified tooth morphology nomenclature follows Reig et al. (1987). Notations in super- or subscript refer to specific (upper or lower, respectively) tooth rows, as traditionally used in tooth formulae nomenclature (*e. g.* M^4), but when no specific row is meant, we chose not to use super- or subscript (*e. g.* M4).

Results

Frequency of occurrence

The frequency of supernumerary molars occurrence in each of the investigated species was calculated based on adult specimens with four molars erupted, as the number of individuals presenting any extra tooth divided by the total number of specimens examined for that species. The frequency of supernumerary teeth is 0.7% (1/141) in *C. minimus*; 1.2% (1/82) in *C. philander*; 0.5% (3/655) in *D. albiventris*; 0.3% (1/337) in *D. aurita*; 1.0% (9/872) in *D. marsupialis*; 2.8% (1/36) in *P. andersoni*; 0.8% (2/244) in *P. frenata*; and 0.3% (2/767) in *P. opossum*.

Tooth morphology and position

The location of the supernumerary tooth found is reported in table 1. Supernumerary teeth were found at all molar rows; however, they were more frequent at the upper rows.

Caluromys philander

The only specimen (MZUSP 11591) found with an extra tooth presents it at the end of the right inferior molar series (Fig. 1). It is slightly smaller than the M4. Cuspids are distinguishable with the protoconid excessively developed in comparison to the paraconid and metaconid that are reduced. The talonid is slightly reduced, and is divided antero-posteriorly by a crest, not present in the normal teeth, that creates two basins and makes the identification of the talonid cusps more difficult. This tooth is aligned with the molar series in occlusal view, but its crown is slightly tilted to the lingual side.

Chironectes minimus

The only occurrence of a supernumerary molar for this species (MZUSP 16545) is an extra molar erupting behind the right M_4 (Fig. 2). The tooth is not fully erupted (only the protoconid, and the tips of the metaconid and entoconid emerge from the bone), but its crown pattern is clearly visible and identifiable with conids and cristids pattern identical to the M_4. The tooth is clumped, as there is no space available for it in the mandibular ramus and is erupting

Table 1. Individuals observed with supernumerary teeth, with respective species, museum number, sex, locality of origin and location of supernumerary molars. Legend: M: Male; F: Female; UL: Upper left row; UR: Upper right row; LL: Lower left row; LR: Lower right row. Museum acronyms as in text

Species	Museum Number	Sex	Locality	Location of supernumerary molar			
Caluromys philander	MZUSP 11591	M	Fordlândia, Pará, Brasil		UR		
Chironectes minimus	MZUSP 16545	F	Cametá, Pará, Brasil				LR
Didelphis albiventris	AMNH 63852	M	Utcuyacu, Junin, Perú			LL	LR
Didelphis albiventris	DZUFMG 120	M	Santa Luzia, Minas Gerais, Brasil		UR		
Didelphis albiventris	MN 22250	F	Brasília, Distrito Federal, Brasil	UL	UR	LL	LR
Didelphis aurita	AMNH 133034	M	Paraiba do Sul, Rio de Janeiro, Brasil	UL	UR		
Didelphis marsupialis	AMNH 33243	M	Esmeraldas, Ecuador		UR		
Didelphis marsupialis	AMNH 93978	F	Norte do Rio Amazonas, Faro, Pará, Brasil				LR
Didelphis marsupialis	AMNH 95345	M	Rio Tapajós, Igarapé Amorim, Pará, Brasil				LR
Didelphis marsupialis	AMNH 95361	M	Rio Tapajós, Inajatuba, Pará, Brasil		UR		
Didelphis marsupialis	AMNH 209179	M	Beni, Bolivia	UL	UR	LL	LR
Didelphis marsupialis	USNM 280966	M	Villanueva, Colombia		UR		
Didelphis marsupialis	USNM 51092	M	Rio Tapajós, Caxiricatuba, Pará, Brasil		UR		LR
Didelphis marsupialis	USNM 545457	F	Belém, Pará, Brasil		UR		
Didelphis marsupialis	FMNH 22199	M	Sierra de Mérida, Mérida, Venezuela	UL			
Philander andersoni	AMNH 72017	F	Rio Curaray, Loreto, Perú	UL			
Philander frenata	MC 267	M	Maricá, Rio de Janeiro, Brasil	UL	UR		
Philander frenata	MN 5769	M	Santa Teresa, Espírito Santo, Brasil	UL	UR		
Philander opossum	AMNH 34373	?	Bagadó, Chocó, Colombia	UL	UR		
Philander opossum	USNM 337643	M	El Recreo, Zelaya, Nicaragua	UL	UR		

with its crown tilted about 45 degrees lingual and anteriorly in comparison to the remaining molars.

Didelphis albiventris

Specimen DZUFMG 120 presents a single supernumerary molar, erupted behind the right M^4 (Fig. 3). It is a small tooth (approx. 1/3 of the size of the normal M^4), with an oval crown, with two cusps connected by cristae. Its reduced size and abnormal crown shape makes it difficult to identify what these cusps and cristae are equivalent to in normal teeth. The tooth is very tight, as there is no place for it on the maxilla, behind the M^4. The crown of this tooth is approximately in the same occlusal plane as normal molars, but it does not occlude with any inferior tooth.

Specimen MN 22250 possesses one supernumerary molar at the end of each series. The extra tooth on the left superior series is smaller than the M^4 and similar in shape, yet with much reduced stylar cusp C, and slightly compressed, so that the stylar cusp E (metastyle) is closer to the paracone than in the M^4. All remaining cusps are clearly identifiable. It is also slightly rotated counter-clockwise. Its crown lies beneath the occlusal plane of the rest of the series but occludes with the extra molar of the inferior series. The extra tooth on the right superior side is identical in shape to the M^4, and of about half its size. Unlike the tooth previously described, orientation and cusps are similar to the M^4, and apart from the size difference, there is no deformation or other shape difference. Its crown also lies beneath the occlusal plane of the M^4, and apparently does not occlude. The left inferior extra tooth (Fig. 4) is overall similar to the M_4, especially the trigonid is identical to the M_4 trigonid, with all cusps identifiable. In the talonid, however, the hypoconulid is closer to the hypoconid, giving the

whole talonid a more elongated or triangular shape. Finally, the supernumerary molar on the right mandible (Fig. 5) also presents a trigonid identical to the M_4 trigonid, but with a slightly different talonid, with a hypoconulid somewhat farther from the trigonid than in the latter.

Didelphis aurita

Specimen AMNH 133034 possesses one supernumerary molar in each side of the superior row. Both extra teeth have a molariform shape but are slightly reduced. The extra tooth on the right superior series is posteriorly directed, probably due to the lack of space in the row, and is not at the oclusal plane of the remaining teeth. Its cusps are present and distinguishable with a crown pattern resembling a normal M^4. The other extra tooth at the left superior series is not at the occlusal plane of the remaining row and its cusps, although distinguishable, do not resemble a normal M^4 pattern.

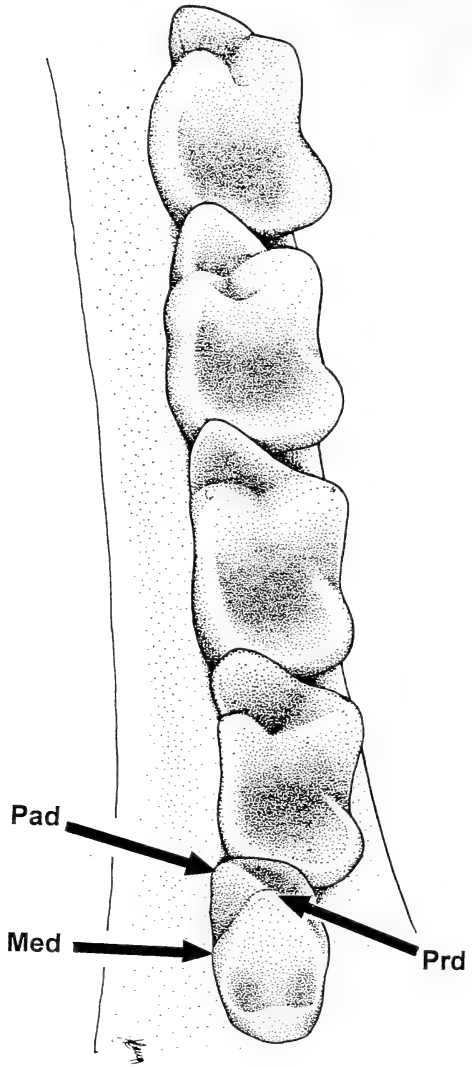

Fig. 1. Right inferior molar series of *Caluromys philander* (MZUSP 11591), with a supernumerary molar (arrow). Occlusal view. Protoconid (Prd), paraconid (Pad), metaconid (Med).

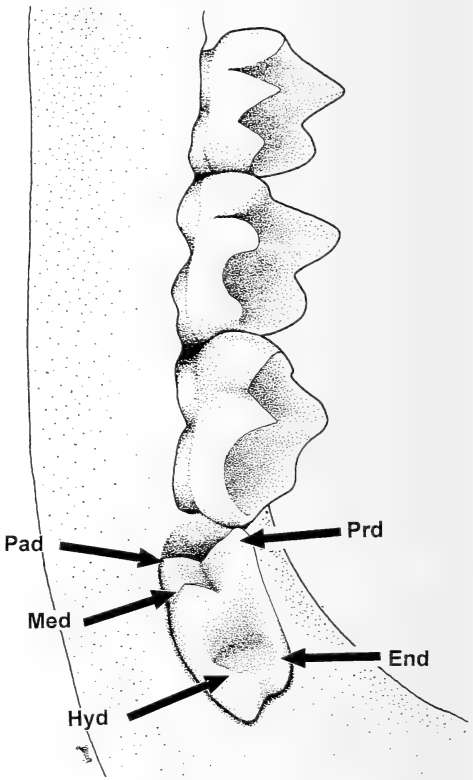

Fig. 2. Right inferior molar series (M2–M4) of *Chironectes minimus* (MZUSP 16545), with a supernumerary molar (arrow), viewed from the occlusal plane of the extra tooth. Protoconid (Prd), paraconid (Pad), metaconid (Med), entoconid (End), hypoconid (Hyd).

D. marsupialis

Specimen AMNH 93978 possesses one extra tooth on each side of the superior rows. Both are reduced but with a molariform shape. The extra teeth at the right has some cusps visible (but hardly identifiable), and a crista, which is apparently the centrocrista, oriented with the antero-posterior axis of the skull.

Philander frenata

Specimen MC 267 presents one extra molar on each side, at the end of the upper molar series. On the left side (Fig. 6), the supernumerary tooth is smaller than the M^4. Some cusps are discernible, as well as what appears to be the centrocrista. Protocone, paracone and metacone are identifiable, but the cusp present on the opposite side

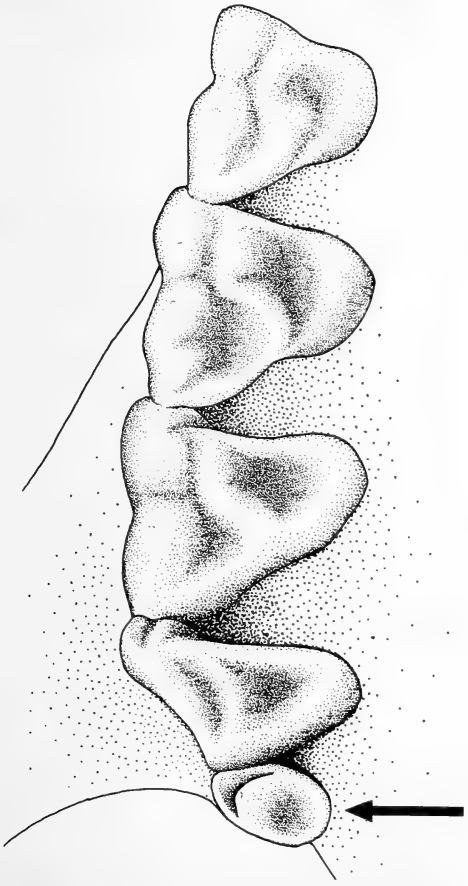

Fig. 3. Right superior molar series of *Didelphis albiventris* (DZUFMG 120), with a supernumerary molar (arrow). Occlusal view.

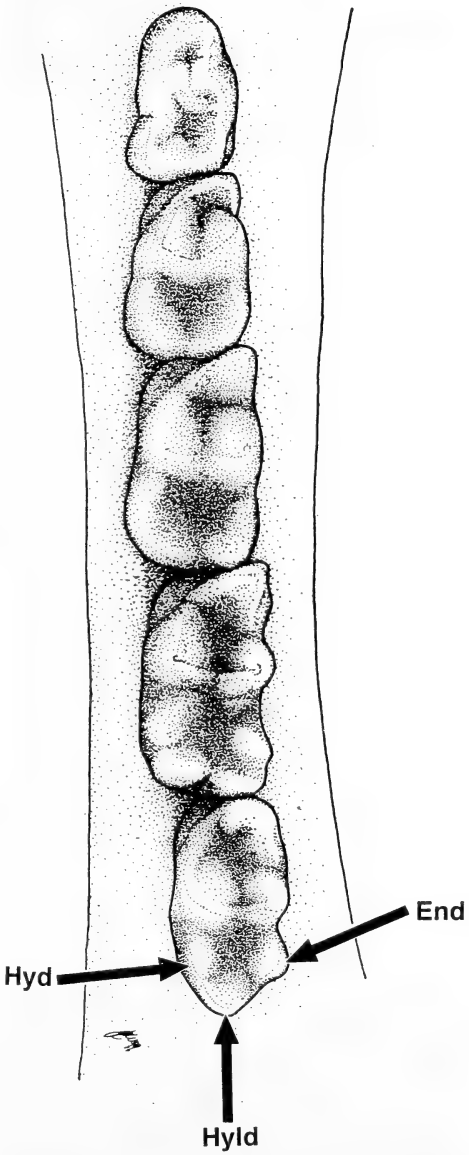

Fig. 4. Left inferior molar series of *Didelphis albiventris* (MN 22250), with a supernumerary molar (arrow). Occlusal view. Entoconid (End), hypoconid (Hyd), hypoconulid (Hyld).

of the centrocrista cannot be identified. Actually, this extra tooth resembles a normal M^4 as described by Hershkovitz (1997) for *Philander*, and the M^4 resembles a normal M^3: On the right side the extra tooth is more deformed, somewhat ovally shaped with some cusps visible (but hardly identifiable), and a partially formed crista (apparently the centrocrista, oriented with the antero-posterior axis of the skull). Unlike on the left side, the right tooth shows some degree of wear on the cusps and outer cristae. In both cases teeth are partially cluttered on the M^4, and crowns are on a different occlusal plane than the remaining molars (roots are more developed).

Specimen MN 5769 also presents one extra molar on each side, behind the upper left and right M^4. On the right side (Fig. 7), the extra molar is partially erupted. It is dislocated, due to the lack of space on the den-

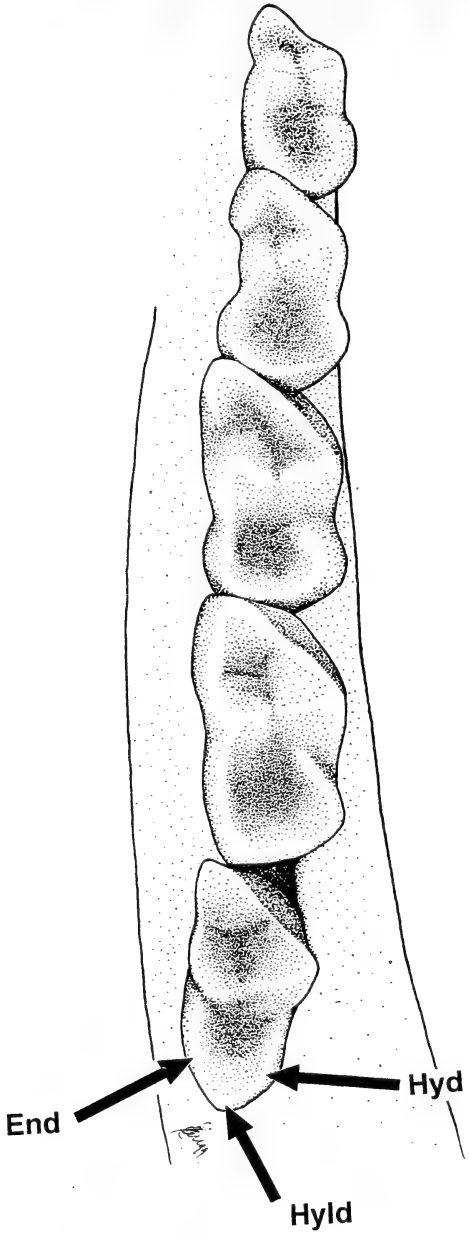

Fig. 5. Right inferior molar series of *Didelphis albiventris* (MN 22250), with a supernumerary molar (arrow). Occlusal view. Entoconid (End), hypoconid (Hyd), hypoconulid (Hyld).

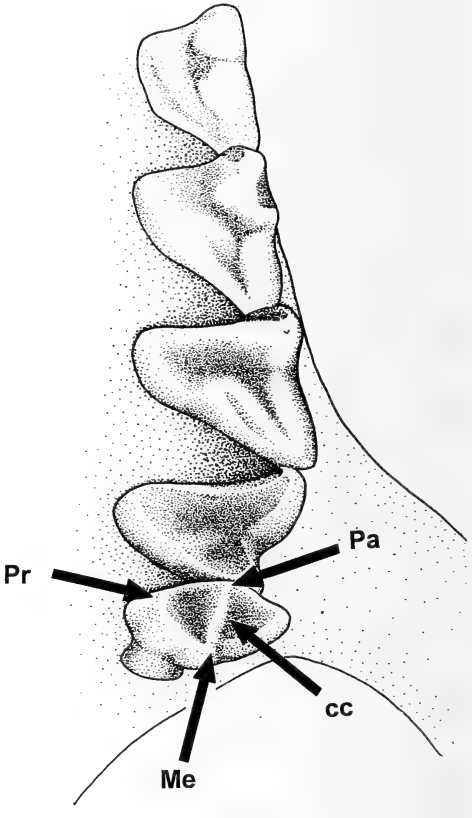

Fig. 6. Left superior molar series of *Philander frenata* (MC 267), with a supernumerary molar (arrow). Occlusal view. Protocone (Pr), paracone (Pa), metacone (Me), centrocrista (Cc).

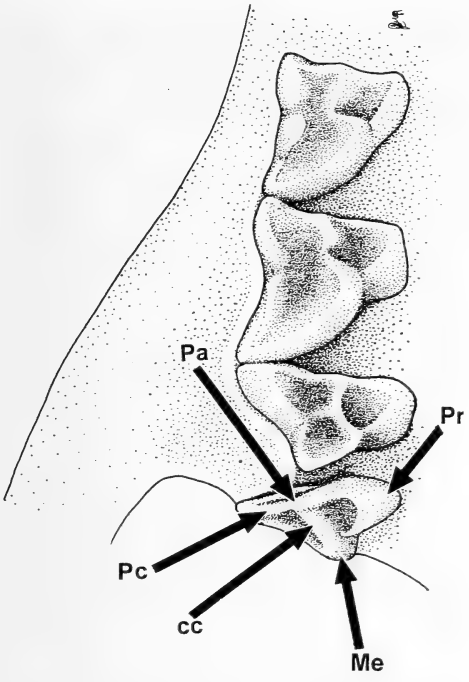

Fig. 7. Right superior molar series of *Philander frenata* (MN 5769), with a supernumerary molar (arrow). Occlusal view. Protocone (Pr), paracone (Pa), metacone (Me), centrocrista (Cc), paracrista (Pc).

tary behind the M^4, with its occlusal plane of the tooth posteriorly directed. A centrocrista is also recognisable, as well as protocone, paracone and metacone. The paracrista is also present, and the tooth lacks stylar cusps C, D and E. On the left side. the extra tooth is more oddly formed, with a crown of ovoid shape. Cusps are perceptible, such as an inner crista, probably the centrocrista. The occlusal plane, however, is aligned with the remaining molars of the series.

P. opossum

One specimen (AMNH 34373) presented a single supernumerary tooth at the end of each superior row. The extra tooth at the left side is reduced, but otherwise much similar to a normal M^4 in cusp patterns. It is also at the same occlusal plane of the remaining teeth. The extra tooth at the right superior side is occluding anteriorly oriented, and seems to be pushing forward the row. It is reduced, with distinguishable cusps.

Discussion

The occurrence of dental abnormalities such as supernumerary teeth is a rare and unpredictable phenomenon that makes the study of its specific developmental causes and processes very unlikely. Although the alternative explanations to the supernumerary teeth phenomenon are not always exclusive we provide a critical evaluation of some possible explanations.

Altough rare, the frequencies of supernumerary molars reported here for the Didelphidae fall within the range of those found in other mammal (placental) groups where the phenomenon has been reported (e.g. 1.6% (9/550) in European lynxes (*Lynx lynx* (Linnaeus, 1758)) Kvam 1985; 0.2% (1/580) in red deers. (*Cervus elaphus* Linnaeus, 1758) and 0.8% (1/130) in wapitis (*Cervus canadensis* Linnaeus, 1758) Pekelharing 1968; 3.7% (4/109) in mooses (*Alces alces* (Linnaeus, 1758)), Steele and Parama 1979.

First it is important to consider if these supernumerary teeth are a return to a lost primitive condition, thus being an atavistic character. For instance, Takahashi (1974) suggested that the presence of supernumerary incisors is an atavistic character of some *Didelphis* specimens. However, Berkovitz (1978) states that no more than five incisor tooth germs were ever observed in *Didelphis*. Thus, the supernumerary incisors studied by Takahashi (1974) doubtfully can be interpreted as atavistic characters. Furthermore, an atavistic explanation presents some limitations in our case, as the basic marsupial dental formula, exhibited by extant Didelphidae ($I_4^5C_1^1P_3^3M_4^4$) differs from the basic therian formula at the time of metatherian divergence from eutheria by the lost of premolar teeth on the former (Barbour 1977). Besides the proposition of some authors that the third deciduous premolars (dP3) could in fact be first molars and the subsequent molars being M2 to

M5 (e.g. Hershkovitz 1992), there is no mention of a truly additional fifth molar in marsupials (living or fossil). The only known exception would be the Australian numbat *Myrmecobius fasciatus* Waterhouse, 1836 (Myrmecobiidae), which can present 5 or 6 molars (Thenius 1989). In this case however, it is believed that the molar number is a secondary specialisation resulting from jaw elongation and not related to any ancestral condition, or primitive trait. Hence, an atavistic explanation could be advanced for a possible supernumerary premolar but not for molars. In fact there is no fossil record relating the occurrence of five molars in marsupials.

Another hypothesis relates an excessive size development to the emergence of an extra tooth at the end of the tooth row. However, as all specimens studied here presented standard sizes for their species, such a hypothesis does not seem to be the case. Furthermore, as we reported, in many cases there is actually a lack of space for these teeth to develop, which however did not prevent the teeth from appearing and the amount of space available does not seem to be related to the completeness of the tooth formation.

In some reports the occurrence of supernumerary teeth had been related to developmental disorders, such as splitting of the tooth germ (Krutzch 1953; Long and Long 1965; Pekelharing 1968; Steele and Parama 1979). These developmental alterations on the embryonic germ will likely lead to an incomplete development of one or both duplicated teeth, as observed in cervids, and in some cases resulting in an extra tooth "mirrored" in relation to the original one (Pekelharing 1968). The supernumerary molars here reported vary from morphological perfect M^4-like teeth to very small vestigial teeth, and never in this "mirrored" situation. In fact, no clear association between lack of space and amount of development of the supernumerary tooth could be found. Furthermore, knowledge on precise tooth development for most of these species is not existant, and all individuals examined are field caught, making an exact determination of the underlying phenomenon hard. Nevertheless, some sort of random developmental disorder could be an explanation for many of the cases we studied here.

Such an explanation is more difficult to accept in extreme cases such as MN 22250 and AMNH 209179, where four almost fully developed molars are present, requiring a simultaneous event of germ duplication in all M4. A genetically based disturbance with simple mendelian inheritance is also unlikely, as one of the specimens studied (MC 267) was field caught but maintained alive for captive breeding, and none of the offspring presented any similar phenomenon.

An alternative explanation could be that the premolariform P3 had erupted without loss of the molariform dP3. If this is the case, the cheek teeth observed would in fact be, in order: P1, P2, P3, dP3, M1, M2, M3 and M4. The eruption of the P3 would displace the whole molar series (at the time of eruption of the P3, only M1 and M2 are present), thus forcing the M3 and M4 to the end of the maxillar bone, which in case of lack of space could explain the deformations eventually observed. According to Berkovitz (1978), in *Didelphis virginiana* the third premolar develops in the embryonic dental lamina between the second premolar and the deciduous molar. Thus, if the deciduous molar was displaced posteriorly instead of falling, the sequence of the teeth after eruption would be the one previously stated. However, both upper and lower deciduous premolars are morphologically different from first permanent molars; dP^3's are narrower than M^1's, and dP_3's have narrower trigonids than M_1's, and their talonids are bigger in relation to the trigonid than in the M_1. In all animals examined here the first molar in the series has all characteristics of an actual M1, and not of a dP3, which denies this hypothesis.

The different shape variations observed in these teeth can be explained by the classic field model of mammalian heterodonty. This model postulates that heterodonty derived by the existence of three morphogenetic fields (incisor, canine, and molar).

These fields determine what the final form of a developing tooth bud will be (Butler 1939) but conflicting functional aspects are also important. In the genus *Peromyscus* Gloger, 1841, for instance, correlations among cheekteeth make M^3 and M_3 widths somewhat independent (van Valen 1962). The characteristics of each type of teeth appear early in tooth ontogeny although initial buds are undifferentiated (Archer 1974; Berkovitz 1978; Butler 1978). At weaning *Didelphis* has three functional molariform teeth. As it grows the deciduous premolar (which is molariform) is shed at the same time of the eruption of M3 (Tribe 1990). In this sense the deciduous P3's would actually be molars because when they grow they are located in a molar field (Archer 1974). Allometric growth of the bones changes the fields causing the so-called deciduous premolar to be shed and substituted by the P3's now growing in a premolariform field. Different allometric rates among taxa would then explain the differences in ontogeny of dentition among didelphids observed by Tribe (1990) and us (Astúa de Moraes and Lemos, unpubl. data).

Apparently it is possible that ancestors of metatherians had two dentitions like the placentals, since some secondary incisive and canine buds appear but are resorbed later in *Antechinus flavipes* (Waterhouse, 1838) (Archer 1974). Thus the dental lamina of the oral epithelium seems to have the potentiality to develop more teeth buds than teeth that effectively erupt. The supernumerary teeth could then be a congenital accidental anomaly. The resorption of the buds may be determined by the fixation of the teeth above them. With available space above buds (lack of teeth), these buds would develop into supernumerary teeth. In fact, supernumerary incisives and molars are more frequent (being the only ones so far described) because there is the available space in the diastema, between incisives and canines and also behind the cheek teeth row. Supernumerary incisives appear on the premaxillary bone only (Takahashi 1974). The additional teeth usually show the characteristic morphology of the teeth of the region where they appear, Exceptions are valid in cases when where there is no space for the tooth to fully develop into its normal morphology. Thus, varied morphology can be expected to appear.

Regardless of an explanation these dental abnormalities do not seem to be especially selectively disadvantageous, as all animals reached adulthood before being captured.

Acknowledgements

We are grateful to G. A. B. Fonseca (DZUFMG), A. L. Gardner (USNM), L. F. B. Oliveira, and L. O. Salles (MN), B. Patterson (FMNH), M. de Vivo (MZUSP), and R. Voss (AMNH) for access to the collections under their care. To M. A. R. Mello and Lena Geise for translation and corrections in the Zusammenfassung. Arianna Camardella gave us precious help sharing her knowledge on didelphid molar morphology, as well as J. A. W. Kirsch regarding dental formulas in *Myrmecobius*. Jair da Silva did the drawings. We thank two anonymous referees for suggestions. The work was partially supported by grants from CNPq, FAPERJ, FAPESP, FUJB, PROBIO/MMA and PRONEX.

Zusammenfassung

Überzählige Molaren bei neotropischen Beuteltieren (Didelphimorphia, Didelphidae)

Abweichungen von der arttypischen Zahnzahl wie das Auftreten zusätzlicher Zähne, werden in vielen placentalen Säugetiergruppen gefunden. Die Untersuchungen an neotropischen Beuteltieren haben ebenfalls überzählige Molaren ergeben bei: *Didelphis aurita, D. albiventris, D. marsupialis, Philander opossum, P. frenata, P. andersoni, Chironectes minimus* und *Caluromys philander.* Die Häufigkeit des Auftretens überzähliger Zähne bei diesen Arten bleiben innerhalb eines Bereiches, der ähnlich demjenigen bei anderen Arten ist. Folgende Möglichkeiten zur Deutung dieses Phänomens

werden erwogen: 1) Erscheinung der Extrazähne als Folge einer übermäßigen Entwicklung der Schädelgröße; 2) Atavismus; 3) Persistenz des dritten Milchprämolaren bei Erscheinen des Dauerzahnes; 4) Wachstumsstörungen, die zur Verdoppelung eines Zahnkeimes führen. Die erste Hypothese wird verworfen, da alle Einzelindividuen eine arttypische Größe haben. Kein fossiler Hinweis unterstützt auch die zweite. Die Morphologie der beobachteten Zähne unterstützt auch die dritte nicht, da es sich um Zähne des Dauergebisses handelt. Schließlich ist es schwierig, Beweise gegen oder zugunsten der vierten Hypothese zu finden, da keine Informationen vorhanden sind, über die Entwicklung der Zähne bei den bearbeiteten Museumsexemplaren.

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Mamm. biol. **66** (2001) 204–214

http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

A habitat analysis of badger (*Meles meles* L.) setts in a semi-natural forest

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Receipt of Ms. 27. 07. 2000
Acceptance of Ms. 22. 12. 2000

Abstract

We studied the size, distribution and habitat characteristics of badger (*Meles meles* L.) setts in a largely forested area near the city of Zurich, Switzerland. The distribution of the setts was non-random, as revealed by testing nearest neighbour distances. To evaluate the habitat characteristics that determine sett locations, different parameter categories describing topography, vegetation cover and structure of the forest habitat were analysed with a multiple regression analysis and with a digital terrain model of the forest using a Geographical Information System (GIS). Preferred sett sites were the convex slopes with an inclination of 20–40°. These sites are well drained and offer many opportunities for digging entrances and tunnels, and thus gives the badger the option to leave the sett from several directions. Ideal sett sites were found above 600 metres a.s.l., closer to the forest boundary and adjoining agricultural zones than the random points. These sett sites probably guarantee access to a good food supply year-round and allow badgers to adapt their foraging behaviour to seasonal changes in food availability both within the mixed forest stands and in the agricultural fields and meadows outside the forest. Setts were found more than 50 metres from the nearest path and in areas with sparse ground cover. Coniferous stands were avoided. However, single old spruces within deciduous forest stands were frequently used as sett sites for setts consisting of one or two entrances only. Spruce trees have shallow roots, which facilitate digging and help prevent the roof of the sett from collapsing. Vegetation cover played an important role in the choice of a sett site. However, just "being out of view" (be it through topographic characteristics or distance from the nearest path) could be a type of cover as well. In this study, the small-scale topography around the setts seemed to play a key role in the choice of sett site. The results presented here suggest that a large, deciduous forest with a pronounced topographical variation represents a good badger habitat.

Key words: *Meles meles*, sett distribution, entrance type, sett site, habitat analysis

Introduction

In general, carnivores not only show great interspecific diversity in their behavioural ecology (Bekoff et al. 1984; Gittleman 1986) but also marked intraspecific variability (Wilson 1975). The European badger (*Meles meles* L.) is an example of a species that shows a high degree of plasticity in its behaviour, adapting its social and spatial organisation to

1616-5047/01/66/04-204 $ 15.00/0.

different environments and food availability. In high-population-density areas with an abundant and highly predictable food availability throughout the year, badgers usually live in groups, defend small territories and occupy distinctive main setts (Cheeseman et al. 1981, 1987, 1988; Kruuk 1978; Kruuk and Parish 1982, 1987; Nolet and Killingley 1986; Rodriguez et al. 1996; Roper et al. 1986; Woodroffe and Macdonald 1992, 1993). In areas with a seasonally changing, unpredictable food availability, population densities are lower and badgers live in small groups or solitarily, have large overlapping home ranges and use several setts within a range (Bock 1986; Cresswell and Harris 1988; Graf et al. 1996; Pigozzi 1989; Skinner and Skinner 1988). Doncaster and Woodroffe (1993) suggested that the spatial organisation of badgers may be influenced by the distribution of suitable sett sites in a given area. Parameters affecting the distribution of badger setts include the type of soil, the amount of cover and the hilliness of the terrain (Neal 1986). Most assessments of suitable badger setts have been undertaken in mixed wood- and arable land (e. g. Cresswell et al. 1990). These studies showed an active selection for woodland as sett location. However, open fields and meadows were used as foraging grounds and had an important effect on sett choice (Hofer 1988; Skinner et al. 1991).

The goal of this study was to examine sett density, sett type and the specific habitat parameters affecting the distribution of setts in a highly forested habitat (Sihlwald, Switzerland), offering both ideal digging conditions as well as good foraging grounds. Furthermore, the correlation between the distribution of the setts in certain parameter categories and the availability of those categories in the study area was explored.

Material and methods

The study area

The Sihlwald forest is situated approximately 10 km south of the city of Zurich, Switzerland (47°15′ N, 8°34′ E). It is characterised by a diverse mosaic pattern ot mixed deciduous forest dominated by beech (*Fagus silvatica*), with smaller proportions of ash (*Fraxinus excelsior*), other deciduous trees, white pine (*Abies alba*) and the introduced Norway spruce (*Picea abies*). Declared a nature reserve in 1994, it covers approximately 1 000 ha of a forested hill chain, ranging from 470 metres a.s.l. at the bottom of the valley to over 900 metres a.s.l. on the ridge. It belongs to the Swiss plateau and consists of subalpine molassic sandstone with partly morrainic cover. The dominant soil types contain sandy to silty clay and argillaceous sand. The extreme relief and well-drained soils make Sihlwald an ideal place for digging setts.

Methods

The study area was searched for setts from March until August 1996. A sett was defined as at least one entrance leading more than two metres underground, measured with a two-metre flexible stick. If two entrances were farther than 25 metres apart, they were considered as two separate setts. We assumed that practically all setts were found. The setts were classified into small (1 or 2 entrances), middle-sized (3 or 4 entrances) and large (>4 entrances) setts. Five different entrance types were distinguished: entrances dug directly into the ground, under a boulder/rock, under a spruce (*Picea abies*), under a deciduous tree and under a stump.

This study did not differentiate between fox dens and badger setts for the following reasons. Although it is known that fox dens usually have fewer entrances and a different shape and smell than badger setts (Stubbe 1980), the criteria were not as clear-cut in Sihlwald with dens/setts consisting of one or two entrances that were sporadically used by one or both species. Badger hairs were found in many setts consisting of one entrance only, indicating the presence of badgers in single entrance setts as well. Analysis of sett characteristics based on sett size revealed no statistical difference between setts. Therefore, all setts were included in the habitat analysis presented here. However, to compare main sett density with those in the literature, all setts with more than two entrances and definite badger signs were considered "main setts" (Kruuk 1978). In order to test the distribution of the setts for non-randomness, nearest neighbour distances between the setts were compared with a Monte-Carlo-Simulation of nearest neighbor distances (random distribution,

1000 samples of 123 points) and then tested using a Chi2-test for two independent samples.

The habitat parameters chosen for the analysis are summarised in table 1. The parameters were either measured in the field (field data), or obtained from a Geographical Information System (GIS) using the software ArcInfo, which also contained a digital terrain model of the forest based on 10 metre-contour lines (Tab. 1). The field data were measured within a radius of 25 metres of the approximate centre of the sett. The habitat analysis was calculated by using a stepwise backward logistic regression. The parameters "topography" and "vegetation unit" were used as categorial variables (equivalent to the traditional group of "dummy variables") (NIEVERGELT 1981). The parameters derived from the GIS and the field data could not be analysed together, as the parameters derived from the GIS were available for the whole forest, whereas the field data were available only for the sett sites. For the analysis of the parameters derived from the GIS, a goodness-of-fit test compared the number of observed setts with the number of expected setts for each parameter:

$$\text{number of expected setts} = \frac{\text{area of the parameter}}{\text{area of the forest}} \times \text{total number of observed setts}$$

To measure the availability of the habitat parameters measured in the field (i. e. the parameters that could not be derived from the GIS database), the number of setts was compared with the number of random points for each parameter by a χ^2-test for two independent samples. Due to a strong correlation between "altitude" and "distance to forest boundary", the "distance to forest boundary" was analysed separately. The habitat parameters for which the distribution of the setts was non-random were further analysed to see which categories (Tab. 1) best explain the sett distribution. Every parameter category was tested for deviation from the expected value by using a χ^2-test in conjunction with a Bonferroni z statistic (NEU et al. 1974).

Results

Sett size and sett type

123 setts were found in the 1 000 ha study area of Sihlwald (12.3/100 ha). The setts were classified according to entrance number (one to two, three to four, more than four) and entrance types (five classes, see below). Small setts were most common (71.6%), followed by middle-sized (19.5%) and large (8.9%) setts. Using KRUUK's (1978) definition of "main setts" (setts with >2 entrances), the density of main setts in the forest was 3.5/100 ha. The number of entrances per sett varied from one to eleven with an average number of 2.3 entrances per sett. Of the total 279 entrances, 207 (74.2%) were dug into the ground, while the rest were dug under some type of structure (11.1% under spruces, 2.5% under deciduous trees, 7.9% under boulders, 4.3% under tree stumps).

Sett spacing

The average nearest neighbour distance between two setts was 111 metres, compared to 158 metres for the average nearest neighbour distance between two generated random points. Thus, the observed distribution of the setts was significantly different from random (χ^2-test for two independent samples, $p < 0.001$).

When the nearest neighbour distance was calculated for the "main setts" only, the average nearest neighbour distance was 311 metres, compared to the 314 metres for the average nearest neighbour distance between two generated random points. The distribution of "main setts" did not differ from random.

Habitat analysis of the setts

The results of the stepwise backward logistic regression show that sett sites were positively associated with the parameters "convex slope", "inclination" and "distance to nearest path" but negatively associated with "concave slopes", "flat areas", "gentle slopes", as well as "moss-", "herb-" and "middle layer coverage" (Tab. 2). The results for the different parameter categories are as follows:

Forest parameters and vegetation cover: The forest parameters and vegetation cover seemed to play a key role. The results showed that the parameters of the setts differed significantly from the availability of those parameters for "lower layer cover-

Table 1. Habitat parameters for setts. The parameters were either measured in the field (field data), or were obtained from the Geographical Information System (GIS)

Parameter	Subscales	Categories	Source of data
Sett location	X-coordinates Y-coordinates	continuous	Field data
Altitude	metres a.s.l.	≤ 600 m; ≤ 700 m; ≤ 800 m; > 800 m	GIS
Inclination	degrees	0–10°; 11–20°; 21–30°; 31–40°; > 40°	Field data
Aspect	degrees	N; NE; E; SE; S; SW; W; NW	GIS
Topography*	flat gentle slope concave slope convex slope crest	–	Field data
Vegetation cover	tree cover (> 1.3 m) shrub cover (0.5–13 m) herb cover (0–0.5 m) moss cover	BRAUN-BLANQUET (1964): 0, 1–5%, 6–25%, 26–50%, 51–75%, > 75%	Field data
Forest parameters**	lower-, middle and upper layer coverage	BRAUN-BLANQUET (1964): 0, 1–5%, 6–25%, 26–50%, 51–75%, > 75%	GIS
	lower-, middle- and upper coniferous layer coverage	BRAUN-BLANQUET (1964): 0, 1–5%, 6–25%, 26–50%, 51–75%, > 75%	GIS
	vegetation unit		GIS
	stage of development	1 = young growth; 2 = pole wood; 3 = young timber wood; 4 = middle timber wood; 5 = old timber wood I; 6 = old timber wood II; 7 = old timber wood III	GIS
Distance to nearest path	metres	≤ 50 m; ≤ 100 m; ≤ 150 m; ≤ 200 m; > 200 m	GIS
Distance to nearest water	metres	≤ 50 m; ≤ 100 m; ≤ 150 m; > 150 m	GIS
Distance to forest boundary	metres	≤ 100 m; ≤ 200 m; . . .; ≤ 900 m; > 900 m	GIS

* gentle slope: a slanting surface neither curving inward nor outward concave slope: a slope curving inward convex slope: a slope curving outward, like a segment of a globe.

** data from the forest superintendent's office (Waldamt der Stadt Zürich). lower layer coverage density: canopy density that reaches at most 1/3 of the dominant tree height. middle layer coverage density: canopy density that reaches 1/3–2/3 of the dominant tree height. upper layer coverage density: canopy density that reaches at least 2/3 of the dominant tree height.

age" and "lower-" and "middle coniferous layer coverage" (Tab. 3 a). However, more setts than expected were found only in areas lacking a "middle coniferous layer coverage" (Tab. 4; Bonferroni z statistic, $p < 0.05$). The parameters of the setts differed significantly from the random points for herb- and moss coverage (Tab. 3 b; χ^2-test for two independent samples, $p < 0.05$ and $p < 0.01$, respectively), as setts were more frequently found in areas with little "herb-" and no "moss coverage" (Tab. 4; Bonferroni z statistic, $p < 0.05$ and $p < 0.01$ respectively).

Table 2. Habitat parameters that best explain the occurrence of the setts. Multiple logistic regression (backward, stepwise), Model-$\chi^2 = 92.36$; df = 10; $p < 0.001$; $R^2 = 0.77$

Habitat parameter	B	df	p-value
Inclination	0.0695	1	0.0006
Topography		4	0.0247
flat	−0.6172		0.6818
gentle slope	−0.2514		0.8821
concave slope	−1.5706		0.1194
convex slope	0.8271		0.3550
Distance to nearest path	0.0144	1	0.0006
Middle layer coverage	−0.0288	1	0.0486
Herb coverage	−0.3226	1	0.0351
Moss coverage	−0.8196	1	0.0053

Table 3. Comparison of the habitat parameters of the setts derived from the GIS with the availability of those parameters within the study area (a); comparison of the habitat parameters of the setts with those of the random points (b). Only the parameters for which the distribution of the setts is significantly non-random are listed here. Goodness-of-fit test; df = degrees of freedom. For (b): $n_1 = 123$; $n_2 = 85$

a) Comparison with availability	p-value	χ^2	df
Altitude	$p < 0.001$	128.23	3
Aspect	$p < 0.02$	16.78	7
Lower layer coverage	$p < 0.02$	12.69	4
Lower coniferous layer coverage	$p < 0.005$	12.39	2
Middle coniferous layer coverage	$p < 0.02$	10.89	3
Distance to forest boundary	$p < 0.05$	17.61	9
Distance to nearest path	$p < 0.001$	18.10	3
Distance to nearest water	$p < 0.05$	10.82	4
b) Comparison with random points	p-value	χ^2	df
Inclination	$p < 0.001$	52.41	4
Topography	$p < 0.001$	40.04	4
Herb coverage	$p < 0.05$	19.63	5
Moss coverage	$p < 0.01$	15.44	2

Inclination and topography: Comparison of the habitat parameters of the setts measured in the field with those of the random points (Tab. 3 b) showed that setts differed significantly from random points for "inclination" and "topography" (both: χ^2-test for two independent samples, $p < 0.001$). "Convex slopes" with the inclination categories $\leq 30°$ and $\leq 40°$ were significantly preferred sett sites (Tab. 4; Bonferroni z statistic, $p < 0.001$).

Distances to forest boundary, forest roads and trails, and water: The distribution of the setts was decidedly non-random for these three parameters (Tab. 3 a). Setts are found significantly closer (≤ 100 m) to the forest boundary than expected (Tab. 4; Bonferroni z statistic, $p < 0.05$). Significantly more setts than expected were found ≥ 50 m but ≤ 100 metres to the nearest road or trail (Tab. 4; Bonferroni z statistic, $p < 0.001$). No difference was obtained for any category of the parameter "distance to nearest water". Altitude and aspect: The distribution of the setts was non-random for "altitude" (Tab. 3 a; χ^2-test for two independent samples, $p < 0.001$) as well as for "aspect" ($p < 0.02$). More setts were found

Table 4. Bonferroni Confidence Intervall (NEU et al., 1974) for all significant parameter categories positively affecting sett distribution. c. i. stands for confidence intervall

Parameter	Category	Availability	Demand	Estimate	Estimate in %	Lower c. i.	Upper c. i.	Bonferroni parameters	p-value
Middle coniferous layer coverage	0	55.35	69	55.193	0.4487	0.4492	0.6727	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 10.92$ $p < 0.01$
Herb coverage	1–5%	11	30	15.733	0.1279	0.1417	0.3461	n = 6; p = 0.05; z = 2.6383	$\chi^2 = 43.17$ $p < 0.05$
Moss coverage	0	51	100	72.942	0.5930	0.7252	0.9008	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 27.01$ $p < 0.001$
Inclination	≤ 30%	14	53	20.259	0.1647	0.3159	0.5459	n = 5; p = 0.05; z = 2.5758	$\chi^2 = 125.85$ $p < 0.001$
	≤ 40%	5	23	7.235	0.0588	0.0964	0.2775	n = 5; p = 0.05; z = 2.5758	$\chi^2 = 125.85$ $p < 0.001$
Topography	convex slope	12	62	17.163	0.1395	0.3879	0.6202	n = 5; p = 0.05; z = 2.5758	$\chi^2 = 144.17$ $p < 0.001$
Distance to forest boundary	≤ 100 m	8	24	11.576	0.0941	0.0948	0.2954	n = 10; p = 0.05; z = 2.8071	$\chi^2 = 55.23$ $p < 0.05$
Distance to path	≤ 100 m	33.33	47	33.331	0.2710	0.2727	0.4915	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 18.19$ $p < 0.001$
Altitude	≤ 700 m	23.4	45	23.402	0.1903	0.2574	0.4743	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 128.23$ $p < 0.001$
	≤ 800 m	12.03	28	12.031	0.0978	0.1332	0.3221	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 128.23$ $p < 0.001$
	> 800 m	0.02	10	0.020	0.0002	0.0198	0.1428	n = 4; p = 0.05; z = 2.4977	$\chi^2 = 128.23$ $p < 0.001$

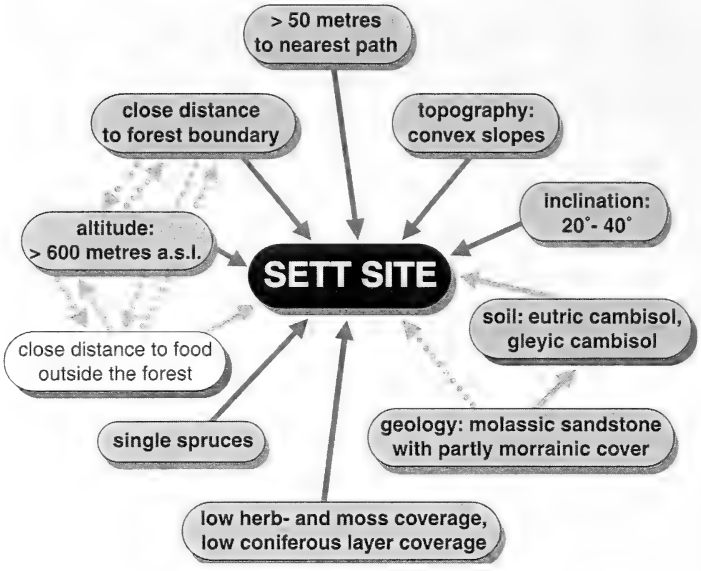

Fig. 1. Parameters positively affecting sett site in Sihlwald. Grey ovals: parameters measured in this study or taken from available data sets for the study area. White ovals: parameters that are difficult to assess but probably influence the choice of sett sites. Arrows indicate the interrelations between the parameters.

> 600 metres a.s.l. (Tab. 4; Bonferroni z statistic, $p < 0.001$). No significant difference was obtained for any category of "aspect" other than North, for which fewer setts than expected were found (Tab. 4; Bonferroni z statistic, $p < 0.05$). Figure 1 illustrates the different parameters positively affecting sett sites in Sihlwald.

Discussion

Sett size and sett type

The number of entrances per sett in Sihlwald, ranging from one to eleven, was well below the average found in the literature (1 to 21: KRUUK 1978; 1 to 38: ANRYS and LIBOIS 1983; 1–80: ROPER 1992 a, b), even compared to that of the other studies in Switzerland (1–28: GRAF et al. 1996; 1 to 15: FERRARI 1997; 2–23: MONNIER, unpublished data; 1–34: DOLINHSAN, unpublished data). Badgers seem to prefer burrowing more setts but with fewer entrances in the forest than in the agriculture zone where sett sites are restricted to the little patches of forest between the agricultural fields and meadows (DOLINHSAN, unpublished data). We suggest that badgers living in Sihlwald can optimise their foraging efficiency by using different setts within their home range according to the proximity of the seasonally most profitable food patches. Future analysis of the seasonal sett-use together with seasonal variations in foraging behavior in the study area will provide the necessary data to test this hypothesis.

In Sihlwald, 28.4% of the setts found showed more than two entrances and could indicate main setts (KRUUK 1978). However, their distribution did not differ from random and therefore did not show a spacing-out mechanism indicating territories according to the fixed-territory model proposed by DONCASTER and WOODROFFE (1993) for a high-density badger population.

With regard to the entrance types, it is surprising that 31 entrances (11%) were dug under relatively large spruces. Although sett locations have been analysed in several studies, only BOCK (1986) classified different sett types. However, his study did not mention anything about setts dug under spruces. The spruces in Sihlwald were all in mixed forests. A possible explanation is that spruce trees are normally shallow rooted

(Köstler et al. 1968; Blanckmeister and Hengst 1971), compared to the dominant beech trees in Sihlwald. Shallow roots facilitate digging; also the roots keep the roof of the sett from collapsing. It is also of interest to note that 22 entrances (7.9%) were dug under a boulder/rock. To our knowledge, single rocks as a possible habitat parameter for sett location, providing shelter and good thermal insulation has only been mentioned in one other study (Virgos and Casanovas 1999).

Cover as key factor

The habitat parameters affecting the distribution of setts in Sihlwald correspond closely to those identified by Neal (1986) and Thornton (1988): digability, hilliness and (tree-) cover. Cover allows the badgers to leave inconspicuously, and it allows the young cubs to play near the entrance without being visible to potential predators. A closer look at the vegetation cover around the preferred sett sites in Sihlwald shows that these sites are areas of sparse ground cover (i. e. low herb- and moss coverage). High herb and moss coverage often is correlated with humidity and therefore avoided by badgers as sett sites. As observed in other studies (Neal 1986; Zejda and Nesvadbova 1983), coniferous stands providing little vegetation cover and found in rather flat areas were avoided in Sihlwald. The preference for convex slopes with a high inclination (20–40°) as well as the preference for a minimum distance of 50 m from the next path suggest that the variable "cover" is not necessarily equivalent to vegetation cover; the small-scaled topography around the sett and the distance to the nearest path (just "being out of view") can indirectly be a type of cover as well. Topography, i. e., the physical shape of the area in which a sett is dug, is a parameter that has never been stressed in the literature before and seems to play a key role in the choice of sett site in Sihlwald. Paying attention to the small-scale topography (∅ 50 metres) around the sett appears to be important. Setts dug in convex slopes have several advantages. The badger can pick up scents from different directions without having to leave the security of the sett and thus have several directions from which to leave a sett. It is also possible that setts on convex slopes are easier to enlarge because the rounded shape of the slope gives the badgers more opportunities for digging entrances and connecting tunnels than an unstructured slope. Inclination ("hilliness" according to Thornton 1988) is also closely associated with topography. Setts are usually dug in slopes (Neal 1986; Skinner et al. 1991). The hilliness of the study area is advantageous to the badger in various ways. Digging in a slope facilitates the removal of the excavated soil, which spills down the slope. A particularly favourable stratum of soil for digging is more easily found on a slope since it is more likely to be exposed. Sloping land is usually well drained so that the sett is more likely to be warm and dry, and in colder parts a depth below ground is quickly attained which is frost free (Neal 1986).

Sett density and population density

The density or setts in Sihlwald (12.3/100 ha) is very high compared to the density of the nearby agricultural zone (2.7/100 ha, DoLinhSan, unpublished data). This implies that suitable sett sites are not a limiting factor in the forest, as suggested by Roper (1993) for British areas. Other regions of Switzerland (Canton of Neuchâtel: 0.02–0.2/100 ha, Monnier, unpublished data; Canton of Berne: 4.2/100 ha, Graf et al. 1996) have also lower sett densities. Still, Sihlwald has a significantly lower sett density than found in Britain (up to 26/100 ha, Cresswell et al. 1990). The density of possible main setts in Sihlwald (3.5/100 ha) is comparable to that in the high-badger-density areas in Britain (Clements et al. 1988, see Kowalczyk et al. 2000, for review). Based on the available earthworm biomass, which is the most important food source for badgers in Sihlwald, the minimum population size is estimated to be 2.5 to 3 individuals per 100 ha (Hindenlang, unpub-

lished data). Therefore, also the badger density in Sihlwald is high compared to the published densities across Continental Europe, but, in contrast to the main sett density, lies much lower than the estimated population densities of the British Isles (Kowalczyk et al. 2000). Kowalczyk et al. (2000) showed that log densities of badger setts correlate negatively with the percent forest cover in the area. This is certainly not the case in Sihlwald where forest covers approximately 70% of the area used by badgers living in the Sihlwald (pers. observation). In the nearby agricultural zone with a much lower sett density forest covers approximately 17% of the area. We argue that this high sett density and considerably high badger density in Sihlwald is attained through a combination of ideal sett-site conditions as well as a rich and varied food supply. According to the literature, a mixture of woodland and pastures, and woodland and arable land is among the habitat types preferred by the badger (Broseth et al. 1997; Hofer 1988; Neal 1977; Zedja and Nesvadbova 1983). Also, the setts in Sihlwald are found significantly closer to the forest boundary and adjoining agricultural zones than random points. Other studies have noted that badger setts tend to be situated close to habitat edges, i. e. on boundaries between two habitat types (O'Corry-Crowe et al. 1993; Virgos and Casanovas 1999). The proximity of setts to the forest boundary and adjoining agricultural zones makes access easier to an optimal food supply year-round without forfeiting optimal sett sites that the forest offers with its pronounced topography. The diverse pattern of mixed deciduous forest stands in Sihlwald itself contains good worm patches even in dry periods (Hindenlang, unpublished data). Badgers can therefore adapt their foraging to the seasonal changes in food availability, both within the mixed forest stands and in the agricultural fields and meadows outside the forest. We suggest that the spatial organisation of badgers living in the Sihlwald area is primarily determined by the seasonal availability of food resources.

Acknowledgements

We thank Gerulf Rieger and Werner Suter for the helpful comments on the drafts. Furthermore, we would like to thank Lorenz Gygax and Wolf Blankenhorn for the statistical advice and Susanne Reimann for helping us draw figure 1. We are also very indebted to all those who helped us find numerous setts. K. Hindenlang was supported by the Swiss National Fund ("Adjustment of spatial behaviour of European badger (*Meles meles* L.) in response to a heterogeneous environment", Nr. 3100-40846.94/3100-52988.97).

Zusammenfassung

Eine Analyse der Habitatcharakteristika von Dachsbauen (*Meles meles* L.) in einem naturnahen Wald

Größe, Verteilung und Habitatcharakteristika von Dachsbauen wurden in einem naturnahen Wald untersucht. Die Verteilung der Dachsbaue im Untersuchungsgebiet war nicht zufällig, wobei jeweils die Distanzen zum nächst benachbarten Bau mit den Distanzen zu Zufallspunkten verglichen wurden. Für die Bestimmung der charakteristischen Habitatfaktoren, die die Verteilung der Baue im Untersuchungsgebiet erklären, wurden verschiedene Kategorien von Habitatparametern für Topographie, Vegetation und Struktur des Waldhabitats mittels Multipler Regressions-Analyse und mithilfe eines digitalen Geländemodells in einem Geographischen Informations-Systems (GIS) analysiert. Bevorzugte Standorte waren konvexe Hangrippen mit einer Inklination zwischen 20° und 40°. Sie sind gut entwässert und bieten dem Dachs die Möglichkeit, Baueingänge und -röhren zu graben, die ein Verlassen des Baus und das Aufnehmen von Witterung aus verschiedenen Himmelsrichtungen erlauben. Bevorzugte Standorte für Dachsbaue befanden sich in Höhenlagen über 600 Meter ü. M. sowie näher am

Waldrand und damit auch näher an den umliegenden landwirtschaftlich genutzten Flächen als die Zufallspunkte. Diese Baue gewährleisten den Dachsen das ganze Jahr über Zugang zu einem optimalen Nahrungsangebot, sei es in den vielfältigen Mischwaldbeständen innerhalb des Waldes oder sei es auf den landwirtschaftlich genutzten Äckern und Wiesen außerhalb des Waldes. Die Dachse können so ihre Nahrungssuche den saisonalen Veränderungen im Nahrungsangebot optimal anpassen. Baue wurden meistens in Flächen mit wenig Bodenbedeckung und weiter als 50 Meter vom nächsten Weg entfernt gefunden. Nadelwaldbestände wurden gemieden. Einzelstehende, alte Fichten (*Picea abies*) in Laubwaldbeständen jedoch wurden oft als Standorte für Baue mit ein bis zwei Eingängen genutzt. Ihr flaches Wurzelwerk erleichtert das Graben und verhindert das Einstürzen des Baues. Ein hoher Deckungsgrad der Vegetation und damit ein guter Sichtschutz spielte eine wichtige Rolle für die Auswahl der Baustandorte. Sichtschutz kann jedoch auch durch andere Faktoren, wie Topographie und Entfernung zum nächsten Weg, gewährleistet werden. Insbesondere die kleinräumig diverse Topographie um die Baue scheint ein bisher wenig beachteter Schlüsselfaktor für die Anlage eines Baues zu sein. Die Ergebnisse dieser Studie sprechen dafür, dass ein großes Laubwaldgebiet mit einer stark ausgeprägten Topographie ein sehr gutes Dachshabitat darstellt.

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Mamm. biol. **66** (2001) 215–227
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Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Age and sex distributions in the catches of belugas, *Delphinapterus leucas*, in West Greenland and in western Russia

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Receipt of Ms. 14. 02. 2000
Acceptance of Ms. 06. 11. 2000

Abstract

Age and sex were determined for belugas or white whales, *Delphinapterus leucas*, harvested in West Greenland in 1985–86 and 1989–1997. There was a clear segregation of whales in the drive fishery conducted during autumn in Qaanaaq and Upernavik. Primarily immature whales of both sexes together with mature females were taken. Age was estimated from Growth Layer Groups (GLGs) in sectioned teeth, assuming the currently accepted criteria of 2 GLGs forming annually. The mean and median ages were increasing slightly in both sexes from Upernavik from 1985 through 1994. Both immature and mature whales were taken on the wintering grounds from Disko Bay and south. Estimation of survival was confounded by the large number of whales where only a minimum age could be assigned because of tooth wear at the crown (i. e. no neonatal line in the dentine). The apparent survival rates for belugas from West Greenland were estimated as 0.81 and 0.79 for females and males, respectively. Correction of these estimates for an observed population decline of 4.7% per year revealed true survival rates of 0.85 and 0.82 for females and males, respectively. The estimates of true survival rates are less than those determined for beluga populations in the White and Kara seas and in Alaska for comparable age truncations. Since the exploitation levels are much lower in these areas the low apparent survival rate from West Greenland strongly supports the evidence of a population decline. Colour change from grey to white occurs at mean ages of 8.5 yr and 9.1 yr and median lengths of 367 cm and 445 cm in females and males, respectively.

Key words: *Delphinapterus leucas*, age structure, Greenland, Russian Arctic

Introduction

Large numbers of belugas (white whales), *Delphinapterus leucas*, have been taken in commercial fisheries and Inuit harvests throughout the Arctic during the last 100 years. In Greenland the accumulated catches of belugas in this century amounts to more than 50 000 whales (Heide-Jørgensen 1994). Despite the availability of samples verv little is known about the sex and age frequencies in different harvesting situations; let alone survival rates calculated from catch-at-age data.

The belugas that are harvested along West Greenland are believed to be part of the

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stock(s) of belugas that summer in the Canadian High Arctic (HEIDE-JØRGENSEN 1994). This stock is supposed to winter in West Greenland south of Disko Bay and aerial surveys of the population densities of belugas on these wintering grounds have indicated a substantial decline between 1982 and 1994 (HEIDE-JØRGENSEN and REEVES 1996). The most likely explanation for this apparent population reduction is that the large level of exploitation during the 1980s has exceeded the replacement yield of the stock. With this background it was considered important to further evaluate the status of the stock.

SERGEANT (1973) provided the first age frequencies from catches of belugas in Hudson Bay and while he realised the detrimental impact of tooth wear on age estimations he was able to show that maximum longevity was at least 25 yr for both sexes, under the assumption of deposition of two Growth Layer Groups (GLGs) per annum. BURNS and SEAMAN (1986) provided age frequencies from Alaska with a maximum life span of 38 yr but did not present details on the distribution for males and females. DOIDGE (1990) showed from age frequencies obtained in Northern Quebec that belugas have a maximum longevity of at least 31 and 33 yr for males and females, respectively. By use of a smoothing technique of the age frequencies from teeth without wear DOIDGE (1990) estimated annual survivorships for both sexes combined ranging from 0.69 to 0.93 for whales between 0 and 9 yr of age and between 0.94 and 0.97 for whales between 10 and 37 yr of age. Survivorship estimates for worn and unworn teeth lumped together were slightly lower for all age classes. The survival rates were slightly higher in Northern Quebec compared to Alaska especially after age 12 yr, but both studies were evidently violating the assumptions of both equilibrium of the population prior to sampling and representativeness of samples for the population age frequencies.

This study examines the changes in the age- and sex selectivity of the harvesting of belugas in West Greenland. The survival rates calculated for West Greenland belugas are compared to survival rates from belugas in the White and Kara seas.

Material and methods

Age frequencies from West Greenland

Lower jaws were collected from the catches of belugas in West Greenland (Fig. 1). The jaws were registered and stored at freeze houses and kept frozen before and during shipment to the laboratory in Copenhagen. Teeth were extracted and stored frozen until sections were prepared according to methods described in HEIDE-JØRGENSEN, et al. (1994). Two trained readers independently counted the number of Growth Layer Groups (GLGs – see PERRIN and MYRICK (1980) for definition of GLG) in the teeth and age was determined as the mean of the two readings. 'Minimum age' refers to those teeth where an unknown number of GLGs were missing due to wear of the crown of the tooth. 'Complete age' refers to those teeth in which all GLGs, including the neonatal line, could be counted. Two GLGs were assumed to be deposited annually (HEIDE-JØRGENSEN et al. 1994). The same two persons made all the readings of GLGs except for the samples from 1993–94 where another trained reader replaced one of them. If the discrepancy between the two readers exceeded 3 GLGs the tooth was checked again by one of the readers and if the discrepancy was maintained, the age estimate would either be discarded or another tooth was prepared. Sex was determined by DNA analysis of skin samples extracted from the lower jaws (PALSBØLL et al. 1992).

The samples collected were stratified with regard to sex, area, and year. For each area and year, the mean, its standard deviation and the median of ages were calculated for both sexes. This was done separately for samples restricted to whales with minimum age and to whales with complete age.

Colouration of skin was classified to three groups; brown or brownish-grey, grey and white, for a subsample of 147 females and 119 male belugas that were examined before being flensed. Classification of skin colouration from the skin remains on the samples of lower jaws alone proved to be unreliable, whereas all the whales with length measurements had been examined by the first author before they were flensed. For the change in colouration from grey to white colouration mean age and associated variance was determined by use of the method of DEMASTER (1978) after smoothing of a curve fitted to the data.

Age frequencies from the White and Kara seas

Age frequency data from the beluga harvest in the White and Kara seas was compared with the age distribution from West Greenland. A sample of 570 whales was collected from the commercial hunt in the White and Kara seas in the 1970s and early 1980s (see Ognetov 1981 for a description of a subset of the sample).

The growth of belugas in the White and Kara seas resembles the West Greenland belugas more than any other beluga population (Heide-Jørgensen

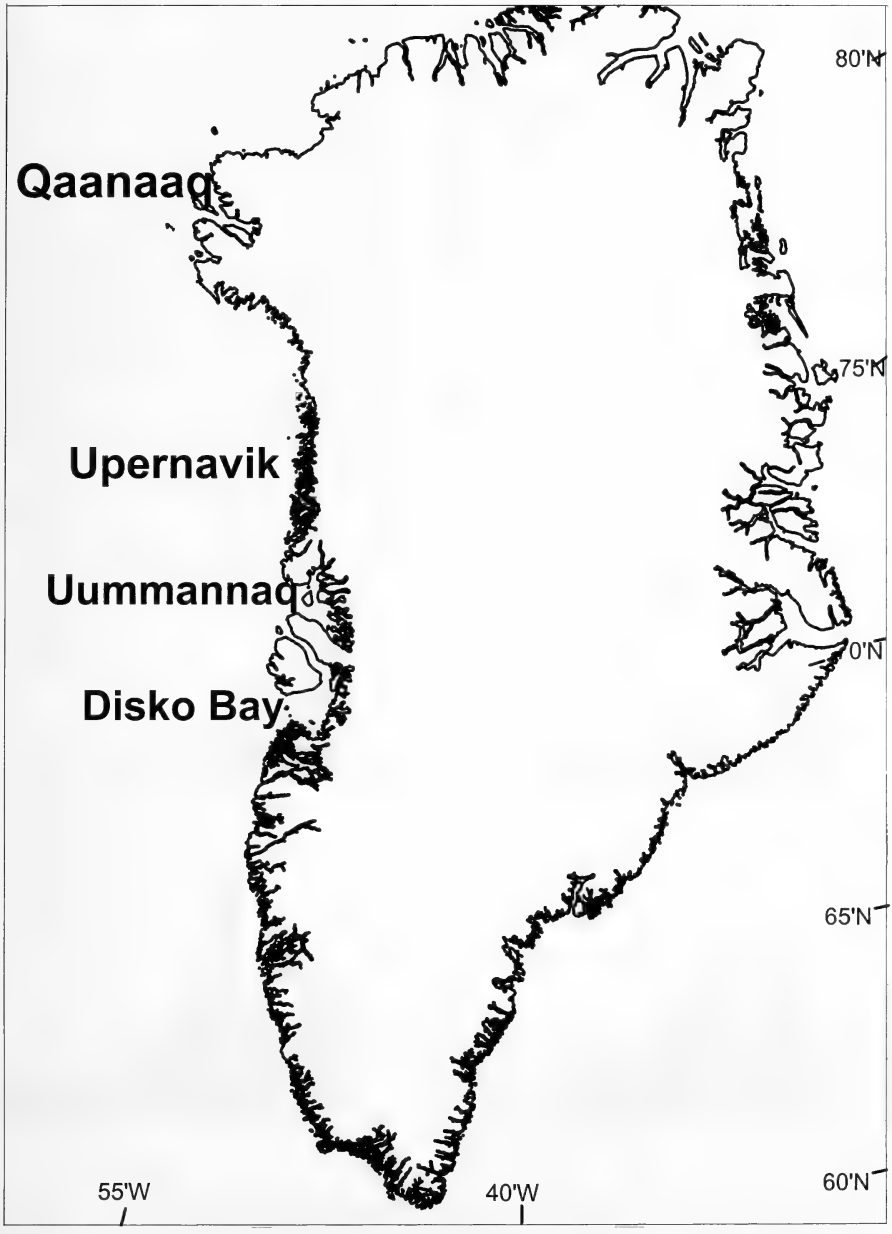

Fig. 1. Map of municipalities and areas in West Greenland mentioned in the text.

and TEILMANN 1994) although their tooth wear begins at a much later age (HEIDE-JØRGENSEN et al. 1994).

Estimation of survival rates

Apparent survival rates (i. e. survival rates uncorrected for population changes) were estimated for the age frequencies from West Greenland and the White and Kara seas according to the method of ROBSON and CHAPMAN (1961). Because of underrepresentation of the youngest age classes in all samples, all age frequencies were recoded from the modal age class upwards. Apparent survival rates were also calculated by fitting a negative exponential curve where the natural logarithm of the exponent is equivalent to the annual survival rate.

Statistical analysis

Data management and comparisons of means were conducted in Statview for Windows (version 5.0) and non parametric tests and non linear regressions were carried out in S-Plus (version 4.5). Unless otherwise stated, significance was always determined at the 5% level.

Results

Selectivity in the beluga harvest in West Greenland

All sex and age classes of belugas are subject to harvesting in West Greenland (Fig. 2). Sampling during ten years between 1985 and 1997 resulted in an overall mean age of 7.7 yr in females and 6.5 yr in males of the harvested population older than 1 year in all municipalities and minimum and complete ages combined. In the samples more females than males were taken (712 vs. 596), but there was an equal proportion of both sexes among calves less than 1 year of age in Greenland (44 females, n = 89).

The limited number of samples from the municipality of Qaanaaq (formerly called

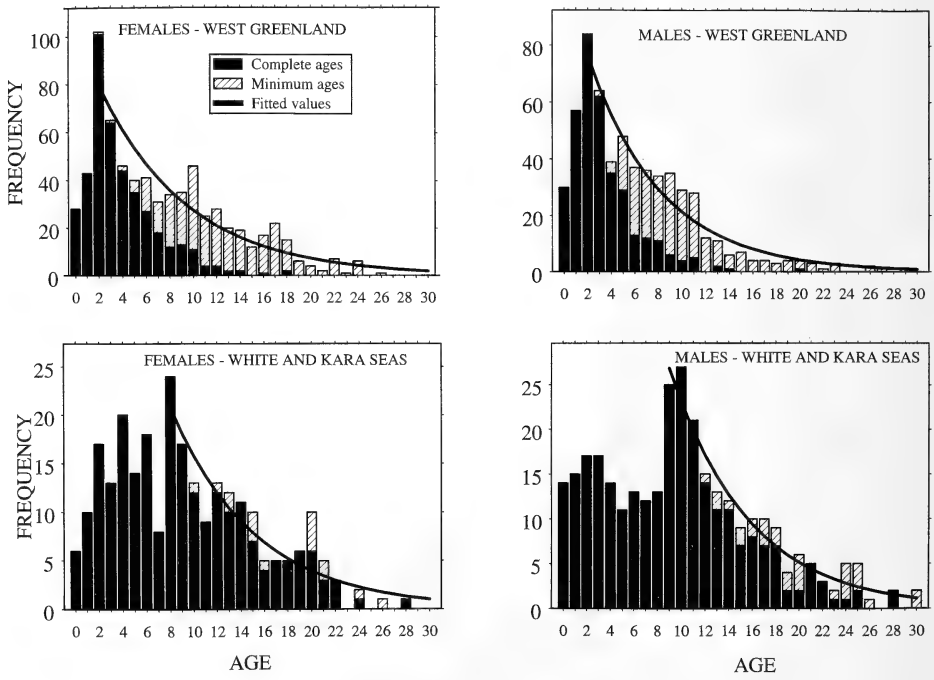

Fig. 2. Age-frequency distributions of male and female belugas from West Greenland and the White and Kara seas. Frequencies of complete and minimum ages are shown together with the negative exponential fit (F = a*exp(b*AGE)) from the modal age class. See table 2 for values of parameters from fitted functions.

Avanersuaq, see Fig. 1) collected in September 1993 showed that the catch primarily consisted of young animals (Tab. 1). The mean age of the samples from the municipality of Upernavik collected in late September and early October 1985 through 1994 or in 1993 alone were not significantly different from those collected in Qaanaaq (ANOVA, $p > 0.2$). The samples of whales taken in Uummannaq in the autumns of 1993 through 1996 indicated similar age structure as in Qaanaaq and Upernavik. Mainly young whales were taken in all three areas.

When contrasting the age and sex frequencies obtained from the autumn drive fisheries in Qaanaaq, Upernavik and Uummannaq, with that from the ice edge and open water hunt in Disko Bay and south, it is obvious that older whales are taken in Disko Bay (Tab. 1). This was evident both from comparisons of mean ages from all whales (older than 1 year) and from those with complete ages (t-test). Also, the samples collected from winter and spring catches in Disko Bay showed that less than 30% of the whales could be aged without bias (complete age) in contrast to Upernavik and Qaanaaq where more than 60% had complete age (Tab. 1).

Trends in mean age in the catches

Linear regressions of mean age on time showed that there was a significant increase in the mean age of harvested female and male belugas for which minimum age had been determined from 1985 through 1994 from Upernavik (ANOVA). The increase was also evident when groups where minimum and complete age had been determined were combined but could not be confirmed for females when complete age was considered alone. For the area from Disko Bay and south no signifcant trends in mean age could be detected between 1990 and 1997 for minimum age or minimum and complete ages combined. However, a significant increase was observed using complete age data for males but not for females ($p = 0.0588$). Since the minimum ages tend to be truncated at the age when the neonatal is worn away this category of teeth is less reliable for detecting an increase in the mean age of catches. Thus the category with complete ages should be given more weight, which implies that there is a tendency for older males being harvested in both Upernavik and Disko Bay since the mid 1980s.

Comparison with age distribution in the White and Kara seas

The observed potential minimum life span of 30 yr in belugas from West Greenland was similar to what was found in the sample from the harvest in the White and Kara seas. This was, however, the only common feature of the two age distributions (see Fig. 2). Whereas immature belugas constituted the largest number of samples in West Greenland, mature whales of more than 7 yr constituted the majority of the samples from the White and Kara seas, where the mean ages also deviate significantly from West Greenland (Tab. 1). Because of the late onset of tooth wear in the belugas from the White and Kara seas less than 16% of the teeth had lost their neonatal line.

Survival rates of belugas

As tooth wear increases with age individuals with incomplete (minimum) age estimates are much more frequent in older age classes. Thus the apparent survival rates were generaily much higher when individuals with minimum ages were included. Moreover, inclusion of minimum age estimates still leads to an underestimate of survival rates because the minimum age estimations underestimate the true age of the whales.

No significant differences were detected for apparent survival rates (age > 9, t-test) or frequency distributions of all age samples from north and south of Disko Bay (Kolmogorov-Smirnov two sample test). Thus the two data sets were pooled.

The combined age distribution from West Greenland showed an underrepresentation of age classes 0 and 1 (Fig. 2), thus for the

Table 1. Mean ages of belugas older than 1 yr harvested in four different areas in West Greenland between 1985 and 1997 and in the White and Kara seas in the 1970s and 1980s. 'ALL' refers to both teeth with 'minimum' and 'complete' age

Years	QAANAAQ				UPERNAVIK				UUMMANNAQ				DISKO BAY AND SOUTH				WHITE AND KARA SEAS			
	1993				1985–1994				1993–1996				1986–1997				1970–1980			
	Formales		Males		Formales		Males		Formales		Males		Formales		Males		Formales		Males	
	All	Complete ages	All	Complete ages	All	Complete ages	All	Complete ages	All	Complete ages	All	Complete ages	All	Complete ages	All	Complete ages	All	Complete ages	All	Complete ages
Mean	6.2	4.8	6.0	3.7	6.0	4.1	5.3	3.6	8.2	2.8	6.6	6.3	10.4	6.0	8.4	5.1	9.4	8.9	10.1	9.0
SD	3.9	2.6	4.6	1.9	4.4	2.6	4.1	2.1	3.1	0.4	5.4	6.5	6.1	3.8	5.0	3.3	6.1	5.8	6.7	5.9
Median	5.5	4.0	5.0	3.5	4.5	3.5	3.5	3.0	9.0	2.8	5.5	3.5	10	5.5	8	5.0	9.0	8.0	10.0	10.0
N	41	31	27	17	364	258	283	209	11	2	13	8	283	79	253	67	258	242	312	282
Max age	16	10.5	23	8	22.5	18.5	26.5	13	11.5	3	20.5	20.5	26	18	29	14	28	28	30	28
% with complete age	76		63		71		74		20		62		28		27		94		90	

calculation of survival rates these age classes were excluded.

The age distributions from the White and Kara seas were radically different from what is seen in West Greenland. Whereas West Greenland age distribution peaks at 2 yr of age for both sexes the samples of belugas from the White and Kara seas were almost constant from age 0 to the peak at 8 yr in females and 10 yr in males (Fig. 2). Estimation of apparent survival rates for the White and Kara seas was thus conducted for the age frequencies older than 7 yr and 9 yr for females and males, respectively (Tab. 2).

The apparent survival estimates for the White and Kara seas were larger, albeit not significantly larger, than the estimates for West Greenland for similar truncations of the age classes (Tab. 2). However, significant difference (t-test) was only detected for the survival rate for male belugas estimated from the negative exponential model.

Change in colouration

Some beluga calves are born brown and others are grey, but usually the brown colouration changes at an earlier age (< 5 yrs) and shorter length (< 300 cm) than the grey colouration (Figs. 3 and 4). There is obviously a large overlap in the brown (or brownish-grey) and the grey classification which probably indicates diffculties in distinguishing between these two categories. The colour change from grey to white seems to be completed at a mean age of 8.5 yr for females (SD = 0.6) and 9.1 yr for males (SD = 0.5) and a median length of 367 cm and 445 cm for females and males, respectively (Figs. 3 and 4).

Discussion

Reliable calculation of survival rates for belugas taken in harvest operations depend on a variety of assumptions:

Table 2. Survival estimates for belugas from West Greenland and the White and Kara seas estimated by the method from ROBSON and CHAPMAN (1961) and by fitting a negative exponential curve (frequency = a*exp(b*age)). Only age classes older than 1 year of age are included in the estimations for West Greenland. For the White and Kara seas only age classes older than 7 yr for females and 9 yr for males, respectively, are included. 95% Cl are shown in parenthesis

	SURVIVAL RATES	
	ROBSON and CHAPMAN	Negative exponential model
FEMALES – WEST GREENLAND		
Recoded ages from > 1 yr (n = 625)	0.86 (0.85–0.88)	0.88 (0.85–0.90)
Recoded ages from > 9 yr (n = 232)	0.81 (0.79–0.83)	0.84 (0.80–0.87)
MALES – WEST GREENLAND		
Recoded ages from > 1 yr (n = 500)	0.83 (0.82–0.85)	0.85 (0.83–0.87)
Recoded ages from > 9 yr (n = 123)	0.79 (0.75–0.82)	0.73 (0.69–0.78)
FEMALES – WHITE AND KARA SEAS		
Recoded ages from > 7 yr (n = 152)	0.84 (0 .82–0.87)	0.87 (0.85–0.90)
MALES – WHITE AND KARA SEAS		
Recoded ages from > 9 yr (n = 161)	0.84 (0.81–0.86)	0.85 (0.83–0.87)

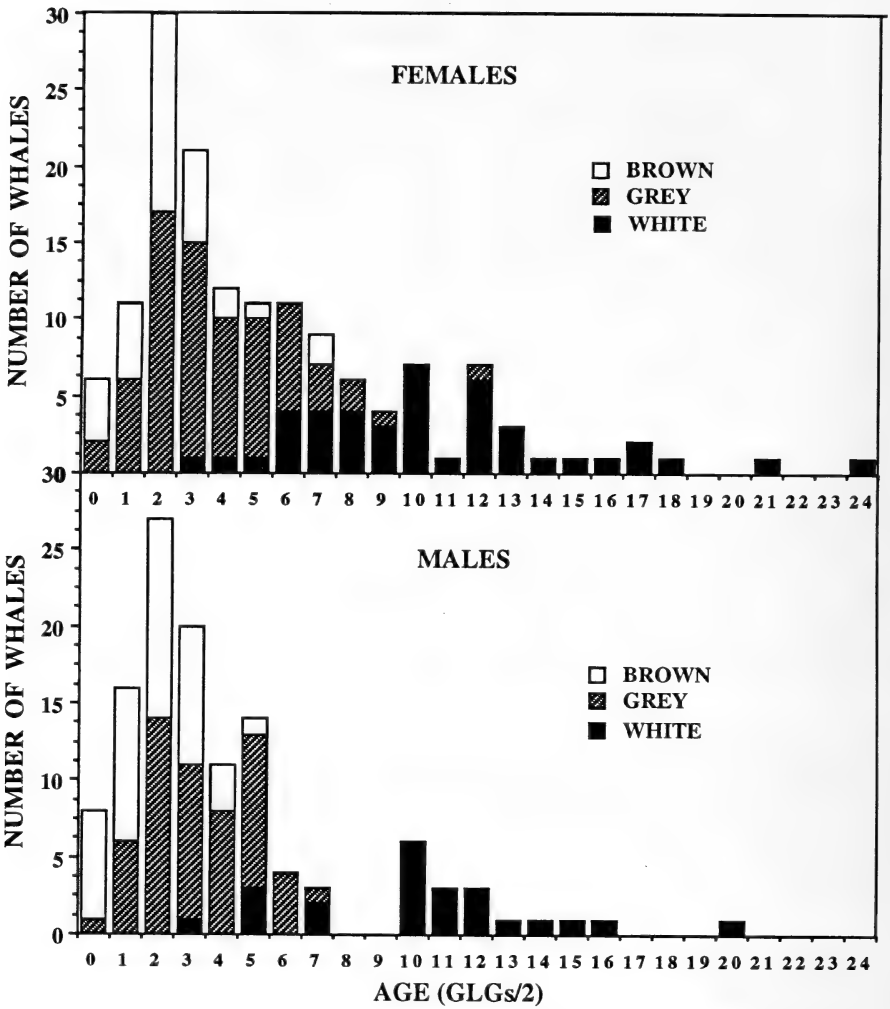

Fig. 3. Changes in colour phases in relation to age for female and male belugas from West Greenland.

1. Similar or identical methods for age estimation must be employed and preferably the techniques need validation from known age animals.
2. The samples collected from the harvest should be representative of the population and bias – if any – should be clearly discernible.
3. The survival need to be constant over time for the age groups involved in the estimation of survival and the population should be constant over the period when the age material was collected.

Age estimation technique

Identical methods for age estimation were used for all samples from Greenland and at least one person made readings of all teeth. Thus it seems reasonable to assume that the samples from Greenland are consistent with regard to age estimation and reading of GLGs. It is uncertain if the Russian samples are entirely comparable with those from Greenland. For validation of the age estimation method see HEIDE-JØRGENSEN et al. (1994).

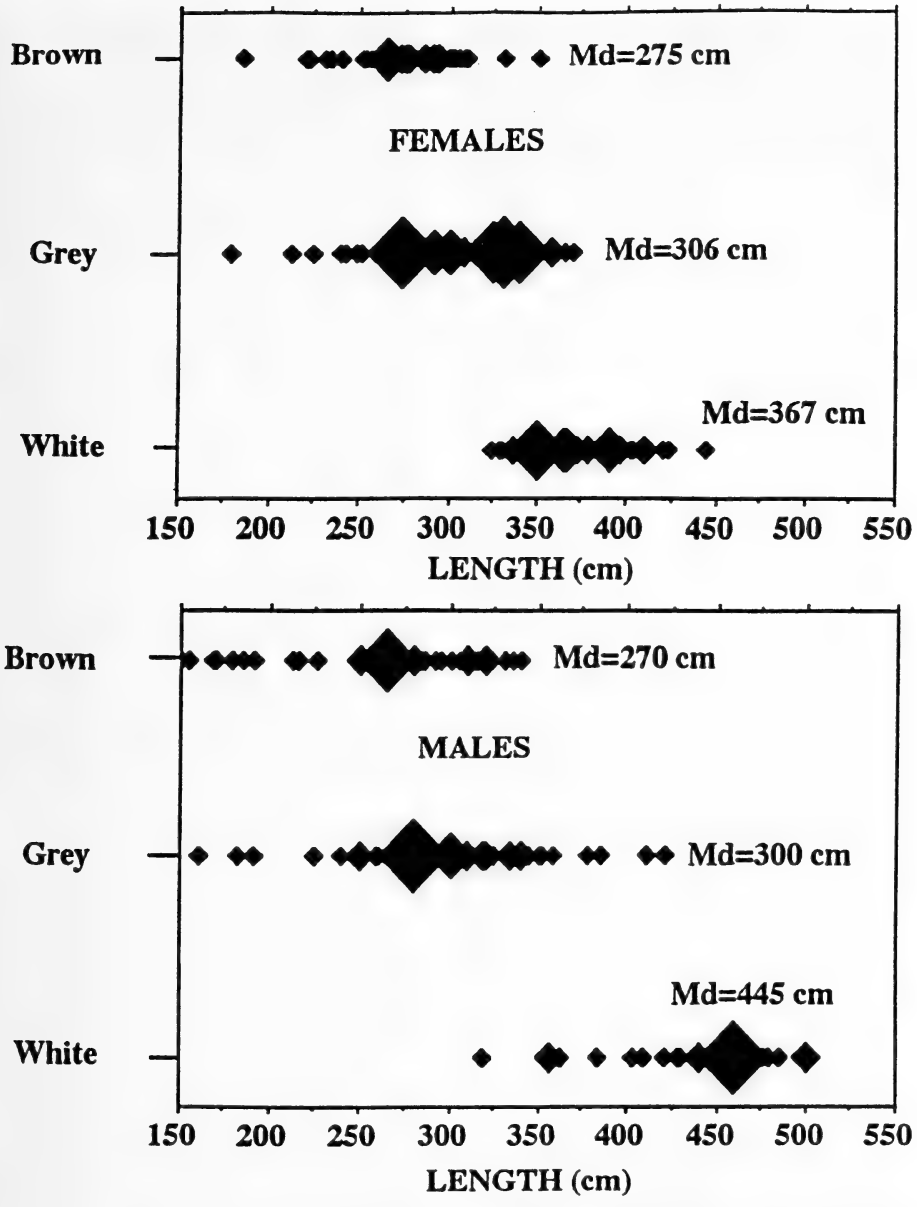

Fig. 4. Changes in colour phases in relation to length for female and male belugas from West Greenland. Md = median of cumulated numbers in each colour classification. Size of diamonds indicate the relative number of animals.

Bias in samplings

The samples collected for this study do not have an unbiased representation of the age and sex structure of the beluga population as the selectivity varies with different hunting methods and seasons. The catches in Qaanaaq and Upernavik are taken in a drive fishery during a short period, usually the last week of September in Qaanaaq or

the first week of October in Upernavik. The catches usually consist of entire herds of belugas ranging in size from 20 to 250 whales. The catches can be considered as random samples of the segment of the beluga population that migrates south in a coastal corndor. There may be different composition of the herds encountered and there is probably some selectivity towards larger herds. However, the samples from the catch in Upernavik can at least be expected to reflect the annual composition of that particular fishery better than any of the other samples.

According to HEIDE-JØRGENSEN et al. (1994) mean age at tooth wear, i. e. when neonatal line disappears, for female and male belugas from West Greenland is 7.7 and 6.0 yr of age, respectively. For the samples from Upernavik this implies that less than 30% of the samples were from whales that exceed these ages. It also indicates that females are generally older for the Upernavik samples than the males, because they have a higher mean age but a similar proportion of 'minimum age' classifications. Age at sexual maturity in belugas from West Greenland is around 4–7 yr for females and 6–7 yr for males (HEIDE-JØRGENSEN and TEILMANN 1994). Thus few mature males were taken in Upernavik, whereas some mature females were included in the catches at least until 1992. In 1993 and 1994 an increasing proportion of mature animals of both sexes were taken. This fact and the apparent increase in mean age of whales taken in Upernavik may be a result of the intensive exploitation of the younger age segments of the population. The whales that were caught in 1993 and 1994 were taken around 1 October as in previous years, few whales were available to be driven and nothing suggested any decrease in hunting effort (HEIDE-JØRGENSEN own observations). The gradual shift to older segments of the population may be explained by a depletion of young whales that exceeded the recruitment to the population. The hypothesis of a general decline in the beluga population is supported by results from aerial surveys conducted at the wintering grounds between 1981 and 1994 (see HEIDE-JØRGENSEN and REEVES 1996).

The mean age of the whales taken in the autumn catches in Upernavik in 1993 was indistinguishable from the mean age of belugas taken in Qaanaaq earlier in the same season. Both samples were similar in their age distribution to samples collected at Grise Fjord presumably in the autumn (STEWART 1994). Because there were temporal differences in age classes taken in Upernavik, the selectivity in the harvest is likely due to different availability of certain age classes during the autumn migration.

The hunt in Disko Bay is conducted from powered boats in open water during November through January or from the ice edge in spring during March through May. Mature whales of both sexes have for several of the years been found on the wintering grounds around Disko Bay. Since the open-water and ice edge hunt in this area is characterised by catches of small herds (<10) of whales or single animals it may be considered to reflect the age structure of the population more randomly than the autumn drive fishery for large herds. This is because pods of mature males are often separated from mature females with young of both sexes.

Changes in population size

Estimation of survival rates is confounded by both selectivity in catches and a large proportion of whales with minimum ages which results in underestimates of maximum life span and survival. However, due to differences in tooth wear (HEIDE-JØRGENSEN et al. 1994) the sample from the White and Kara seas have less whales with incomplete age and probably reflect the true age more accurately. Apparent survival rates calculated for West Greenland including only females >7 yr and males >9 yr indicated survival rates that were lower albeit not significantly lower than those estimated for the White and Kara seas. Some of the difference between the two areas can be attributed to differences in tooth wear.

The largest catches of belugas in the White and Kara seas took place before 1966 when vessel hunting was stopped (OGNETOV pers.

comm.). During the period when the samples were obtained the beluga population in the White and Kara seas had been subject to some harvesting although exact statistics are not available. The Report of the International Whaling Commission (1982) list catch figures between 135 and 672 belugas per annum for 1976–1982 with years without catches in the White, Barents and Kara seas. Other researchers estimate that catches in this area during 1975–1980 remained below 1 200 whales (Ognetov pers comm.). In the 1980s catches have been dwindling (according to IWC reports from 1985 to 1991) and ceased after 1990 (Ognetov pers. comm.). The reasons for the declining catches are more likely related to a reduced economical incentive for selling beluga products than to a reduced availability of the resource (Stanislav Belikov pers comm., Ognetov pers. comm.). Recently it has been suggested that the beluga population in the western Russian Arctic is in a non-declining state and could potentially support a harvest of up to 530 belugas (Ognetov pers. comm.).

During the 1980s catches have remained high in Greenland with an annual reported mean of 740 whales and there are no signs of a decline in hunting effort or in the economical incentives for the hunt (Heide-Jørgensen 1994). But aerial surveys of population densities on the wintering grounds in West Greenland indicate a linear decline of 4.7% (95% CI: 2.1–7.2) per year between 1981 and 1994 (Heide-Jørgensen and Reeves 1996). This population decline will severely affect the apparent survival rates calculated from the age material collected from the harvest. The apparent survival rates (q) can be converted into true annual survival rates (p) by $p = q/\lambda$, for the Robson and Chapman method and by $p = \exp(\ln q + (\lambda - 1))$ for the exponential model where λ, is the observed rate of population change. The true survival rates thereby become 0.85 and 0.83 for females and males, respectively, for the Robson and Chapman method applied to the belugas older than 9 yr in West Greenland. Similarly the true survival rates for the exponential model become 0.88 and 0.77 for females and males, respectively. These estimates are closer to the estimates derived from the age samples from the White and Kara seas.

In a study of harvested belugas in Alaska, Burns and Seaman (1986) estimated age for 528 belugas collected between 1977–79 and 1980–83 and found several whales older than 30 yr and two as old as 38 yr. From the distribution of 332 males and females older than 5 yr they estimated a mean mortality rate of 0.094, equivalent to an annual survival of 0.91 for both sexes. This estimate was based on both minimum and complete age classifications and is therefore again an underestimate of true survivorship. The onset of tooth wear may occur a few years later in Alaska than in Greenland, but that is probably not the main explanation for the large and significant difference in survival in the two areas. The catches in Alaska have been reported to be between 241 and 345 belugas per year during 1980 to 1983 or an estimated 1.9% to 2.6% of the provisional population estimates and with no indications of a population decline over that period (Lowry et al. 1989). Compared to the exploitation status in West Greenland it thus seems reasonable to assume that the apparent survival rates calculated for Alaskan belugas are less biased than estimates of survival in West Greenland. If the West Greenland age distribution is recalculated from age 5 yr (as for the Alaskan sample), females and males combined and corrected for population change with the negative exponential model, then the true annual survival rate becomes 0.9136, which is similar to the estimate from the far less exploited Alaskan population.

Changes in colour phase

Our estimates of change in colour phases are not entirely comparable to estimates from other studies, because several other researchers (e. g. Burns and Seaman 1986) have used four colour phases rather than the three as chosen for this study. We found that using three colour phases was less sub-

jectively based. The age for change from grey to white as reported from other areas is fairly similar to what we have seen in West Greenland (Sergeant 1973; Ognetov 1981), but detailed comparisons are not possible because the statistical methods used for deriving the mean age at change of colour are not specified. However, for belugas in East Baffin, Brodie (1971) reported that whitening occurs after 6 and 7 yr in females and males respectively, which is also evident from this study.

Acknowledgements

This study was supported financially by the Fisheries Directorate of the Greenland Home Rule Government and it was conducted by the Greenland Fisheries Research Institute. The beluga hunters in West Greenland are thanked for providing the samples of their harvest. We thank Royal Greenland and Greenland Trade Department for help with collection of samples. J. Jensen, J. Teilmann, F. Thomsen, and P. Barner Neve did the age determinations and the data entry. G. N. Ognetov (SEV-Pinro, Arkhangelsk) kindly made his data on white whale age frequencies in the White and Kara seas available. P. Møller Lund and U. Siebert are gratefully acknowledged for making the map and the German translation of the abstract.

Zusammenfassung

Alters- und Geschlechtsverteilung von Belugafängen, *Delphinapterus leucas*, in Westgrönland und Westrußland

Alter und Geschlecht wurden von Belugas oder Weißwalen *Delphinapterus leucas*, bestimmt, die von 1985–86 und 1989–97 von Eskimos in Westgrönland erlegt wurden. Der Probenumfang umfaßte 712 Weibchen und 596 Männchen. Es gab eine klare Trennung der Wale in der Jagdfischerei, die während des Herbstes in Qaanaaq (früher als Avenersuaq bekannt) und Upernavik, das nördlich des 74 °N Breitengrades liegt, stattfindet. Vor allem nicht geschlechtsreife Wale beider Geschlechter wurden zusammen mit geschlechtsreifen Weibchen gefangen. Zähne dienten der Altersbestimmung. Das Alter wurde an Jahreszuwachsringen (GLGs) im Dentin ermittelt unter der Annahme, daß zwei Zuwachsringe pro Jahr entstehen. Mittelwert und Median für Alter nahmen bei beiden Geschlechtern aus Upernavik von 1985 bis 1994 langsam zu. Sowohl nicht geschlechtsreife als auch geschlechtsreife Wale wurden in den Überwinterungsgebieten der Disko Bucht und südlich des 70 °N Breitengrades entnommen. Die Überlebensrate wurde nach zwei Methoden bestimmt: nach Robson und Chapman (1961) und über den natürlichen Logarithmus des negativen Exponenten einer an die Altersfrequenz angepaßten Kurve. Die Abschätzung der Überlebensrate wurde erschwert durch eine große Anzahl von Walen, denen bedingt durch eine Abnutzung der Zahnkrone nur ein Minimalalter zugeordnet werden konnte (d. h. keine Neonatlinie im Dentin). Die offensichtliche Überlebensrate von Belugas vor Westgrönlands wurde auf 0,81 und 0,79 für Weibchen bzw. Männchen geschätzt. Korrekturen dieser Abschätzung für eine beobachtete Bestandsabnahme von 4,7% pro Jahr ergaben eine tatsächliche Überlebensrate von 0,85 und 0,82 für Weibchen bzw. Männchen. Die Schätzwerte der tatsächlichen Überlebensrate sind geringer als die, welche für die Belugapopulation im Weißen Meer und der Karasee ermittelt wurden, fiir die Altersdaten aus den 70er und frühen 80er Jahren zur Verfügung standen, sowie publizierten Raten für Belugas aus Alaska (1977–83) mit einer vergleichbaren Alterszusammensetzung. Da der Grad der Bejagung in diesen Gebieten wesentlich niedriger ist, bestätigt die geringere Überlebensrate vor Westgrönland deutlich eine Abnahme der Population. Der Wechsel in der Hautfärbung von Grau zu Weiß tritt im mittleren Alter von 8,5 und 9,1 Jahren und bei einer mittleren Länge von 367 cm und 445 cm bei Weibchen bzw. Männchen auf.

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Mamm. biol. **66** (2001) 228–237
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

A new species of *Aepeomys* Thomas, 1898 (Rodentia: Muridae) from the Andes of Venezuela

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Receipt of Ms. 25. 04. 2000
Acceptance of Ms. 20. 09. 2000

Abstract

A new species of Neotropical rodent of the genus *Aepeomys* is described based on 24 specimens collected in the Andean region of Venezuela (Lara and Trujillo States). Among the diagnostic characters are: large size; first and fifth digits of pes not extending beyond the commissure of digits 2–3 and the first interphalangeal of digit four, respectively; posterior margin of zygomatic ramus of the maxilla with a distinctive notch; palate extending to the posterior border of M^3 or behind this molar; and paraflexus of M^1 and M^2 divided by an enamel bridge. In addition, the new species shows the following karyological features: 22 chromosomal pairs (2n = 44); 46 autosomal arms (FN = 46); a low proportion of two-armed elements; automosal chromosomes with abundant heterochromatin around the pericentromeric areas; and short arms of chromosomes X and Y entirely heterochromatic. According to the most recent systematic revision of the species assigned to *Aepeomys*, only two forms could be considered as members of this genus: *A. lugens* (the type species) and the taxon described herein. Both have geographic distributions restricted to highlands from the northern Andes, where the new species inhabits primary cloud forests and páramos located in the northeastern extreme of the Venezuelan Andean Cordillera.

Key words: *Aepeomys,* Thomasomyine, Taxonomy, Andes, Venezuela

Introduction

Neotropical sigmodontine rodents of the genus *Aepeomys* are members of the thomasomyine group, together with six additional genera whose systematic and phylogenetic relationships remain unclear: *Delomys* Thomas, 1917; *Phaenomys* Thomas, 1917; *Rhagomys* Thomas, 1917; *Rhipidomys* Tschudi, 1844; *Thomasomys* Coues, 1884; and *Wilfredomys* Avila-Pires, 1960 (Aguilera et al. 1994, 2000; Gómez-Laverde et al. 1997; Musser and Carleton 1993; Reig 1986; Voss 1993). After the original description of *Aepeomys* by Thomas (1898), some authors have considered this taxon as a synonym of *Thomasomys* (e. g., Cabrera 1961; Ellerman 1941; Handley 1976). Nevertheless, the results of the most recent systematic revision of these Andean genera (Pacheco unpubl. data) and several previous publications (e. g., Aguilera et al.

1616-5047/01/66/04-228 $ 15.00/0.

1994; Gardner and Patton 1976; Musser and Carleton 1993; Reig 1986; Soriano and Ochoa 1997; Soriano et al. 1998) are coincident in considering them as differentiated taxa.

Four nominal species of *Aepeomys* have been described (Cabrera 1961; Musser and Carleton 1993), although at the present time only two of them are recognized as valid taxa (both have geographical distributions restricted to highlands in the northern Andes): *Aepeomys lugens* (Thomas, 1896), recorded in several localities from western Venezuela to Andean Ecuador; and *A. fuscatus* (Allen, 1912), known from the western and central Andes of Colombia. However, the highly differentiated cranial morphology shown by *A. fuscatus* with respect to *A. lugens* (the type species of the genus) and other related forms, has been used among the arguments to consider *A. fuscatus* as representative of a neglected taxon whose evolutionary lineage could be more related with the oryzomyine tribe, representing perhaps an undescribed genus (Pacheco and Voss unpubl. data).

As part of the results of a field study on the small mammal communities inhabiting highland ecosystems from the Andean region of Venezuela (Lara and Trujillo States), we caught a series of thomasomyine specimens whose general morphology corresponds to *Aepeomys* (sensu stricto), although their external, cranial, and karyological features are not referable to previously known species assigned to this genus. Apparently, they represent a new species that we describe below. Some of these specimens, in addition to others collected in the Venezuelan Andes and cited herein as representatives of the new taxon, were formerly recorded as *Aepeomys lugens* or *Aepeomys* sp. by Handley (1976), Soriano et al. (1990), and Aguilera et al. (1994, 2000).

Material and methods

Specimens examined (all adults) are deposited in the following institutions: American Museum of Natural History (AMNH); the Colección de la Estación Biológica de Rancho Grande (EBRG), Maracay, Venezuela; the Colección de Vertebrados de la Universidad de Los Andes (CVULA), Mérida, Venezuela; and the Colección de Vertebrados de la Universidad Simón Bolívar (CVUSB), Caracas, Venezuela. Species, individuals and localities corresponding to this material are as follows: *Aepeomys fuscatus* (1; holotype). Colombia: Valle del Cauca, San Antonio, near Cali, 2 135 m (AMNH-32230). *Aepeomys lugens* (21, including two topotypes). Venezuela-Merida State: Páramo Los Conejos, 24 km W Mérida, 2 928 m (AMNH-96169; holotype of *A. ottlevi*); 5.5 km E + 2 km S Tabay (Middle Refugio), 2 600 m (EBRG-15569 and 15570); 1 km N + 2 km W Mérida (Santa Rosa), 2 020 m (EBRG-15571 and 15572); El Morro, 9 km SSW Mérida City, 2160 m (EBRG-22009 and 22010; topotypes). Tachira State: Páramo Los Colorados (Parque Nacional Páramos Batallón y La Negra), 12 km SSE El Cobre, 3200 m (EBRG-21513 to 21523; CVULA-5747, 5751, and 5753). *Aepeomys reigi* (15). Venezuela-Lara State: El Blanquito, 17 km SE Sanare, Parque Nacional Yacambú, 1 600 m (CVULA-2738; EBRG-4208, 21735, 21440, and 22580 to 22582); Road El Blanquito-Sanare, km 6, Parque Nacional Yacambú, 1 700 m (EBRG-10621); El Avileño, near El Blanquito, 9 km SE Sanare, Parque Nacional (Yacambú, 1 600 m (CVULA-2710 and 2718). Trujillo State: Macizo de Guaramacal, 9 km ESE Boconó, Parque Nacional Guaramacal, 3 100 m (CVULA-3350); Guaramacal, 5 km E Boconó, Parque Nacional Guaramacal, 2 230 m (CVULA-3139); Pica La Toma, 7 km E Boconó, Parque Nacional Guaramacal, 2 300 m (EBRG-22714); 14 to 15 km E Trujillo, near Hacienda Misisí, 2 225 to 2 350 m (EBRG-15567 and 15568). *Thomasomys hylophilus* (5). Venezuela: 35 km S + 22 km W San Cristobal (Buena Vista), Táchira State, 2395 m (EBRG-15597 to 15601). Thomasomys laniger (5) Venezuela: 4 km S + 6.5 km E Tabay (La Coromoto), Mérida State, 3 170 m (EBRG-15227 to 15230); 5 km S + 7 km E Tabay (near La Coromoto), Mérida State, 3 251 m (EBRG-15231). Thomasomys vestitus. (1) Venezuela: El Baho, 3 km SE Santo Domingo, Mérida State, 3 010 m (EBRG-32012).

Age criteria follow Voss (1991). Cranial measurements were taken according to Voss (1988, 1991). Nomenclature of the occlusal components of molar teeth follows Reig (1977). Karyological analyses were carned out on 13 specimens of *A. lugens* and nine specimens representing the new taxon (five from Lara State and four from Trujillo State), including the sample described by Aguilera et al. (2000). Bone marrow metaphase chromosomes were obtained by a modification of Ford and Hamerton's (1956) in vivo colchicine

technique. C- and G-banding patterns were obtained as described by BARROS and PATTON (1985) and CHIARELLI et al. (1972), respectively. Chromosome nomenclature followed LEVAN et al. (1964). Fundamental numbers (FN) are autosomal arm numbers.

Results

Aepeomys reigi new species

Holotyoe: A female (dry skin, skull, and karyotype analysis; CVUSB-928) with adult pelage, fused sphenoccipital suture, and the third molar erupted (age class IV). Collected by MARISOL AGUILERA et al. in August 1986 at El Blanquito, Parque Nacional Yacambú, 17 km SE Sanare, Lara State, Venezuela, 1 600 m (approx. 9°40′ N; 69°37′ W; Fig. 1).

Paratypes: Seven specimens (6 as dry skins and skulls; one in alcohol) with karyotype analysis: Lara State, Parque Nacional Yacambú, El Blanquito, 17 km SE Sanare, 1 600 m; 3 males and 1 female collected by

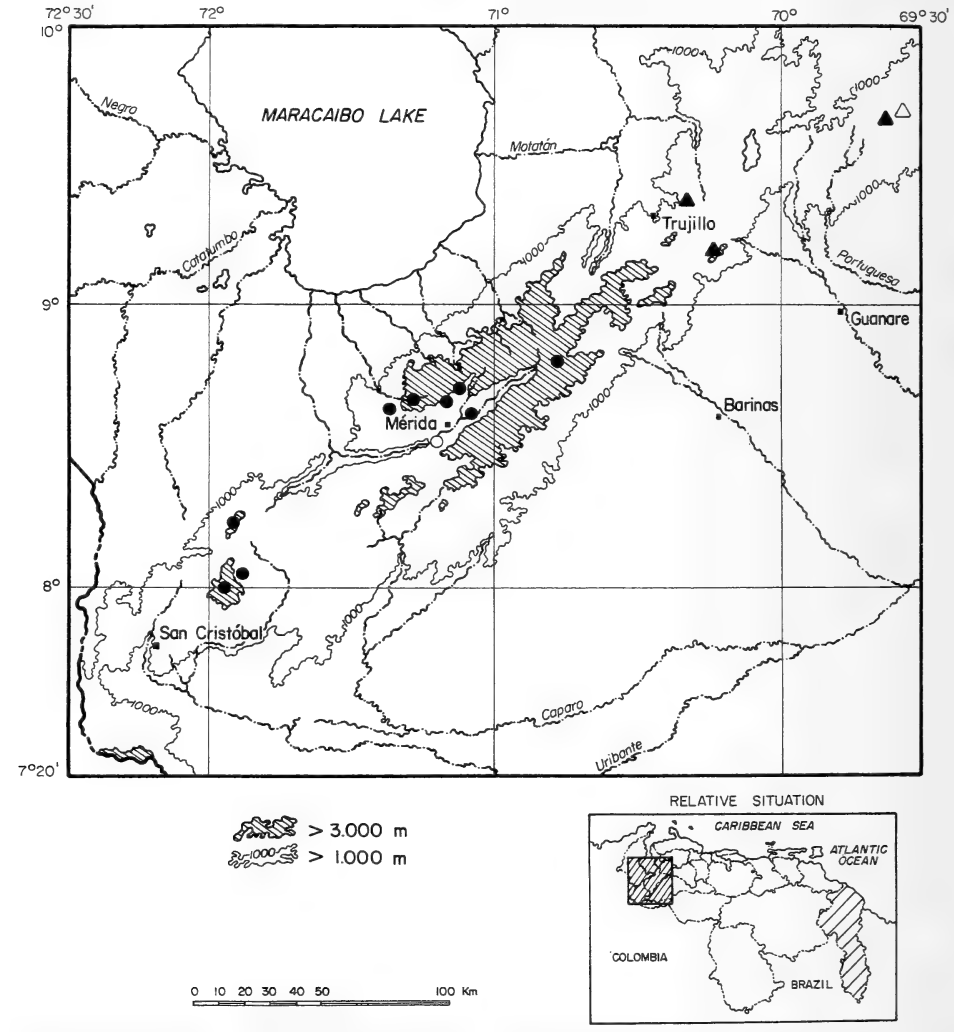

Fig. 1. Distribution of *A. reigi* (triangles) and *A. lugens* (circles) in Venezuela. White symbols correspond to the type localities.

M. Aguilera et al. (CVUSB-927, 1365, 1419, and 1420). Trujillo State, Parque Nacional Guaramacal (approx. 9°15′ N; 70°12′ W), Pica La Toma, 7 km E Boconó, 2 300 m; 1 male and 2 females collected by J. Ochoa et al. (EBRG-22715 to 22717).

Etymology: The epithet *reigi* honors the memory of Dr. Oswaldo Reig, who devoted his life to the study of the systematics and evolution of South American rodents, and made important contributions to the education and encouragement of many Latin American mammalogists.

Distribution: Known only in highlands (1 600–3 230 m) from the northeastern extreme of the Venezuelan Andes (Lara and Trujillo States).

Diagnosis: Size large for the genus as indicated by external and cranial measurements (Tab. 1), in addition to postcranial skeleton development; first and fifth digits of pes not extending beyond the commissure of di-

Table 1. Selected external and cranial measurements (in millimeters) of adult specimens of *Aepeomys reigi* and *Aepeomys lugens* (age classes 2–4) from Venezuela. Data are: Mean ± SD, (range), and sample size.
[1] Sample includes two topotypes and the holotype of *Aepeomys* (see specimens examined).

Measurement	*A. reigi*	*A. lugens*[1]
Length of head and body	113.6 ± 5.88 (104–125)15	110.1 ± 7.54 (100–119)7
Length of tail	127.1 ± 8.29 (116–142)15	121.7 ± 4.15 (114–127)7
Length of hind foot	27.9 ± 1.30 (25–30)15	27.0 ± 3.96 (20–30)7
Condylo-incisive length	27.8 ± 0.84 (26.6–29.3)16	26.6 ± 0.58 (25.8–27.6)17
Length of diastema	8.6 ± 0.31 (8.0–9.0)18	8.2 ± 0.25 (7.7–8.7)18
Length of molars	4.5 ± 0.11 (4.3–4.8)18	4.3 ± 0.12 (4.0–4.4)18
Length of incisive foramen	5.6 ± 0.22 (5.2–6.0)16	5.5 ± 0.20 (5.1–5.9)18
Breadth of incisive foramen	2.4 ± 0.18 (2.2–2.7)16	2.3 ± 0.14 (2.0–2.5)18
Breadth of rostrum	5.0 ± 0.23 (4.6–5.3)14	4.5 ± 0.27 (4.0–5.1)16
Breadth of palatal bridge	3.8 ± 0.16 (3.5–4.0)17	3.5 ± 0.25 (3.0-4.0)17
Breadth of zygomatic plate	1.8 ± 0.13 (1.6–2.1)18	1.8 ± 0.14 (1.5–2.0)18
Least interorbital breadth	6.1 ± 0.17 (5.9–6.4)17	6.0 ± 0.26 (5.6–6.4)18
Breadth of braincase	13.3 ± 0.22 (12.9–13.7)17	13.1 ± 0.35 (12.4–13.8)18
Zygomatic breadth	14.8 ± 0.37 (14.2–15.6)15	14.1 ± 0.38 (13.6–14.9)17
Depth of incisors	1.3 ± 0.11 (1.0–1.4)17	1.2 ± 0.11 (1.0–1.4)18
Length of orbital fossa	9.1 ± 0.24 (8.6–9.6)17	8.4 ± 0.21 (8.0–8.8)17

gits 2–3 and the first interphalangeal of digit four, respectively; posterior margin of zygomatic ramus of the maxilla with a distinct notch; palate extending to the posterior border of M^3 or behind this molar; interparietal length (along an antero-posterior axis) near half of parietal length; and parafiexus of M^1 and M^2 divided by an enamel bridge that crosses from the paracone to the base of the anteroloph. Karyotype with 22 chromosomal pairs (2n = 44), 46 autosomal arms (FN = 46), a low proportion of two-armed elements, the automosal chromosomes with abundant heterochromatin around the pericentromeric areas, and the short arms of the chromosomes X and Y entirely heterochromatic.

Description: Length of head and body 104–125 mm. Tail approximately as long as body (Tab. 1), sparsely covered by short dark-brown hairs and unicolored (dark above and below). Legs, heels, and dorsal surface of pes sparsely covered by brown hairs. Body pelage dense and soft (longer in specimens from the highest altitudes). Dorsal coloration ranging from dark gray-brown to reddish gray-brown, with moderately to intensively hoary appearance. Dorsal fur consisting of shorter hairs (approx. 9–12 mm) with golden tips and scattered longer hairs (approx. 12–15 mm) with dark brown tips (in a few cases with whitish tips); both having the basal 75% gray. Ventral pelage shorter (approx. 7 mm) and paler than dorsum, ranging from moderately to intensively hoary (hairs with golden tips and the basal 75% gray). Pinnae 18–21 mm long and furred on both sides; inside part yellowish, contrasting in color with the dorsal fur. Manus cream-colored and paler than hind feet. Pes narrow and long (adapted for terrestrial life; Tab. 1); first and fifth digits not extending beyond the commissure of digits 2–3 and the first interphalangeal of digit four, respectively.

Incisors narrow and moderately developed (not robust), with sharp tips. Upper incisors with the anterior surface slightly concave. Maxillary and mandibular toothrows relatively short (Tab. 1; Fig. 2); first molars antero-posteriorly elongated (length averages approximately 50% of their respective toothrows). Upper molars with rounded protocone and hypocone, and the paracone and metacone antero-posteriorly sharp. Paraflexus of M^1 and M^2 divided by an enamel bridge that crosses from the paracone to the base of the anteroloph, producing an internal fosseta. M^3 with triangular shape in dorsal view. M_1 with a distinctive protolophid in most specimens, which reaches the cingulum.

Skull with general appearance resembling a typical *Aepeomys* (see Fig. 2 and 3 for comparisons with *A. lugens*). Rostrum narrow and elongated (approx. 1/3 of the greatest length of skull), with acute profile and only the external capsule of the nasolacrimal foramen exposed in dorsal view; nasal and premaxillary bones extending beyond the anterior surface of incisors and the gnathic process to form a distinct rostral tube. Nasals laterally concave and flat in dorsal profile, forming a continuous surface with the premaxillae; posterior border extending to the level of the zygomatic plate. Interorbital constriction relatively broad, without concealing (in dorsal view) the labial ridge of maxillary and the molars. Braincase moderately inflated and slightly concave in dorsal profile; the posterior surface concealing the occipital condyles in dorsal view. Interparietal length (along an antero-posterior axis) near half of parietal length. Lambdoidal ridges scarcely developed. Zygomatic arches completely ossified, filamentous and fragile. Zygomatic plate relatively narrow (Tab. 1; Fig. 3), with the posterior edge extending to the first molar (Fig. 2). Posterior margin of zygomatic ramus of the maxilla with a distinct notch. Lumen of the infraorbital foramen compressed laterally and expanded dorso-ventrally. Gnathic process scarcely developed. Masseteric tubercle large. Palatal bridge moderately long (Tab. 1; Fig. 2), extending to the posterior border of M^3 or behind this molar. Posterior margin of palate without medial process in most specimens; therefore, the anterior margin of the mesopterygoid fossa has a shallow shape. Incisive foramina extending posteriorly beyond the masseteric tubercle,

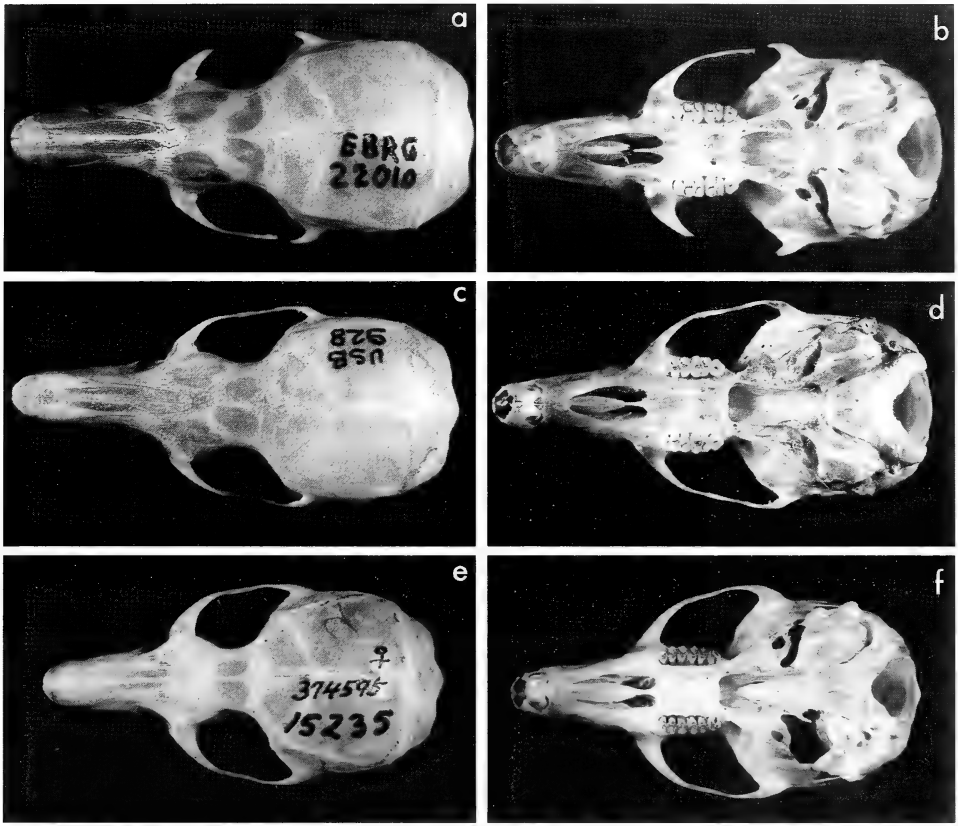

Fig. 2. Dorsal and ventral views of crania of *Aepeomys lugens* (topotype; a, b), *Aepeomys reigi* (holotype; c, d), and *Thomasomys laninger* (e, f). Approx. X1.9.

without reaching the level of the first molar; margins of the anterior half strongly convergent anteriorly. Postglenoid foramen compressed dorso-ventrally and expanded antero-posteriorly. Foramen magnum with the inferior border almost reaching the level of the auditory bulla. Auditory bulla moderately inflated. Mandible with the tip of the condylar process behind the angular process.

Karyotype with 22 chromosomal pairs (2n = 44), 46 autosomal arms (FN = 46), and low proportion of two-armed elements (Aguilera et al. 1994). Automosal chromosomes with abundant heterochromatin around the pericentromeric areas. Short arms of chromosomes X and Y entirely heterochromatic (Aguilera et al. 2000).

Comparisons: Among the thomasomine group, the genus most closely related to *Aepeomys* is believed to be *Thomasomys* (Aguilera et al. 2000; Gardner and Patton 1976), whose cranial morphology is clearly differentiated from *A. reigi* and *A. lugens* in the following features (Fig. 2 and 3): shorter rostrum; zygomatic arches more expanded laterally; narrower interorbital region; braincase less inflated at the level of lambdoidal ridges; broader zygomatic plate; larger incisive foramina (almost reaching the first molars); and shorter palate (posterior border not extending beyond the third molar). In addition, Venezuelan species of *Thomasomys* are larger (*T. aureus*, *T. hylophilus*, and *T. vestitus*) and/or have much paler brownish fur (*T. hylophi-*

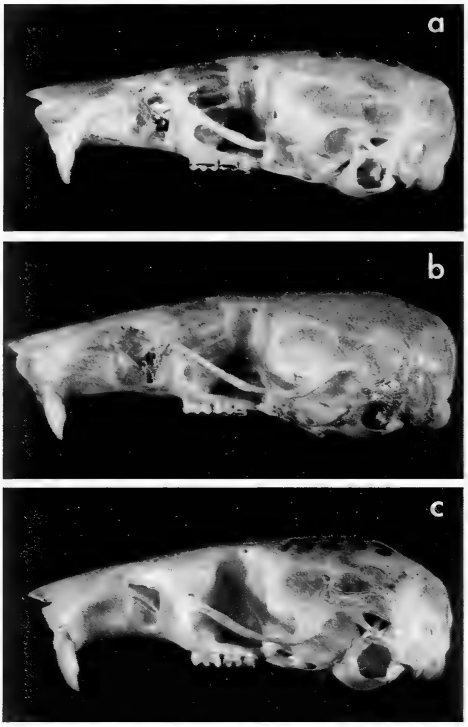

Fig. 3. Lateral views of crania of *Aepeomys lugens* (topotype; a), *Aepeomys reigi* (holotype; b), and *Thomasomys laniger* (c). Approx. X1.8.

lus, *T. vestitus* and *T. laninger*) than *Aepeomys lugens* and *A. reigi*.

With respect to the species previously included within *Aepeomys*, *A. reigi* resembles the external and cranial morphology of *A. lugens*, except for the following differences: size larger (Tab. 1); fur on head and body shorter and rougher; manus and pes broader; legs, heels, and dorsal surface of pes sparcely haired (densely haired in *A. lugens*); first and fifth digits of pes shorter; posterior margin of zygomatic ramus of the maxilla with a distinct notch, rather than shallow as in *A. lugens* (as consequence, in *A. reigi* the orbital fossa is larger, Tab. 1); incisive foramina broader, with margins showing a more convergent position anteriorly; interparietal longer in most specimens (antero-posterior midline near half of the parietal length, rather than 30–40% as in *A. lugens*); palate extending to the posterior border of M^3 or behind this molar (near or before the posterior border of M^3 in *A. lugens*); posterior margin of palate without medial process in most specimens (therefore the anterior margin of the mesopterygoid fossa is shallow rather than incipiently biconcave as in *A. lugens*); maxillary toothrow relatively longer; M^3 larger and triangular in dorsal view (rounded in *A. lugens*); M^1 and M^2 with paraflexus divided by an enamel bridge (continuous in most specimens of *A. lugens*); coronoid and condylar processes broader and larger, producing deeper sigmoid and angular notches, respectively. M_1 with a distinctive protolophid in most specimens, which reaches the cingulum (reduced or absent in *A. lugens*). Some of these features (particularly those related with cranial and dental morphology) show the maximun divergence in specimens of *A. reigi* from Lara State. In addition, *A. lugens* has a very different karyotype, with fewer chromosomal pairs (2n = 28 vs 2n = 44), more autosomal arms (FN = 48 vs FN = 46), and a lower concentration of heterochromatin (especially conspicuous in the short arms of two autosomal pairs and the Y chromosome; AGUILERA et al. 1994, 2000). These chromosomal variations were consistent when we compared *A. reigi* with specimens of *A. lugens* from two localities in Venezuela: the type locality (El Morro, Mérida State) and Páramo Los Colorados, Táchira State (AGUILERA et al. 2000).

Regarding *A. fuscatus* the external and cranial features of this species show a high degree of differentiation with *A. reigi*, revealing a morphological pattern that appears to be taxonomically separated from the thomasomyine group and perhaps corresponds to a taxon whose evolutionary lineage is more related with the oryzomyine tribe (PACHECO and Voss unpubl. data). Among the most conspicuous characteristics in *A. fuscatus* supporting this assessment are: darker fur coloration; shorter and broader rostrum (without the acute profile shown by *A. reigi* and *A. lugens*); anterior portion of zygomatic arches more expanded and broader; broader zygomatic plate; narrower interorbital breadth; braincase less inflated; short-

er incisive foramina and palate; and broader mandibular branches. These features, in addition to the extremely high number of chromosomal pairs (2n = 54) and autosomal arms (FN = 62) reported by GARDNER and PATTON (1976) for *A. fuscatus* are clear evidences of a differentiated evolutionary pattern with respect to *Aepeomys*.

Discussion

The morphological variation between *A. reigi* and *A. lugens*, in addition to the high degree of differentiation in the number and structure of chromosomes, support the hypothesis of evolutionary divergences in both species, such as it has been proposed for other thomasomyine rodents (GARDNER and PATTON 1976; GÓMEZ-LAVERDE et al. 1997). Despite the higher diploid number in *A. reigi* with respect to *A. lugens* (44 vs 28), and based on their similarities in fundamental numbers (46 vs 48, respectively), we postulate that karyological differences found in these species could be reached by chromosomal rearrangements evolving principally robertsonian changes (AGUILERA et al. 2000).

An important aspect within the evolutionary context of *Aepeomys* species, is the direction of chromosomal transformation in *A. reigi* and *A. lugens*. According to GARDNER and PATTON (1976), thomasomyine karyotypes are characterized by a generalized condition of diploid number of 42 or 44, in addition to a predominantly acrocentric autosomal complement. This generalized condition is present in *A. reigi* and allows to consider it as a primitive form. This fact, together with the great proportion of two-armed elements shown by the karyotype of *A. lugens*, are arguments to postulate this last species as a derived form (AGUILERA et al. 2000). Some complementary evidences supporting this hypothesis are the differences in quantity and distribution of the constitutive heterochromatin: low and chromosomal restricted in *A. lugens* vs abundant and distributed in chromosomes of *A. regi*; the last pattern has been associated with a primitive condition in eukariotic chromosomal evolution (IMAI 1991).

The geographic distribution of *A. reigi* seems to be allopatric with respect to *A. lugens*, at least in the northeastern extreme of the Venezuelan Andean Cordillera. However, we do not reject the possibility of sympatric distribution in highlands (>1 500 m) near to the border of Merida and Trujillo States. Future karyological studies, in a more extensive area, are required to provide a further diagnosis on the biogeographic patterns of these taxa. Other non-volant small mammals recorded at Yacambú and Guaramacal are: *Caluromys philander*, *Didelphis albiventris*, *Didelphis marsupialis*, *Gracilinanus dryas*, *Marmosops fuscatus*, *Micoureus demerarae*, *Cryptotis meridensis*, *Mustela frenata*, *Sciurus granatensis*, *Heteromys anomalus*, *Akodon urichi*, *Ichthyomys hydrobates*, *Microryzomys minutus*, *Neacomys tenuipes*, *Oecomys flavicans*, *Oligoryzomys fulvescens*, *Oryzomys meridensis*, *Rhipidomys venustus*, *Rhipidomys venezuelae* and *Thomasomys laninger* (SORIANO et al. 1990).

The known ecological distribution of *A. reigi* corresponds to primary cloud forests (humid montane forest according to HUBER and ALARCÓN 1988) and small patches of páramos surrounded by continuous masses of cloud forests; these ecosystems, in addition to seasonal forests and evergreen dry forests, have been previously recorded among the ecological conditions used by *A. lugens* (HANDLEY 1976; SORIANO et al. 1990). *A. reigi* appears to be a relatively uncommon species along its ecological range. Even though field data for páramos are insufficient, sampling efforts of 3 724 trap-nights in cloud forests, accumulated during inventories conducted by the authors, allowed to catch 27 individuals of *A. reigi* that represented 10.6% of total non-volant small mammals trapped in this ecosystem (*Oryzomys albigularis* and *Heteromys anomalus* were the dominant species). Collected specimens have been found on the ground in densely forested sites (beside logs, at the base of trees, in rocky places, along trails, or near small streams) or in open areas (close to the

ecotone between páramos and forests) covered by shrubs and herbaceous vegetation (mainly *Espeletia schultzii* and grasses). We used as bait a mixture of sardine or bacon with oats, peanut butter, and/or kitchen oil. Some specimens maintained in captivity were fed with insects (Orthoptera), domestic fruits, and seeds. Hairs and insect remains (Coleoptera) were found in the stomach content of one specimen from Yacambú. Three males collected in August and December showed inguinal testis.

Acknowledgements

We would like to thank the assistance given during field work by Jhonny Murillo, Richard Gavidia, Amelia Díaz de Pascual, Tina Oliveira, Rosa Moscarella, Eladio Márquez, Ernesto Panier, Mariapia Bevilacqua, Lourdes Suárez, Norberto Rebolledo, Eisamar Ochoa, Mariángela Ochoa, Elizandra Delgado, INPARQUES, and the Asociación Venezolana para el Estudio de los Mamíferos. Javier Sánchez and Robert Voss gave important comments to the first draft of the manuscript and allowed revise the specimens housed in the Colección de la Estación Biológica de Rancho Grande and the American Museum of Natural History, respectively. Antonio Pérez Zapata (†) and Marcela Gómez provided valuable information used in this description. Field researches of the senior author are supported by Wildlife Conservation Society. This study is a contribution of the project "Diversidad de Pequeños Mamíferos en Ecosistemas de Tierras Altas del Norte de Venezuela" (CONICIT-RP-VII-240056).

Zusammenfassung

Eine neue Art von *Aepeomys* Thomas, 1898 (Rodentia: Muridae) aus den Anden von Venezuela

Es wird eine neue Art der neotropischen Nagergattung *Aepeomys* beschrieben. Grundlage bildet eine Serie von 24 Exemplaren, die in Andenregionen (Lara und Trujillo) von Venezuela gesammelt wurde. Diagnostische Merkmale sind unter anderem; große Art; erste und fünfte Zehe reichen nicht über die Kommissur der zweiten und dritten Zehe hinaus; Hinterrand des zygomatischen Astes des Maxillare mit deutlichem Knoten versehen; Palatinum zieht bis zum Hinterrand des M^3 oder darüber hinaus; Paraflexus am M^1 und M^2 durch eine Schmelzbrücke geteilt. Die neue Art ist auch durch einen Karyotyp von 2n = 44, NF = 46 gekennzeichnet; die perizentromerische Region der Autosomen weist viel Heterochromatin auf; die kurzen Arme der X- und Y-Chromosomen sind vollständig heterochromatisch. Die Ergebnisse einer systematischen Revision zeigen, daß nur zwei Arten der Gattung *Aepeomys* angehören: *A. lugens* (Typusart) und die hier beschriebene neue Art, *A. reigi* n. sp. Beide sind in ihrer Verbreitung auf die nördlichen Anden beschränkt, wo die neue Art primäre Nebelwälder und Paramos im äußersten Nordosten Venezuelas bewohnt.

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Mamm. biol. **66** (2001) 238–250
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Developmental stability and protein heterozygosity in a local population of Iberian hares (*Lepus granatensis*)

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Receipt of Ms. 11. 04. 2000
Acceptance of Ms. 13. 09. 2000

Abstract

Various studies have revealed a positive effect of heterozygosity on developmental stability in animals of diverse taxa. In homeothermic vertebrates, however, no clear picture has so far emerged in this context. Here, we test the influence of heterozygosity on the developmental stability of adult-sized skulls of 63 Iberian hares (*Lepus granatensis*) from a local population in Portugal. 44 allozyme and blood protein loci were screened by horizontal starch gel electrophoresis, agarose electrophoresis, and isoelectric focusing. This yielded eleven polymorphic loci, that were used to calculate individual heterozygosity. Levels of fluctuating asymmetry (FA) of three morphological character systems (15 epigenetic dental characters, ten non-metric skull traits, six metric skull variables) were determined and used as indicators of the levels of developmental homeostasis of single hares. Overall individual heterozygosity did not correlate with respective FA levels in any of the three morphological character systems. However, a trend towards a negative relationship between metric FA and heterozygosity suggested that there might be a slight positive influence of heterozygosity on developmental stability of the morphometric system, but it could be masked by various seasonal exogenic factors.

Key words: *Lepus granatensis*, heterozygosity, fluctuating asymmetry, developmental homeostasis

Introduction

Developmental homeostasis, i. e., the ability to buffer against minor random deviations from metabolic pathways during growth, can be reduced by environmental and genetic stress (e. g., Møller and Swaddle 1971). The level of fluctuating asymmetry (FA) is commonly used to evaluate the degree of developmental stability (e. g., Zakharov 1981; Palmer and Strobeck 1986; Novak et al. 1993). FA is defined as random departures from the ideal bilateral symmetry of morphological traits with a population mean around zero and a normal distribution (e. g., Palmer 1994). More symmetric animals apparently have higher fitness, as indicated by diverse fitness components, than asymmetric (Møller 1997). It has been proposed that heterozygosity stabilizes the ontogenetic development, so that genetically determined pathways are more

1616-5047/01/66/04-238 $ 15.00/0.

precisely expressed in the phenotype of an organism (e. g., HANDFORD 1980; FLEISCHER et al. 1983; MITTON and GRANT 1984; MITTON 1993 a, b, 1995).

In local populations of adult brown hares (*Lepus europaeus*) from central Europe FA was negatively correlated with population-specific allozyme heterozygosity in non-metric but not in metric skull characters. This suggested a differential effect of heterozygosity on the developmental stability of non-metric and metric skull characters (HARTL et al. 1995). However, no such relationship was found in brown hares from Britain and New Zealand, that had lower levels of genetic variability than central European brown hares (SUCHENTRUNK et al. 2000), and FA in both character systems was even lower than in brown hares from central Europe (SUCHENTRUNK et al. 1998). Such inconsistencies of the relationship between heterozygosity and FA might result from different evolutionary histories of population sets. In addition, varying levels of environmental stress may conceal effects of heterozygosity on FA to different degrees (e. g., PANKAKOSKI 1985; PANKAKOSKI et al. 1992; PALMER and STROBECK 1986; BORISOV et al. 1997; MØLLER and SWADDLE 1997; ZAKHAROV et al. 1997 a).

Here we, examine whether or not heterozygosity has a significant effect on developmental homeostasis of Iberian hares (*Lepus granatensis*) from one local population in a relatively homogeneous environment. In particular we examine whether overall individual heterozygosity is negatively correlated with FA in three character systems of the skull; and if so, whether such a relationship becomes generally apparent in all three character systems.

Material and methods

Collection of specimens and samples for genetic analysis

Sixty three adult-sized Iberian hares (*Lepus granatensis*) were collected at Pancas (38°48′ N/ 8°57′ W), approx. 15 km east of Lisbon, Portugal, during regular hunts between October 1997 and October 1999. Pancas is situated in a lowland region (29 m a. s. l.) that has a Mediterranean climate, with 500–600 mm average annual rainfall, mainly in October–April, and 16 °C mean annual temperature (C. N. A. 1983). The vegetation is characterized by tree stands of *Quercus suber*, *Pinus pinea*, as well as marshy areas, pastures, and arable land.

All hares were sexed by inspection of their primary reproductive organs. They were classified as "adults", based on body size and weight, absence of the epiphyseal protrusion of the ulna (cf. SUCHENTRUNK et al. 1991 for European brown hares), the ossification pattern of skull sutures, and the shape and size of the processus supraorbitales (e. g. PALACIOS and LOPEZ 1980).

Blood samples were taken shortly after the death of the animals by cardiac puncture and collected in ETDA-coated tubes. Red blood cells were separated from plasma by centrifugation at 1 500 g for 5 min at 4 °C and stored at –20 °C. Liver, kidney, and spleen tissue samples were taken and frozen at –20 °C.

Protein heterozygosity

Fourty-four loci encoding for allozymes and blood proteins were initially screened for genetic variability. This set largely included loci that were already studied by HARTL et al. (1989, 1990, 1992, 1993, 1994, 1995) for brown hares (*L. europaeus*), SUCHENTRUNK (1993, 2000), SUCHENTRUNK et al. (1998, 1999, 2000 a, b, c, SUCHENTRUNK, unpubl. data) for brown hares, mountain hares (*L. timidus*), Iberian hares, and several hare species from Mexico, and by ALVES et al. (2000) for Iberian hares. Direct side-by-side comparisons of migrating allozymes on the same gels were made to infer alleles at polymorphic loci from zymograms (cf. HARRIS and HOPKINSON 1976). Eleven loci revealed allelic polymorphism and were considered in the present analyses. They are listed in table 1 along with the respecitve allozyme/blood protein names, E. C. numbers, and methodological specifications.

Allele frequencies, locus-specific heterozygosities (h_o, h_e), and exact Fisher's tests for deviation of observed genotypes from Hardy-Weinberg expectations were calculated by using the BIOSYS-1 pc package, release 1.7 (SWOFFORD and SELANDER 1989). For the combined analysis with the morphological data, genotypes at all polymorphic loci were categorized as "homozygous" or "heterozygous", irrespective of allele composition. The overall heterozygosity (H) of an individual was calculated as the percentage of heterozygous loci.

Table 1. Enzyme systems/blood proteins and respective loci used in the combined analyses with fluctuating asymmetry of Iberian hares from Pancas. For allele frequencies, see Tab. 4. h_e – unbiased locus-specific heterozygosity, h_o – direct count (observed) locus-specific heterozygosity. Methodological specifications of protein screening (method. specific.) are in the footnote.

enzyme systems/blood proteins (name, code, E.C. number)	locus	method. specific.	h_e	h_o
NADH-diaphorase (DIA, 1.6.2.2)	Dia-2	SGE/G	0.258	0.143
Esterases (ES, 3.1.1.1)	Es-1	SGE/G	0.481	0.548
Acid phosphatase (ACP, 3.1.3.2)	Acp-2	SGE/G	0.016	0.016
Peptidase B (PEPB, 3.4.11)	Pep-B	SGE/A	0.338	0.320
Aminoacylase-1 (ACY-1,3.5.1.14)	Acy-1	SGE/G	0.182	0.127
Mannose phosphate isomerase (MPI, 5.3.1.8)	Mpi	SGE/G	0.284	0.176
Hemoglobin alpha chain (HBA)	Hba	SGE/A	0.501	0.366
Transferrin (TF)	Tf	AGE	0.154	0.083
Hemopexin (HPX)	Hpx	IEF	0.272	0.308
Vitamin D binding protein (GC)	Gc	IEF	0.146	0.154
Properdin factor B (BF)	Bf	IEF	0.370	0.333

SGE/A – horizontal starch gel electrophoresis and protein staining according to Alves et al. (2000), SGE/G – horizontal starch gel electrophoresis and protein staining according to Grillitsch et al. (1992), AGE – agarose gel electrophoresis (Teisberg 1970), IEF and HIEF – isoelectric focusing in carrier ampholytes and hybrid pH-gradients according to (Alves et al. 2000).

In a few individuals ambiguous allele interpretations at one or more loci resulted in a slightly reduced number of polymorphic loci for calculation of H. Hence, H-values were used in further analyses only if based on at least nine polymorphic loci. Sex-dependence of locus-specific heterozygosity (h) and H was tested by Mann-Whitney U-tests, respectively. Associations of homozygous or heterozygous genotypes among pairs of loci were checked by exact Fisher's or chi^2 tests, based on the Sequential Bonferroni procedure (alpha = 0.05) to account for multiple and partly dependent tests (Rice 1989). The Sequential Bonferroni procedure was also applied in all further test series involving non-metric characters, metric variables, as well as in test series of combined morphological and genetic data sets.

FA of epigenetic (non-metric) occlusal characters

Epigenetic occlusal characters in Leporids concern basically presence or absence of enamel folds, notches, grooves or islands, conformation patterns of enamel margins, and presence or absence of cement in folds (e. g., Forsyth Major 1898; Hibbard 1963; Angermann 1966; Palacios and Lopez 1980). Initially, 40 dichotomized (0/1) occlusal characters were scored for right/left differences in their respective character states (cf. Suchentrunk 1993; Suchentrunk et al. 1994, 1996, 2000 a, b). Bilateral asymmetry of a character was given, if different (0/1, 1/0) character states occurred on the right and left body sides. Only 15 characters were found with clear right/left-differences. They were used for the FA analysis; table 2 details the descriptions of the characters, character states, and character-specific bilateral asymmetry levels. The latter were calculated as percentages of individuals with asymmetric characters.

A Wilcoxon matched-pairs signed-rank test was run for each character to check for occurrence of FA or directional asymmetry (DA) (Palmer and Strobeck 1986). Since no character showed DA, all were considered indicators of developmental homeostasis (Palmer and Strobeck 1986; Palmer 1994; Møller and Swaddle 1997). Associations of FA between pairs of characters and sex-dependence of single characters were tested by exact Fisher's tests, respectively. Individual overall FA of occlusal characters (FA_{OC}) was calculated as the proportion of

Table 2. Fluctuating asymmetry (FA) of epigenetic occlusal characters of Iberian hares from Pancas. Current character numbers (CN) and tooth allocation, character description, dichotomized character states (0/1), and level of FA in percent of unequal, i. e., (1)/(0) or (0)/(1) character states are given for each character.

CN	Tooth	Description of characters	dichotomized character states	FA
C-1	P_3	Mesial re-entrant fold (filled with cement):	present(1)/absent(0)	1.6
C-2	P_3	Additional mesial re-entrant fold (with cement):	present(1)/absent(0)	3.3
C-3	P_3	Anterior lingual re-entrant fold (with cement):	present(1)/absent(0)	13.1
C-4	P_3	Posterior external re-entrant fold breaking through the lingual enamel wall and separating trigonid and talonid completely:	yes(1)/no(0)	3.3
C-5	P_3	Margin of posterior external re-entrant fold forming one extra fold in its most lingual section, extending mesiad and/or distad:	yes(1)/no(0)	1.6
C-6	P_3	Mesial margin of posterior external re-entrant fold plicate (strong or slight plication)	yes(1)/no(0)	8.2
C-7	P_3	Distal margin of posterior external re-entrant fold plicate (strong or slight plication):	yes(1)/no(0)	8.2
C-8	P_3	Distal margin of posterior external re-entrant fold forming one distinct step or extra fold in its lateral part:	yes(1)/no(0)	11.5
C-9	P_3	Margin of anterior external angle with rather strong plication:	yes(1)/no(0)	1.6
C-10	P_3	Cement layer of mesial re-entrant fold stretching lingually (covering also anterior lingual re-entrant fold, if present):	yes(1)/no(0)	3.3
C-11	P_4	Distal margin of lateral fold with extra fold in the buccal section:	yes(1)/no(0)	1.7
C-12	M^2	Enamel island filled with cement lingually or buccally of lingual fold (hypostria):	present (1)/absent(0)	1.6
C-13	P^2	central fold with plicated margin:	yes(1)/no(0)	3.3
C-14	P^2	lingual fold with plicated margin:	yes(1)/no(0)	5.2
C-15	I^1	labial groove with cement:	yes(1)/no(0)	2.1

Table 3. Non-metric bilateral skull characters used for assessing fluctuating asymmetry (FA). Code, morphological designation, description of dichotomized (0/1) character states, and levels of FA (%) are given. f. – foramen (foramina).

code	description and character states (0/1)	FA
NM1	Foramen nervi hyperglossi internale: (0) two f. present, (1) > two f. present	6.6
NM2	Foramen nervi hypoglossi internale accessorium: (0) f. absent, (1) one or more f. present	27.9
NM3	Foramen condylare: number of f. on both sides: (0) equal, (1) unequal	51.6
NM4	Foramen alisphenoidale: number of f. on both sides: (0) equal, (1) unequal	29.5
NM5	Foramen ethmoidale accessorium: (0) absent, (1) present	30.0
NM6	Foramen palatinus: (0) one f. present, (1) two f. present	1.6
NM7	distinct foramen on os maxillare medial of P^2–M^1: (0) no, (1) yes	6.3
NM8	Foramen frontale mediale: (0) f. absent, (1) f. present	19.4
NM9	Foramen mandibulare: (0) one f. present, (1) more than one f. present	3.2
NM10	Foramina along the rostral sulcus of the mandibular ramus (0) equal, (1) unequal number	66.1

asymmetric characters of the total set of occlusal characters studied per individual (Leary et al. 1985). Sex-specific variation of FA_{OC} was tested by a Mann-Whitney U-test.

FA of non-metric skull characters

Ten non-metric skull characters (foramina) were scored on both body sides. They could be easily scored and are largely a subsample of those characters that were used in FA analyses in brown hares (*Lepus europaeus*, see Hartl et al. 1995; Suchentrunk et al. 1998). Character descriptions, dichotomized character states (0/1), and respective asymmetry values appear in table 3. Statistical procedures were analogous to those for dental characters. Calculation of the individual-specific index of overall FA of non-metric skull characters (FA_{NM}) was based on all ten characters.

FA of metric skull variables

Six bilateral skull and mandible measurements (Fig. 1) were taken with digital calipers to the nearest 0.01 mm. Measurements were taken exclusively by one of the authors (PCA) to eliminate the possible inter-observer variability (Lee 1990), and were repeated once to obtain a data basis for evaluating the influence of measurement error on the FA estimation. The effect of measurement error on FA values of single variables was calculated by a two-way ANOVA for each variable, based on sides and repeated measurements in each individual. The influence of measurement error on the asymmetry measurement was considered insignificant, if the sum of mean variance of the side factor and the mean variance of the side/individual interaction factor was at least twice as high as the residual mean variance (Hartl et al. 1995; see also Palmer 1994).

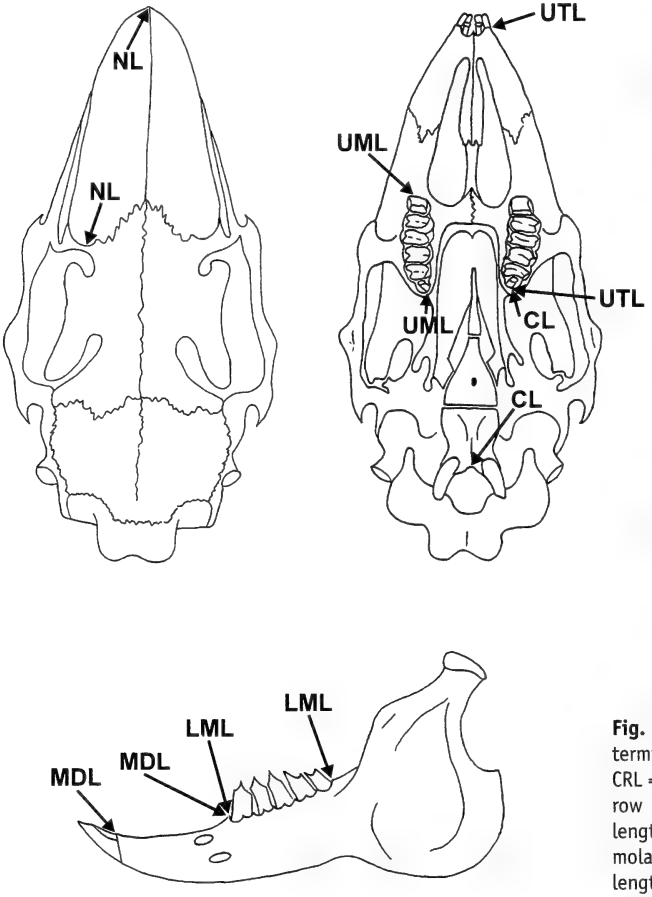

Fig. 1. Skull measurements used for determination of fluctuating asymmetry. CRL = cranium length, LML = lower molar row length, MDL = mandibular diastema length, NL = nasalia length, UML = upper molar row length, UTL = upper tooth row length.

Occurrence of DA or antisymmetry (AS) was tested for each variable by a sign test (right minus left measurements), and by a Kolmogorov-Smirnov test of the frequency distribution of the right-left paired differences, respectively (PALMER and STROBECK 1986; HARTL et al. 1995). To check for size-dependence of asymmetry, a Spearman correlation between individual values of |right-left| differences and respective arithmetic means was performed in each variable. Despite absence of a correlation, we used an FA index for single metric variables that allowed the calculation of overall individual FA indices, even in cases of missing data for single values in partly damaged skulls. For single variables the following FA index was used:

$$|R - L|/[(R + L)/2],$$

where R and L are the measurements on the right and left sides, respectively (cf. PALMER and STROBECK 1986; HARTL et al. 1995; PALMER 1994). Sex-dependence of FA of each variable was checked by a one-way ANOVA. Pairwise correlations of FA of variables were tested by Spearman correlations. Overall FA of metric variables (FA_M) was calculated as the arithmetic mean of FA indices of the six (CRL, LML, MDL, NL, UML, UTL), and only in few partly damaged skulls based on five variables. Sex-dependence of FA_M was checked by a one-way ANOVA and size-dependence by a Pearson correlation between FA_M and individual condylobasal length (CBL) (e. g., PALMER 1994).

Relationships between non-metric and metric FA

Relationships between non-metric dental and skull characters were examined by Fisher's exact tests, and those between non-metric and metric variables by Mann-Whitney U-tests. Relationships between FA_{OC}, FA_{NM}, and F_{AM} were examined by Spearman correlations, respectively.

FA, skull length, and protein heterozygosity

Relationships between either FA_{OC}, FA_{NM}, F_{AM}, CBL, and H were tested by Spearman correlations, respectively. For the relationship between FA_M and heterozygosity, the following additional statistical approach was carried out: H-values were classified as low (< 20%) and high (20–45. 5%); and within each group FA values of single variables were calculated by:

$$\text{var}\,[(R - L)/(R + L)/2],$$

where R and L are the right and left side measurements per individual and var is the H-group variance. To maximize the information on FA of all variables and individuals in a comparison of metric FA between the two heterozygosity groups, we performed a two-way ANOVA with variable and group as factors (cf., PALMER 1994).

Results

The allele frequencies at polymorphic loci are presented in table 4. One significant deviation of genotype frequencies from Hardy-Weinberg expectations at the Dia-2 locus was found; it was due to a slight heterozygote deficiency. Locus-specific expected heterozygosities ranged between 0.016–0.501 and direct count heterozygosities between 0.016–0.548 (Tab. 1). There were no sex-specific differences of frequencies of homozygote and heterozygote genotypes at any locus. Also, no significant pairwise associations of homozygous or heterozygous genotypes were found among loci. H values ranged from 0.0% to 45.5% with a mean of 22.52% and a standard deviation of 12.68%. H values did not vary significantly between the sexes.

Levels of asymmetry of non-metric characters appear in tables 2 and 3 and those of metric variables in table 5. Only one metric variable (DIA) showed DA. No character showed AS. Apart from DIA, all metric characters were used as indicators of developmental homeostasis (PALMER and STROBECK 1986). In single non-metric characters and metric variables no sex-specific differences of FA were found. Also, no significant associations or correlations of symmetric or asymmetric expressions were detected between pairs of non-metric characters or metric variables, respectively. The two-way ANOVA of measurement repeats and side (Tab. 5) did not suggest that FA values of the six metric variables used for FA calculations were confounded by measurement errors.

FA of single metric variables and FA_M values were not significantly correlated with CBL. Also, in non-metric characters no significant differences of CBL values were

Table 4. Allele frequencies (%) of polymorphic loci in hares from Pancas. Allele designations are not necessarily in alphabetical or numerical order because alleles were assigned in a combined analysis of *L. granatensis* and *L. europaeus* and some alleles were not found in the hares from Pancas. Allele designations of the loci Gc, Pep-B, HBA, Bf, and Hpx conform to those in ALVES et al. (2000)

locus	allele	frequency	locus	allele	frequency	locus	allele	frequency
Dia-2	A	0.857	Acy-1	A	0.100	Bf	1	0.786
	B	0.082		B	0.900		2	0.107
	C	0.061					3	0.060
							5	0.048
Mpi	A	0.157	Acp-2	A	0.992	Tf	C	0.083
	B	0.833		B	0.008		D	0.917
	C	0.010						
Es-1	B	0.643	Pep-B	1	0.800	Hpx	1	0.846
	C	0.333		3	0.150		2	0.115
	D	0.012		4	0.050		3	0.010
	F	0.012					4	0.029
Gc	1	0.923	Hba	3	0.451			
	3	0.019		4	0.549			
	4	0.058						

Table 5. FA of single metric skull variables selected for estimating overall metric skull FA of hares from Pancas. n = sample size, m. e. = measurement error (see material and methods), (R + L)/2 – mean of the variable size, s. e. = standard error of mean. Mean and standard errors of the differences between the sides (R–L) are also given to indicate the absence of DA (cf. PALMER 1994) in conjunction with the not significant sign-test results, based on the Sequential Bonferroni procedure. For variable acronyms and calculation of the FA index, see material and methods.

variable	n	m. e.	(R + L)/2 (+/–s. e.)	(R–L) mean (+/–s. e.)	FA index mean s. e.
CRL	59	3.3 : 1	29.70 (0.145)	0.046 (0.036)	0.007 (0.001)
LML	61	2.0 : 1	17.90 (0.08)	0.044 (0.043)	0.013 (0.002)
MDL	61	3.5 : 1	20.42 (0.13)	–0.083 (0.045)	0.013 (0.001)
NL	61	15.1 : 1	40.11 (0.2)	–0.097 (0.047)	0.007 (0.001)
UML	61	3.72 : 1	16.80 (0.07)	–0.06 (0.03)	0.011 (0.001)
UTL	61	2.92 : 1	43.46 (0.17)	0.048 (0.035)	0.005 (< 0.001)

found between symmetric and asymmetric character states. And there were neither significant correlations between CBL and FA_{OC} or FA_{NM} values nor significant correlations between FA_{OC}, FA_{NM}, FA_M values. No significant correlations between FA_{OC}, FA_{NM}, FA_M, CBL, and H were found. However, there was a slight tendency towards lower FA_M values in hares with greater H values. The respective correlation coefficients and associated significance levels are listed in table 6. The two-way ANOVA of the variance-based metric FA in-

Table 6. Relationships between overall individual heterozygosity (H) and overall fluctuating asymmetry of non-metric occlusal characters (FA_{OC}), non-metric skull characters (FA_{NM}), metric skull variables (FA_M), condylobasal length (CBL). One-tailed Spearman rank correlation coefficients (r_s), individual numbers (n), and significance levels (p) are given; n. s. = not significant.

		FA_{OC}	FA_{NM}	FA_M	CBL
H	r_s	0.0485	–0.0017	–0.2164	0.0824
	n	48	49	49	48
	P	0.372 n. s.	0.495 n. s.	0.068 n. s.	0.289 n. s.

Table 7. Fluctuating asymmetry (FA) values of single metric skull variables in hares with low (< 20%) and high (> 19%) heterozygosity. Means (M), standard errors (SE), minimum (MIN), maximum (MAX), and sample sizes (n) are given for each variable and heterozygosity group. M, SE, MIN, and MAX values are multiplied by 10^4. For acronyms of variables, see Fig. 1.

		FA index | R – L |/[(R + L)/2]			
Variable	N	M	SE	MIN	MAX
group: heterozygosity < 20%					
CRL	21	90.79	17.32	6.82	307.27
LML	20	145.66	25.58	5.3	373.68
MDL	20	153.31	27.24	13.54	444.44
NL	21	77.49	12.94	2.65	191.87
UML	21	115.73	20.88	0.0	402.68
UTL	20	44.38	6.83	2.22	126.26
group: heterozygosity 20–45.5%					
CRL	26	47.00	10.51	0.00	183.36
LML	26	101.05	18.96	0.00	341.83
MDL	25	109.17	21.43	0.00	387.81
NL	26	68.09	10.97	2.51	235.12
UML	28	103.3	17.8	6.13	341.3
UTL	27	56.22	8.24	0.00	222.09

dices revealed a significant effect by variables ($p < 0.0001$) but only a tendency ($p = 0.019$; Bonferroni criterion for multiple testing: $p = 0.01$) towards an H group effect. The H group/variable interaction factor was not significant ($p = 0.457$). The means, standard errors, and extreme values of FA in single metric variables are listed in table 7, separately for each H group.

Discussion

Heterozygosity is commonly considered to indicate levels of genetic variability within individuals and populations (e. g., Mitton and Pierce 1980; Nei 1987). Hares with high heterozygosity may harbour less homozygous genotypes with rare recessive alleles that are detrimental to certain metabolic processes than hares with low heterozygosity. Hence, low heterozygosity could lead to higher developmental instability ("dominance hypothesis"). According to the "overdominance hypothesis" individuals with heterozygote genotypes at many unlinked polymorphic loci should have a better capability of buffering biochemical processes against various adverse environmental effects during ontogenesis (e. g., Turelli and Ginzburg 1983; Mitton 1993 b). In Oldfield mice (*Peromyscus polionotus*) the ability of an individual to maintain stable developmental trajectories under fluctuating environmental conditions is related to its genetic variability (Teska et al. 1991). Higher genetic variability may lead to the production of a higher variability of biochemical products to buffer diverse environmental influences. This in turn should lead to a more regular expression of bilateral symmetric morphological traits of an organism (e. g., Ginzburg 1979; Mitton and Grant 1984; Mitton 1995; Møller and Swaddle 1997).

Bilateral asymmetry of morphological characters is only indicative of developmental homeostasis if they show fluctuating asymmetry (FA) (Palmer and Strobeck 1986; Palmer 1994; Møller and Swaddle 1997). Among all traits presently studied, the only case of directional asymmetry (DA) was found in one metric variable (DIA). We do not have a convincing biological explana-

tion for this significant deviation from FA. It might result from a systematic measurement bias due to different positions of the skulls when holding them for taking right and left measurements. Whatever reason, we excluded this variable from all combined analyses with heterozygosity. In three other metric variables (MDL, NL, UML) the standard errors of right-left differences (R–L) were quite low compared to the respective means (table 5). This might suggest DA in these characters. Nevertheless, we included these variables in the calculations of metric FA because of nonsignificant sign-tests when based on the Sequential Bonferroni procedure.

Our results demonstrate that there is FA in all three morphological character systems studied, but no concordance of FA levels among the three morphological systems. And we did not find a significant relationship between FA and heterozygosity. This corresponds to the "poikilotherm-homeotherm hypothesis" (Handford 1980; Wooten and Smith 1986; but see Hartl et al. 1995), according to which a negative relationship between FA and heterozygosity should be more likely in poikilothermic animals because of their supposedly greater sensitivity to environmental conditions, whereas homeotherms experience a more stable development during their ontogeny (see also Møller and Swaddle 1997). In some poikilothermic vertebrates, single-locus heterozygosity was found to be negatively correlated with FA (Mitton 1993 a, b, 1995 for overview). However, here we did not check for relationships with single-locus heterozygosity, to avoid too stringent significance levels by the Sequential Bonferroni procedure (see Palmer 1994).

Nevertheless, in the metric skull characters a tendency towards increased FA in hares with low heterozygosity became apparent. A weak inverse relationship might indeed exist, but could be largely masked by effects of diverse exogenic factors, despite the quite small and homogeneous study area. Mulvey et al. (1994) found a negative relationship between genic variability and FA in the fish *Gambusia holbrooki* only in certain environmental contexts. Exogenic factors might include diverse weather components or food stress in different seasons. At Pancas hares are born all year round (leverets can be observed in any season). Seasonal changes of ground temperature and moisture, wind and rainfall, together with varying food availability for leverets and lactating does could modify levels of FA of hares born in different seasons. Increased dental FA was observed in mice that were born and raised in cold environments (Siegel and Doyle 1975 a). Rats (*Rattus norvegicus*) exposed to cold and heat stress increased FA of long bones (Gest et al. 1986). FA of humeri of cotton mice (*Peromyscus gossypinus*) and Florida mice (*P. floridanus*) was raised by cold stress (Siegel and Doyle 1975 b). Levels of parasitic infections may also have varied within the sampling period. FA of antlers of a Norwegian reindeer (*Rangifer tarandus*) herd was enhanced by abomasal nematode infections, and there was a negative relationship between certain immune parameters and FA (Lagesen and Folstad 1998). In addition, seasonal changes of levels of psychogenic stress due to variable predation pressure by foxes, raptors etc. with possible effects on various hormone-based regulation systems may influence developmental stability. Social stress had a negative impact on FA of non-metric skull traits in laboratory rats (*Rattus norvegicus*) (Valetsky et al. 1997).

Palmer and Strobeck (1986), and Palmer (1994), among others, recommended variance-based FA indices and comparisons of FA at the population/group level. In a meta-analysis, Vøllestad et al. (cf. Møller and Swaddle 1997) found a tendency towards an inverse relationship between FA and heterozygosity at the population level in poikilotherms but no clear pattern in homeotherms. In fact, in central European brown hares (*Lepus europaeus*) a significant negative relationship between non-metric FA and heterozygosity was only apparent at the population level Hartl et al. 1995). This might result from a better estimate of genic variability by groupspecific

heterozygosity than by individual heterozygosity (Palmer and Strobeck 1986). To increase the power of the comparison of FA between groups of individuals (populations etc.), Palmer (1994) recommended combining the FA information of several traits in a two-way ANOVA with group and trait factors. By this variance-based approach, the initially found (not significant) tendency towards increased FA of metric skull variables in hares with low heterozygosity was also evident. However, we emphasize that in this second variance-based test of FA between the two heterozygosity groups, sample sizes per group were naturally lower compared to the full set of individuals in the correlation analysis between H and F_{AM}. Moreover, this second approach resulted in a more stringent significance level to account for multiple (and partly dependent) testing (Rice 1989). This might have reduced the chance of detecting a significant difference.

It has been questioned whether measuring heterozygosity at a comparatively small number of loci provides a good estimate of overall genome heterozygosity. Heterozygosity estimates might be valid particularly if: a) a large amount of the genome is structured in blocks, i. e. when there is a large amount of linkeage disequilibrium, b) there is a high degree of inbreeding, and c) there is non-random mating due to small population size and isolation (Møller and Swaddle 1997). The largely absence of concordant locus-specific deficiency of heterozygous genotypes does not particularly indicate a severe level of inbreeding in the hares from Pancas. We also did not find any significant linkage disequilibrium in our sample and we do not have any information on the mating structure of hares at Pancas. However, there is a substantial level of gene flow between the Pancas population and other populations in Portugal (Alves and Ferrand 1999). To increase the predictor quality of heterozygosity, we analysed most of the protein loci that have been found to be polymorphic in the genus *Lepus* (Hartl et al. 1990, 1992, 1993, 1995 for brown hares; Grillitsch et al. 1992; Alves et al. 2000; Suchentrunk et al. 1998, 1999, 2000, and unpublished data for diverse hare species).

Based on eleven polymorphic loci, we did not find a significant positive effect of overall individual heterozygosity on developmental stability. This, however, does not necessarily mean that there is no such effect. We found a tendency for a negative correlation between metric skull FA and heterozygosity; and such a relationship might indeed exist, but it could be masked by the combined influence of various unperceived seasonal environmental stressors. Weather parameters or food availability, among other stressors, might exert seasonal influences on growing hares. If so, such exogenic stress components would have a clearly higher overall effect on developmental stability than cross genic variability of the hares. This, however, should be tested by a further study based on hares from different birth seasons.

Acknowledgements

We thank Mr. Rafael Vinhais, the manager of the Pancas hunting estate, the commandant of the Campo de Tiro de Alcochete, and all hunters for their help to obtain the samples. Mrs. Anita Haiden (Vienna), Mrs. Helena Goncalves, Mrs. Ana Monteiro, Mr. Christiano Lima, Mrs. Joana Castro and Mrs. Catarina Ferreira (all Vila do Conde) provided help during field and lab work, Mr. Rudolf Willing (Vienna) provided statistical advise, and Mr. A. Körber (Vienna) prepared the figure. Financial support for this study was provided by the Instituto de Cooperação Cientifica e Tecnológico International (Ministério da Ciéncia e da Tecnologia (Portugal), the ÖAD (Austrian Academic Exchange Service, Vienna), and by the Direção-General de Florestas (Portugal).

Zusammenfassung

Heterozygotie und Entwicklungshomöostase bei Iberischen Hasen (*Lepus granatensis*) aus einer lokalen Population in Portugal

Bisherige Untersuchungen haben vielfach einen positiven Einfluß des Heterozygotiegrades auf die Entwicklungsstabilität von Tieren ergeben. Homeotherme Vertebraten zeigen diesbezüglich allerdings kein einheitliches Bild. In dieser Arbeit wird der Einfluß des individuellen Heterozygotiegrades von Iberischen Hasen aus einer lokalen Population in Portugal auf ihre Entwicklungshomöostase untersucht. Die Analyse von 44 proteinkodierenden Loci mittels Stärke- und Agarosegelelektrophorese sowie isoelektrischer Fokusierung ergab bei 63 Hasen elf polymorphe Loci, die zur Berechnung des individuellen Heterozygotiegrades herangezogen wurden. Das Niveau der Entwicklungshomöostase einzelner Hasen wurde anhand der fluktuierenden Asymmetrie (FA) in nicht-metrischen und metrischen Merkmalssystemen (Zahnmerkmale, Schädelmeßstrecken und Foramina) ermittelt. Das Ausmaß der individuellen FA war in keinem der drei Merkmalssysteme mit dem Heterozygotiegrad korreliert. Die FA der Schädelmeßstrecken zeigte aber tendenziell einen negativen Zusammenhang mit der Proteinheterozygotie. Solch ein (schwacher) Zusammenhang könnte tatsächlich bestehen, aber durch nicht erfaßte (kaum erfaßbare) exogene Streßfaktoren weitestgehend verdeckt sein.

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Mamm. biol. **66** (2001) 251–255
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Notes on the ecology of sympatric small carnivores in southeastern China

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Receipt of Ms. 30. 10. 1998
Acceptance of Ms. 20. 02. 2001

Key words: *Herpestes urva, Paguma larvata, Vivenicula indica,* activity, home range

The civets are diverse and prominent elements of old world tropical communities, demonstrating more ecological diversification in trophic specialization and substrate use than any other family of carnivores (Eisenberg 1981). They are also the least known carnivore group in the world (Wemmer and Watling 1986), especially in Asia, even though many species have ecological and economic significance and have long been harvested for their pelts, meat, and musk. We radio-tracked 5 masked palm civets (*Paguma larvata* H. Smith, 1827), 2 small Indian civets (*Viverricula indica* Demarest, 1817) and 1 crabcating mongoose (*Herpestes urva* Hodgson, 1836) in northern Jiangxi Province, southeastern China during April 1993–November 1994 to understand more about the small carnivore community there.

The study site near Taohong Village is located in northern Jiangxi Province about 15 km south of the Yangtze River and about 490 km WSW of Shanghai. It is in a small, V-shaped vallev about 6 km long at the foot of Mount Taohong and surrounded by a stretch of low and undulating hills (50–530 m above sea level). The climate is moist monsoon type with typical temperate climate seasonal changes. The average annual temperature is around 16.3 °C, and the annual precipitation is 1 326 mm, of which over 40% falls as rain during May–July.

All the arable lands at the bottom of the valley are under cultivation and many gentle hills and slopes also are now farmland. Above the farmland the major vegetation is a combination of tall grasses (*Themeda triandra*, *Imperala cylindirca*, and *Arundinella* spp.) and secondary growth of shrub species (*Lespecdeza bicolor*, *L. formosa*, *Rhus chinensis*, and *Rhododendron simsii*) that is maintained by annual firewood collection and frequent fires. Only in some remote areas or regions posted by the local forest farms do small patches of deciduous broadleaf and, in rarer frequency, evergreen-deciduous broadleaf forest remain.

The northwest part of Taohong Village is included in the Taohongling Sika Deer Reserve that was established to protect a remnant population of the endangered subspecies of sika deer (*Cervus nippon kopschi* Swinhoe, 1873) in 1981. A general survey on the fauna and flora of the reserve was carried out in and near the reserve during 1988–89; this is the only source of background information for that area (Ding 1990).

Most of the study animals were caught by the local trappers with traditional bamboo foothold snares (Han 1960); only one masked

1616-5047/01/66/04-251 $ 15.00/0.

palm civet was captured in a cage-type live trap. Captured animals were weighed to calculate drug dose, then immobilized with Telezol (Tiletamine HCL and Zolazepam HCL) or Ketaset (Ketamine HCI) at a dosage of 10 mg/kg body weight. After sex was determined and body measurements recorded, each animal was fitted with radiocollar (with 15-cm whip antennas) weighing < 5% of their body weight. All immobilized animals were held in cages then released after full recovery from the drugs' effects.

Activity of marked animals was determined by listening for changes in radio signal strength during a 60-second period. Consecutive readings were taken with an interval of at least 30 minutes. The activity level (% active) was calculated as the number of active readings divided by the total number of readings. Collared animals were generally located a minimum of 3 times a week by walking in on the animals' resting site during periods of inactivity. The term "daybed" is used to designate those resting sites (RABINOWITZ 1991). The general external characteristics of daybeds were recorded to categorize them. Daily movements were calculated as the linear distances between 2 consecutive daybeds. Re-use rates of daybeds were calculated as the total number of locations divided by the number of different daybeds (PALOMARES and DELIBES 1993, 1994). The resting home ranges of the marked animals were calculated as minimum convex polygons (MOHR 1947) with the RANGES V program (KENWARD and HODDER 1996), based on the locations of daybeds and capture sites (PALOMARES and DELIBES 1994).

Masked palm civets were active > 50% of the time between 18.00 and 05.00 hours (Tab. 1). Their activity declined throughout

Table 1. Percent of checks indicating activity for radio-marked carnivores studied near Taohong Village, southeastern China during April 1993–November 1994

	Masked palm civet		Small Indian civet		Crab-eating mongoose	
Hour	No. of checks	Percent active	No. of checks	Percent active	No. of checks	Percent active
01.00	1	100	2	100	–	–
02.00	7	57	–	–	–	–
03.00	8	100	2	100	–	–
04.00	19	53	–	–	–	–
05.00	40	68	1	100	–	–
06.00	94	45	3	33	–	–
07.00	101	39	2	0	–	–
08.00	104	21	–	–	1	0
09.00	135	15	1	0	–	–
10.00	144	22	–	–	4	25
11.00	112	9	–	–	4	25
12.00	90	3	–	–	3	100
13.00	48	14	2	0	3	67
14.00	51	14	2	0	–	–
15.00	66	17	2	0	3	67
16.00	137	14	6	17	4	100
17.00	178	33	12	42	2	100
18.00	167	74	20	85	2	50
19.00	60	88	6	100	–	–
20.00	45	89	4	100	–	–
21.00	42	93	–	–	–	–
22.00	27	89	4	100	–	–
23.00	13	93	1	100	–	–
24.00	6	83	–	–	–	–

the morning, with a nadir at 12.00 hours, then remained moderately low until 18.00 hours. Limited data for small Indian civets seemed to mirror that of masked palm civets, but the crab-eating mongoose was clearly very active (56% of 25 readings) when monitored between 10.00 and 18.00 hours (Tab. 1). Masked palm civets have been reported elsewhere to have 2 nocturnal peaks of activity (ZHANG et al. 1991), and small Indian civets apparently have either 1 (WANG et al. 1976; RABINOWITZ 1991) or 2 (SHENG and XU 1990). Like we found, GAO (1987) indicated that crab-eating mongooses were diurnal.

All the daybeds of the masked palm civets were underground burrows, mainly the abandoned dens of porcupines (*Hystrix brachyura* Cuvier, 1822). In contrast, all the daybeds of the small Indian civets we examined were on the ground, usually under dense bushes or among tall grass. In some cases adjacent daybeds were located so close to each other (e. g., 4 daybeds with an area of 2 m^2) as to practically form daybed groups. The few daybeds used by the crab-eating mongoose were underground dens. RABINOWITZ (1991) reported that the small civets (including small Indian civet and masked palm civet in his study) were located in tree beds 86% of the time; we did not find use of tree beds by the masked palm civets though there were enough big trees within their habitat. GAO (1987) observed that masked palm civets commonly rest in dens in winter and spring and often use the dense bush in the hot summer. Thus, factors other than the availability of proper-sized trees would seem to affect civet daybed selection.

All 3 species did not use permanent dens but moved among numerous daybeds. The average daybed reuse rate was 2.5 times for the 5 masked palm civets (range 1.2–4.2), but increased with the total number of locations obtained ($r^2 = 0.86$, 4.d.f., $P = 0.005$), as might be expected. The reuse rate was 3.6 for the small Indian civet. However, the animals did not use their daybeds randomly but showed strong preferences. Overall, masked palm civets used their daybeds only once (59% of 124), twice (14%) or 3 times (11%), but some daybeds were frequently used; 7 were used 6–10 times each and 5 were used 10–17 times each. Similarly, small Indian civets often used their daybeds only once (43% of 14) or twice (29%), but 4 were used 6–10 times each.

The daybeds of the small Indian civet and crab-eating mongoose were located solely in the foothill region adjacent to the farmland. Some daybeds of masked palm civets were located in the low bushes and tall grass that covered the hilly region bordering farmland, but many were also farther above in the woods. This difference in habi-

Table 2. Altitude (m asl) of daybeds used, distance (m) between consecutive daily locations, and resting home range sizes (ha) of radio-marked sympatric small carnivores studied near Taohong Village, southeastern China during April 1993–November 1994

Species	Sex	No. of locations	No. of different daybeds	Daybed altitude			Distance between locations		Tracking period	Home range size
				$x \pm SD$[2]	Min.[b]	Max.[c]	$x \pm SD$	Max.		
Masked palm civet	F	104	25	92 ± 23	45	145	560 ± 448	1960	04/93–11/93	288
	F	89	31	85 ± 17	46	125	248 ± 313	1155	06/93-12/93	190
	M	21	17	151 ± 91	53	363			12/93-07/94	410
	M	39	23	122 ± 31	65	170	681 ± 414	1450	03/94-11/94	182
	M	64	28	97 ± 66	30	363	177 ± 223	805	10/93-07/94	346
Small Indian civet	M	47	13	86 ± 18	40	108	613 ± 686	2395	03/94-06/94	227
	M	3	3	59 ± 14	43	70			06/94-07/94	7
Crab-eating mongoose	F	7	6	78 ± 33	30	105			02/94-03/94	100

tat use was showed clearly by the altitudes of the locations of the tracked animals (Tab. 2). Although many daybeds of these 3 species occurred in close proximity to farmland and trails used by humans, most marked carnivores that were resting were not disturbed by nearby human activity. Elsewhere, masked palm civets prefer dense forest (RABINOWITZ 1991), and small Indian civets prefer disturbed habitats or forest/agricultural edges (WEMMER and WATLING 1986; SHENG and XU 1990; WANG 1990), similar to our results and indicating an important difference in overall habitat use between those 2 species.

The average distance moved between consecutively used daybeds ranged from 177–681 m (max. = 1 960 m) for masked palm civets, and 613 m for the small Indian civet (max. = 2 395; Tab. 2). Although masked palm civets and small Indian civets returned to their previous daybeds with similar frequency (32% of 203 movements vs. 38% of 37 movements, respectively), movements to different daybeds were usually shorter for masked palm civets (53% vs. 15% of moves < 500 m to different daybeds; $X^2 = 9.37$, 1 d.f., $P < 0.01$).

The resting home ranges of the 5 masked palm civets located 20–104 times ranged from 182–410 ha (Tab. 2) and did not vary with number of locations ($P > 0.56$). The resting home range for the small Indian civet located 47 times was similar in size (227 ha). The monthly home range for the small Indian civet was 158 ha (n = 24) in April and 156 ha (n = 20) in May. Although the crab-eating mongoose was only located 7 times, its home range was at least 100 ha.

The home ranges of the 2 small Indian civets overlapped, and they and 4 other individuals were caught in the same area. Local hunters told us that both masked palm civets and crab-eating mongooses were seen in packs of 3 to 4 individuals. Two marked masked palm civets were found sharing the same daybeds more than 20 times. In addition, footprints showed that small Indian civets were usually solitary while crab-eating mongooses often moved in small packs or family groups.

In spite of their dietary similarity (WANG 1999), the resting home ranges of these 3 species overlapped extensively. Even though only an unknown portion of all individuals of any 1 species were marked in the study area, daytime home ranges of crab-eating mongooses overlapped 35% and 36%, those of small Indian civets overlapped 60% and 82%, and those of masked palm civets overlapped 76% and 99% with those of other species. However, none of the radio-marked individuals of any 1 species used the same daybed simultaneously with any other marked individual of another species.

In the only other telemetry study of masked palm civets, RABINOWITZ (1991) radio-tracked a single adult female for 12 months. Its total home range was 370 ha, the average daily movement distance was 620 m, and the longest daily movement was 1 800 m, figures rather close to those we recorded. RABINOWITZ (1991) also reported that an adult male small Indian civet followed for 6 months had an overall home range of 310 ha, an average daily movement of 500 m, and the longest distance of 2 400 m, findings that were again, similar to ours. The home ranges we calculated, however, were certainly minimums because they were calculated solely from daybed locations and capture sites, while RABINOWITZ (1991) used both the daybeds and locations obtained by triangulation at night.

Acknowledgements

We are grateful for the field assistance of TANG DAXONG and the logistical assistance of J. QING, S. MENG, W. WANG, B. WANG, J. ZHANG, and G. LI.

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Mamm. biol. **66** (2001) 256
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Zeitschrift für Säugetierkunde

Book reviews

MANN, JANET; CONNOR, R. C.; TYACK, P. L.; WHITEHEAD, H. (eds.): **Cetacean societies. Field studies of dolphins and whales.** Chicago, London: University of Chicago Press 2000. Paperback or cloth, 433 pp., numerous black and white pictures and colour plates. $ US 24.50 or 56.00.
ISBN 0-226-50341-0 or 0-226-50340-2.

This book gives an account of the state-of-the-art in field studies of dolphin and whale social biology. Thirteen authors from Canada, USA, and England contribute to this publication.
After an introductory chapter on the social lives of Cetacea, the first part of the book, consisting of three chapters, deals with the history of studying cetacean societies as well as with the dynamics of social life and structure. In the second part the social relationships and characteristics of four whale species are dealt with, each of which is presented in a separate chapter, namely, the bottlenose dolphin (*Tursiops truncatus*), the killer whale (*Orcinus orca*), the sperm whale (*Physeter macrocephalus*) and the humpback whale (*Megaptera novaeangliae*). In these four chapters detailed information on these species is supplied, not only on behaviour and social relationships, but on biological aspects in general. The social behaviours of these four cetacean species are very different: The bottlenose dolphin lives in a "fission-fusion society", the killer whale is an active hunter in highly co-ordinated groups. Female sperm whales live a very social life, but males of this same species are "rovers" which separate from the female-calve-groups and migrate polewards. The humpback whale, on the other hand, shows a strong annual cycle with seasonal feeding and breeding.
The third section of the book discusses results of comparative studies and deals with conservation aspects. For example, reproduction in females and males is discussed in two chapters. The information on life histories and calf care, as presented by WHITEHEAD and MANN is of general interest and presents information on a large number of odontocete and mysticete species. In a separate chapter functional aspects of cetacean communication – behavioural and acoustic – is presented. Finally, conservation, protection and management of wild cetaceans and an outlook on future behavioural studies are discussed in two chapters.
The first appendix to the book presents a diagram depicting cetacean phylogeny; in the second appendix a detailed list on cetacean taxonomy (six pages) follows. The list of references is really overwhelming, it fills more than 57 pages, each with more than 30 citations! A citation index referring to authors of original papers mentioned in this book follows and the publication is concluded by a subject index of 19 pages.

P. LANGER, Giessen

COLE, T. C. H.: **Wörterbuch der Tiernamen; Latein-Deutsch-Englisch, Deutsch-Latein-Englisch.** Heidelberg, Berlin: Spektrum Akademischer Verlag 2000. Geb., 970 pp. DM 148,–. ISBN 3-8274-0589-0.

Zur praxisnahen Begutachtung des vorliegenden Wörterbuches wurden stichprobenhaft in der Säugetierkunde gebräuchlichen Artnamen überprüft. Der Referent nutzte dazu eine von ihm anhand des Werkes von WILSON und REEDER (1993): Mammal species of the world, 2nd ed., zusammengestellte Material-Liste von Eutheria, welche von den Insectivora bis zu den Artiodactyla sieben Ordnungen umfaßte. Bei dieser willkürlichen Auswahl ergab sich, daß die Mehrzahl der 47 in der Namens-Liste berücksichtigten Arten im Wörterbuch zu finden sind. Drei Vertreter der Goldmulle (Chrysochloridae) werden nicht genannt (*Amblysomus hottentotus*, *Chrysotalpa duthieae*, *Ch. sclateri*). Die karibische Seekuh oder Nagel-Manati, *Trichechus manatus*, wird ebenfalls nicht aufgeführt. *Pecari tajacu* wird noch als *Tayassu tajacu* und *Moschiola meminna* als *Tragulus meminna* bezeichnet. Im Wörterbuch yon Cole findet sich die Schreibweise *Mazama gouazoubira*, wo WILSON und REEDER *Mazama gouazoupira* schreiben. Das Zwergflußpferd wird an zwei Stellen aufgeführt, unter *Hexaprotodon liberiensis* und unter *Choeropsis liberiansis*. Gleiches gilt für das Begriffspaar *Dama dama – Cervus dama*. Bei den deutschen Artnamen folgt COLE der neuen Rechtschreibung: *Rupicapra rupicapra* ist die Gämse. Im zweiten Teil des Bandes, der die deutsch-lateinisch-englische Namenstabelle bietet, finden sich folgende Hinweise: „Gämse, Gamswild (Gemse)" und „Gemse, Gamswild (jetzt: Gämse)".
Zoologen, einschließlich der Mammalogen, sind THEODOR C. H. COLE zu Dank für sein Wörterbuch verpflichtet. Diesem ist ein weiter Benutzerkreis zu wünschen. Es ist zu hoffen, daß eine zukünftige Auflage unter Hinzuziehung der dann aktuellen Namenslisten bearbeitet wird!

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URBAN & FISCHER Verlag
Jena/Germany

ISSN 1616-5047
Mamm. biol. · 66(2001)4 · 193-256

Contents

Abstracted/Indexed in
Animal Breeding Abstracts/Biological Abstracts/Biological Environmental Sciences/BIOSIS database/Current Advances in Ecological and Environmental Sciences/Current Contents - Agriculture, Biology & Environmental Sciences/Dairy Science Abstracts/Fisheries Review/Helminthological Abstracts/Index Veterinarius/Key Word Index to Wildlife Research/South Pacific Periodicals Index/Veterinary Bulletin/Wild Review (Fort Collins)/Zoological Record

Mammalian Biology

Zeitschrift für Säugetierkunde

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ISSN 1616-5047
Mamm. biol. · 66(2001)5 · 257-320
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Mammalian Biology

Zeitschrift für Säugetierkunde

IMPRESSUM
Publisher: Urban & Fischer Verlag GmbH & Co. KG, Branch Office Jena, P.O. Box 100537, D-07705 Jena, Germany; Phone: ++49(0)3641/626-3, Fax: ++49(0)3641/62 65 00, E-mail: journals@urbanfischer.de
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Terms of delivery (2001): 1 volume consisting of 6 issues.
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Type setting and printing, binding: druckhaus köthen GmbH

As of vol. 61, number 1 (1996) the paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Printed in Germany

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Mamm. biol. 66 (2001) 257–268
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Original investigation

The vomeronasal complex in strepsirhine primates and *Tarsius*

By Angela Wöhrmann-Repenning and M. Bergmann

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Receipt of Ms. 11. 09. 2000
Acceptance of Ms. 05. 03. 2001

Abstract

The vomeronasal complex (VNC) of several different strepsirhine primates and two *Tarsius* species was studied with respect to comparative anatomy. All investigated species possess a well developed vomeronasal organ (VNO) in the center of this complex. As *Tarsius* possesses an extremely small nose, a correspondingly small VNO is present. Its organ is – different to the Strepsirhini and most other mammals – almost completely outlined by an olfactory epithelium. With regard to its histological appearance, however, the VNO should play an important role in all investigated primates concerning sensory ability. It is evident that the VNC in primates follows the progressive developmental line of placental mammals. In this connection the rostral part of the paraseptal cartilage is an intricate structure and normally forkes into a dorsal and a ventral branch, where the latter usually fuses with the cartilage of the nasopalatine duct. While several Strepsirhini fit into this pattern, some other tend to differ from this scheme, mainly caused by nasal metamorphosis connected with facial reorganisations. All Strepsirhini possess a naked rhinarium split ventrally by a median philtrum, which communicates with the sulcus papillae palatinae. Inside this sulcus, taste buds occur quite frequently at the lateral walls of the palatine papilla. *Tarsius* a haplorhine primate differs completely by having an unsplit, freely movable, hairy upper lip.

Key words: *Tarsius*, Strepsirhini, vomeronasal organ, vomeronasal complex

Introduction

The vomeronasal organ (VNO) is a paired accessory olfactory organ present in most mammals and located at the base of the rostral nasal septum. This organ belongs to an autonomous intranasal system with a complicated morphology called the vomeronasal complex (VNC) (Broom 1898; Wöhrmann-Repenning 1984 a, b). The comparative anatomy of this VNC testifies to its functional importance (Bailey 1978; Wöhrmann-Repenning 1991) and allows limited conclusions concerning phylogenetic relationships within the class of mammals (Broom 1898; Wöhrmann-Repenning 1984 a, b, 1993 b). As a rule, the morphology of the VNC within a mammalian order follows the same type of construction, and usually the respective species show little in-

1616-5047/01/66/05-257 $ 15.00/0.

dividual variations. Those orders that do not fit into this scheme, like insectivores (Wöhrmann-Repenning 1984 b) and bats (Wible and Bhatnagar 1996), are of particular interest. From this point of view, the order of primates should be of special significance, since it is well known that within the ascension of this order the sense of smell has decreased from macro- to microsmaty. Involved in this process are both olfactory systems, the primary nasal, as well as the vomeronasal olfaction, which in the catarrhine radiation might even have been lost entirely (Frets 1912; Maier 1997).

Beyond the fact that the facial skull in primates was subject to considerable change during phylogeny (Starck 1953; Biegert 1957; Hofer and Spatz 1963) in this process the eyes oppressed the nasal cavity by moving progressively into a frontal position. In general, the nose tended to shorten in length almost simultaneously, with the VNC involved.

Only few specific publications on the VNC of some species are available (Schilling 1970; Jordan 1972; Hedewig 1980; Starck 1982; Maier 1997; Bhatnagar and Meisami 1998). Reference was made to these publications, since they helped to complete the present study whose purpose is to investigate the comparative anatomical characteristics of the VNC in a greater number of mainly basale primates with regard to recorded developmental inquiries.

Material and methods

For the present study the noses of several, mainly adult primates were available as follows:

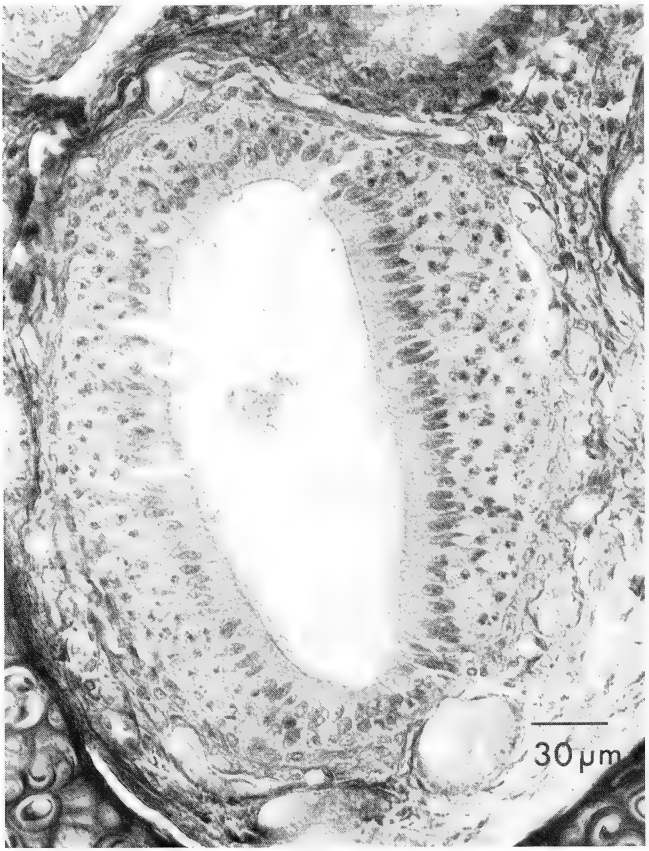


Fig. 1. Cross section of the VNO of *Tarsius bancanus borneanus*. 10 µm. Azan.

Subordo Strepsirhini: *Microcebus murinus* (Cheirogaleidae, Lemuroidea), *Lemur catta* (Lemuridae, Lemuroidea), *Arctocebus calabarensis* (Lorisidae, Lorisoidea), *Nyticebus coucang* (Lorisidae, Lorisoidea), *Galago crassicaudatus*, adult and fetus, 43 mm total length (Galagidae, Lorisoidea) *Galago senegalensis*, neonatus (Galagidae, Lorisoidea).
Subordo Haplorhini: *Tarsius bancanus borneanus* (Tarsidae), *Tarsius syrichta* (Tarsidae).

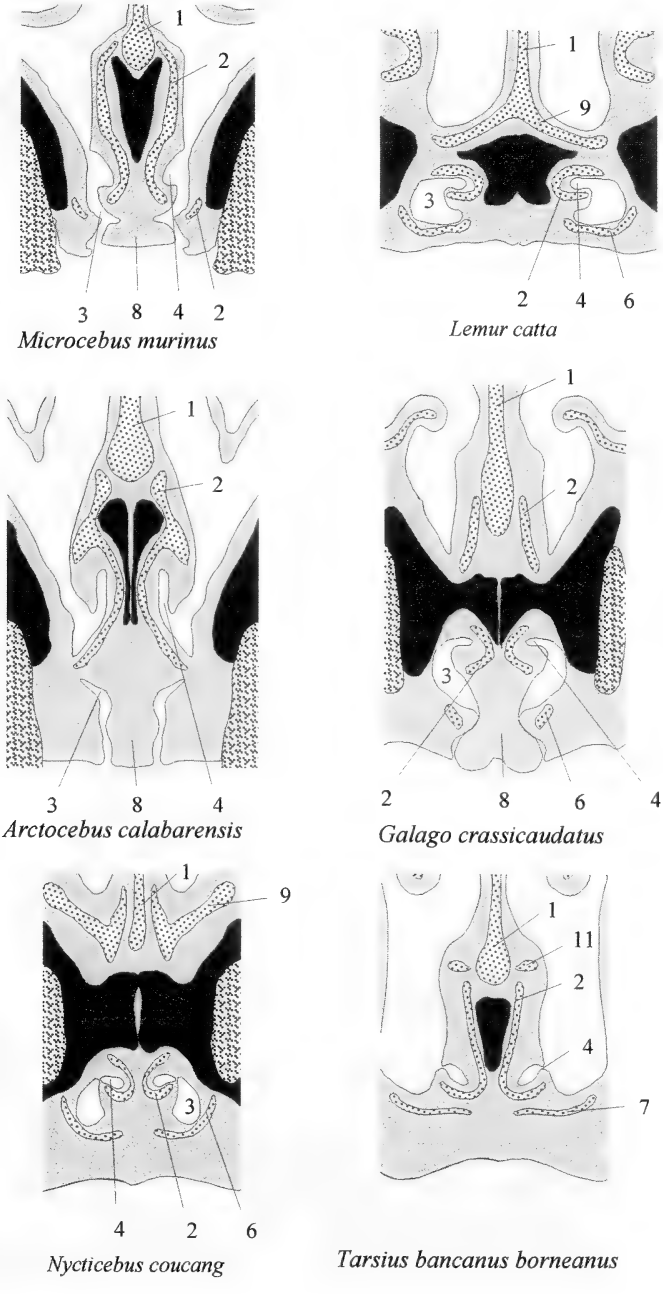
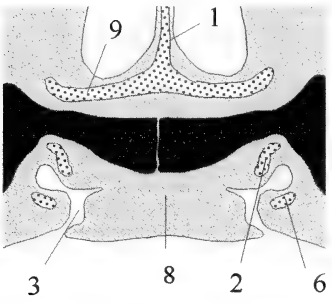
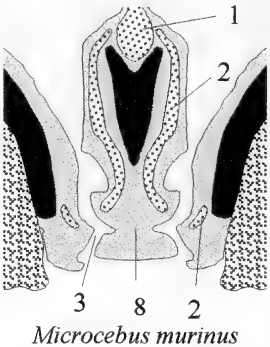


Fig. 2. Schematic and comparative representation of the merging of the VNO in the investigated species in six cross sections. Black – bone; stippled – cartilage; 1 – nasal septum; 2 – cartilago paraseptalis; 3 – ductus nasopalatinus; 4 – ductus vomeronasalis; 5 – vomeronasal organ; 6 – cartilago ductus nasopalatini; 9 – lamina transversalis anterior; 10 – outer bar; 11 – unnamed cartilage.

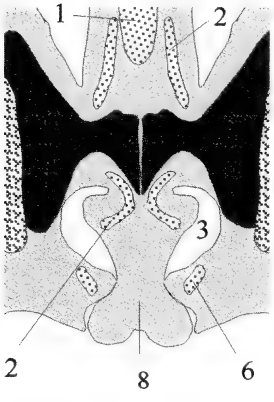
The primate material originated to a great extent from the collection of the late Prof. Dr. H. O. HOFER. A series of differently stained cross sections of the rostral noses were studied with the aid of a light microscope.



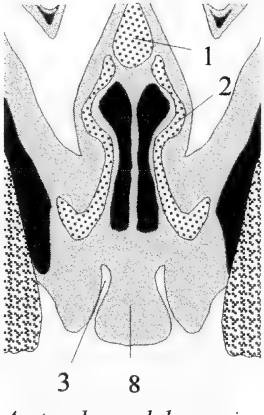
Lemur catta



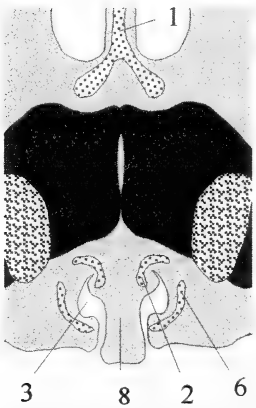
Microcebus murinus



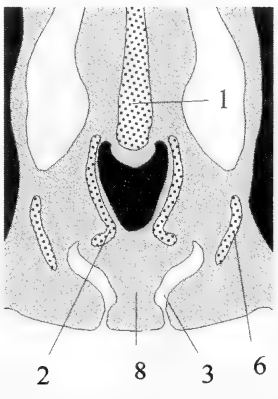
Galago crassicaudatus



Arctocebus calabarensis



Nycticebus coucang



Tarsius bancanus borneanus

Fig. 3. Schematic and comparative representation of the palatine papilla in the investigated species in six cross sections. See Fig. 2 for further explanations.

Results

Vomeronasal organ

Apparently, the VNO in all investigated primates is well developed. In Strepsirhini the sensory epithelium covers only the medial side of the organ, while the lateral part is coated by a respiratory epithelium. This coincides with the situation found in most mammals. In *Tarsius*, however, the organ is almost completely covered with olfactory epithelium, and only a few small islands of respiratory epithelium are embedded in this area (Fig. 1). This is probably a consequence of the extremely compressed snout of this species, which allows the VNO only to extend up to a length of about 3 mm. In addition, cross sections of the organ reveal it to be circularly rounded, while in most mammals the organ is somewhat laterally compressed. Rostrally, the organs of both sides merge into the paired nasopalatine ducts (Fig. 2). In *Lemur*, *Galago*, and *Nycticebus* this happens in the middle of the ducts deep inside the palate. In *Arctocebus*, as well as in *Microcebus*, the ducts penetrate the gum extremely vertically, while their VNOs merge into the ducts closely neighboured to the nasal floor. Probably therefore the orifices of the VNO are exceptionally oriented towards the oral cavity. In *Tarsius*, cross sections show these orifices situated deep inside the nasal floor (Fig. 2). In reality, however, this region proves to be the broad funnel-shaped nasal mouth of the nasopalatine duct. In addition, the openings of the VNO are no small, short ducts like in the other species, but extended longitudinal slits.

Rostral palate and palatine papilla

All the investigated species possess a well-developed mushroom-shaped palatine papilla, which obviously has the function of a plug, as described in other mammals (Wöhrmann-Repenning 1991) (Fig. 3). In *Lemur*, the papilla is related to its pronounced exceptionally large snout and possesses a very broad surface. In Strepsirhini, like in all mammals with a well-developed naked rhinarium, the sulcus surrounding the lateral sides of the papil communicates directly with the philtrum, which actually is a ventral furrow splitting the rhinarium (Fig. 4). A cleft exists between their frontal incisors. In accordance their frontal incisors are separated from each other by a median cleft. *Tarsius*, however, differs from this situation (Fig. 5). As in all haplorhine primates (Hofer 1979), the tip of the nose is a rounded, hairy part connected to uniform

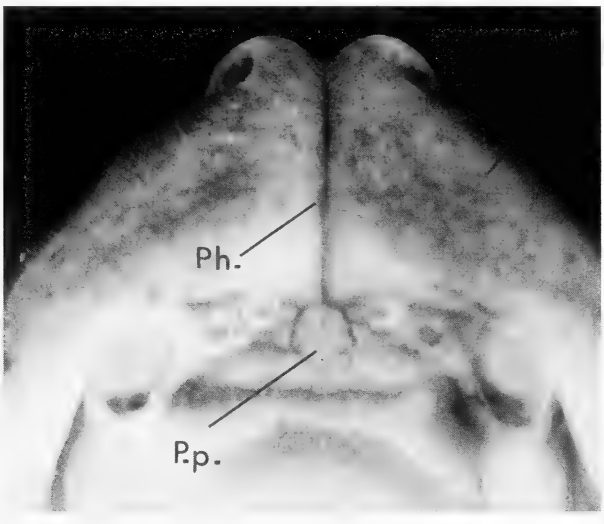


Fig. 4. Rostral view of the palate of *Galago crassicaudatus*. p.p. – palatine papilla; ph. – philtrum.

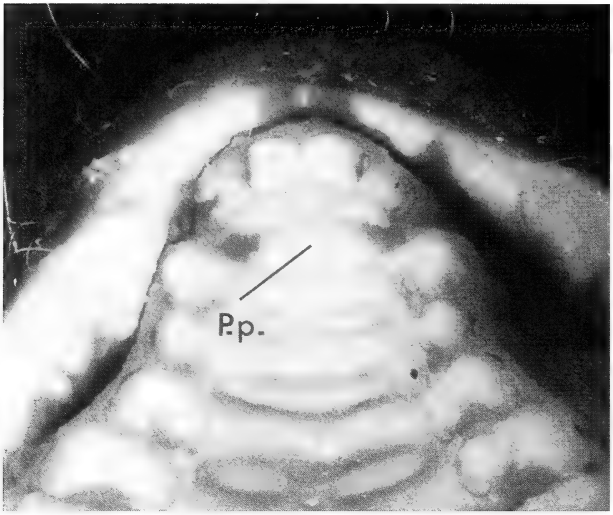


Fig. 5. Rostral view of the palate of *Tarsius bancanus borneanus*. p.p. – palatine papilla.

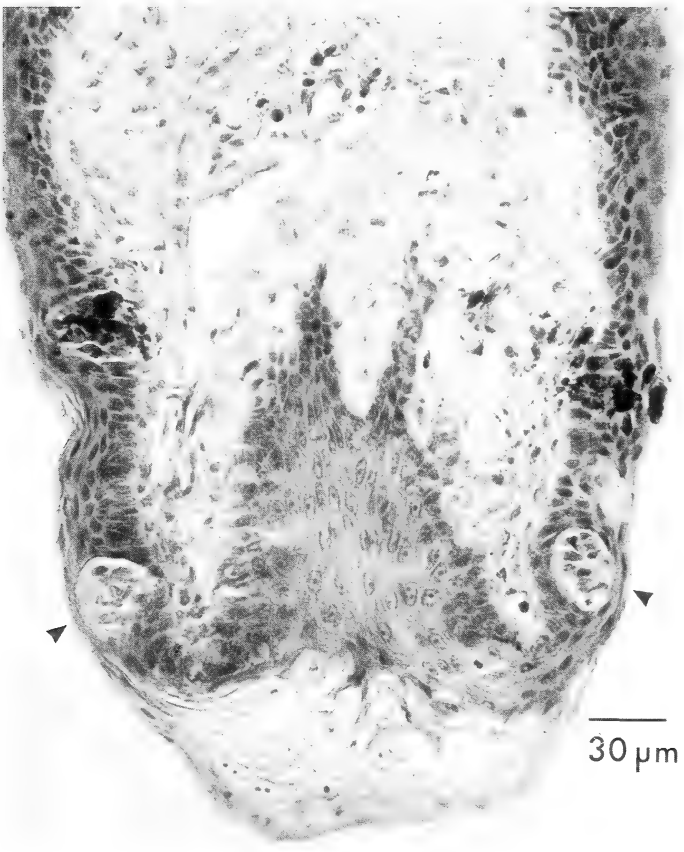


Fig. 6. Cross section of the palatine papilla of *Microcebus murinus* with taste buds (arrows). 10 µm Delafield's hematoxylin and eosin.

freely movable upper lips. No median furrow separates the incisors, instead they are situated closely together. The palatine papilla, not being very prominent, is mainly marked by two small lateral furrows, which are the actual nasal openings of the nasopalatine ducts.

The palatine papilla is a site where taste buds quite often appear in mammals (Wöhrmann-Repenning 1978, 1993 a). The latter studies have shown that they do appear in several strepsirhine primates for instance in *Galago*, *Nycticebus* and *Microcebus* (Fig. 6). Hofer (1977) found taste buds in *Peridicticus potto* as well, while no taste buds occur in *Lemur, Arctocebus* and *Tarsius.*

Cartilages of the VNC

In general, the paraseptal cartilage is a central element of the VNC in mammals, since it is most closely associated to the VNO itself. It accompanies the organ along its entire length, thus forming a gutter-like support. In both Strepsirhini and *Tarsius*, the paraseptal cartilage reveals a construction typical for most mammals. Its medial edge exceeds the lateral fold significantly in height. An outer bar, which is a cartilaginous annular buckle often surrounding the rostral end of the VNO is not commonly distributed in the investigated primates. It is only well-developed in *Arctocebus*, where it is situated caudal to the opening of the VNO, thus forming an extended tubular structure (Fig. 7). *Nycticebus* tends to have an outer bar of varying form. One individual showed an outer bar that was developed only at its right side, while in the other animal both annular bars were developed. These bars, however, are not completely closed, with the lateral fold only showing close contact with the medial side. Here only the perichondria fuse, but not the cartilages themselves. Obviously exceptionally, there is a distinct outer bar developed in one juvenile *Galago crassicaudatus*, while this is missing in the adult specimen.

With only one exception, i. e. *Arctocebus*, the paraseptal cartilage in Strepsirhini has a rostrally forked region. In *Microcebus*, where the organs open near the back wall of the nasopalatine ducts, this forked region occasionally is situated rostral to the opening of the organ. The dorsal branch of this fork is always continuous anterior to the lamina transversalis, while the ventral part en-

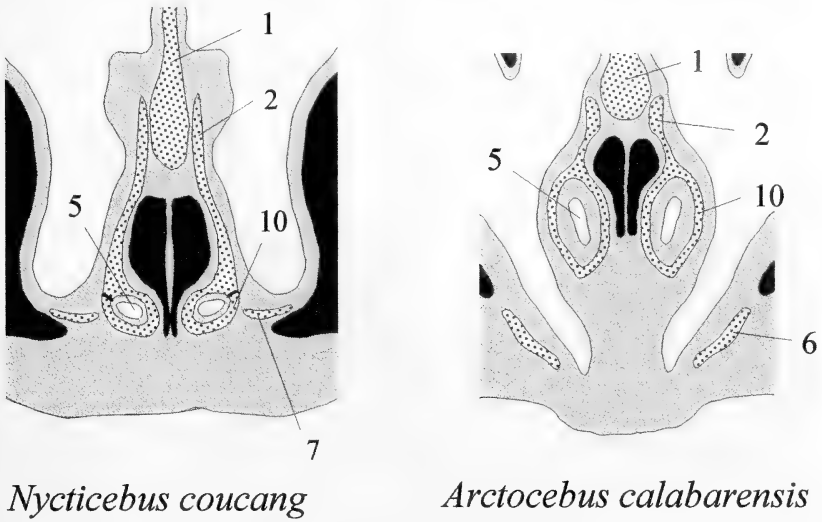


Fig. 7. Schematic representation of the outer bar of the paraseptal cartilage in *Nycticebus* and *Arctocebus*. See. Fig. 2 for further explanations.

circles the VNO until it opens into the nasopalatine duct. In *Tarsius*, this part is variable in its construction. Here the forked region seems to be an unstable, delicate element. While such a region was not found in the only investigated individual of *T. syrichta*, it was present in all three specimens of *T. bancanus*, but only in one case, the forked region was distinctly well developed.

In both *Nycticebus* and *Tarsius*, the ventral branch or part of the paraseptal cartilage rostrally fuses with the cartilage of the nasopalatine duct, which is common in many other mammals as well (WÖHRMANN-REPENNING 1984a, b) From this combination a characteristic sickle-shaped cartilage results which encircles the nasopalatine duct dorsally (Fig. 8). This seems normal for most mammals, but such a sickle is missing in individuals of *Tarsius* without a forked region. In those cases there is a solid cartilaginous nodal point instead. This sickle formed by two fused cartilages is not existent in both *Lemur* and *Galago*. A special situation is present in *Microcebus*. This species possesses a completely isolated sickle shaped cartilage. SCHILLING (1970) first described and called it "portion en faucille du cartilage paraseptal". It encircles the very rostral part of the VNO. The lateral part of this

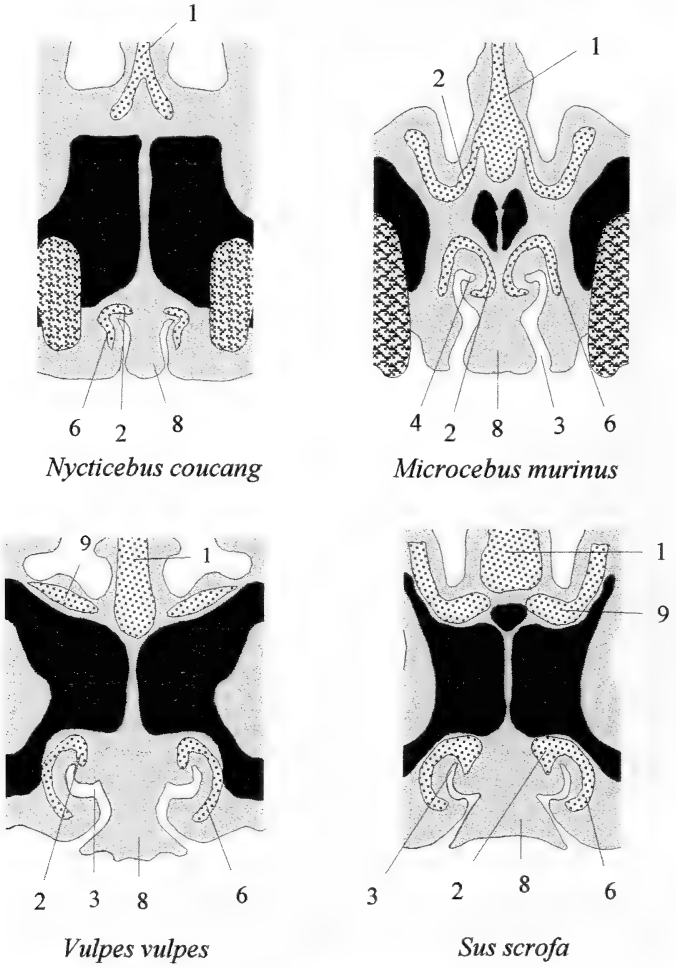


Fig. 8. A comparative representation of the sickle-shaped cartilage in two strepsirhine primates and two non-primate mammals. See Fig. 2 for further explanations.

sickle caudally ends abruptly. This special anatomical detail will be discussed later.

All investigated species possess a palatine cartilage which serves as a horizontally orientated skeletal plug for the incisive window. Except in *Microcebus* it was found to be closely connected with the cartilage of the nasopalatine duct which supports the duct laterally.

A papillar palatine cartilage is not commonly found in the investigated primates. Moreover, this cartilage seems to occur seldomly, and irregularly. Schilling (1970) did not describe it in *Microcebus*, while the studied individual has a small cartilage inside the papil. Correspondingly, it is present and even well developed in only one individual of an adult *Galago crassicaudatus*.

Finally, another rather odd cartilage in *Tarsius* should be mentioned, since it tends to fuse in some cases caudally with the medial edge of the paraseptal cartilage. This element, already noted and described by Starck (1982) supports the septal bulge situated dorsal to the VNC (Fig. 2). In *T. bancanus* it is either connected with the paraseptal cartilage or nonexistent. In *T. syrichta* it remains in certain distance to the paraseptal cartilage. This skeleton seems to be an unstable and varying element, primarily meant to stabilize a tuberosity of the nasal septum.

Discussion

From the present results it might be concluded that all strepsirhine primates and all members of the Tarsiiformes have a well developed and functionable VNO. This, however, is not surprising, since all these species possess a distinct marking behavior in which they use urine and/or special glandular secretions (Eibl-Eibesfeld 1953; Seitz 1969; Niemitz 1974; Epple 1976) and it is suspected that especially pheromones are closely related to a functioning VNO (Estes 1972; Meredith et al. 1980; Schilling et al. 1990; Sasaki et al. 1999). The special histological situation of the VNO in *Tarsius* might be a consequence of the narrow intranasal space in this species.

In placental mammals the VNC is either based on a primitive or a progressive type of construction. From several comparative studies it can be assumed that the origin of the division into two different lines took place during the early development of the Placentalia. Thus, we find the primitive type in Scandentia, Macroscelidea, Solenodontidae as well as in a modified form in Rodentia and Lagomorpha (Broom 1898; Wöhrmann-Repenning 1980, 1981, 1982, 1984 a, b, 1987). In contrast to this, the majority of placental mammals – also including the majority of insectivores – exhibits a progressively developed VNC. In this case the rostral part of the VNO tends to subside orally, deep into the palate, where it merges directly into the nasopalatine duct, often traversing the palate in an extremely oblique manner. Due to this situation the arrangement of the cartilaginous elements is rather complicated.

There is no doubt that primates – in case they have a VNC – with regard to their construction, follow the progressively developed line. Here in this investigation we found that Strepsirhini often demonstrate a pattern which might even be called exemplary. Some studied species, however, show slight modifications which can be interpretated as first reactions to the tendency in primates to change and alter the facial skull. This, for instance, leads to some special features in *Microcebus murinus*, a species with a very short nose. The compression of its snout has obviously shifted the VNC. By this means the merging of the VNO is moved to the backside of the nasopalatine duct, and the forked region of the paraseptal cartilage is occasionally situated rostral to this site. From this aspect the isolated "sickle-shaped" cartilage (Schilling 1970) should be the common combination of the paraseptal cartilage and the cartilage of the nasopalatine duct, since this feature is too similar to the situation found in other mammals. Accordingly, the caudal cartilage supporting the lateral wall of the nasopalatine duct in *Microcebus* is – taking the shifted VNC into account – the rostral part of the palatine cartilage, which does not

fuse in any case with the cartilage of the nasopalatine duct. The as yet unpublished results of own investigations, show that the two cartilages develop both independently and successively to each other.

The results of the investigations conducted on *Arctocebus calabarensis* should also be discussed, since at the first sight they seem to differ greatly from the normal progressive constructional type. This impression arises from the fact that this species has no forked paraseptal cartilage and the fusion of its VNO seems to be situated rather inside the nasal cavity than in the nasopalatine duct. Cross sections, however, reveal that in this primate the VNC is orientated in an extreme vertical position. Due to this position, the VNC of *Arctocebus*, which originates without doubt from the progressive line, curiously regains features of the primitive VNC. Thus, the nasopalatine duct passes through the palate straight down to the oral cavity. Thereby the nasal floor subsides steadily into its tight crater-like opening. Thus in cross sections a missheading impression is gained that the openings of the VNO are still situated inside the nose. Additionally, the vertical oriented VNC in *Arctocebus* renders a forked paraseptal cartilage, because the nasopalatine duct passes straight through the incisive foramen. With reference to the primitively constructed VNC, the paraseptal cartilage in *Arctocebus* has a well-developed outer bar, which, however, is rather an elongated tube than a small bar. In other strepsirhines an outer bar is more or less an exceptional structure.

Finally *Tarsius* should be mentioned. It is remarkable that this species, with a nose almost completely compressed, still has a surprisingly well developed VNC (STARCK 1982). In general, it shows several conformities to those features found in strepsirhines. The forked region of the paraseptal cartilage however seems to have lost its functional importance with the very small nose. It is only well-developed in one individual. At the same time, none of the investigated species demonstrates as clearly as *Tarsius* that the VNC can be altered greatly for example, when the nasal cavity is forced to transform, and thus forced to reduce structures because of dramatic facial changes.

Regarding the external situation of the VNC in strepsirhine primates we find a situation characteristic for many mammals. These remarkable structures are closely connected to the functional mechanism of the VNO (HOFER 1977, 1980; WÖHRMANN-REPENNING 1991). The rostral palatal features in *Tarsius* differ from this in that it belongs to the haplorhine primates. In strepsirhine primates taste buds are commonly found at the ventro-lateral sides of the papilla palatina. They are mainly situated near the entrance of the nasopalatine duct. Their role in connection with sensory abilities of the VNO in mammals was generally discussed in a previous study (WÖHRMANN-REPENNING 1993 a). The presence of taste buds indicates a dual chemosensory system combining smell and taste for functions of the VNC. In those cases, where taste buds are missing at the palatine papilla, as it can be seen in *Lemur*, *Arctocebus* and in *Tarsius*, one may assume that lingual taste buds interact with the VN-olfaction.

Acknowledgements

We would like to thank MARION KÜHN for kindly revising the English text.

Zusammenfassung

Der Vomeronasalkomplex bei strepsirhinen Primates und *Tarsius*

Der Vomeronasalkomplex (VNC) verschiedener strepsirhiner Primates und von zwei *Tarsius* Species wurde unter vergleichend anatomischen Aspekten untersucht. Alle Arten besitzen ein gut entwickeltes Vomeronasalorgan (VNO). Bei *Tarsius* ist das VNO auf Grund seiner winzigen Nasenhöhle entsprechend klein ausgebildet. Offensichtlich um dies zu kompensieren, ist das Organ – anders als bei den

Strepsirhini und den meisten anderen Mammalia – in seinem gesamten Lumen fast vollständig von olfaktorischem Epithel ausgekleidet. Das VNO aller untersuchten Primaten läßt auf Grund seiner histologischen Beschaffenheit vermuten, daß ihm eine wichtige Funktion im sensorischen Leben der Tiere zukommt. Die Befunde lassen klar erkennen, daß der VNC der Primates dem progressiv entwikkelten Typus zuzuordnen ist. Charakteristisch für diese Entwicklungslinie ist ein im rostralen Abschnitt diffizil gestalteter Paraseptalknorpel, der sich zudem in diesem Bereich in der Regel in einen dorsalen und einen ventralen Ast gabelt. Beide Teile neigen zum Fusionieren mit anderen Knorpeln. Die Mehrzahl der untersuchten Primaten besitzt einen progressiv entwickelten VNC, dessen Gesamtstruktur dem anderer Mammalia bis in kleinste Details ähnelt. Bei einigen Vertretern jedoch lassen sich Besonderheiten ausmachen, die größtenteils im Zusammenhang mit der für Primates charakteristischen Umgestaltung des Fazialschädels zu sehen sind. Alle Strepsirhini besitzen ein nacktes Rhinarium, dessen Philtrum ventral mit dem Sulcus papillae palatinae kommuniziert. In diesen Sulcus aber münden die Ductus nasopalatini ein, und genau in diesem Bereich befinden sich bei einigen der untersuchten Strepsirhini Geschmacksknospen. *Tarsius* besitzt kein Rhinarium, sondern als Angehöriger der haplorhinen Primaten eine ungeteilte, behaarte, frei bewegliche Oberlippe.

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Mamm. biol. **66** (2001) 269–280
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Review

Postnatal brain size decrease, visual performance, learning, and discrimination ability of juvenile and adult American mink (*Mustela vison*: Carnivora: Mammalia)

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Receipt of Ms. 24. 07. 2000
Acceptance of Ms. 17. 10. 2000

Abstract

The decrease in brain size to an amount of 20% during early life from the juvenile to the adult state in mink and other *Mustela* species is still poorly understood and unresolved in its general biological and functional relevance. The same holds true tor the decrease in brain cavity and the flattening of the cranial vault. Since the neocortex and other brain parts with higher integrative and associative sensory and motoric functions are especially involved, the question arises as to whether these size changes have any functional consequences, i. e., are the functional capacities reduced concomitantly? This was tested for the visual system in 8 juvenile (4, 4) and 8 adult (4, 4) mink (*Mustela vison energumenos*) of wild descent using twofold-choice discrimination trials. After conditioning and testing for spontaneous side preferences, the individuals had to discriminate black dots of different sizes against a white plate from 30 cm distance. Altogether, 16 000 individual data-sets were statistically analysed for differences in visual performance, in learning velocity, and in discrimination ability. No differences occurred between the juvenile and the adult group concerning learning velocity. However, significant differences were found in discrimination ability with regard to age (juvenile mink performed better than adults) and sex (females performed better than males). These results are discussed with regard to the importance of visually guided behaviour of the species, with the behaviour of juveniles and adults in general, and with the ontogenetic decrease in mass of the central nervous tissue. According to this study, there is no indication of any functional impact of the ontogenetic reduction in brain size on the capacity of the visual system.

Key words: *Mustela vison*, ontogenesis, vision, brain size

Introduction

Unlike most other mammals, some species of the *Mustela* genus exhibit a peculiar postnatal brain ontogeny, i. e., their brain significantly decreases in size in both sexes shortly before the adult stage is reached. This phenomenon was confirmed by brain and skull comparisons in the two domesticated forms of ranch mink (*Mustela vison* f. dom.; Kruska 1977, 1979, 1993) and ferret (*Mustela putorius* f. furo; Apfelbach and

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KRUSKA 1979; ESPENKÖTTER 1982) as well as in wild populations of feralized ranch mink (WIIG 1982, 1985) and the weasel (*Mustela nivalis*; SCHMIDT 1992). Furthermore, brain size decreases due to domestication were additionally found. This results from comparisons of adult wild American mink with adult ranch mink (KRUSKA 1996, KRUSKA and SCHREIBER 1999) as well as polecat with ferret (ESPENKÖTTER 1982). However, these changes of brain size in the course of domestication differ considerably from those in ontogenesis (KRUSKA 1987) since different brain parts are involved in the two respective processes to highly diverse degrees (KRUSKA 1993, 1996). Although not all species have been investigated so far, it can be assumed that the ontogenetic decrease in brain size appears in all *Mustela* species, including the American wild mink.

In comparative brain anatomy, intra- or interspecific differences in the mass of brain substance are usually discussed in connection with a functional increase or decrease in general central nervous capacity (KRUSKA 1988 a). Because ontogenetic brain size decrease mainly occurs at an individual age from 5 to 7 months in mink, its biological relevance is especially puzzling. This is the time when the maternal family breaks up and the subadults disperse, searching for their own future home ranges (KRUSKA 1988 b). A decrease in central nervous capacity at this stage of ontogeny appears unlikely.

Quantitatively, the diencephalon decreases by 9.5% in size independently of body size, but the most extreme decrease was found in the telencephalon, this being 22% smaller in size in adults compared with 5-month-old individuals. Here, the total neocortex (23%) and especially its grey matter (27%) are most dramatically decreased (KRUSKA 1993).

As these impressive size reductions affect brain parts with especially higher associative, coordinative, and integrative central nervous functions, they should have a bearing on general ethology or special behavioural performance, if functionally relevant at all. In this framework, the present study aims at comparing the capacities of one exemplary sensory system in juvenile vs. adult wild mink (*Mustela vison energumenos*) namely visual performance, visual learning, and visual discrimination ability. The concerned brain parts, especially the occipital neocortex grey matter are especially involved in these general visual functions.

Material and methods

Animals

In total 16 (8 m, 8 f) wild mink (*M. vison energumenos*) were used in this study. Eight (4 m, 4 f) juvenile and 8 (4 m, 4 f) adult individuals were born at the Institut für Haustierkunde of the University of Kiel. They were first generation offspring of wild parents that were caught in the vicinity of Whitehorse (Yukon Territory, Canada), transported to Kiel, and kept there in large open air enclosures. The test animals were fed mainly on newly hatched chicks and housed separately in differently sized (22 m^2–35 m^2) wire mesh surrounded open air enclosures on natural ground with vegetation, nest boxes, and water basins. White spots different in size and pattern on the pelage of throat, breast, and belly made them individually recognizable. Additionally they were named using G as initial letter for the juveniles and F for the adults. The juvenile mink were on average 3.6 months (range: 98–117 days) old at the start of the experiments, the adult ones 11.2 months (range: 337–343 days).

Experimental arena

Twofold-choice discrimination trials were run in a simple experimental arena of wood (1.7 m in length, 0.5 m in breadth and 0.2 m in height). This arena (Fig. 1) consisted of one discrimination chamber (A) covered with wire mesh and two adjacent reward boxes (B) covered with a wooden plate. Lockable one-way swinging doors (C), 16×16 cm in dimension, allowed access to each of the reward boxes if unlocked. Plates with visual discrimination test stimuli could easily be placed on these swinging doors. There was also a partition wall (D) between these swinging doors protruding 30 cm into the discrimination chamber, thus forming a left and a right tunnel at its lower end. Entrance to the arena was only possible through a trap door (E) that could not be opened

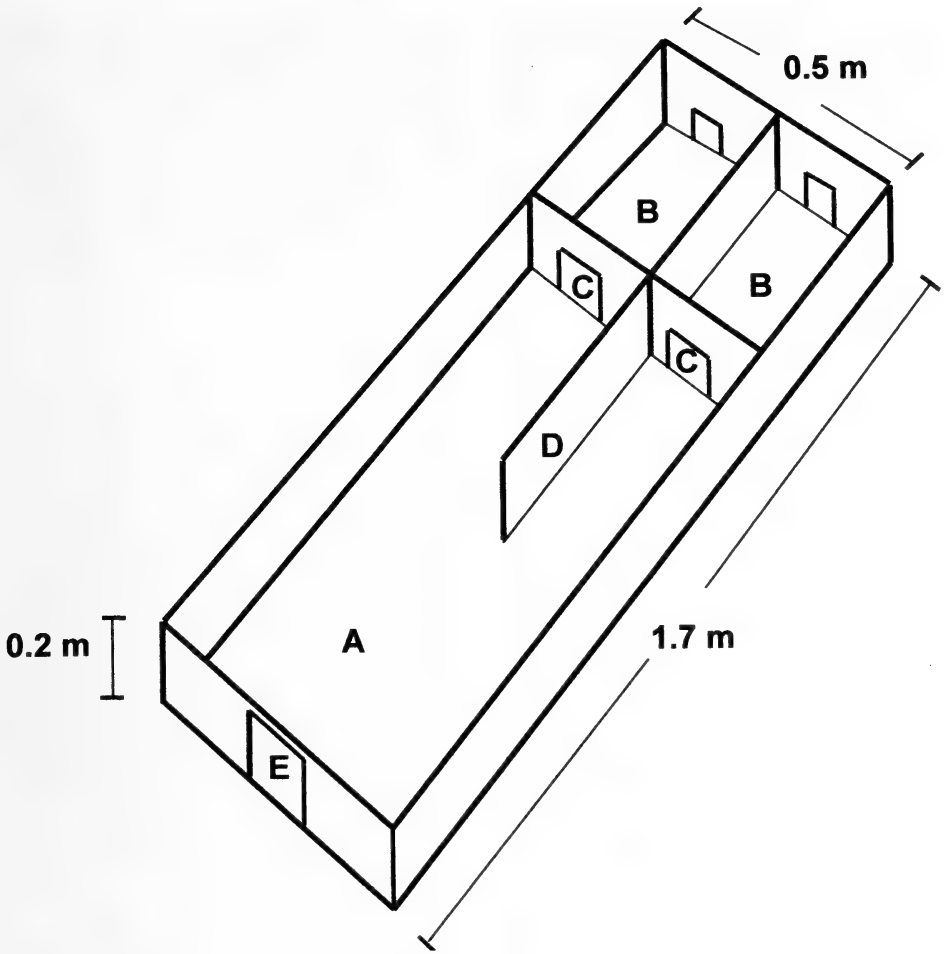


Fig. 1. Scheme of the experimental arena.
A – discrimination chamber; B – reward boxes; C – one-way swinging doors; D – partition wall; E – entrance trap door

by the animals. One-way swinging doors at the end of the reward boxes were the exits from the arena.

Experimental tests

The arena was placed in the diverse rearing enclosures of the mink, thus trials were run in accustomed environments during normal daylight. The mink were tested to discriminate visually between a totally white, blank plate and diverse white plates with central black circles of different diameter (70, 30, 25, 20, 15, 12, 9, 5, 3, and 1 mm). The experiments were performed in four phases identical for all animals tested. During Phase 1 each of the mink was habituated to the arena and observer (K. S.). At this time all the doors were kept unlocked and pieces of food (chick parts) were randomly placed in one of the reward boxes only. Access was possible through the entrance, so the mink was conditioned to the one-way path through the arena. During Phase 2 individual side preference and its constancy were tested. Equally sized pieces of food were now offered simultaneously in both reward boxes during each trial. Each animal performed 100 runs over 2 to 3 successive days. The random right or left side choices

were recorded. During Phase 3 the animals were tested for spontaneous preference of visual stimuli. Now, for the first time the discrimination plates were affixed to the still unlocked swinging doors leading to the reward boxes both loaded with food rewards. In the first trial, the white plate was presented on one side against the white plate with a central black circle 70 mm in diameter on the other side. Each animal had to run 50 trials on one day. During these trials the position of the plates was changed from left to right and vice versa in accordance with the schedule of GELLERMAN (1933). Hereby it was ensured that (1) the subsequent side (left/right) was unpredictable to the animals, (2) no plate was offered more than maximally three times on the same side in consecutive trials to avoid possible side preferences, and (3) both sides (left/right) occurred overall at the same frequency. Phase 4 finally represents the entire tests aimed at for visual discrimination and learning. In this, the white plate was designated the incorrect choice and consequently the swinging door bearing this plate was locked during all following trials, although the associated reward box always contained equal quantity of meat reward. This controlled for choices made on possible olfactory cues.

In each trial, the mink had to make their decision at a 30 cm distance from the swinging doors and choices were evaluated by the observer (K. S.) as positive or negative. These evaluations followed stringent criteria. Choices were counted as positive only in cases where animals ran to the positive sign immediately after entrance into the discrimination chamber. In cases where they showed preference for the wrong side or started to move towards the negative stimulus, this was counted as a negative choice even if they seemed to recognize the failure and corrected their choice later.

Trials with the same plates were run 50 times on one day by each of the mink followed by a day of relaxation and 50 trials on the subsequent day. A higher number of trials daily led to erratic performance in later trials, probably due to satiation after the positive rewards.

The time point at which conditioning to the 70 mm circle had occurred was very clearly recognisable through a change in behaviour. From that moment on, mink moved rather rapidly and directly towards the correct sign. The number of runs preceding this conditioning was taken as a measure of individual learning velocity. The entire 100 discrimination trials with the 70 mm circle were conducted after conditioning had taken place. Only after completing the 100 trials on the 70 mm circle during two days the next smaller sign was tested in the same manner, regardless of the animal's prior performance, and the trials continued in the same way for all smaller circles. The order in which the individual animals were tested and the time of day (08.00 h–12.00 h) the trials were run was constant throughout the experiment. Each of the 16 mink therefore completed a total of 1 000 test trials. Thus, altogether 16 000 runs yield the data base for statistical treatment.

Data analysis

Choices during Phase 1 were not analysed statistically. Habituation to the apparatus and conditioning to find food were continued until the animals performed efficiently. Choices of Phase 2 and 3 were treated statistically. The significance of spontaneous preferences for side (right/left; Phase 2) and visual stimuli (stimulus present/absent; Phase 3) was assessed by a replicated goodness-of-fit χ^2-test. During the learning phase, mink were considered as trained to the visual stimulus if they correctly chose 63 out of 100 trials. This corresponds to a probability of $p = 0.99$, i. e. the mean rate of correct choice is significantly larger than expected at random (= the lower limit of the 99% confidence interval for the mean rate of correct choice exceeds 0.5; SOKAL and ROHLF 1995). The total of 16 000 individual trials of the entire Phase 4 was jointly analysed using a log-linear model for frequency data (BISHOP et al. 1975; SOKAL and ROHLF 1995). By this approach we examined the influences of age, sex, and sign size on the discrimination efficiency as well as the various interactions among these factors.

Results

General behaviour of the individuals

The individual mink differed slightly in general behaviour prior to as well as during the experiments. The adult mink, e. g., were accustomed to their enclosures for a longer period and were minimally disturbed by humans. During Phase 1, they acted rather hesitantly and shyly. The juveniles, in contrast, seemed to be more bold and curious. Adult individuals required up to 20 sec. for a run through the experimental arena, while juveniles clearly operated faster, on average only 4–8 sec. per run. Apart from this, some

individuals of both age groups were especially shy, labile, and less concentrated during the trials (Gira, Giwa, Feka), while others remained comparably calm and difficult to motivate (Galbus, Fabea, Felia, Fedor, Falkano, Fargo). In contrast, still others acted very excited, concentrated, and fast. They often vocalised the typical twitters of excitement (Gilia, Galicia, Gaius, Gagarin, Godu, Fiona, Fibius) during trials. Sex-specific differences were especially marked. In cases of a wrong decision, for example, adult males tended to be aggressive and bit, scratched and tore at the locked entrance to the reward box but such behaviour was never observed in females. In comparable situations, females only corrected their erroneous decision by running to the positive sign with the food reward. Thus, although such a choice was negatively evaluated for the trial, females showed a somewhat greater plasticity in such situations. This is also reported for many other mustelids. Females, both adults and juveniles, were also more active in general compared to males, especially during the habituation and conditioning phases. Males were clearly less motivated and comparably disinterested. All the animals, however, completed all trials although in individually different ways.

Table 1. Individual side preference prior to conditioning (100 runs per animal)

Age	Sex	Individual	side choice	
			left	right
juvenile	female	Gilia	56	44
		Gira	41	59
		Galicia	38	62
		Giwa	40	60
	male	Galbus	54	46
		Gaius	39	61
		Godu	62	38
		Gagarin	42	58
adult	female	Fiona	50	50
		Felia	62	38
		Feka	50	50
		Fabea	52	48
	male	Fedor	56	44
		Falkano	56	44
		Fibius	54	46
		Fargo	58	42

Side preference and spontaneous preference for visual stimuli

Summarised results of the test for spontaneous side preference and side constancy of choices are given in table 1. There was no significant overall side preference (replicated goodness-fit: $\chi^2_{pooled} = 0.25$, $df = 1$, $p = 0.617$), but the side preference was significantly heterogeneous among individuals (replicated goodness-fit: $\chi^2_{heterogeneity} = 40.00$, $df = 15$, $p < 0.001$). This was caused by four individuals exhibiting a spontaneous side preference, significant at $p < 0.05$. Albeit this preference was only slight (62 : 38 at maximum) and symmetrical (two individuals preferred left, two right), the potential influence of individual side preference on the visual discrimination efficiency was estimated in a separate log linear model.

Most mink showed no preference for either a blank white plate or a 70 mm black circle. Based on 50 runs per animal and a significance level of $p = 0.05$, only two individuals seemed to slightly prefer the circle, while three others did so with the white plate.

Learning velocity

Regarding individual learning velocity, the juvenile mink clearly showed less variability of run numbers (range: 57 to 95) than the adults (range: 51 to 200) prior to conditioning (Tab. 2). This was caused by two particular adults (Fibius, Feka) learning very slowly, with 200, respectively, 150 trials prior to conditioning. However, all the other adults reached values within the variance of the juveniles. Over all, there were no significant differences among the four groups, i. e., juvenile and adult mink of both sexes (Kruskal-Wallis-Test: $H = 4.83$, $df = 3$, $p = 0.185$). Thus, learning velocity during conditioning of individual mink can be considered identical and independent of age and sex.

Table 2. Learning velocity during conditioning (runs per animal until they were considered conditioned; see methods for details).

Age	Sex	Individual	number of runs
juvenile	female	Gilia	89
		Gira	95
		Galicia	57
		Giwa	73
	male	Galbus	75
		Gaius	79
		Godu	80
		Gagarin	71
adult	female	Fiona	51
		Felia	81
		Feka	150
		Fabea	80
	male	Fedor	76
		Falkano	82
		Fibius	200
		Fargo	81

Table 3. Significant factors determining visual discrimination ability, given as % variation explained (result of a log-linear model analysis).

Factor	DF	χ^2	p	% of variation explained
Sex	1	13.25	<0.001***	4
Age	1	46.65	<0.001***	14
Sign size	9	116.41	<0.001***	35
Interaction sex vs. age	1	10.32	0.001***	3
Interaction age vs. sign size	9	45.41	<0.001***	14
total explained variation	–	–	–	70
unexplained variation	–	–	–	30#

#From 30% unexplained variation, 10% could be attributed to individual side preferences (as indicated by a separate log-linear model).

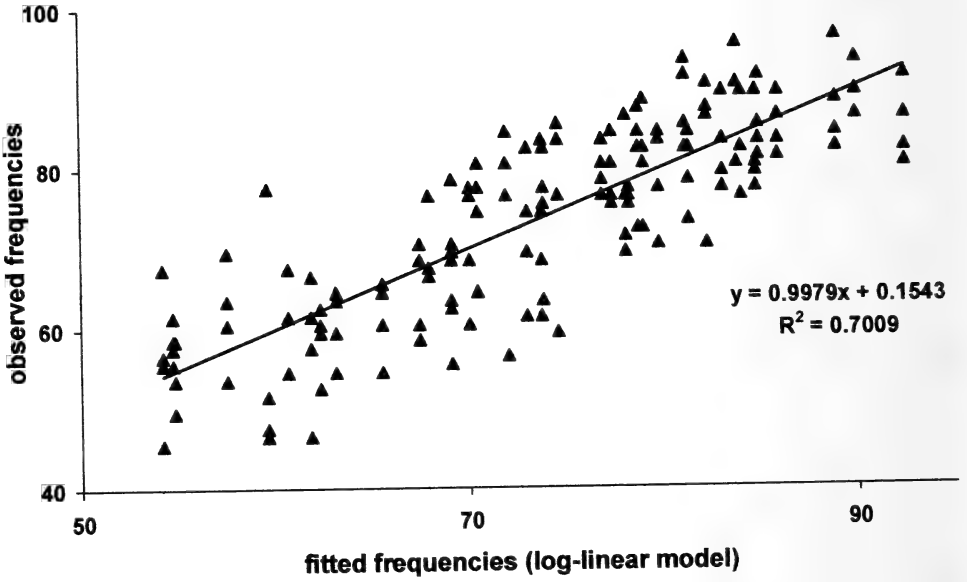


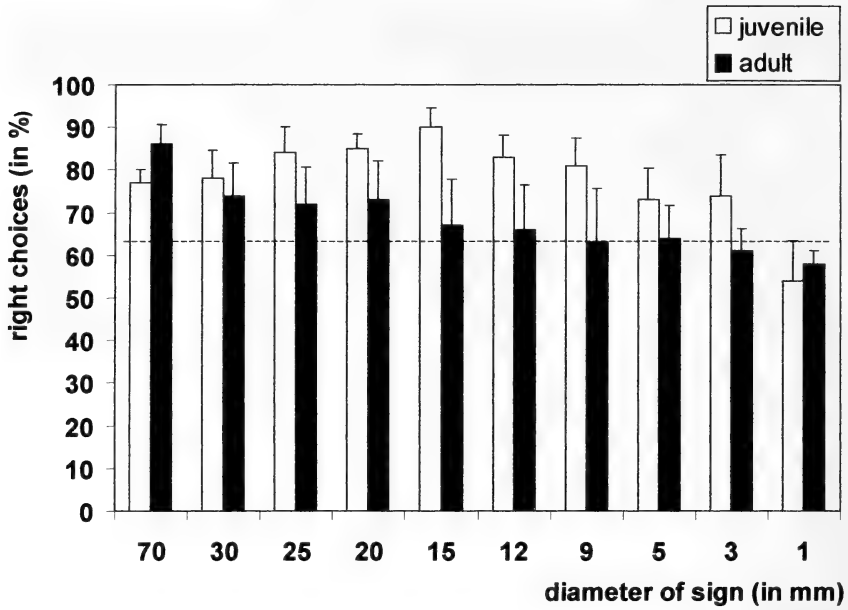
Fig. 2. Correlation between fitted and observed frequences of correct choices in the visual discrimination experiment, when sex, age, sign size and the two interactions sex vs. age and age vs. sign size are included in the log-linear model.

Table 4. Individual visual discrimination efficiencies of the juvenile and the adult mink. Numbers of positive choices are presented out of 100 runs on each of the black circles different in diameter. Grey shaded fields indicate performances below the significance level of 63%. Mean values of groups ($\bar{x}$) and standard deviations (SD) are also given.

			Diameter (in mm) of black circle positive sign									
age/sex		name	70	30	25	20	15	12	9	5	3	1
juvenile	♀	Gilia	77	82	89	81	89	89	87	75	76	53
		Gira	76	80	79	86	93	82	90	77	85	49
		Galicia	75	88	77	89	86	89	86	82	83	58
		Giwa	75	72	80	83	93	76	70	63	59	49
juvenile	♂	Galbus	80	69	90	85	84	83	78	69	61	55
		Gaius	75	71	80	83	82	77	73	61	68	56
		Godu	76	86	95	91	96	79	84	74	74	45
		Gagarin	84	76	80	81	88	89	82	82	83	67
juvenile	$\bar{x}$		77.3	78.0	83.8	84.9	88.9	83.0	81.3	72.9	73.6	54.0
	SD		2.99	6.65	6.16	3.40	4.54	5.12	6.57	7.44	9.46	6.34
adult	♀	Fiona	86	77	83	84	80	77	67	70	65	52
		Felia	82	83	80	82	84	80	76	78	64	62
		Feka	80	70	76	87	76	64	76	69	60	60
		Fabea	91	84	78	72	56	74	66	55	54	59
adult	♂	Fedor	91	76	70	69	63	61	46	54	63	58
		Falkano	93	77	68	63	59	46	47	61	60	57
		Fibius	82	68	60	68	64	57	51	61	53	55
		Fargo	85	60	58	62	54	66	77	67	69	61
adult	$\bar{x}$		86.3	74.4	71.6	73.4	67.0	65.6	63.3	64.4	61.0	58.0
	SD		4.58	7.50	8.63	9.08	10.7	10.5	12.5	7.61	5.10	3.08
females	$\bar{x}$		80.3	79.5	80.3	83.0	82.1	78.9	77.3	71.1	68.3	55.3
	SD		5.43	5.74	3.86	4.85	11.3	7.69	8.81	8.27	10.9	4.79
males	$\bar{x}$		83.3	72.9	75.1	75.3	73.8	69.8	67.3	66.1	66.4	56.8
	SD		6.04	7.22	12.6	10.3	14.5	13.7	15.3	8.28	8.69	5.80

Visual discrimination efficiency

According to the log-linear model, the key determinant of the visual discrimination efficiency was the sign size (accounting for 35% of the variation in discrimination efficiency), followed by age and sex, explaining 14% and 4% of the variation found, respectively (Tab. 3). Two two-factor interactions were significant, the interactions age vs. sign size and age vs. sex, accounting for 14% and 3% of the found variation in discrimination efficiency, respectively. Altogether, these factors explained 70% of the present variation and yielded a good fit between observed discrimination efficiency and values expected by the model (Fig. 2). Of the remaining 30% variation unexplained, about 10% can be attributed to individual side preferences (as indicated by a separate log-linear model), while the remaining 20% apparently represents individual differences and stochastic errors. Individual efficiencies to discriminate differently sized black circles are summarized in table 4. Evidently, the mink were generally unable to recognize a black dot sign 1 mm in diameter (except for one juvenile male). Additionally, six out of the 16 animals had also difficulties to discriminate the 3 mm sign. Thus, to discriminate a motionless sign of this size from a distance of about 30 cm may be problematical for mink in general. In this context, adult males are peculiar because of their different efficiencies from sign to sign. This specifically poor performance of adult males – especially with smaller signs – is the apparent expla-



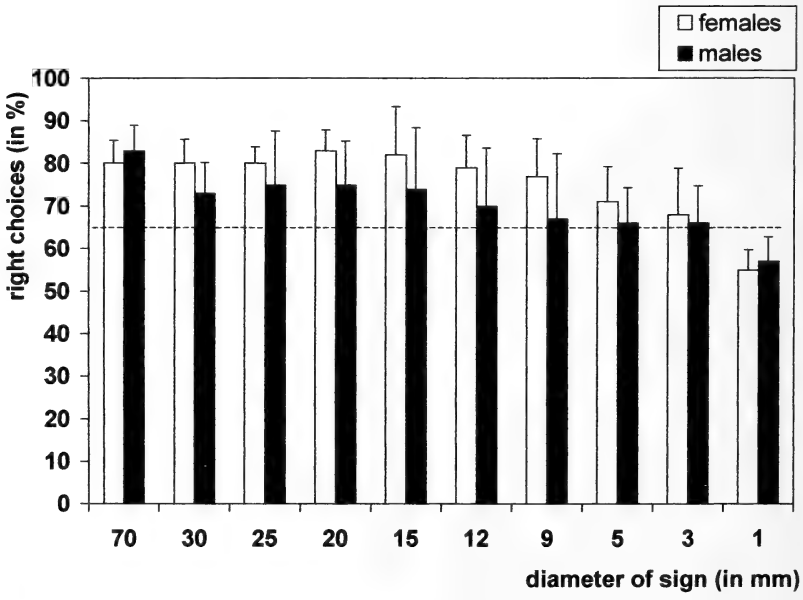


Fig. 3. Arithmetical means of positive choices for the differently sized signs of juvenile vs. adult and of female vs. male mink. Dotted line indicates the 63% level; vertical lines indicate standard deviations.

nation for the two significant factor interactions (age vs. sign size; age vs. sex). Very obviously their minor concentrations on the tasks are reflected in these results. Nevertheless, except for the smallest signs mink chose on average significantly more frequent correct than wrong, regardless of their sex and age (Fig. 3).

Discussion

In connection with the aim of this study it seems worth mentioning what is known about the importance of visually guided behaviour in the biology of the investigated species. Thus mink – like other *Mustela* species – are in general basal carnivores with only little anatomical specialisation (Ewer 1973). They are predators which regionally and seasonally prey on different vertebrates and invertebrates, hunting and chasing on land but since they are adapted to a semi-aquatic life style larger parts of food are also taken from rivers, lakes, or the sea. They are very efficient hunters, reacting quickly both in air and under water. They are thus dependent on their sensory organs for detection of prey, chasing, and killing but also for recognizing their own predators. Concerning their general orientation, they often are said to be sensory-guided mainly by olfaction followed by hearing and then by vision. However, such ranking in the importance of sensory organs and central nervous circuits for species-specific biological peculiarities seems rather meaningless since according to our own observations and those of others as well, mink very efficiently hunt fish in muddy waters even during dark times of the day and also in clear, reflecting waters during bright sunshine. Thus, it can be suggested that at least during these hunts they are mainly guided by sensory functions of the vibrissal system rather than by olfaction, hearing, or vision. Therefore, it seems more likely to conclude that all sensory systems are of certain importance for the biology of mink with different priorities at given situations. However, mink have well developed eyes and differentiated central nervous visual structures. The duplex retina is built up by highly differentiated and extremely polarized rods and cones, with the rods being more numerous (Dubin and Turner 1977; Braekevelt 1990; Steffen 2000). The lateral geniculate body as the main termination nucleus of visual perception is well differentiated (Guillery et al. 1979) showing certain laminae and an input of approximately about 75% to 80% crossed and 20% to 25% uncrossed fibres (Sanderson 1974; Sanderson et al. 1975). Accordingly, the striate area at the occipital lobe of the neocortex is well organized and histologically clearly distinct from surrounding areas (LeVay et al. 1987; Guillery and Obersdorfer 1977; Guillery et al. 1979). In relative size this highest sensory field accounts for about 6.8% of the total neocortical grey matter (own preliminary results). All these anatomical characters can without doubt be indicative for what normally is called good vision in contrast to poor eyesight. This is also confirmed by ethological and physiological tests and findings (Dunstone 1993; Dunstone and Sinclair 1978a, b). Acuity of predators for stationary objects (like dots) is less poorly developed than for moving objects. A recognition of black dots different in size might therefore be of limited importance for the biology of a species but at least documents its visual acuity and functional complexity. However, as our results indicate the animals acted in response to these stimuli and they were able to discriminate different sizes. Thus, the reactions of the animals on the experimental tasks may serve as a measure for functional sensory and central nervous capacities.

In order to uncover a probable relationship between the size of a brain structure and its complex functional capacity, the quantitative structural changes of central nervous tissue from juvenile to adult mink (Kruska 1993) can be correlated with quantitative functional differences as resulted from the visual test procedures presented here. Concerning such a relation, however, no unequivocal conclusions can be drawn, as apparent correlation may appear coinciden-

tally. As example, juvenile mink, known to possess significantly larger neocortical and diencephalic brain regions, generally showed significantly better results in reactions to visual discrimination tasks than adults both in female and male individuals. Consequently, this could be considered an indication for greater functional capacities of juveniles due to larger central nervous structures. This is, however, contradicted by the finding that learning velocity is independent of age. On the other hand, differences were observed among sexes concerning their discrimination ability, although mass and proportioning of the brain did not differ among sexes, either within the larger brained juveniles or within the adults (KRUSKA 1993). For these reasons, the postnatal overshooting of brain size has most probably no functional consequences for the biology of mink, at least not for the capabilities of the visual system. The fact that juvenile individuals are more playful, curious, easier to be conditioned, open for learning and consequently more efficient in behavioural experiments than adults is commonly known from many other mammalian species (WÜSTEHUBE 1960; GOETHE 1964; RENSCH 1973; TEMBROCK 1982) including those with normal brain size development. Thus, the postnatal brain size decrease most probably has no effects on visual functions and still remains unsolved in its biological relevance.

Acknowledgements

We greatly thank Prof. Dr. O. ANNE E. RASA, University of Bonn, for competent criticism on an earlier version as well as linguistic and stylistic advice. We also thank Mrs. ASTRID INGWERSEN, Institut für Haustierkunde, University of Kiel for general technical assistance.

Zusammenfassung

Postnatale Hirngrößenabnahme, visuelle Leistung, Lernen und Unterscheidungsvermögen von juvenilen und adulten amerikanischen Minken (*Mustela vison*: Carnivora: Mammalia)

Die Abnahme der Hirngröße im Ausmaß von 20% während der Entwicklung vom juvenilen zum adulten Stadium beim Mink und anderen *Mustela*-Arten ist nach wie vor wenig verstanden und in ihrer generellen biologischen und funktionellen Bedeutung ungeklärt. Entsprechendes gilt für die einhergehende Verkleinerung des Hirncavums, vornehmlich bedingt durch Abflachung des Hirnschädels. Da der Neocortex und andere Hirnteile mit höheren integrativen und assoziativen sensorischen und motorischen Funktionen besonders betroffen sind, erhebt sich die Frage, inwieweit diese Größenänderungen funktionelle Konsequenzen haben; d. h. sind funktionelle Kapazitäten dieser Hirnstrukturen gleichzeitig gemindert? Dieses wurde für das visuelle System bei 8 juvenilen (4,4) und 8 adulten (4,4) Nachkommen von Minken (*Mustela vison energumenos*) aus freier Wildbahn unter Einsatz einer Zweifach-Wahl-Apparatur getestet. Nach Konditionierung und Test auf spontane Seitenstetigkeit mußten die Individuen schwarze Punkte unterschiedlicher Größe von weißen Flächen aus 30 cm Entfernung unterscheiden. Insgesamt wurden 16 000 individuelle Datensätze erhoben und statistisch auf Unterschiede in visueller Leistung, Lerngeschwindigkeit und Unterscheidungsvermögen analysiert. Es ergaben sich keine Unterschiede in der Lerngeschwindigkeit zwischen juvenilen und adulten Individuen. Allerdings resultierte ein signifikanter Einfluß von Alter (juvenile Tiere zeigten bessere Ergebnisse) und Geschlecht (Fähen zeigten bessere Ergebnisse) im visuellen Unterscheidungsvermögen. Diese Ergebnisse werden im Zusammenhang mit der biologischen Bedeutung des Gesichtssinns für diese Tierart, mit generellen Verhaltensunterschieden zwischen juvenilen und adulten Individuen und mit der ontogenetischen Abnahme zentralnervöser Masse diskutiert. Im Hinblick auf diese Untersuchungen gibt es keine Anzeichen für einen funktionellen Zusammenhang zwischen der ontogenetischen Hirngrößenabnahme und Leistungsfähigkeit des visuellen Systems.

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Mamm. biol. **66** (2001) 281–289
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Differential predation upon sex and age classes of tuco-tucos (*Ctenomys talarum*, Rodentia: Octodontidae) by owls

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Receipt of Ms. 22. 05. 2000
Acceptance of Ms. 05. 04. 2001

Abstract

Predation by burrowing (*Athene cunicularia*) and short-eared (*Asio flammeus*) owls upon sexes and age-classes of the subterranean herbivorous rodent *Ctenomys talarum* were studied by comparing characteristics of field-trapped and preyed-upon individuals. Owls took a greater proportion of males than females in comparison with their respective field densities. This sex-biased pattern of predation was most marked during the breeding season of *C. talarum* and mainly affected subadult males. A set of ecological features of *C. talarum*, such as food habits and above ground mobility, that might explain differential vulnerability by sex was analysed and did not support the observed pattern. We suggest that it is determined by higher above ground exposure of subadult males during the breeding season because they interact above ground with adult males and search for settlement sites to establish their own burrows.

Key words: *Ctenomys talarum*, owl predation, prey vulnerability, Argentina

Introduction

A complex set of behavioural and morphological characteristics of prey and predator species determines the likelihood that an animal will be captured. Prey activity patterns and prey habitat use are behavioural traits that may modify predation risk; while a predator's attack biomechanics, activity time or habitat use, may likewise cause certain classes of prey to be at higher risk.

Non-random predation upon prey species of different size is well known among raptorial birds (Halle 1988; Marks and Marti 1984; Marti 1974; Schoener 1968; Smith and Murphy 1973; Storer 1966; Vassallo et al. 1994). Even within a single prey taxon, selection of a given size often occurs, with the young or smaller individuals often preyed upon more frequently than expected (Smith and Murphy 1973; Kotler 1985; Longland and Jenkins 1987; Donázar and Ceballos 1989; Zalewski 1996).

Predators are thought to be important factors in shaping population traits and habitat use of their mammalian prey (Kotler 1984; Jaksic 1986; Palomares and Delibes 1997; Wolff 1997; Saitoh et al. 1999). Although evidence that predation limits mammalian abundances is weak, the role of predation as a primary selective force remains undisputed in population studies. Owls and

1616-5047/01/66/05-281 $ 15.00/0.

hawks are important predators of small mammals (Marti and Hogue 1979; Korpimäki and Norrdahl 1989; Jaksic et al. 1992; Marti et al. 1993). Prey selection in these visually oriented predators is constrained mainly by prey vulnerability, generally an unknown function of prey size (Marti and Hogue 1979; Zamorano et al. 1984; Bozinovic and Medel 1988), prey colour (Kaufman 1974a; Götmark et al. 1997), prey activity (Kaufman 1974b; Longland and Price 1991), and the synergistic effects of these factors (Halle 1993). Generally, the more conspicuous sex (usually males) is more vulnerable to predators in sexually dimorphic prey (Selander 1965, 1966; Geist 1971). Moreover, even in apparently monomorphic species, body size may exhibit differences in variances between sexes, which can affect vulnerability to predation. Monomorphic species may also exhibit behavioural differences that make one sex more vulnerable than the other.

South American caviomorph rodents of the genus *Ctenomys* (locally known as tuco-tucos) are the group with most species of fossorial rodents in the world. Of about 125 living species of hypogeic rodents, 55 belong to this genus (Reig et al. 1990). Species of *Ctenomys* are sexually dimorphic, specifically male, *C. talarum* are 33% larger in body mass and 6% in body length than females (Zenuto et al. 1999).

The aim of this study is to assess the characteristics of owl predation upon sexes of *C. talarum* and to evaluate some behavioural and ecological features of *C. talarum* that might explain differential vulnerability by sex and age.

Material and methods

Four censuses of tuco-tucos, *Ctenomys talarum*, were conducted every three months starting November 1987 and throughout 1988 at Necochea (38°36′ S, 58°48′ W), Buenos Aires Province, Argentina. Each census took place in a 1.5 ha plot for five consecutive days. Each plot was staked in a grid pattern to establish the spatial location of captured animals. Animals were trapped without injury using plastic livetraps, which were placed at the entrances of all burrows and repeatedly checked and re-set until nearly all animals present within the grid were caught. Removal of individuals from census grids should have had little effect on prey availability, as total hunting area used by owls would have been much larger than the grids.

The censuses provided information on: 1) population density, 2) reproductive status, 3) body weight distribution, 4) the ratio adults: subadults, and 5) sex ratio. Fifty-nine *C. talarum* were captured, and each individual was killed by ether inhalation and autopsied to obtain information on reproductive condition, pregnancy, and relative age. Females were classified as immature (narrow, pale uterine horns and closed vagina) or mature (thick uterine horns, and open or plugged vagina). Males were also classified as immature (lack of spermatozoa in epididymis) or mature (spermatozoa in epididymis). *C. talarum* attains sexual maturity at an average weight of 95 g. Pregnant females occurred only from July to March (Malizia et al. 1991). This well-defined reproductive period in this species allowed comparisons between preyed-upon and trapped individuals during both the breeding and non-breeding seasons.

Fresh pellets from burrowing owl, *Athene cunicularia* (n = 149), and short-eared owl, *Asio flammeus* (n = 124) were collected simultaneously with our censuses. Total area for pellet collection was 10 km^2, which included our census grids. Pellet collection took place at known roosts, perches, or nests. Because sampling took place along consistent routes, sampling intensity did not vary among periods. Thus, number of preyed-upon individuals found in pellets should reflect predation intensity through time.

Ctenomys talarum prey remains were catalogued and then identified to species level by reference to dissected and cleaned skeletal elements of locally collected voucher specimens. The minimum number of single or double anatomical elements such as skulls, mandibles, or tooth rows estimated the minimum number of individuals in pellets. Although skulls of *C. talarum* in owl pellets were frequently found to be partially crushed, a set of skull variables could be measured. Length of maxillary toothrow, rostral width, length of diastema, mandibular length, cranial width, and basilar length were measured with a hand vernier calliper (precision 1/20 mm) and applied in the estimation of body mass and to determine sex of preyed-upon individuals. Estimation of body mass was accomplished through simple linear regression equations. Most regression equations be-

tween skull variables and body mass provided adequate models, thus allowing estimation of body mass with reasonable accuracy. Masses of prey were estimated using that variable which had the smallest sum of prediction error. Determination of sex of prey was undertaken through linear discriminant analysis (Cooley and Lohnes 1971). Skull measurements were entered as variables for investigating within- and between group variability, testing differences in composition of groups, and finally assigning unknown prey to sex for many preyed-upon individuals. Linear discriminant as well as regression equations afforded reliable means for estimating sex and body mass of prey individuals (Tab. 1).

Additional information from a neighbour population of *C. talarum* at Mar del Cobo (37°52′ S, 57°23′ W) was analysed in order to establish presumable correlates with differential sex predation. Data from a capture-recapture study (Busch et al. 1989) were used to obtain information on capture frequency distributions and above ground mobility possibly related to dispersal. A second study using microhistological techniques (Del Valle et al. 2001) provided information on *C. talarum*'s diet characteristics. The proportion of aerial plant parts in the diet and the similarity of diet composition of an individual to that of the vegetation sourrounding each individual's burrow entrance were compared in both sexes.

Diet-vegetation similarity was expressed using the Morisita's index (Ludwig and Reynolds 1988). Kolmogorov-Smirnov tests were used to compare the distribution of capture frequencies between sexes. Nonparametric Mann-Whitney U tests (Zar 1984) were used to compare the proportion of aerial plant parts in the diet, distances moved between successive captures, and diet-vegetation similarity indexes between sexes. Mean prey mass distributions of trapped and preyed-upon individuals were analysed with one-way ANOVA with subsequent Student-Newman-Keuls multiple comparison of means tests. Intraspecific departures from random predation were tested by calculating an expected number of individuals of each sex and age category. This was done by multiplying the proportion of each sex or age category in field censuses by the total number of individuals found in pellets. Differences between observed and expected numbers of prey in pellets were tested using Chi-Square tests (Sokal and Rohlf 1981). Alpha was initially set to 0.05 in all statistical analyses and adjusted using sequential Bonferroni corrections for the total number of comparisons in each analysis (Rice 1989).

Results

Linear discriminant analysis based on skull morphometrics produced significant separation between known males and females of *Ctenomys talarum* (Wilks' Lambda = 0.244 F = 19.783 d. f. = 5, 32 P < 0.001). We assigned skulls of *C. talarum* from owl pellets to male or female categories if the probability of correct sexual classification was ≥ 0.90. Of 112 *C. talarum* individuals found in pellets 39 skulls were intact and thus provided measurements in those variables necessary for the discriminant analysis. Regressions of body mass on skeletal measurements provided reliable estimates of body mass, allowing the assignment of

Table 1. Cranial variables and statistics of linear regressions and discriminant analysis used to estimate body mass and sex, respectively, of preyed-upon individuals of *Ctenomys talarum*. BL basilar length; CW cranial width; LD length of diastema; LMT length of maxillary toothrow; ML mandibular length; RW rostral width. Number of observations = 39.

	Body mass				
	Constant	Coefficient	r^2	Sex	
LD	−91.13	19.68	0.86	Constant	8.83
LMT	−284.48	51.83	0.67	LD	0.31
BL	−142.33	15.27	0.88	LMT	2.64
RW	−175.63	34.22	0.88	BL	0.42
ML	−179.15	17.79	0.86	RW	−3.86
				CW	−0.55
				% CORRECT	97.36

preyed upon individuals to adult and subadult age categories. Of the 39 *C. talarum* found in pellets we assigned 26 to males (9 adult and 17 subadult), 9 to females (7 adults and 2 subadult), and the remaining 4 were not classified (Fig. 1).

Owls showed contrasting consumption of *C. talarum*. *A. cunicularia* took most tuco-tucos during the breeding season, while *A. flammeus* preyed most heavily during the non-breeding season.

Differences in sex ratios, age category, and mean body masses of *C. talarum* were apparent between trapped and preyed-upon individuals during both breeding and non-breeding seasons (Tab. 2). Male *C. talarum* were preyed upon significantly more often than expected based on sex ratio of trapped individuals by *A. cunicularia* during the breeding season ($\chi^2 = 5.43$, $P = 0.02$). During the non-breeding season no individuals preyed upon by *A. cunicularia* were recorded. Sex ratio of *C. talarum* preyed upon by *A. flammeus* did not differ with respect to that expected based on trapped individuals either during this period or during the non-breeding season ($\chi^2 = 0.73$, $P = 0.39$ and $\chi^2 = 1.09$, $P = 0.29$, respectively).

Males preyed-upon by *A. cunicularia* during the breeding season were significantly smaller than those field-trapped (SNK test, $P = 0.034$). The same was observed for males preyed upon by *A. flammeus* during the non-breeding season (SNK test, $P = 0.017$).

On the other hand, body mass of females preyed upon by *A. cunicularia* during the breeding season and by *A. flammeus* during the non-breeding season did not differ from that of field-trapped females (SNK test, $P = 0.290$ and $P = 0.878$, respectively).

That males preyed upon by owls were smaller than those field-trapped, concurs with a biased adult : subadult ratio as compared to the ratio observed in field-trapped males. Hence, subadult males were significantly overconsumed by *A. cunicularia* ($\chi^2 = 30.68$, $P < 0.001$) and *A. flammeus* ($\chi^2 = 53.78$, $P < 0.001$) during the breeding and non-breeding seasons, respectively. In both periods, the adult : subadult ratio of preyed-upon females did not show significant de-

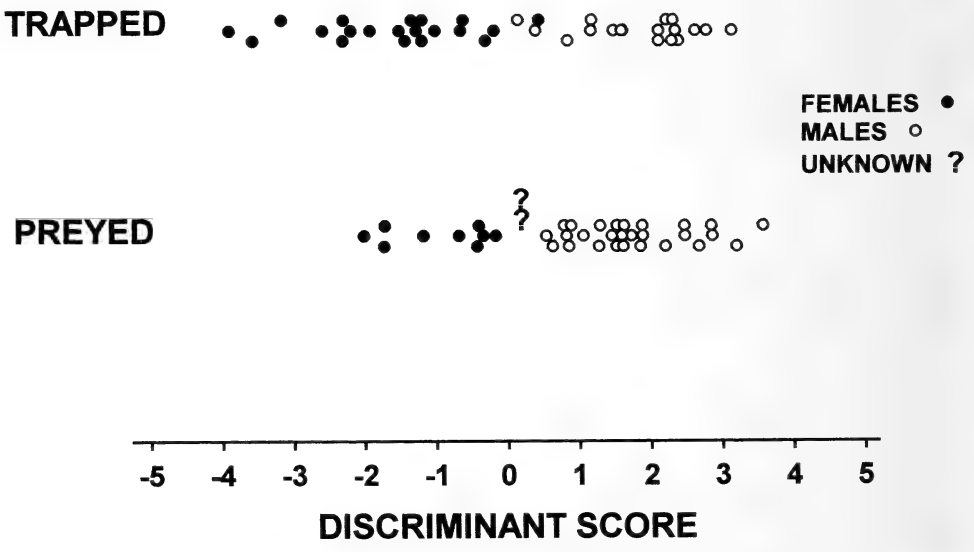

Fig. 1. Sex determination of *Ctenomys talarum* eaten by owls. Discriminant scores are given for individual craniometric measurements from known (trapped) males and females. Individuals of unknown sex in owl pellets had a probability of correct sexual classification ≥ 0.90.

partures from that observed for field-trapped individuals ($\chi^2 = 1.34$, P = 0.25 and $\chi^2 = 0.07$, P = 0.78, respectively).

The observed proportion of male *C. talarum* in both owls' pellets for the breeding season was significantly higher than that for the non-breeding season as compared to expected proportions based on field densities and sex ratios in both periods ($\chi^2 = 10.05$, P = 0.001). On the contrary, the proportion of females in owls' pellets did not differ between periods ($\chi^2 = 1.41$, P = 0.23).

A set of attributes that might indicate differential exposure to owl predation, possibly accounting for higher predation upon one sex was analysed. For this purpose we compared data on capture frequencies, distance moved between successive trappings and diet composition between sexes.

Comparisons between distributions of capture frequencies (number of individuals that were caught 1, 2, or n times) may denote differences in site fidelity between sexes, but we did not find significant differences in this regard (males 1.4 ± 0.7, females 1.6 ± 1.2; Kolmogorov-Smirnov test, D = 0.28, P = 0.92).

Distances moved between successive captures larger than the average length of the burrow system (14 m; Antinuchi and Busch 1992) were considered as above ground mobility related to dispersal, taking in account that in this species dispersal occurs above ground. Average distance for males (mean ± 1 SD, 45.36 ± 34.31 m) did not differ from that for females (43.85 ± 14.55 m; Mann-Whitney test, U = 29, P = 0.52). The proportion of these transient individuals in the population did not differ between sexes (males = 0.72, females = 0.68; $\chi^2 = 0.05$, P = 0.83).

Two attributes of the diet of *C. talarum* were presumed to be related to above ground exposure: the proportion of above ground plant parts in the diet, and the similarity between the botanical composition of the diet and that of the vegetation surrounding each individual burrow entrances. A higher proportion of above ground plant parts in the diet, and a lower similarity between diet and surrounding vegetation for one sex would indicate that this sex is more exposed to owl predation. Neither the proportion of above ground plant parts (males = 86.25 ± 12.78, females = 81.70 ± 17.61) nor diet-vegetation

Table 2. Number of male and female individuals trapped in field censuses, body mass (g; mean ± 1 SD), and observed (expected in parentheses) number of each sex and age category of *Ctenomys talarum* preyed-upon by owls.

Source of specimens and parameter	Breeding season		Non-breeding season	
	Males	Females	Males	Females
Trapped				
Total	18	23	10	8
Adults	16	16	9	2
Subadults	2	7	1	6
Body mass	129.2 ± 31.0	103.9 ± 26.5	125.4 ± 18.5	82.9 ± 20.3
Asio flammeus				
No.preyed	2 (0.9)	0 (1.1)	9 (6.7)	3 (5.3)
No. of adults	2 (1.8)	0	1 (8.1)	1 (0.7)
No. of subadults	0 (0.2)	0	8 (0.9)	2 (2.3)
Body mass	115.9 ± 0.42		83.5 ± 11.1	92.9 ± 24.8
Athene cunicularia				
No. preyed	15 (9.2)	6 (11.8)	0	0
No. of adults	6 (13.3)	6 (4.2)	0	0
No. of subadults	9 (1.7)	0 (1.8)	0	0
Body mass	88.3 ± 17.6	130.0 ± 17.0		

similarity (males = 0.36 ± 0.18, females = 0.36 ± 0.21) differed between sexes (Mann-Whitney test, U = 337.5, P = 0.29; U = 198, P = 0.57; respectively).

Discussion

Although tuco-tucos are subterranean rodents, they occur above ground when searching for food in the vicinity of burrows, as suggested by the high proportion of aerial plant tissues found in their diet (Del Valle et al. 2001; Comparatore et al. 1995) and when dispersing (Malizia 1994). Unexpected high levels of above ground mobility have been noted in *C. talarum* (Busch et al. 1989) as well as in *C. australis* (E. Oudshoorn, pers. comm.). These above ground activities differ from what was reported for other subterranean rodent species of Spalacidae and Bathyergidae, where surface exposure is considered incidental (Heth 1991, Jarvis and Bennett 1991). The regular above ground activity of tuco-tucos would suggest that predation, principally by visually oriented raptors, is more common than previously assumed in *Ctenomys* (Vassallo et al. 1994; Busch et al. 2000).

Our study shows that subadult male *Ctenomys talarum* underwent higher predation risk by owls than females during the breeding season. As a probable correlate of higher predation risk for males we compared measurements related to territory fidelity and above ground mobility between sexes and did not find significant differences. A recent experimental study concerning demographic and reproductive attributes of dispersers in *C. talarum*, at the study site of Necochea, showed a 1 : 1 sex ratio of dispersers, transients, and residents. In addition, dispersers did not differ from residents in age composition or body mass (Malizia et al. 1995). Thus, dispersal does not appear to be the cause of the observed predation pattern.

If males and females of a prey species are equally vulnerable to predation, they should occur in owl diets in proportions approximating the sex ratio in the local environment. What characteristics of male *C. talarum* (particularly subadult males) might account for their higher vulnerabilities?

The first possibility is that subadults simply lack the experience or sensory skills necessary to avoid owl predation. Young individuals of some rodent species became prey soon after leaving maternal care due to inexperience with their new environment (Lay 1974). Young subterranean rodents leave maternal care rather late and experience the environment outside their natal nests within their mother's burrow. Size of subadult males preyed upon by owls indicate that these individuals had developed sufficient experience with their environment to be almost equally vulnerable as adult males. It is noteworthy that sizes of preyed upon males (around 85 g) clearly depart from those of natal dispersers, which are approximately 3 months old and weighed around 60 g (Malizia and Busch 1991; Malizia et al. 1991). Lower body masses of individuals captured at their exclusive burrow were around 60 g, indicating that burrow settlement occurs shortly after dispersal from their natal burrow. This suggests that preyed upon males had already established their own burrows when captured by owls.

Based on the examined information we do not have evidence to conclude that males are more vagile above ground than females. However, the possibility exists that without being more vagile, males (and particularly subadult individuals during the breeding season) stay longer above ground than females. We ask whether differential predation upon subadult males is due to coincidence of either the surface activity patterns and microhabitats used by subadult male tuco-tucos, and whether adult tuco-tucos increase the predation risk of juveniles by forcing them to stay longer above ground in more open areas.

We have no evidence concerning differences in microhabitat characteristics, i. e. differences in plant cover which eventually determine unequal exposure to visual raptors; between adult and subadult males (Comparatore 1990; Comparatore et al. 1992). However, data from semi natural enclosures concerning social and reproductive behaviour

of *C. talarum* show that adult males turn from tolerance towards young individuals to higher levels of aggression toward grown-up males (Zenuto 1999). This observation fits with the high occurrence of scars in field-trapped males (Busch et al. 1989). When searching for territories – and/or a place within the social hierarchy – a considerable number of young males should be involved in aggressive interaction, which probably expose them to visually guided raptors. As opposed to females, young males near adulthood are compelled to interact and gain access to mates.

Different sources of evidence (Zenuto et al. 1999) indicate that *C. talarum* has a polygynyc mating system in which male to male competition usually takes the form of aggressive interaction leading to dominance ranks (Zenuto et al. 2001). Taking in account that, compared to other subterranean rodent species, *C. talarum* makes extensive use of the above ground habitat (Busch et al. 2000), it is conceivable that a substantial portion of social interactions – including but not restricted to inter male aggression – is performed out of their burrows. Tuco-tucos inhabit exclusive burrow systems (Contreras and Reig 1965; Antinuchi and Busch 1992); only during the breeding season one of the sexes must leave its burrow and enter the other sex's burrow for mating. If males visit female burrows during the breeding season travelling above ground it is expected that males would suffer higher predation risks during this period. However, it is expected that adult males would suffer increased predation under this assumption. Some interaction between both male categories might explain higher exposure of subadult males above ground. We suggest that both the higher level of intolerance from established adult males, and the active search of a place within the social hierarchy expose subadult males near maturity to higher vulnerability to owls.

Acknowledgements

This research was supported by a grant from the International Foundation for Science, Sweden (C/1706-1), and from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), PID) N° 3-1049006/88. We wish to express our gratitude to our colleagues at Laboratorio de Ecofisiología for their constant interest and encouragement.

Zusammenfassung

Alters- und geschlechtsbedingte Unterschiede bei der Prädation von Tuco-Tucos (*Ctenomys talarum*, Rodentia: Octodontidae) durch Eulen

Die Prädation von Kaninchenkauz (*Athene cunicularia*) und Sumpfohreule (*Asio flammeus*) auf die Geschlechter und Altersklassen des unterirdisch lebenden, herbivoren Nagers Tuco-Tuco (*Ctenomys talarum*) wurde untersucht, indem Freilandfänge und Beutespektrum miteinander verglichen wurden. Die Eulen erbeuteten einen höheren Anteil von Männchen als nach den Dichten im Freiland zu erwarten war. Die Bevorzugung war während der Fortpflanzungsperiode von *C. talarum* besonders ausgeprägt und betraf insbesondere die Gruppe der subadulten Männchen. Verschiedene ökologische Merkmale von *C. talarum* wie Nahrungsspektrum und oberirdische Aktivität, die unterschiedliche Gefährdung der beiden Geschlechter erklären könnten, wurden analysiert, lieferten aber keine Erklärung für die Beobachtung. Wir vermuten daher, dass die vermehrte Prädation subadulter Männchen während der Fortpflanzungsperiode Folge einer vermehrten oberirdischen Aktivität ist, die durch oberirdische Interaktionen mit adulten Männchen und die oberirdische Suche nach freien Siedlungsplätzen für die Anlage eigener Baue bedingt wird.

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Mamm. biol. **66** (2001) 290–300
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Kleinsäuger auf forstwirtschaftlich unterschiedlich behandelten Windwurfflächen eines Bergwaldes

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Receipt of Ms. 01. 12. 1999
Acceptance of Ms. 18. 04. 2001

Abstract

Small mammal distribution on differently managed storm areas of a mountain forest

In 1995, two uprooted forest stands and an old growth area were investigated regarding small mammal distribution. Each stand was 10 ha in size and all were located at the borderline of Styria and Lower Austria. The age of the forest stands at all three study sites was approximately 200 years old. One study area, the windfallen stand was cleared from thrown and broken trees after the disturbance, the other one was left untreated. The aim of the study was to document small mammal communities in a mountain forest area in the Northern Limestone Alps and also, to investigate if habitat preferences of yellow-necked mouse (*Apodemus flavicollis*) and bank vole (*Clethrionomys glareolus*) were similar in mountain forests compared to previously studied areas at lower elevations. The largest number of Muridae were captured on the untreated storm area. Trapping data showed that the yellow-necked mouse (*Apodemus flavicollis*) was dominant on all three study sites followed by the bank vole (*Clethrionomys glareolus*), wood mouse (*Apodemus sylvaticus*), and field vole (*Microtus agrestis*). Yellow-necked mice were most often caught at the untreated site and in general were captured in young as well as grass and herb stands. The number of male yellow-necked mice captured was significantly larger on the three study sites as a whole. But taking the respective study sites selectively, the number of males was significantly larger only in the old growth stand. Trapping success suggests that seasonal habitat change occurs with the yellow-necked mouse. Trapping success for the bank vole was highest on the cleared plot and closely associated with young stands, old stands, and forest edge. Trapping success on the three study sites as a whole corresponded with habitat preferences as described in the literature.

Key words: *Apodemus flavicollis, Clethrionomys glareolus,* mountain forest, windfallen stand, forest managment

Einleitung

Ausgelöst durch ein starkes Sturmtief über Mitteleuropa, mit Windgeschwindigkeiten bis zu 160 km/h, wurden im März 1990 in Österreich große Waldbestände entwurzelt. Kleinsäuger, speziell Mäuse, reagieren verstärkt auf bodennahe Standortveränderungen, wie etwa plötzlich auftretende strukturelle Veränderungen durch Totholz und

1616-5047/01/66/05-290 $ 15.00/0.

daraus resultierende Deckungs- und Klimagegebenheiten. Aber sie sind auch in der Lage, sich schnell anzupassen und als Pioniere neu entstandene Lebensräume rasch zu besiedeln. Untersuchungen zu Kleinsäugern und ihrer Habitatwahl in Tieflagen sind zahlreich (z. B. Flowerdew 1985), über montane und subalpine Bereiche hingegen sind eher nur spärlich Daten vorhanden.
Ziel der Untersuchung war es, Daten über die Kleinsäugerbesiedlung der Bergwaldstufe (im Bereich des nordöstlichen Ausläufers der Nördlichen Kalkalpen) zu erhalten. Ebenso war zu untersuchen, ob die aus der Literatur bekannten unterschiedlichen Habitatansprüche von Gelbhalsmäusen (*Apodemus flavicollis*) und Rötelmäusen (*Clethrionomys glareolus*) in tieferen Regionen auch auf Sonderstandorte, wie jene forstwirtschaftlich unterschiedlich behandelten Windwurfflächen (naturnahe und intensive Bewirtschaftung) des montanen Waldes, übertragbar sind.

Material und Methoden

Untersuchungsgebiet

Das Untersuchungsgebiet der Windwurf- und Sukzessionsforschung liegt in den Steirisch-Niederösterreichischen Kalkalpen auf rund 1 100 m Seehöhe (derzeitiger Status: IUCN Kategorie I a „Wildnisgebiet Dürrenstein", Natura 2000 – Vorschlag) und wird von hohen Bergmassiven großräumig begrenzt. Klimatisch geprägt ist das Gebiet durch ein ozeanisch-subozeanisch überlagertes Alpenrandklima mit hohen Jahresniederschlägen, relativ milden Lufttemperaturen, aber schneereichen Wintern. Die Untersuchungen der hier vorliegenden Arbeit konzentrierten sich auf drei je 10 Hektar große und etwa 30 m voneinander entfernt liegende Flächen mit einem Bestandesalter von rund 200 Jahren: Die sogenannte „Edelwiesfläche" wurde nach dem Windwurf nicht in forstwirtschaftlich üblicher Weise aufgeräumt, sondern unbehandelt belassen (U = ungeräumt). Nördlich davon liegt, durch eine Forststraße getrennt, die geräumte Fläche (G = geräumt): das hier angefallene Sturmholz wurde bis auf Wurzelteller und „Fratten" (in Bahnen aufgeschichtetes Astmaterial) beseitigt. Nordwestlich von U befindet sich der Altbestandbereich (A), der in seinem Bestandesalter dem der Windwurfflächen U und G entspricht, aber nicht vom Sturmereignis betroffen war. Er diente in der Untersuchung als Kontrollfläche.

Kleinsäugerfang

Die Kleinsäuger wurden während der Vegetationsperiode vom 18. Juni bis 24. September 1995 mit Lebendfallen vom Fallentyp „Holzkastenfalle" (Wippbrett-Falltüren-Prinzip; Fa. Deu Fa, Neuburg/Inn) gefangen und mit einem Gemisch aus Erdnußbutter, Haferflocken, Apfelstückchen und Pflanzenöl geködert (vgl. Radda 1968). Holzwolle und ein über die Falle gestülpter leerer Saftkarton schützten die Tiere vor Kälte und Nässe. Die gefangenen Tiere wurden zur Bestimmung direkt von der Falle in einen Tiefkühlbeutel entlassen und mit einigen Tropfen Äther betäubt. An den Tieren wurden Art, Geschlecht, Gewicht und Reproduktionszustand erhoben. Eine Markierung war zuerst nicht vorgesehen, da sie für die Fragestellung nicht relevant war (Populationsschätzungen wurden nicht durchgeführt). Ab der 3. Fangperiode wurde angesichts der hohen Fangergebnisse der Fangperioden 1 und 2 und dem Interesse am Umfang der Wiederholungsfänge mit einer Markierung begonnen. Die Tiere wurden mit einem wasserfesten Farbstoff (Xanthin, gelöst in 70%igem Alkohol) auf der Ventralseite durch einen Farbpunkt als „gefangen" markiert. Die Fänge wurden allerdings individuell nicht unterschieden. Bei jedem Wiederfang wurde der Ventralseite dann ein weiterer Farbpunkt hinzugefügt (Markierung im Uhrzeigersinn im Bereich des rechten Vorderfußes beginnend, 4. Punkt: Bereich des rechten Hinterfußes, 5. Punkt: Bauchmitte), wodurch die Anzahl der Wiederholungsfänge pro Individuum registriert werden konnte. Im weiteren erwähnte Wiederfänge beziehen sich immer nur auf die Fangperioden 3–6. Die insgesamt 120 Fallen wurden auf den drei Untersuchungsflächen zu gleichen Teilen verteilt.
Die Fallen wurden, abgesehen von wetterbedingten Verschiebungen (Fangperiode 4 auf U entfallen), im Intervall von zwei Wochen in jeweils dreitägigen Fangperioden fängig gestellt und einen Tag (durchschnittlich 24 Stunden) danach kontrolliert. Insgesamt entsprachen die Fallen der sechs hier berücksichtigten Fangperioden (10 Fangnächte) 1160 Fallennächten (FP1 „Ende Juni": 18.–20. Juni, FP2 „Mitte Juli": 14.–16. Juli, FP3 „Ende Juli": 31. Juli–02. August, FP4 „Mitte August": 15.–16. August, FP5 „Ende August": 31. August–01. September, FP6 „Ende September": 22.–24. September).

Witterungsbedingt notwendige Fangzahlenkorrektur

Für die wetterbedingt entfallene Fangperiode Mitte August (FP4) auf der Fläche U wurden die Fangzahlen für Gelbhals- und Rötelmaus interpolierend korrigiert, um dennoch einen direkten Vergleich der Fangzahlen zwischen den verschiedenen Untersuchungsflächen zu ermöglichen: als Bezugsfläche zur Korrektur wurde wegen der Ähnlichkeit der Fangerfolge G herangezogen. Die Differenz der Gesamtfangerfolge (ohne Fangperiode Mitte August, FP4) der einzelnen Arten zwischen U und G wurde berechnet und durch die Anzahl der berücksichtigten Fangnächte (9) dividiert. Der so für jede Kleinsäugerart erhaltene Korrekturfaktor K wurde zum jeweiligen Fangerfolg der Fangperiode 4 auf G hinzugezählt bzw. abgezogen und ergab den theoretischen Fangerfolg der ungeräumten Windwurffläche U für die Fangperiode Mitte August (FP4; K = Differenz der Gesamtfangerfolge zwischen U und G/Anzahl der berücksichtigten Fangnächte).

Fallenverteilung

Aufgrund extremer Verhältnisse auf den ungeräumten Windwurfflächen konnte eine rasterartige Fallenverteilung mit den zur Verfügung stehenden Hilfsmitteln nicht realisiert werden. Daher wurden die Kleinsäugerfallen nach der Beliebtheit der unterschiedlichen Mikrohabitate verteilt und nach eingehender Literaturstudie Habitatpräferenzen für die im Untersuchungsgebiet in Frage kommenden herbi- und granivoren Kleinsäugerarten Gelbhalsmaus (*Apodemus flavicollis*), Waldmaus (*A. sylvaticus*), Rötelmaus (*Clethrionomys glareolus*) und Erdmaus (*Microtus agrestis*) abgeleitet (vgl. Gelbhalsmaus: Bergstedt 1965; Hansson 1971; Zejda 1961; Mazurkiewicz und Rajska-Jurgiel 1978; Niethammer 1978; Mazurkiewicz 1984; Rajska-Jurgiel 1992; Waldmaus: Felten 1952; Tellería et al. 1991; Jamon 1994; Tatersall und Whitbread 1994; Rötelmaus: Kikkawa 1964; Radda 1968; Hansson 1971; Miller und Getz 1976; Bäumler 1981; Kirkland 1990; Erdmaus: Schindler 1972; Chelkowska et al. 1985; Viitala und Hoffmeyer 1985; Kirkland 1990; Niemeyer 1993). Diesen Präferenzen entsprechend kamen mehr Fallen in von Kleinsäugern häufig aufgesuchten Mikrohabitaten zum Einsatz (vgl. Adams und Geis 1983) und verhältnismäßig weniger an Mikrohabitaten mit geringerer Präferenz (s. Tab. 1). Der Abstand zwischen den einzelnen Fallen betrug mindestens 10 m.

Auf den Untersuchungsflächen wurden folgende sechs Mikrohabitate als Fallenstandorte gewählt (Habitataufnahme: Quadrat von 2×2 m, Fallenstandort als Zentrum; s. Tab. 1): 1. Jungwuchs: bis 7 cm Brusthöhendurchmesser (BHD); 2. Gras: reine Grasstandorte; 3. Kraut/Strauch: krautige Pflanzen, deren unverholzte, oberirdische Stengel im Herbst absterben, und verholzte Pflanzen, die den Winter oberirdisch überdauern mit einer Höhe bis 2 m (z. B. Brennessel, Heidelbeere, Himbeere); 4. Fels/Stein: anstehendes Gestein oder Bereich mit Steinen über 20 cm Durchmesser; 5. Bestand: ab 10 cm BHD, 6. WT;WR^{A}: Wurzelballen entwurzelter Bäume. Auf der Kontrollfläche im Altbestand A wurde der Standort Wurzelteller durch den Standort Waldrand ersetzt.

Tabelle 1. Fallenverteilung (je Untersuchungsfläche) in Mikrohabitaten, die nach Literaturangaben für verschiedene Kleinsäugerarten als unterschiedlich attraktiv gelten. Die Punkte in den Feldern entsprechen der nach Literaturhinweisen vermuteten Nutzungsintensität der Mikrohabitate durch die Kleinsäugerarten (•••• sehr stark genutzt, ••• stark genutzt, •• genutzt, • wenig genutzt, – nicht genutzt). Aus der Anzahl der Punkte ergibt sich vertikal die Anzahl der Fallen je Mikrohabitat und horizontal die Anzahl der Fallen, die einer Art auf einer Untersuchungsfläche zugedacht sind.
^{A}: auf der Kontrollfläche im Altbestand wurde der Standort Wurzelteller (WT) durch den Standort Waldrand (WR) ersetzt.

Mikrohabitate	Jungwuchs	Gras	Kraut/Strach	Fels/Stein	Bestand	WT; WR^{A}	Fallenzahl je Kleinsäugerart
Rötelmaus	•••	•	•••	–	–	•••	10
Erdmaus	•	••••	•••	•	–	•	10
Gelbhalsmaus	•••	•	•	••	•••	–	10
Waldmaus	••	••	••	–	•••	•	10
Fallenzahl je Mikrohab.	9	8	9	3	6	5	40

Vegetationsaufnahmen

In der Nähe der Fallenstandorte wurden nach Braun-Blanquet (1964) Mitte Juli (FP2) insgesamt 18 Vegetationsaufnahmen durchgeführt. Teilweise waren es Wiederholungsaufnahmen aus bereits vorhergegangenen Untersuchungen. Aufgrund des Mosaikcharakters der Bodenvegetation wurde für die Aufnahme eine Flächengröße von 2 m×2 m gewählt. Die Aufnahmen wurden bewußt an Standorten mit unterschiedlichen Außenbedingungen (Exposition, Neigung, Sonneneinstrahlung, etc.) durchgeführt (je vier Aufnahmeflächen auf G und A, sowie zehn auf U – letztere im Hinblick auf die dort viel größere strukturelle Diversität). Der Abstand der Aufnahmeflächen betrug mindestens 10 m.

Ergebnisse

Während des Untersuchungszeitraums wurden 309 Kleinsäuger der Familien Muridae (*Apodemus flavicollis, Apodemus sylvaticus*; zus. = 206) und Cricetidae (*Clethrionomys glareolus, Microtus agrestis*; zus. = 103) gefangen.

Die Fangergebnisse der drei Untersuchungsflächen insgesamt unterschieden sich auf den beiden Windwurfflächen wenig. Der prozentual größte Anteil der insgesamt gefangenen Tiere wurde auf den Windwurfflächen U (37%) und G (35%) erreicht, geringer fiel der Anteil auf der Altbestandfläche A mit 28% aus. Deutliche Unterschiede waren hingegen bei der Zahl der gefangenen Arten zu bemerken (Tab. 2). Rund 2/3 der gefangenen Tiere auf U waren Gelbhalsmäuse, die restlichen 36% entfielen auf Rötel-, Wald- und Erdmäuse. Aufgrund der geringen Fangzahlen werden Wald- und Erdmäuse hier in weiterer Folge nicht mehr berücksichtigt.

Gelbhalsmaus

Die Gelbhalsmaus war, in Fangzahlen gesehen (n = 179), auf allen drei Untersuchungsflächen die dominante Species (Tab. 2). Auch unter Berücksichtigung der Wiederfänge (9% auf U; 5,4% auf G, 31% auf A) war der Fangerfolg bei Gelbhalsmäusen auf allen drei Untersuchungsflächen am höchsten. Mitte Juli (FP3) und Ende September (FP6) wurden Gelbhalsmäuse häufig auf der Fläche A gefangen, ab Juni war ein deutlicher Anstieg auf U zu erkennen (Abb. 1). Ende September war insgesamt gesehen die erfolgreichste Fangzeit.

Die Anzahl der gefangenen Jungtiere und Subadulten war auf U im Sommer höher als auf A und kehrte sich gegen Ende des Untersuchungszeitraums wieder um:

juvenil + subadult A : U: Fangperiode Ende Juni (FP2) 3 : 4, Fangperiode Mitte Juli (FP3) 3 : 15, Fangperiode Ende August (FP5) 5 : 6, Fangperiode Ende September (FP6) 12 : 5.

Das Geschlechterverhältnis der Fänge fiel auf der Fläche A und auf allen Untersuchungsflächen insgesamt signifikant zugunsten der Männchen aus. Auf A unterschied sich die Anzahl der weiblichen und männli-

Tabelle 2. Artenspektrum und Fangerfolg (in 100 Fallennächten FN). U: ungeräumte Windwurffläche (insg. 360 FN), G: geräumte Windwurffläche (insg. 400 FN), A: Altbestandfläche (insg. 400 FN).
*: theoretischer (korrigierter) Fangerfolg. Um den direkten Vergleich der 3 Untersuchungsflächen zu ermöglichen, wurde die wetterbedingt entfallene Fangperiode interpolierend korrigiert. Korrekturfaktor K wurde zum jeweiligen Fangerfolg der entfallenen Fangperiode auf G hinzu- bzw. weggezählt (K = Differenz der Gesamtfangerfolge zwischen U und G/Anzahl der berücksichtigten Fangnächte).

Kleinsäugerarten	U		G	A	Flächen ges.	
Gelbhalsmaus *(Apodemus flavicollis)*	23,6*	(20.0)	13	13,8	16,8*	(15,6)
Waldmaus *(Apodemus sylvaticus)*	1,9*	(1,9)	2,8	2,3	2,3*	(2,3)
Rötelmaus *(Clethrionomys glareolus)*	9,4*	(8,9)	11	4,5	8,3*	(8,1)
Erdmaus *(Microtus agrestis)*	0,6*	(0,6)	0,5	1,25	0,8*	(0,8)
Arten gesamt	35,5*	(31,4)	27,3	21,9	28,2*	(26,8)

chen gefangenen Tiere hoch signifikant voneinander, auf allen Flächen zusammen höchst signifikant ($p < 0{,}01$; $p < 0{,}001$; Tab. 3). In vier der sechs Fangperioden wurden auf A mehr adulte Männchen gefangen, in der Fangperiode Anfang September war der Unterschied signifikant. Einzig auf G konnte in einer Fangnacht Anfang September ein höherer Fang an Weibchen verzeichnet werden.

Ein Großteil der Gelbhalsmäuse wurde in verkrauteten Standorten und Jungwüchsen gefangen (Tab. 4).

Rötelmaus

Die Rötelmaus war mit 94 gefangenen Tieren die am zweithäufigsten gefangene Art und bevorzugt auf G und U anzutreffen. Ihre Wiederfangrate auf diesen Flä-

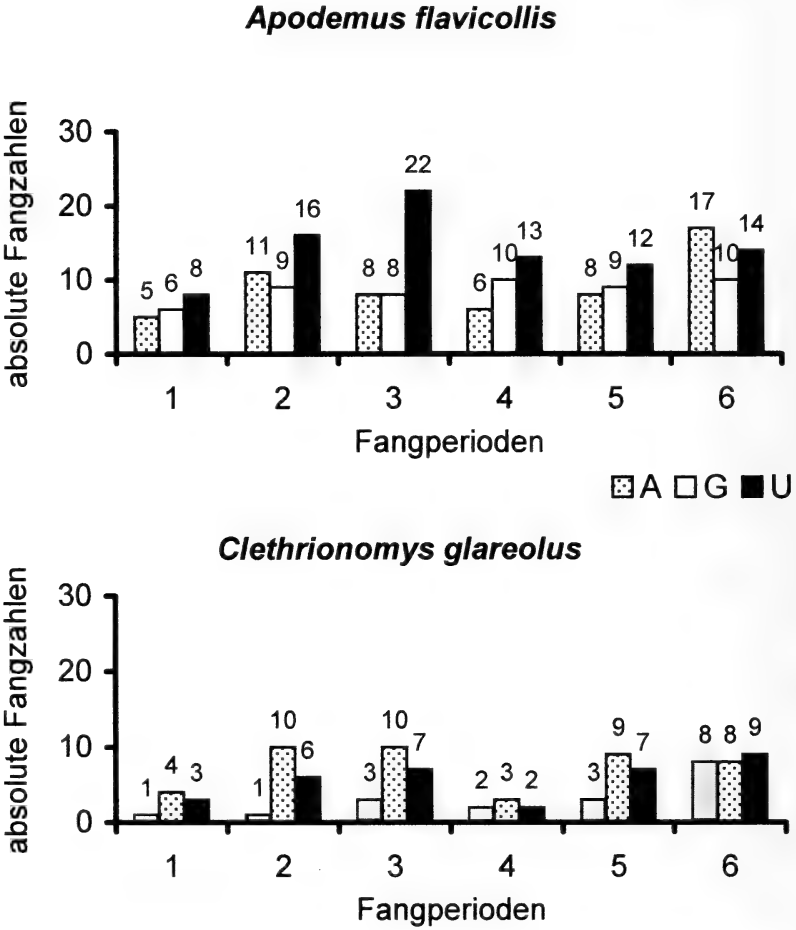

Abb. 1. Fangergebnis der Untersuchungsflächen für Gelbhalsmaus (*Apodemus flavicollis*) und Rötelmaus (*Clethrionomys glareolus*). A: Altbestand, G: geräumte Windwurffläche, U: ungeräumte Windwurffläche. Fangperiode 4 auf U: theoretischer Fangerfolg. Um den direkten Vergleich der 3 Untersuchungsflächen zu ermöglichen, wurde die wetterbedingt entfallene Fangperiode interpolierend korrigiert. Korrekturfaktor K wurde zum jeweiligen Fangerfolg der entfallenen Fangperiode 4 auf G hinzu- bzw. weggezählt (K = Differenz der Gesamtfangerfolge zwischen U und G/Anzahl der berücksichtigten Fangnächte). Zeitraum der Fangperioden: FP1: 18.–20. Juni, FP2: 14.–16. Juli, FP3: 31. Juli–02. August, FP4: 15.–16. August, FP5: 31. August–01. September, FP6: 22.–24. September.

chen war mit je 17% höher als die der Gelbhalsmaus. Die meisten Fänge konnten auch bei dieser Art Ende September erzielt werden. Deutliche Schwankungen in den Fangerfolgen waren auf U und G zu erkennen, wo die Zahl der Fänge Ende Juni (FP1) und Mitte August (FP4) die niedrigsten Werte erreichte (Abb. 1). Auf A war im Verlauf der Untersuchungen ein stufenartiger Anstieg der Fangerfolge zu erkennen, wenn auch die Fangperiode Mitte August (FP4) etwas unter dem erwarteten Wert lag. Auf keiner der Flächen war bei den Fängen ein signifikanter Unterschied im Geschlechterverhältnis aufgetreten (Tab. 3). Insgesamt wurden auf A und U mehr weibliche Tiere gefangen (53% bzw. 56%), auf G mehr männliche (60%). Rötelmäuse nutzten vor allem Wurzelteller bzw. in A Waldrandbereiche (31% bzw. 69%), Fels/Steinhabitate und Bestandesinseln (= ehemaliger Unterbestand; Tab. 4).

Vegetation und Witterung

Auf den beiden Windwurfflächen U und G waren zum Untersuchungszeitpunkt Kahlschlaggesellschaften mit Himbeeren (*Rubus idaeus*) und Berg-Reitgras (*Calamagrostis varia*) – mit starken bzw. gedämpften Tag-Nacht-Schwankungen der Temperatur – vorherrschend, im Altbestand eine Schneerosen-Buchen-Assoziation („Helleboro nigri-Fagetum Zukrigl 1973").
Für Gelbhals- und für Rötelmäuse wurden auch bei tieferen Temperaturen (im Mittel 5 °C) hohe Fangerfolge erzielt (Abb. 2). In der Untersuchungszeit von Ende August (FP5) bis Ende September (FP6) lag das Temperaturmittel bereits unter zehn Grad Celsius. Obwohl nur drei der insgesamt 10 hier berücksichtigten Fangnächte in diesen Temperaturbereich fielen, wurden 45% der Rötelmäuse in diesem Zeitraum gefangen. Andere Witterungsverhältnisse schienen wenig relevant gewesen zu sein: hohe Fang-

Tabelle 3. Geschlechterverhältnis (Weibchen/Männchen w/m) auf den Untersuchungsflächen. U: ungeräumte Windwurffläche, G: geräumte Windwurffläche, A: Altbestandfläche. Untersuchungszeitraum von Juni–September 1995, 6 Fangperioden. Signifikanzniveau (Binomial Test): ***: $p < 0{,}001$; **: $p < 0{,}01$).

Kleinsäugerarten	U w/m	n	G w/m	n	A w/m	n	gesamt w/m	n
Gelbhalsmaus	0,62	68	0,6	48	0,38**	54	0,52***	170
Rötelmaus	1,29	32	0,68	42	1,14	15	0,98	89

Tabelle 4. Angebot und Nutzung. Anzahl der Fallennächte (FN) je Mikrohabitat und Summe der Kleinsäugerfänge während 6 Fangperioden (Juni–September 1995). U: ungeräumte Windwurffläche, G: geräumte Windwurffläche, A: Altbestand. WT: Wurzelteller, WR: Waldrand, [A]: im Altbestand wurde der Standort Wurzelteller durch den Standort Waldrand ersetzt.

Mikrohabitat	Fallenzahl U, G, A, ges.	Anzahl FN	Fangerfolg (in 100 FN): Gelbhalsmaus	Rötelmaus	Summe
Jungwuchs	27	261	16,9	10,0	26,9
Gras	24	232	12,5	1,6	14,1
Kraut/Strauch	27	261	19,2	6,5	25,7
Fels/Stein	9	87	14,9	11,5	26,4
Bestand	18	174	12,1	10,9	23,0
WT; WR[A]	15	145	15,2	12,4	27,6
Summe	120	1 160	90,8	52,9	143,7

ergebnisse wurden sowohl bei Sonnenschein als auch bei Regenwetter erzielt, die geringsten während bedeckter bzw. bewölkter Tage.

Diskussion

Nach Untersuchungen von Gerlach (1996) scheinen Sturmschadensflächen, unabhängig von der Art der Bewirtschaftung, Kleinsäugern einen idealen Lebensraum zu bieten. Werden sie nach dem Windwurf forstwirtschaftlich geräumt, entsprechen sie Kahlschlägen, deren Strukturierung sich auf zurückgeklappte Wurzelteller und Fratten reduziert und deren Vegetation nach einiger Zeit von typischen Kahlschlaggesellschaften mit dichtem Unterwuchs geprägt wird. Freie Flächen dieser Art sind Witterungseinflüssen und kleinklimatischen Schwankungen verstärkt ausgesetzt. Durch das Belassen von Totholz auf Sturmschadenflächen hingegen entsteht ein reich strukturierter Lebensraum mit mosaikartigem Charakter (vgl. Harris 1984).

Kleinsäuger, wie aus den hier untersuchten Unterfamilien Murinae und Cricetinae, unterscheiden sich im Hinblick auf Verhalten und Lebensraumwahl. Die sich oberirdisch fortbewegende Waldmausart *Apodemus flavicollis* ist ein ausgezeichneter Kletterer (vgl. Hoffmeyer 1973; Viitala und Hoffmeyer 1985). Sie nutzt horizontale Strukturen in ihrem Habitat zur Fortbewegung und lebt bevorzugt im Waldesinneren. Die Wühlmaus *Clethrionomys glareolus* hingegen lebt vorwiegend unterirdisch in Habitaten mit dichtem Unterwuchs und Strauchbestand. Sie kann durch Verbiß von Baumkeimlingen, -trieben, -knospen, -wurzeln und durch das Schälen von Rinde in

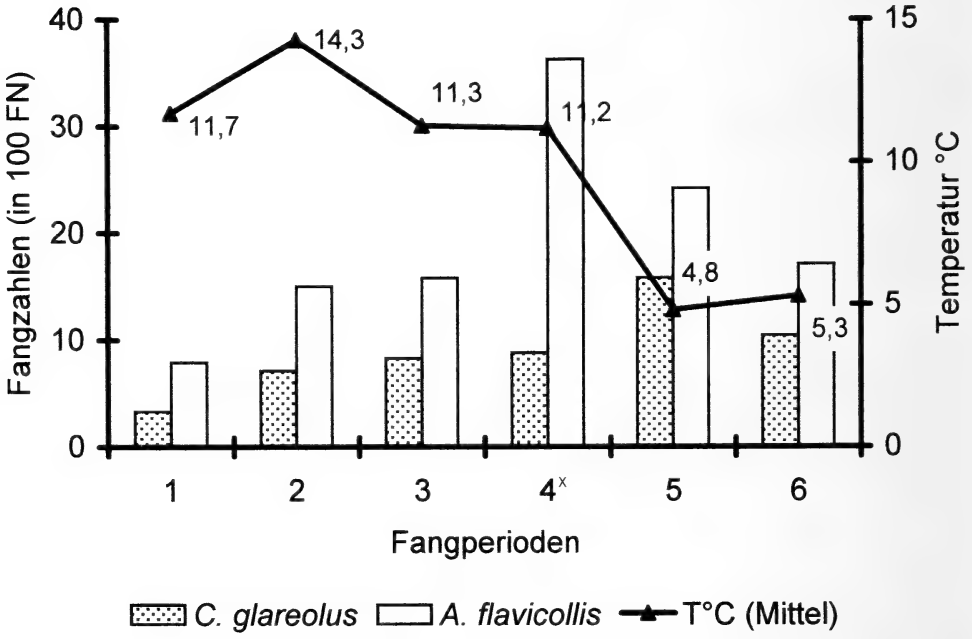

Abb. 2. Fangzahlen (in 100 Fallennächten FN) und mittlere Lufttemperatur. ^{X}: theoretischer Fangerfolg. Um den direkten Vergleich der 3 Untersuchungsflächen zu ermöglichen, wurde die wetterbedingt entfallene Fangperiode interpolierend korrigiert. Korrekturfaktor K wurde zum jeweiligen Fangerfolg der entfallenen Fangperiode auf G hinzu- bzw. weggezählt (K = Differenz der Gesamtfangerfolge zwischen U und G/Anzahl der berücksichtigten Fangnächte). Zeitraum der Fangperioden von Juni bis September 1995 wie in Abb. 1.

der Forstwirtschaft akute Schäden verursachen.

Gelbhals- und Rötelmäuse waren den Fangzahlen nach dominante Kleinsäugerarten im untersuchten Bergwald im Altbestand wie auf den Sturmflächen. Die höchsten Fangergebnisse mit Gelbhalsmäusen wurden auf der ungeräumten Windwurffläche U erzielt. Die morphologisch zum Klettern begünstigten Tiere konnten durch die reiche Strukturierung der Fläche (liegende Stämme, Astwerk) ihr Territorium in weitere Ebenen, horizontal und vertikal, ausdehnen (Fangerfolg Wurzelteller: 5,3 pro 100 Fallennächte).

Auffallend war der saisonale Verlauf der Fangergebnisse auf den Untersuchungsflächen. Die Zahl der Fänge im Altbestand A war zu Beginn und am Ende des Untersuchungszeitraums hoch. Obwohl die Fangperiode im Mai in den hier vorliegenden Ergebnissen nicht berücksichtigt wird, da während dieser FP auf A mit nur 24 statt 40 Fallen gefangen wurde, sei hier erwähnt, daß von den sechs Gelbhalsmäusen vier im Altbestand gefangen wurden. Der Fangerfolg auf U verlief entgegengerichtet: er erreichte zur Mitte der Fangsaison seinen Höhepunkt. Die Fangergebnisse auf G hielten sich in einem mittleren, relativ stabilen Bereich.

Als Erklärung kann für Gelbhalsmäuse aufgrund der vorliegenden Ergebnisse ein saisonaler Habitatwechsel in Betracht gezogen werden. Das Nahrungs- wie das Deckungsangebot für samen- und beerenfressende Mäuse war im Sommer und Herbst auf der Windwurffläche wesentlich höher als im Altbestand. Die Zusammensetzung des Köders blieb über den Untersuchungszeitraum unverändert. Zu Zeiten einer möglichen Nahrungsknappheit sollte die Attraktivität des Fallenköders steigen und bessere Fangergebnisse nach sich ziehen. Doch das traf im Falle der hier untersuchten Altbestandfläche nicht zu. Saisonaler Habitatwechsel konnte schon früher einige Male bei *Apodemus*-Arten beobachtet werden (vgl. z. B. Bergstedt 1965; Flowerdew 1974, nach Viitala und Hoffmeyer 1985). Um die hier vorliegenden Ergebnisse statistisch zu belegen, sind jedoch Studien über mehrere Jahre erforderlich.

Kraut/Strauchstandorte wurden von Gelbhalsmäusen erstaunlich häufig aufgesucht, wenn man von bekannten bzw. den für das Untersuchungsgebiet abgeleiteten Habitatpräferenzen ausgeht. In der Fangperiode Ende August (FP5) bei Regenwetter und den niedrigsten Außentemperaturen konnte auf Grasstandorten die größte Zahl an Fängen (3/100 FN) verzeichnet werden. Aus Untersuchungen von Stoutjesdijk und Barkman (1992) ist bekannt, daß Grasstellen (liegende und abgestorbene Gräser) durch ihre kompakte Struktur deutlich höhere Temperaturwerte aufweisen als die Umgebung. Es wäre denkbar, daß Mäuse bei schlechten Wetterverhältnissen Zuflucht in Grasbeständen und den darin plazierten Fallen suchten.

Die Tatsache, daß deutlich mehr Männchen in den Fallen gefunden wurden, steht wahrscheinlich in Zusammenhang mit der Fallenverteilung und dem territorialen Verhalten bzw. der Abwanderneigung der jungen Männchen. Die männlichen Tiere der Gelbhalsmäuse besitzen größere Streifgebiete als ihre weiblichen Artgenossen und vergrößern im fortpflanzungsaktiven Zustand ihren Aktionsraum von 0,3–2 ha auf bis zu max. 5 ha, wobei sie rund 25–40% längere Laufstrecken zurücklegen (vgl. Schwarzenberger und Klingel 1995). Durch die unregelmäßige Verteilung der Fallen wurde die Untersuchungsfläche nicht systematisch erfaßt. Möglicherweise ergab dies für die mobileren Männchen bessere Fangerfolge als für die Weibchen. Auch sind weibliche Säugetiere generell vorsichtiger als Männchen und aus diesem Grund schwerer zu fangen. Ähnliche geschlechtsspezifische Unterschiede bei Fängen von Gelbhalsmäusen konnte auch Rajska-Jurgiel (1992) beobachten.

Rötelmäuse bevorzugten den Fangergebnissen nach die geräumte Windwurffläche G. Als Bewohner von Kulturen mit Kräutern und verholzenden Sträuchern (vgl. Bäumler 1981) bot ihnen diese Untersuchungsfläche mit ausgeprägter Schlagvegetation und stellenweise offenen und trockenen Be-

reichen einen idealen Lebensraum. Reiches Blockwerk, spaltenreicher Untergrund und tiefgründige Böden in den Mulden haben die Mäuseart, die unterirdische Baue und lange Röhren anlegt, begünstigt, was auch das hohe Fangergebnis von Rötelmäusen in steinigen Bereichen zeigt. Ebenso wurden Rötelmäuse sehr häufig in Bestandesflächen und am Waldrand (8,6 Fänge in 100 Fallennächten) gefangen. Erstaunlich bei den Rötelmäusen waren die verhältnismäßig schlechten Fangergebnisse in Gras-, Kraut- und Strauchbereichen, die sonst als Präferenzbereiche gelten.

Auf A und U stiegen die Fangergebnisse gegen Ende des Untersuchungszeitraums an, wobei U allgemein höhere Fangerfolge als A aufwies. Auf G war ein deutlich geringerer Fangerfolg während der 1. und 4. Fangperiode zu verzeichnen. Womit diese Schwankungen in Zusammenhang zu stellen sind, kann aufgrund des kurzen Untersuchungszeitraums nicht geklärt werden. Auf keiner der drei Untersuchungsflächen konnten bei Fängen an Rötelmäusen den Gelbhalsmäusen vergleichbare Geschlechtsunterschiede festgestellt werden. Anders als bei den Gelbhalsmäusen wurden hier auf zwei der drei Untersuchungsflächen etwas mehr Weibchen gefangen. Das schon früher beobachtete Verhalten der erhöhten Mobilität territorialer adulter Weibchen (Andrzejewski und Olzewski 1963; Viitala und Hoffmeyer 1985) kann dazu beigetragen haben, daß sich die Fangerfolge männlicher und weiblicher Tiere nicht signifikant unterschieden. Der von Rajska-Jurgiel (1992) beobachtete Weibchenüberschuß während der Fortpflanzungszeit erklärt ebenfalls den guten Fangerfolg bei Weibchen auf U und A.

Die Fangergebnisse auf den Untersuchungsflächen entsprachen insgesamt den aus der Literatur entnommenen Habitatansprüchen von Gelbhalsmaus und Rötelmaus. Interessant waren allerdings die Fangergebnisse in den einzelnen Mikrohabitaten, die zum Teil von den in der Literatur erwähnten Präferenzen abwichen. Für Gelbhalsmäuse gehörten Kraut/Strauchstandorte in der vorliegenden Untersuchung insgesamt zu den Standorten mit dem höchsten Fangerfolg. Auf Grasstandorten konnten in der kältesten und regnerischen Fangperiode Ende August (FP5) die höchsten Fangzahlen erzielt werden. Sowohl Gras- als auch Kraut/Strauchstandorte gehören laut Literaturangaben nicht zu den bevorzugten Mikrohabitaten der Gelbhalsmaus. Die Fangergebnisse der Rötelmäuse wichen ebenfalls im Mikrohabitat Kraut/Strauch von den erwarteten Ergebnissen ab. Literaturhinweisen zufolge hält sich die Rötelmaus bevorzugt an diesen Standorten auf, die Fangergebnisse waren hier jedoch erstaunlich gering.

Mit Hilfe dieser Studie sollten Informationen über die Kleinsäugerbesiedlung eines windwurfbeeinflußten Bergwaldes im Randbereich der Nördlichen Kalkalpen gewonnen werden. Die Dominanzverhältnisse der Arten waren aufgrund der Fangzahlen eindeutig zuzuordnen. Die aus der Literatur bekannten Habitatansprüche von Gelbhals- und Rötelmaus aus tieferen Regionen trafen weitgehend auch für diesen montanen Bergwald zu. Auf den hier vorliegenden Sonderstandorten bevorzugte die Gelbhalsmaus eindeutig die naturnahe Windwurffläche, die durch ihre strukturelle Vielfalt mit einem Bestandesinneren vergleichbar ist. Für sie kann ein saisonaler Habitatwechsel zwischen Altbestand und ungeräumter Windwurffläche in Betracht gezogen werden. Die Rötelmaus hingegen nutzte die intensiv bewirtschaftete kahlschlagähnliche Fläche mit gutem Unterwuchs, Wurzeltellern und steinigem Untergrund stärker. Da sie zu einem der wichtigsten Forstschädlinge zählt, ist diese Präferenz bei der Wahl der Bewirtschaftungsmethode auch im montanen Bereich zu bedenken. Für die Mikrohabitate Gras und Kraut/Strauch deckten sich die Ergebnisse im untersuchten Bergwald jedoch nicht mit den Literaturangaben.

Danksagungen

Herzlicher Dank gilt dem Institut für Wildbiologie und Jagdwirtschaft der Universität für Bodenkultur, Wien, für die Bereitstellung der Fallen sowie der Rothschild'schen

Forstverwaltung, insbesondere Herrn Ing. T. Fritz, für die Kooperationsbereitschaft. Herzlicher Dank gilt ebenso unseren Kollegen wie auch besonders den unbekannten Reviewern für die kritische Durchsicht des Manuskripts.

Zusammenfassung

1995 wurden im Steirisch-Niederösterreichischen Grenzgebiet, fünf Jahre nach einer schweren Sturmkatastrophe, eine forstwirtschaftlich geräumte und eine nicht geräumte Windwurffläche sowie eine Altbestandfläche faunistisch und floristisch untersucht. Ziel der Untersuchung war es, Daten über die Kleinsäugerbesiedlung der montanen Waldstufe im Bereich des nordöstlichen Ausläufers der Nördlichen Kalkalpen zu erhalten. Ebenso war zu untersuchen, ob die aus der Literatur bekannten unterschiedlichen Habitatansprüche von Gelbhalsmäusen (*Apodemus flavicollis*) und Rötelmäusen (*Clethrionomys glareolus*) tieferer Regionen auch auf Sonderstandorte, wie jene forstwirtschaftlich differenziert behandelten Windwurfflächen (naturnahe und intensive Bewirtschaftung) des Bergwaldes, übertragbar sind.

Zum Zeitpunkt der Untersuchung herrschten auf beiden Sturmflächen Kahlschlaggesellschaften vor. Auf der nicht geräumten Windwurffläche wurde der größte Fangerfolg an Muriden erzielt. Die Gelbhalsmaus (*Apodemus flavicollis*) war auf allen drei Flächen die am häufigsten gefangene Art, gefolgt von Rötelmaus (*Clethrionomys glareolus*), Waldmaus (*Apodemus sylvaticus*) und Erdmaus (*Microtus agrestis*). Gelbhalsmäuse wurden vermehrt auf der ungeräumten Windwurffläche in verkrauteten Standorten und Jungwüchsen gefangen. Rötelmäuse gingen hingegen vermehrt auf der geräumten Fläche in Fallen, die auf Fels/Stein-, Bestand- und Waldrandstandorten plaziert waren. Für Gelbhalsmäuse konnte aufgrund der Fangzahlen ein saisonaler Habitatwechsel in Betracht gezogen werden. Das Geschlechterverhältnis der Gelbhalsmäuse fiel auf einer Fläche sowie auf allen Untersuchungsflächen insgesamt signifikant zugunsten der Männchen aus. Die Fangergebnisse der einzelnen Untersuchungsflächen entsprachen weitgehend den aus der Literatur entnommenen Habitatansprüchen. Interessant war allerdings das Fangergebnis in den einzelnen Mikrohabitaten, das zum Teil von den in der Literatur erwähnten Präferenzen abwich.

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Mamm. biol. **66** (2001) 301–304
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

The occurrence of roof rats (*Rattus rattus* L., 1758) in Germany during the late 20th century

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Receipt of Ms. 29. 09. 2000
Acceptance of Ms. 02. 02. 2001

Key words: *Rattus rattus*, roof rat, black rat, distribution, Germany

Roof rats (*Rattus rattus* Linné, 1758) have been existant in the area covered by present-day Germany for almost 2000 years. Excavations revealed remains dating back to the second century (Lüttschwager 1968), to the 3rd–5th century (Teichert 1985), and to the early middle ages (Reichstein 1974, 1987). Patterns of their distribution in Central Europe appear not to be linked to natural conditions, such as climate and vegetation, but rather to man-made conditions, which tend to change rapidly. Roof rats may suddenly be introduced by the transport of goods, and they may be extinguished locally when industrial sites are abandoned or farms are modernized (Becker 1978). Pest control operations frequently reduce their populations. The occurrence of roof rats is very dynamic and not characterized by distribution lines used to describe the distribution of endemic species.

Many sites where roof rats become abundant remain unknown to scientists because farmers and pest control operators do not identify the species, and faunistic research projects rarely focus on commensal mammals. Although the roof rat has been classified as "extinct or disappeared" during the 1990s in some federal states of Germany, such as Bayern, Nordrhein-Westfalen, Hessen, Baden-Württemberg, and Rheinland-Pfalz (Nowak et al. 1994), pest control operations targeted this rat in other states.

Roof rats are generally less susceptible than Norway rats (*Rattus norvegicus*) to anticoagulant rodenticides, which have been predominantly used to control commensal rodents during the last few decades. To some degree, they are resistant to warfarin (Endepols and Schuster 1991). Their control is also impeded by the fact that they use smaller home ranges than Norway rats (Telle 1966; Endepols et al. 1989). Incorrect identification of the species during control operations may have resulted in an underestimated abundance of roof rats.

To summarize all occurrences of roof rats in Germany, we collated those that we identified ourselves and those published by others. In addition, we included analyses of owl pellets, and information obtained from data bases from the Landeshygieneinstitut Sachsen-Anhalt (LHI) in Magdeburg and from Bayer Animal Health in Monheim. The data comprise occurrences of roof rats, which were detected by farmers, millers or pest control operators. Such reports were verified when animals were sighted or carcasses found by the authors, by staff of one

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of these institutes or by another hygiene institute. The database of the LHI predominantly contains data from the eastern states of the 1980s. During this time, the LHI advised all rat control programs in the former German Democratic Republic (GDR) and was responsible for the registration of rodenticides.

Most infestations were recorded on farms in Sachsen, Sachsen-Anhalt, and Brandenburg in the 1980s (ERFURT et al. 1986). On large pig farms in these federal states, roof rats established particularly large populations exceeding 10 000 individuals (ENDEPOLS et al. 1989). Poor standards in the extensive animal production in the GDR, such as food spillage, hollow walls and penetrable roofs, supported successful reproduction, even during the cold winters in East Germany (ENDEPOLS 1992).

Simultaneously, roof rats were considered locally extinct in some large federal states

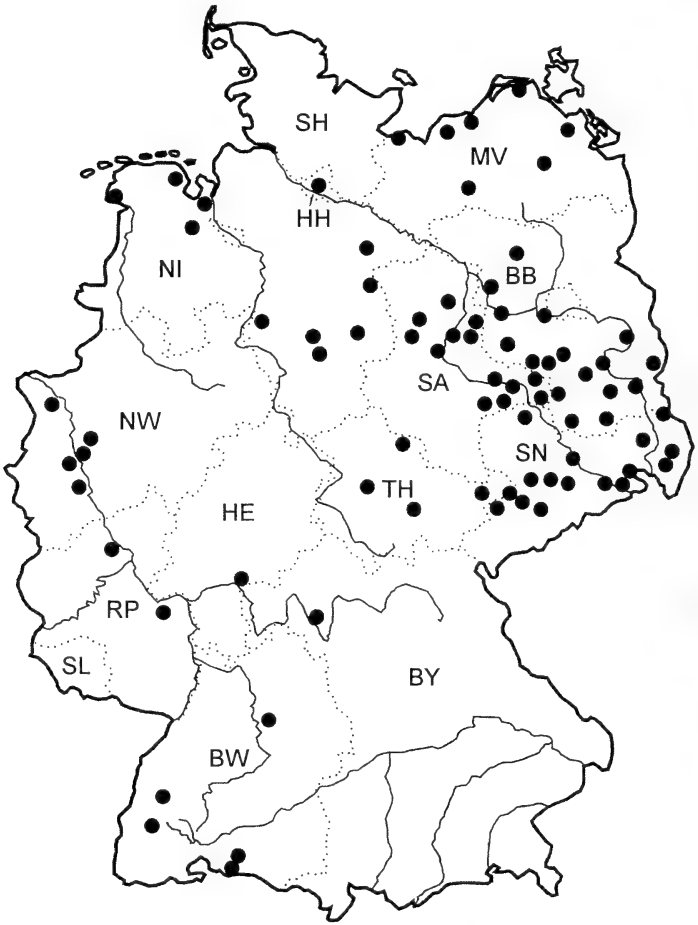

Fig. 1. Occurrences of roof rats (*R. rattus*) in Germany, 1980–1999. Each district where roof rats were recorded is marked by a dot. BB = Brandenburg, BW = Baden Württemberg, BY = Bayern (Bavaria), HE = Hessen (Hesse), HH = Hamburg, MV = Mecklenburg-Vorpommem, NI = Niedersachsen (Lower Saxony), NW = Nordrhein-Westfalen (North Rhine-Westphalia), RP = Rheinland-Pfalz (Rhineland-Palatinate), SA = Sachsen (Saxony), SH = Schleswig-Holstein, SL = Saarland, TH = Thüringen (Thuringia).

in western and southern Germany, such as Rheinland-Pfalz (Grünwald and Preuss 1983, 1987), Baden-Württemberg (Braun 1989), Nordrhein-Westfalen, Bayern, and Hessen (Nowak et al. 1994). Recently, roof rats were re-discovered in some of these areas.

Roof rats were detected in all but two small federal states, Schleswig-Holstein and Saarland, during the last 20 years (Fig. 1). Most populations in western Germany were detected in harbour areas along rivers. We found them in grain mills, food mills and silos along the river Main in the cities of Würzburg (1997) and Hanau (1995), and downstream of the Rhine River in cities, such as Cologne (1999), Düsseldorf (1996), Neuss and Wesel (1995). Roof rats were also detected in southwest Germany (Brünner and Troje 1991), at the Bodensee (lake of Constance) (Wilhelm, Braun, and Dieterlen, pers. comm.) and in the area of the middle Rhine (Dalbeck 1996).

In all regions, we observed the colour variations "rattus", "alexandrinus", and "frugivorus". In Hanau on the river Main and in Cologne on the Rhine River, we found pure populations of black rats. However, due to small sample sizes and specimens lacking fur, such as skulls and bones, characterization of a representative number of populations was not feasible. In general, the three variations of fur colour appear purely or in mixed populations in Germany.

Although large populations of roof rats appeared in habitats such as pig farms, grain mills and silos, light infestations were also detected on small farms, in restaurants and in small food-producing factories. Even in rural residential buildings a few roof rats were observed. Such infestations were reported solely where large rat populations were established nearby. Although many occurrences of roof rats probably remained unnoticed, our data support a previous evaluation that this species is not endangered in Germany (Boye et al. 1998). Conservation measures are neither necessary nor reasonable because roof rats represent a pest in the food industry and agriculture.

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Mamm. biol. **66** (2001) 305–307
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Caecotrophy in pacas (*Agouti paca* Linnaeus, 1766)

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Receipt of Ms. 04. 10. 2000
Acceptance of Ms. 23. 03. 2001

Key words: *Agouti paca*, captivity, caecotrophy

Caecotrophy, a physiological process which was early documented in rabbits (Morot 1882), is recognised to occur in mammals of different species (*Gorilla gorilla*: Harcourt and Stewart 1978; *Phascolarctos cinereus*: Osawa et al. 1993; *Hydrochaeris hydrochaeris*: Borges et al. 1996; *Myocastor coypus*: Takahashi and Sakaguchi 1998). Nevertheless, it has been best documented for lagomorphs and some rodents (Stillings and Hackler 1966; Pickard and Stevens 1972; Björnhag and Sjöblom 1977; Cranford and Johnson 1989; Soave and Brand 1991; Marounek et al. 1995). These herbivores ingest differentiated faeces and absorb the protein and carbohydrates synthesized by caecal microorganisms.

The paca (*Agouti paca*) is the second largest neotropical hystricognath rodent with an adult average body weight of 8 kg. It is distributed from southern Mexico to nortern Argentina, in practically all forest habitats up to 2000 m of altitute (Woods 1984). This species has become locally extinct in overhunted areas of Central America (Emmons 1990), and is considered vulnerable to extinction in some areas of Brazil, because of the reduction of its habitats and hunting pressure (Ayres et al. 1991; Vickers 1991; Bergallo et al. 2000). These mammals are mainly frugivorous (Mondolfi 1972), but Smythe et al. (1983) suggested that pacas could browse on leaves and seedlings during fruit shortage seasons.

A study of the behavioural patterns of 11 pacas in captivity was conducted at the Universidade Estadual Paulista, in Jaboticabal, Brazil between February and March of 1998. Animals were grouped as four mated pairs (three of them with a female offspring) housed separately in 10 m^2 pens, installed in an open outdoor area. The pens had a $1.7 \times 0.7 \times 0.35$ m tank full of water; a brickwork den of $1.0 \times 0.75 \times 1.0$ m with a mobile wood cover at the top, and a 0.30×0.30 m entrance near the floor closed by a mobile metal blind. Although living in captivity, these pacas showed nocturnal habits. Every morning around 9.00 h, faeces and remainding food were removed, drinking water was changed, the water tanks filled, and 1 kg of hay was placed on the floor, 0.8 m from the entrance of the artificial burrows. Each group was fedwith approximatly 240 g of rodent food at 9.00 a. m., and at 5.00 p. m. They received seasonal tropical fruit, green maize, and chopped raw manioc for evening and night consumption. To supply their need for gnawing, three to four fresh pieces of eucalyptus

1616-5047/01/66/05-305 $ 15.00/0.

tus branchs, approximately 1.5 m in length and 5.0 cm in diameter, were provided to each pen, and exchanged for new ones after 15 days. The hay that remained outside the burrows was swept out of the pens every morning. Every ten days, the whole pen floor was washed, even inside the burrows after the hay had been removed, and the water tanks were brushed. All maintenance of the animals was performed by the same two staff persons, who had already been doing this work for at least one year before the study started.

Observations were registered by continuous recording (Martin and Bateson 1986), with all registry done in a descriptive manner by the same observer. Observations began in February 1998, and were conducted from 7.30 h a. m. to 3.00 h p. m. (daylight) for 40 consecutive days, for a total of 148 hours. Nocturnal observations were made from March to July of the same year, from 5.30 h p. m. to 10.00 h p. m., over scattered days for a total of 31 hours. The night schedule was selected, based on a previous study for 72 hours of continuous observation of the activity rhythm. These pacas showed an activity peak from 5.30 h p. m. to 10.00 h p. m. In addition, the animals were observed for two more days, between 6.00 h p. m. to 12.00 h a. m. and 12.00 h a. m. to 6.00 h a. m. In order to acclimate the animals to artificial light, two nights before each nocturnal observation two lamps (with 40 watt each, positioned 5 m equidistant) illuminated the four pens. Observations inside the burrows were possible since one corner of the wood cover was lifted 30 cm with a wire.

Although defecation occurred mainly at night, caecotrophy was detected only once during the nocturnal observations, and this caecotrophy was of already defecated faeces. Ingestion of faeces directly from the anus was, in contrast, only observed during daytime, always occurring inside the burrows. The paca can rest in the burrow using three different positions: with the belly upward and the four limbs flexed near the body; with the bodyside and cheek on the floor and the four limbs stretched perpendicular to the body; and, with the sternum on the floor and the limbs close to the body (i. e.: the sternal position). Caecotrophy occurred when the animals were resting in the sternal position, by raising the chest off the ground, then putting the snout between the hind legs and repeatedly licking the anus; and finally lifting the head and chewing for about ten seconds, swallowing soon after. This cycle was repeated up to ten times. All adults and immature pacas over two months old showed this behaviour daily, throughout the diurnal observation period, however, one adult female performed caecotrophy during nocturnal observations.

Consumption of faeces by captive pacas has previously been reported (Matamoros 1982), but no mention was made of caecotrophy of differentiated faeces.

Since pacas have large intestines with a functional caecum (Bentti 1981) and since they are phylogenetically related to hystricognaths who perform caecotrophy, the consumption of differentiated faces should be interpreted as related to the feeding habits of pacas and not as an abnormal behaviour resulting from captivity (Grier 1984). Although studies concerning the natural feeding habits of this species are lacking, pacas have been considered to be frugivores. The occurrence of caecotrophy and their digestive tract anatomy suggests that pacas may be more herbivorous than expected, often browsing on leaves, and not only when fruits are scarce.

Acknowledgements

We are greatful to Dr. Mauricio Barbanti Duarte for access to the pacas of the Wild Animal Section, at the Universidade Estadual Paulista-Jaboticabal, and to Dr. Carlos Ruiz-Miranda for devoted readings, English revisions and suggestions for the final manuscript. We also thank the anonymous reviewers for their helpful comments on the previous version of this manuscript. Financial support was supplied by the Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq, a Brasilian governmental institution for scientific and technological development.

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Mamm. biol. **66** (2001) 308–311
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Protein polymorphism in two species of *Ctenomys* (Rodentia, Ctenomyidae) from Córdoba province, Argentina

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Receipt of Ms. 09. 10. 2000
Acceptance of Ms. 03. 05. 2001

Key words: *Ctenomys bergi*, *Ctenomys rosendopascuali*, allozymic polymorphism, speciation

Fossorial rodents of the genus *Ctenomys* are widespread in southern South America, from 17° to 54° S (Cabrera 1961; Reig et al. 1990). The genus comprises 60 recognized species originated by an explosive speciation process, promoted mainly by chromosomal rearrangements (Bidau et al. 1996). At present, systematic relationships among species of *Ctenomys* are poorly known and/or controversial.

Thomas (1902) cited the species *C. bergi* for the NW of Córdoba province, Argentina, being Cruz del Eje the type locality. On the basis of geographic criteria, all the populations from the north of that province were included in that species (Bidau et al. 1996).

Chromosomal studies revealed that individuals from the NE of Córdoba have a diploid number 2 n = 52 (FN = 66) but those proceeding from the NW (Salinas Grandes) presented a karyotype of 2 n = 48 (FN = 90) (Reig et al. 1990). This last form was assigned to *C. bergi* and the former was described as a new species and denominated *C. rosendopascuali* (Contreras 1995).

Several authors have emphasized the importance of the application of biochemical and molecular methods in order to confirm and clarify the taxonomic status of different karyotypic forms of *Ctenomys* (Bidau et al. 1996; Mascheretti et al. 2000). The aim of this study is to analyze the allozymic polymorphism in two populations of *Ctenomys* from the north of Córdoba, Argentina assigned to *C. bergi* and *C. rosendopascuali*, in order to determine their level of differentiation at structural loci.

Fourteen specimens of *C. bergi* from Las Toscas (30°11′ S, 64°54′ W, near an extense salt mine called Salinas Grandes) and 16 individuals of *C. rosendopascualis* obtained in the proximity of the mouth of Xanaes river (Mar Chiquita saline lagoon, 30°55′ S 62°44′ W) were used in this study.

Animals were killed by ether anesthesia, liver and kidneys removed immediately and preserved at –30 °C until used. Homogenates, vertical starch gel electrophoresis and staining procedures were carried out as described by Gardenal et al. (1980) and Gardenal and Blanco (1985). The following enzymes were analyzed (loci scored and E. C. numbers in parenthesis): liver and kidney acid phosphatase (Acp_L-1, Acp_L-2, Acp_K-3, Acp_K-4; 3.1.3.2), aspartate aminotransferase (Aat-1, Aat-2; 2.6.1.1), liver soluble esterases ($Es\text{-}1_L$ to $Es\text{-}6_L$; 3.1.1.1), catalase (Cat; 1.11.1.6), phosphoglucomutase (Pgm-1, Pgm-2; 2.7.5.1), leucine aminopepti-

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dase (Lap-1, Lap-2; 3.4.11.1), malic enzyme (Me; 1.1.1.40), lactate dehydrogenase (Ldh; 1.1.1.27), alcohol dehydrogenase (Adh; 1.1.1.1), glycerophosphate dehydrogenase (Gpdh; 1.1.1.8), malate dehydrogenase (Mdh-1,Mdh-2; 1.1.1.37), isocitrate dehydrogenase (Idh-1, Idh-2; 1.1.1.42), 6-phosphogluconate dehydrogenase (6-Pgdh; 1.1.1.43) and glucose-6-phosphate dehydrogenase (G-6-pdh; 1.1.1.49).

The allele coding for the band migrating fastest to the anode was assigned the number 100; that controlling the fastest cathodic band, –100. The other alleles were numbered according to their relative mobility from the origin. Bands with the same mobility were considered homologous.

Proportion of polymorphic loci (95% and 99% criteria), mean observed and expected heterozygosities, Rogers' genetic distance (1972) and Nei's identity (1975) among populations were calculated using the program Biosys-1 (Swofford and Selander 1989).

Sixteen out of 27 loci analyzed were polymorphic at least in one population. Table 1 shows allele frequencies, proportion of polymorphic loci (P), and observed and expected mean heterozygosity per locus (H_o and H_e) for the two populations analyzed. Locus G-6-pdh was the only one presenting a different allele fixed in each population.

Although crossing tests were not performed, the genetic control of the electrophoretic patterns observed was postulated on the basis of similar polymorphisms described for other rodent species where the Mendelian transmission of variants has been demonstrated (Gardenal and Blanco 1985; Gardenal et al. 1980; García and Gardenal 1989). In all cases, the observed genotypic frequencies did not differ significantly from the expected ones according to the Hardy-Weinberg equilibrium.

Rogers' genetic distance and similarity between the two species was 0.094 and Nei's distance and identity were 0.059 and 0.942, respectively.

Levels of polymorphism revealed in this study for *C. bergi* and *C. rosendopascuali* are particularly high when compared with those reported for other subterranean mammals with low vagility and socially-structured mating system (Nevo et al. 1990). Values of heterozygosity obtained in this study are higher than the mean referred for fossorial rodents (H = 0.0311) and for

Table 1. Allele frequencies, proportion of polymorphic loci (95% and 99% criteria) and observed and expected heterozygocity in *Ctenomys bergi* and *Ctenomys rosendopascuali* from Córdoba province (Argentina).

Locus	Allele	*C. bergi*	*C. rosendopascuali*
Lap-2	100	1.000	0.929
	88	0.000	0.071
Acp_K-1	100	0.067	0.036
	90	0.900	0.857
	81	0.033	0.107
Adh	–100	0.867	0.864
	–50	0.133	0.136
Gpdh	100	1.000	0.923
	60	0.000	0.077
Acp_L-3	100	0.094	0.038
	78	0.906	0.962
Acp_L-4	100	0.031	0.000
	71	0.969	1.000
Aat-1	100	0.000	0.0154
	72	0.969	0.0846
	20	0.031	0.000
Es-1	100	0.844	0.855
	93	0.156	0.115
Es-2	100	0.563	0.731
	94	0.438	0.269
Es-3	100	0.906	0.885
	88	0.094	0.115
Es-4	100	0.000	0.077
	89	0.656	0.615
	85	0.344	0.308
Es-5	100	0.000	0.038
	89	1.000	0.962
Es-6	100	0.813	0.269
	77	0.188	0.731
Pgm-2	100	1.000	0.846
	82	0.000	0.154
Me	100	0.063	0.000
	89	0.938	1.000
G 6pdh	100	1.000	0.000
	87	0.000	1.000
P (95%)		33.33	40.74
P (99%)		40.75	48.15
H_O (%)		10.1	12.8
		(s. e. 3)	(s. e. 3.4)
H_E (%)		9.3	11.7
		(s. e. 2.8)	(s. e. 2.9)

several species of *Ctenomys* from Bolivia (Cook and Yates 1994), and Chile (Gallardo and Palma 1992), albeit similar to those obtained in 4 species from southern Brazil (H from 0.11 to 0.17) (Moreira et al. 1991). When rapidly evolving loci as esterases are excluded, H_e falls to 0.041 in *C. bergi* and to 0.067 in *C. rosendopascuali*. However, they are still higher than the mean obtained for fossorial rodents, most of them calculated including esterases. Sage et al. (1986) and Ortells and Barrantes (1994) found lower levels of allozymic polymorphism in other species of *Ctenomys* from Argentina. However, estimates were made, in most cases, on the basis of 1 to 4 individuals, which could explain the results obtained by those authors.

Genetic similarity between *C. bergi* and *C. rosendopascuali* is within the range reported for conspecific populations (King 1993). Notwithstanding, in locus G-6-pdh allele '100' is fixed in *C. bergi* and allele '87' has a frequency of 1 in *C. rosendopascuali*, indicating lack of gene exchange between the two forms.

Several cases of interspecific homogeneity in allozymic frequencies have been reported in *Ctenomys*. Gallardo and Palma (1992) found very low levels of genetic differentiation among *Ctenomys* species from Chile, although being very dissimilar in morphological characters and karyotype. Moreira et al. (1991) reported an S value of 0.91 between *C. minutus* and *Ctenomys sp.* from southern Brazil, inhabiting regions separated by 75 km and a wide river.

The genus *Ctenomys* is characterized by a large karyotypic heterogeneity, being one example of "explosive" speciation accompanied by scarce morphological changes (Bidau et al. 1996; Reig et al. 1990). Fixation of chromosomal re-arrangements would be favored by the population structure characteristic of all species in the genus: small, semi-isolated groups with low vagility and continuous extinction, expansion, and re-colonization in a variety of environments (Reig et al. 1990). The low genetic distance between *C. bergi* and *C. rosendopascuali* would be in agreement with the hypothesis of a rapid speciation by chromosomal re-arrangements, with almost no differentiation at structural loci, as those coding for proteins.

On the basis of morphological, morphometric, paleontological, karyological and distributional data, Contreras and Bidau (1999) have proposed a hypothesis on the evolution of the complex genus *Ctenomys*. *C. bergi* would be closely related to the group designated "mendocinus", which comprises several species with very similar karyotypes that have originated from a west-south radiation. *C. rosendopascuali* would integrate a separate lineage, the so called "oriental" group, presenting less stable diploid numbers and particular morphological features such as sperm asymmetry. However, Mascheretti et al. (2000), on the basis of cytochrome b sequences, found a very close relationship between these two species, placing them in the same molecular lineage. Our results would support this last proposal.

Acknowledgements

We thank Dr. Antonio Blanco for advice and critical revision of the manuscript. This work was supported by a grant from the Consejo de Investigaciones Científicas y Tecnológicas de la Provincia de Córdoba (CONICOR). C.N.G. is a Career Investigator of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina.

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Mamm. biol. **66** (2001) 312–316
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Comparative food preference of *Microtus brandti* and *Ochotona daurica* in grasslands of Inner Mongolia, China

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Receipt of Ms. 14. 12. 2000
Acceptance of Ms. 05. 04. 2001

Key words: *Microtus brandti*, *Ochotona daurica*, food selection, niche overlap

Brandt's voles (*Microtus brandti*) and dahurian pikas (*Ochotona daurica*) are two common small mammal species in typical steppes of Inner Mongolia, China. The burrowing and foraging activities of the voles can impose strong impact on the composition, physiognomy, and productivity of typical steppes (Zhong et al. 1985 a). In Inner Mongolian grasslands, the density of burrow entrances of *M. brandti* reached 5,616/ha in a high density year, and average above ground plant biomass in the area inhabited by voles was only 47% compared to areas without voles (Zhong et al. 1985 b). The voles and pikas are sympatric in this region. Trophic relationships are important to understand the interspecific interactions between these two coexisting species. However, none of previous studies covered seasonal changes in the food habits of *M. brandti* and *O. daurica* and their trophic relationships. The objectives of this study were twofold: (1) to report species composition of natural diets of *M. brandti* during spring, summer and autumn in typical steppes of Inner Mongolia, China, and natural diet composition of *O. daurica* in summer and autumn; (2) to determine the interspecific trophic relationship between *M. brandti* and *O. daurica*.

The study was conducted in Hexiten Banner, Inner Mongolia, China. The study site (43°24′ N, 116°46′ E) was located in a grassland of flat topography. The vegetation is characterized as a *Stipa krylovii, Artemisia frigida, Aneurolepidium chinense* community. The average annual temperature is about –0.1 °C. The average annual rainfall is about 350 mm, and is concentrated in June, July, and August. Snow cover is present from November to March. Plant growth occurs from April to August (Jiang 1985).

We trapped *M. brandti* and *O. daurica* in a 10-ha plot. Snap traps were set at burrow entrances of voles and pikas. Stomachs of captured voles and pikas were removed and preserved in 5% formalin solution. We analysed 22 stomachs of voles in April 1989, 23 in July 1989, and 20 in September 1990. Sample sizes for the pikas were 10 stomachs in July 1989, and 11 in September 1990. All sample sizes were greater than or equal to the minimum sample size for this kind of analysis (Batzli 1985). Stomach contents were analysed following the procedures described by Williams (1962). Reference slides of epidermal layers were made for about 40 plant species of the study site. Epidermal fragments in stomach contents were identified to species whenever possi-

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ble. Percent of each plant species in diet dry weight was estimated following the procedure of SPARKS and MALECHEK (1968). We only listed main food items contributing >1% of diets (BATZLI 1985).

Within plot, above ground biomass was sampled with a 100×100 cm square frame in July, 1989. Ten random frames were chosen. Green plants were cut to the ground. Vegetation samples were sorted to species, and were dried in an oven at 60 °C for 48 consecutive hours. Dried samples were weighed to the nearest 0.1 g. The total biomass of plants in a quadrat (g/m^2) and percent biomass of each plant species in the total biomass were recorded.

We used the proportional similarity index (FEINSINGER et al. 1981), $SI = \sum_i \min(D_j, D_k)$, to calculate the trophic niche overlap between the two mammal species, where $\min(D_j, D_k)$ is the minimum value between D_j and D_k, D_j the proportion of plant species i in diet dry weight of species j, and D_k the proportion of the same plant species in the diet of species k. We computed the jackknife means and variances (ZAHL 1977) of SI for summer and fall, and then followed the t-test procedure of HUTCHESON (1970) to test for differences in the trophic niche overlaps between the voles and pikas. We also used the proportional similiarity index to determine the similarity between the composition of summer diets of the voles and pikas and vegetation. Similarity between diet and vegetation composition measures diet selectivity of voles and pikas. Trophic niche width was determined by Shannon-Wiener diversity index, $H = -\sum D_i \ln(D_i)$, where D_i is the proportion of plant species i in a herbivore's diet. We followed the t-test procedure of

Table 1. Natural diets (diet dry weight percent %) of *Microtus brandti* in spring, summer, and autumn and *Ochotona* daurica in summer and autumn. Blank cells indicate either not used by the voles and pikas or < 1% of diets.

Food items	voles			Pikas	
	spring	summer	autumn	summer	autumn
Monocotyledons					
Aneurolepidium chinense	55.4	40.3	27.4	56.4	21.0
Agropyron cristatum	27.6	4.7	2.8	2.3	4.0
Stipa krylovii	5.1	2.1	1.3	2.3	1.3
Carex duriuscula	2.6				
Keoleria cristata			1.9		
Cleistogenes squarrosa		2.2			
Other monocotyledons	0.7		3.8	0.5	3.1
Dicotyledons					
Astragalus galactites				2.0	
Scutellaria scordifolia				2.0	
Artemisia frigida	1.4	6.5	32.4		30.0
Potentilla acaulis	2.0		1.3		
Ixeris chinensis	1.3		2.3	3.4	
Saussurea amara			1.1		
Melissitus ruthenica		28.9	11.6	3.6	1.5
Potentilla tanacetifolia		2.7	5.8	14.1	16.4
Salsola collina			1.1		
Heteropappus altaicus		7.6		7.2	8.2
Potentilla bifurca		1.5		3.2	
Astragalus adsurgens				1.8	7.0
Other dicotyledons	1.8	3.5	7.2	1.2	7.5
Plant roots	2.0				
Unknown	0.1				

Hutcheson (1970) to detect differences in the niche width between two species as well as between the seasons for the same species. We used preference index (PI = proportion of diet/proportion of forage) to assess if a herbivore responds to availability of a food item, e. g. PI > 1 if consistently preferred, PI < 1 if consistently avoided (Batzli 1985).

In spring, the voles consumed seven main plant species, including four species of monocotyledons and three species of dicotyledons. Monocotyledons made up 91.4% of diet dry weight, and dicotyledons 6.5%. The voles consumed nine main plant species in summer, four species of monocotyledons (49.3%), and five species of dicotyledons (47.2%) (Tab. 1). In summer, vole diet composition was different from plant species composition of the vegetation as the similarity index between the diet composition and vegetation composition was 0.39. Of all available food items, the voles strongly preferred certain dicotyledons in summer (PI $\gg$ 1.0), such as *Potentilla tanacetifolia*, *Heteropappus altaicus*, and *Melissitus ruthenica* (Tab. 2). Although *Artemisia frigida* contributed 6.5% of the summer diet, the voles did not prefer this plant (PI < 1.0). Autumn diets of voles consisted of 11 main plant species, four species of monocotyledons (33.4%) and seven species of dicotyledons (55.6%). *A. chinense* was the favorite food of voles in spring, summer, and autumn in terms of percentage. *A. cristatum* was less important during summer (4.7%) and autumn (2.8%) compared with spring (27.6%). However, *Melissitus ruthenica* and *A. frigida* became more important during summer and autumn.

In summer, the pikas selected 11 main plant species, three species of monocotyledons (61%) and eight species of dicotyledons (37.8%). The pikas also showed preference for certain plants in summer, as the similarity index between the diet and the vegetation composition was 0.33. The pikas preferred *Potentilla tanacetifolia*, *Astragalus galactites*, *Heteropappus altaicus*, *Melissitus ruthenica*, and *Ixeris chinensis* (PI $\gg$ 1, Tab. 2). The pikas selected eight main plant species in autumn, including three species of monocotyledons (26.3%) and five species of dicotyledons (63.1%, Tab. 1). The diet dry weight percent of *A. frigida* increased from 0.5% in summer to 30% in autumn, while the percent of *A. chinense* declined from 56.4% in summer to 21% in autumn. Therefore, diets of the pikas had apparent seasonal changes.

The overlap index of trophic niche between the voles and pikas was 0.54 in summer, and 0.64 in autumn, but did not differ between

Table 2. Percent of main food items of the voles and pikas in the summer above ground biomass of vegetation and preference index (PI). PI > 1.0 indicates consistent preference, PI < 1.0 consistent avoidance.

Food items	% of vegetation biomass	PI of voles	PI of pikas	Food items	% of vegetation biomass	PI of voles	PI of pikas
Aneurolepidium chinense	15.32	2.6	3.7	*Melissitus ruthenica*	4.23	6.8	0.8
Agropyron cristatum	4.47	1.1	0.5	*Astragalus adsurgens*	1.61	0	1.1
Stipa krylovii	7.03	0.3	0.3	*Artemisia frigida*	26.29	0.3	0
Potentilla tanacetifolia	0.03	91	470	*Ixeris chinesis*	0.29	0	11.8
Heteropappus altaicus	0.23	32.9	31.2	*Potentilla bifurca*	1.25	0	2.6
Astragalus galactites	0.03	0	65.3	*Scutellaria scordifolia*	2.48	0	1.2

the two seasons ($P > 0.05$). The trophic niche width of voles was 1.32 in spring, 1.69 in summer, and 1.92 in autumn. Likewise the trophic niche width of pikas increased from summer (1.61) to autumn (1.93). The trophic niche width of the voles differed between spring and autumn ($P < 0.05$), but neither voles nor pikas had significantly different trophic niche widths between summer and autumn ($P > 0.05$). The voles selected more main food items in autumn than in spring, and the voles consumed more monocotyledons in spring (91.4%) than in autumn (37.2%) (Tab. 1). Selection for more food plant species and more even contributions of dicotyledons and monocotyledons in the autumn diet resulted in broader trophic niche of the voles in autumn than in spring. Although the standing crop biomass of the steppes of Inner Mongolia reaches its highest in autumn (Li et al. 1988), the food quality of plants in autumn may be low. Mature plants in grasslands generally have higher fiber content, decreased protein, and increased phenolic content that voles tend to avoid (Lindroth et al. 1986; Marquis and Batzli 1989). The reduction of food quality could lower the availability of food plants in autumn. Consequently, the voles expanded their trophic niche in autumn to respond to the low availability of food. The trophic niche width was not different between the voles and pikas either in summer or in autumn ($P > 0.05$).

Bergman and Krebs (1993) found that the overlap of the diets of collared lemming (*Dicrostonyx kilangmiutak*) and tundra voles (*Microtus oeconomus*) increased when both species foraged in the same habitat. Overlap index of food utilization of voles and pikas under the food selection trial was 0.45 (computed from data of Zhong et al. 1982 and Zhou et al. 1992), while the overlap of trophic niche in the free-ranging conditions was 0.54 in summer. The voles and pikas had overlapping habitat use on our study site. The greater overlap under the free-ranging conditions might result from the lower availability of preferred food plants of pikas in natural vegetation and higher percent of *A. chinense* in the pika's natural summer diet. *A. chinense* made up 6% of daily food consumption in the food selection trial (Zhong et al. 1982), but 56.4% of the natural diet of pikas in summer. The lower availability of preferred *P. bifurca*, *A. bidentatum*, and *A. commutata* might force the pikas to use the more abundant *A. chinense*, one of the dominant plant species in the plant community on the study site. The limited availability of preferred food items in natural vegetation may cause the voles and pikas to share more common and abundant plant species and may result in greater trophic niche overlap under the free-ranging condition.

Acknowledgements

We thank Guanghe Wang for his assistance with the field work. Dr. Bill Mcshea and anonymous reviewers made helpful comments on our manuscript. This work was financially supported by the Inner Mongolia Grassland Ecosystem Research Station, the Chinese Academy of Sciences.

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Mamm. biol. **66** (2001) 317–319
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Records of a few rare mammals from northeastern Peru

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Receipt of Ms. 06. 12. 2000
Acceptance of Ms. 15. 02. 2001

Key words: Didelphimorphia, Rodentia, Peru, distribution records

During 18 months (July 1997 to December 1998) small mammals were collected near Iquitos, Peru, for certain research projects. Sampling was conducted at the Estación Biológica Allpahuayo (S 3°58′; W 73°25′), a 3000 hectare field station operated by the Instituto de Investigaciones de la Amazonía Peruana (IIAP), 25 km south of Iquitos, Department of Loreto, in northeastern Peru. The climate is tropical with a mean annual temperature of 26 °C; the highest average monthly temperature (31 °C) occurs in November and the lowest (22 °C) in July (SALATI 1985). Average rainfall is 2 945 mm per year, with a slightly drier season from June to September (JOHNSON 1976). The elevation of the station ranges from 110 m to 180 m above sea level.

Over 1 000 mammals were collected and prepared. Concerning our knowledge on their distribution several of these specimens represent substantial range extensions for a few species, whereas others are records of mammals not frequently recorded in mammalian surveys. The following accounts summarize information about the species of this region not yet recorded as well as what is already known about the species distributions (EMMONS 1997; EISENBERG and REDFORD 1999). Any measurements (mm) are given using the standard sequence of total length, tail length, hind foot length, and ear length. Specimens are deposited at the Museum of Texas Tech University, Lubbock, Texas, and the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru. Preserved tissues (frozen) include heart, kidney, liver, spleen, lung, and muscle and are deposited at the Museum of Texas Tech University.

Philander opossum (Linnaeus, 1758) and *Philander andersoni* (Osgood, 1913)

The occurrence of these two species of opossum in the study area represents the first record of sympatry, as well as the first record of *P. opossum* north of the Amazon River this far east of the Andes (EMMONS 1997). FLECK and HARDNER (1995) also reported sympatry of these species in Jenerro Herrera, south of the Amazon River. However, Dr. J. L. PATTON of the University of California, Berkeley, examined photographs of the animals and determined that the *P. andersoni* had been misidentified and were in fact *P. mcilhennyi* (pers. comm.). The species identity of my specimens has been verified by cytochrome b sequence analysis conducted by Dr. PATTON. All 39 *P. opossum* were captured in disturbed habitat whereas 12 of 14 *P. andersoni* were cap-

1616-5047/01/66/05-317 $ 15.00/0.

tured in mature forests. *P. andersoni* was captured throughout the year; nursing females (n = 2) were obtained in April and October. The individual captured in April had two pouched young. *P. opossum* was only captured from July to January, with no captures in the spring. Nursing individuals (n = 11), with an average litter size of 4 (2–5), were obtained in July, August, and November.

Gracilinanus kalinowskii Hershkovitz, 1992

This tiny marsupial is extremely rare, known only from seven individuals, three from southern Peru and four from the Guyanan region (HERSHKOVITZ 1992; R. S. Voss, pers. comm.). One young female was captured on 20. 05. 1998 in a Victor rat trap baited with dried, salted fish. The trap was located on the ground in monte alto forest about a 3 h walk north from the road southwest of Iquitos. The animal weighed 4 g and measured 132-76-10-10. The identity of this specimen has been confirmed by R. S. Voss (pers. comm.). This capture represents a substantial range increase and suggests the distribution of this rare species may be quite broad within the Amazon Basin, from southern Peru to the Guyanas.

Monodelphis adusta (Thomas, 1897)

This species is currently known only from Panama and the eastern slopes of the northern Andes in Peru, Colombia, and Ecuador (EMMONS 1997), with a disjunct population in Madre de Dios in southern Peru (WOODMAN et al. 1995). Six individuals were captured in Allpahuayo. Females, with an average weight of 13 g (12–14 g), were substantially smaller than males, with a mean weight of 29 g (28–30 g). Average measurements for females were 130-40.5-12.5-11 (130/130-40/41-12/13-11/11) and for males 164-55-15-12 (157/172-52/57-15/16-11/12). Five of the animals were captured in pitfall traps with a drift fence, as described by Voss and EMMONS (1996). The remaining animal was taken in a Sherman trap baited with a peanut butter/pork fat mixture. They were captured in each of the three types of primary forest present in Allpahuayo (VÁSQUEZ MARTÍNEZ 1997). No reproductive activity was detected for animals captured in the months of November, December, March (both females), May, and August. This represents the first record of any species of *Monodelphis* north of the Amazon River in the Iquitos area and a substantial range increase of *M. adusta*.

Scolomys melanops Anthony, 1924

This genus is known from less than 50 individuals and is suggested to be highly localized in its distribution (PATTON and DA SILVA 1995). It is not necessarily unexpected in the Iquitos area, and may be more widespread in the Amazon Basin than is presently recorded. A large series (24 individuals) was taken during 8 months, but not those of the dry season (June, July, August, and September), and in each of the three types of primary forest present in Allpahuayo (VÁSQUEZ MARTÍNEZ 1997). Eleven individuals were captured in pitfall traps and 9 were taken in Victor traps. Two were taken on fallen logs approximately 1 m high. A total of 5 females and 19 males was obtained, including 2 pregnant females with an average litter size of 2.5 (one each in March and April). Males in reproductive condition (average testes size of 3×6 mm) were captured in March, October, and November. This represents the largest series of *S. melanops* available (PATTON et al. 2000).

Galictis vitata (Schreber, 1776)

This species is broadly distributed throughout the Amazon Basin, but uncommon in its range (EMMONS, 1997). One adult male grison was brought to me by a local hunter on 14. 10. 1997. The animal was shot in upland monte alto forest. No measurements are available.

Acknowledgements

I thank many people and institutions for making this research possible. Dr. VICTOR MONTRUEIL with the Instituto de Investiga-

ciones de la Amazonia Peruana granted permission to conduct research at the biological station. Dr. David Schmidly provided comments on an earlier draft that improved the manuscript. INRENA supplied necessary collecting permits (#21-98-INRENA-DGANPFS-DCFS). This work was supported in part by research grant AI-39800 from the National Institutes of Health.

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Mamm. biol. **66** (2001) 320

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Book review

HUME, I. D.: **Marsupial Nutrition.** Cambridge: Cambridge University Press 1999. 434 pp., 93 line-diagrams, 39 half-tones. Paperback. Us$ 54.95. ISBN 0 521 59555 X.

The reader will hopefully allow the reviewer to do some calculations first before starting with the review, although this might not be a strictly "professional" approach: The present book, as a sequel to "Digestive Physiology and Nutrition of Marsupials" by the same author, which was published in 1982, increased considering the number of pages by approximately 70% and the number of papers cited in the references increased by approximately 90%! As the author himself writes in the preface, this remarkable expansion of knowledge during the last two decades is due to intensified research efforts that have gone into marsupials other than kangaroos. Additionally, authors dealing with South American marsupials have contributed considerably to information on marsupial nutrition, which are meticulously presented here to the impressed reader.

In a detailed introductory chapter the author deals with general physiological and nutritional aspects under the title "Metabolic rates and nutrient requirements". In this important section the frame for all consecutive chapters is supplied: The concept of nutritional niches, significance of metabolic rates, energy requirements for maintenance, aspects of food intake, torpor and hibernation as it can be found in some marsupials, as well as requirements of, e. g., water and protein.

The following chapter deals with carnivorous marsupials, such as American caenolestids, some didelphid species and the only representative of the microbiotheriids, *Dromiciops australis*, or colocolos, as well as Australasian Dasyuridae. In the next chapter HUME presents omnivorous marsupials, such as the American Didelphidae and Australasian Peramelidae, Peroryctidae, Burramyidae, Petauridae, and Acrobatidae. Two chapters deal with hindgut fermenters; one with wombats and the second with arboreal folivores, such as tree kangaroos, the koala (Phascolarctidae) and phalangers as well as pseudocheirids (ring-tails). The following three chapters present foregut-fermenters, such as the Macropodidae (kangaroos and wallabies) and Potoroidae (rat kangaroos). All these chapters are clearly organised, well-written, instructively illustrated (diagrams and half-tones) and full of biological information!

Having been informed about the diversity of the digestive tract, its function and about nutritional and physiological aspects in the Marsupialia, the biologically interested reader expects information and comments on how this richness in species and differentiations came into existence. The reader is not disappointed. HUME presents outlines of the Gondwanian origins of American and Australasian marsupials and discusses their likely foraging and digestive differentiation. He makes clear that his presentation in this part of the book is speculative.

After a relatively short "Future directions", an appendix compiles the classification of marsupials. When browsing through this list, serious deviations from the modern taxonomic reference published by WILSON and REEDER (1993) in association with the American Society of Mammalogists, could not be detected by the present reviewer. 51 (!) pages of references show the remarkable number of publications, on which the book of I. D. HUME is based. An index of 17 pages makes the information presented in this book readily accessible.

P. LANGER, Giessen

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Mammalian Biology

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URBAN & FISCHER Verlag
Jena/Germany

ISSN 1616-5047
Mamm. biol. · 66(2001)5 · 257-320

Contents

Abstracted/Indexed in
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Mammalian Biology

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ISSN 1616-5047
Mamm. biol. · 66(2001)6 · 321-384
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Mammalian Biology

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IMPRESSUM
Publisher: Urban & Fischer Verlag GmbH & Co. KG, Branch Office Jena, P.O. Box 100537, D-07705 Jena, Germany; Phone: ++49(0)3641/626-3, Fax: ++49(0)3641/62 65 00, E-mail: journals@urbanfischer.de
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Type setting and printing, binding: druckhaus köthen GmbH

(∞) As of vol. 61, number 1 (1996) the paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

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Mamm. biol. **66** (2001) 321–331
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Original investigation

Recent recovery of the Italian wolf population: a genetic investigation using microsatellites

By M. Scandura, M. Apollonio and L. Mattioli

Department of Zoology and Anthropology, University of Sassari, Sassari, Italy and Wildlife Management Unit, Provincial Administration of Arezzo, Arezzo, Italy

Receipt of Ms. 20. 09. 2000
Acceptance of Ms. 31. 01. 2001

Abstract

Genetic differentiation within the Italian wolf population was investigated by microsatellite analysis of 38 individuals from 4 distinct sampling sites of the current wolf range throughout the peninsula. A set of 6 microsatellite loci was used, which showed a high level of polymorphism and a combined probability of identity ranging from 10^{-4} to 10^{-6}. The overall DNA variability detected was considerable and only slightly lower than that found for North American grey wolves.
The two largest Italian subpopulations taken into consideration, Tuscan Apennines and central-southern Apennines, proved moderately divergent, and data are consistent with a derivation of the western Alps subpopulation from the former, while the latter showed close similarity to the western coast subpopulation. Gene flow was relatively high across the Italian population and the presence of isolation by distance was supported by our data, as measures of genetic distance were consistent with geographical distribution of sampling sites. High levels of divergence were found between Italian and other European samples. These findings suggest that, despite their absolute mtDNA monomorphism, Italian wolves have preserved a high nuclear DNA heterogeneity and a well-defined genetic identity. A further enlargement of range, which can be expected on the basis of extensive wolf dispersal, might cancel their historical isolation in a few decades, thus favouring a genetic exchange with the east European gene pool.

Key words: *Canis lupus*, microsatellites, variability, population structure, Italy

Introduction

Since the end of the 19th century large predator populations have declined in Italy due to progressive habitat disruption and to direct persecution by humans. As a consequence, different species approached extinction (i. e., brown bear, wolf, and lynx). Changes in human activities, wildlife and wood management, and public opinion have led to the restoration of more favourable environmental conditions and to increased protection of these species. Due to such improvements, in the last 30 years an important predator species, the wolf (*Canis lupus*), has increased in number and enlarged its range (Francisci and Guberti 1993; Boitani and Ciucci 1993; Meriggi

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and Lovari 1996). Wolves in the Italian environment play a key role in wild communities, being the only well-distributed large mammals preying mostly on wild ungulates (Mattioli et al. 1995). During the last two centuries the Italian population became isolated from other European populations, due to the extirpation of the species throughout the Alps (Cagnolaro et al. 1974). The northern border of its range initially moved southwards, towards the central regions, and the presence was restricted to the less accessible areas of the Apennines and to a wooded area along the Tyrrhenian coast (Cagnolaro et al. 1974; Zimen and Boitani 1975). In 1973, the number of wolves inhabiting the Italian peninsula was estimated to be approximately 100 individuals (Zimen and Boitani 1975), after which the population recovered, reaching an estimated size of 400–500 individuals (Boitani 1992).

The demographic recovery of the species was accompanied by a northward expansion of its range, which during the last ten years led to the recolonization of the western Alps, and to the consequent appearance of the wolf in France (Breitenmoser 1998).

The effects of population decline and the subsequent range expansion in the genetic diversity of the Italian wolf population were studied by allozyme and mitochondrial DNA (mtDNA) analyses (Randi et al. 1993; Wayne et al. 1992; Randi et al. 1995; Vilà et al. 1999; Randi et al. 2000). Randi and co-workers (1993), using a set of 40 allozymes over a sample of 38 wolves, found a level of polymorphism and heterozygosity comparable to that of larger North American populations (Kennedy et al. 1991). On the other hand, mtDNA consensus sequences revealed the presence of a single haplotype in all the sampled Italian wolves. This apparent contradiction probably results from the different inheritance systems, based exclusively on female mtDNA transmission.

In order to investigate the actual effects of the population bottleneck and fragmentation on the genetic structure and variability of wolves, nuclear genetic markers, e. g. microsatellites, are more informative. Different studies carried out on North American wolf populations demonstrated the effectiveness of microsatellite loci as a molecular tool for assessing population structure parameters (Roy et al. 1994; Forbes and Boyd 1997), genotyping animals for reintroduction programmes (Garcia-Moreno et al. 1996), evaluating relatedness among individuals (Smith et al. 1996), and estimating genetic variation following natural colonizations (Forbes and Boyd 1996).

The aims of the present study were: 1) to reconstruct the dynamics of the Italian wolf recovery by comparing the genetic pattern of different subpopulations; 2) to evaluate nuclear DNA diversity among and within sub-populations; 3) to estimate the degree of gene flow among different areas. Wolves from historical "stronghold areas" and from recent colonized regions were sampled for comparison.

Material and methods

Sample description and collection

Italian wolf samples were collected from four regions (Fig. 1):

AR – Tuscan Apennines, which probably represented the northern border of the Italian wolf range along the Apennines for half a century (Cagnolaro et al. 1974);

AB – Central-southern Apennines, the part of Italy where the species has always been present in historic times;

VC – Alta Maremma, where the presence of the species was always recorded during the last century, but the area was characterized by continuous new settlements of breeding packs followed by complete or partial eradication (illegal killing);

FR – Alpes Maritimes, France, originating in the early 1990s from individuals moving across from Italy (Randi et al. 2000). Its present size is approximately 20–30 units, of which dispersing individuals are colonizing new areas of the western Alps.

Seventeen tissue samples came from illegally killed wolves, recovered before 1992 in central and southern Italy and obtained from Prof. G. B. Hartl (University of Kiel, Germany). Thirteen specimens are from the northern Apennines, mostly the province of Arezzo: 12 (3 tissues and 9 hairs), supplied by the Provincial Administra-

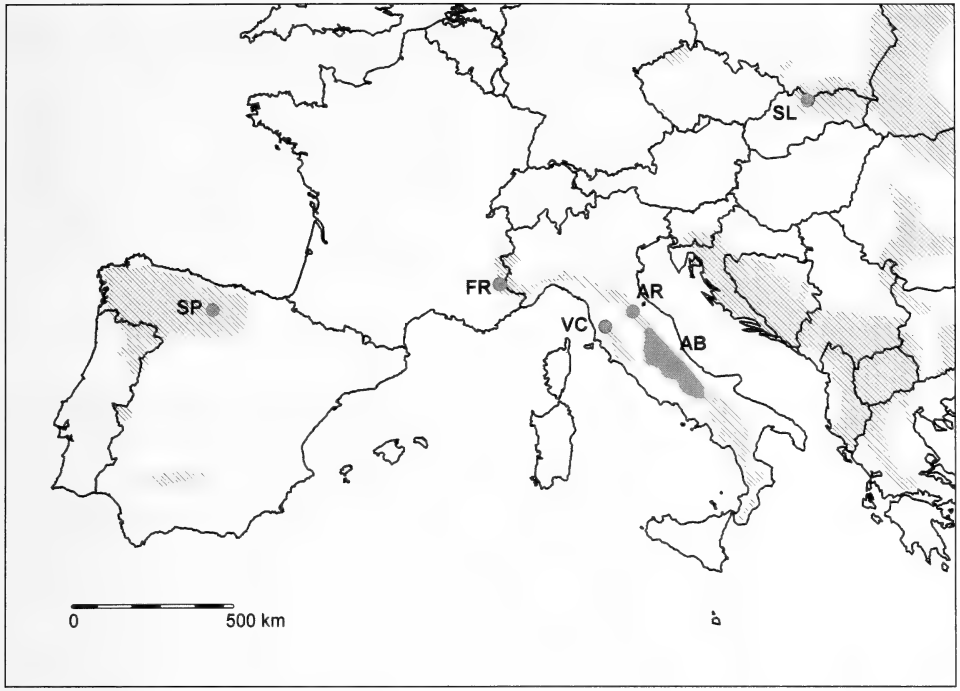

Fig. 1. Geographical location of sampling sites (solid grey) and present distribution range of wolves (hatching).

tion of Arezzo (Tuscany) or by the Corpo Forestale dello Stato, derived from animals dying in the period 1991–1999, whereas one hair sample was collected in the field during a survey in the Foreste Casentinesi National Park. Three samples of the Alta Maremma population were obtained from the Veterinary Service of Volterra (Pisa) and one hair sample was collected in a natural preserve near Volterra. For the Alpine population, 4 tissue samples were provided by Valiere Nathaniel (University of Grenoble, France). In addition, ten wolf samples from Asturias, Spain (SP) and three from Slovakia (SL) were analysed for comparison.

DNA isolation and amplification

Proteinase K digestion and phenol/chloroform standard protocols were used for genomic DNA isolation from tissues. Nuclear DNA was extracted from hair bulbs either according to Higuchi et al. (1988) or by Chelex isolation (Walsh et al. 1991). Samples were genotyped for five dinucleotide $(AC)_n$ polymorphic microsatellite loci and one tetranucleotide locus, previously characterized in dog (Ostrander et al. 1993; Francisco et al. 1996). Amplifications were carried out in 20 µl volume, containing 10 mM Tris-HCl, 50 mM KCl, 2 mM $MgCl_2$, 0.1% Triton X-100, 200 µM each dNTP, 0.5 units Taq DNA Polymerase (Promega), 5 pmol of each primer and 1–4 µl of DNA solution. An initial denaturation step at 94 °C for 3 min was followed by 35 cycles of amplification each of 45 sec at 92 °C, 45 sec at the annealing temperature (55–58 °C) and 60 sec at 72 °C. The reaction terminated with a polymerization step at 72 °C for 5 min.

In order to verify the successful products of single PCRs, 5 µl of reaction solution were run on a 2% agarose gel (Biorad) containing ethidium bromide, and the presence of correctly amplified fragments was detected by comparing their length with a DNA size marker.

Single alleles were sized by running denatured PCR products through capillary electrophoresis in an ABI PRISM 310 automatic sequencer (Perkin-Elmer).

Statistical analysis

By combining alleles at each locus, individual genotypes were obtained. The GENEPOP soft-

ware program version 3.2 a (Raymond and Rousset 1995) was used to calculate allele frequencies and to test data sets for deviation from Hardy-Weinberg equilibrium (HWE) as well as for genotypic linkage disequilibrium. Because many rare alleles were present, HWE departures were also tested "with pooling" (Hartl and Clark 1989), by grouping genotypes into three classes: homozygotes for the most common allele, common/rare allele heterozygotes, and all other genotypes.

Observed heterozygosity (H_o) and unbiased expected heterozygosity (H_e) (Nei 1978) were estimated for each subpopulation. Probability of genotype identity was obtained using the formula

$$\sum_i p_i^4 + \sum_i \sum_{j>i} (2p_i p_j)^2$$

where p_i and p_j are the frequencies of the *i*th and *j*th alleles at a given locus (Paetkau and Strobeck 1994). Single locus probabilities were combined to obtain the total probability over all 6 loci, assuming independence of different loci, as supported by the microsatellite linkage map in the domestic dog (Mellersh et al. 1997).

In order to evaluate the level of genetic variation, the H_e estimated for the overall Italian population ($N = 38$) over five of the six examined loci (109, 123, 204, 250, and 377) was compared with values recalculated for North American populations over the same loci using published data (Roy et al. 1994; Forbes and Boyd 1997).

Allelic and genotypic differentiations were evaluated for each population pair within the Italian range (AR, AB, VC, and FR), and then were pooled and compared with the two other European populations (SP and SL). Two different approaches were used to estimate the level of differentiation between samples by GENEPOP: a Fisher exact test was performed to test the homogeneity of allelic distributions across populations (Raymond and Rousset 1995), whereas a log-likelihood (G) based exact test was used for genotypic differentiation (Goudet et al. 1996). The significance level was always established using Bonferroni's criterion for multiple tests. In both cases, an unbiased estimate of the p-value was obtained, associated with the null hypothesis of identical distribution across populations.

A matrix was created containing the proportions of shared alleles (P_{AS}), over the six loci, for all pairwise comparisons of sampled individuals, as described in Bowcock et al. (1994). In order to obtain a measure of divergence among populations, P_{AS} values were averaged over population pairs and the pairwise distance value D_{AS} was calculated as

$$(1 - \overline{P}_{AS\,ij})$$

where the second term represents the mean P_{AS} calculated over all combinations between the *i*th and the *j*th subpopulation genotypes. Mean distance values were also computed among individuals of a single sample, in order to evaluate intra-group homogeneity. To eliminate the bias originating from different degrees of sample homogeneity, mostly due to different breadths of sampling areas, a new matrix was extrapolated, averaging the differences between inter- and intra-population distance values:

$$D'_{AS\,ij} = \frac{(D_{AS\,ij} - D_{AS\,ii}) + (D_{AS\,ij} - D_{AS\,jj})}{2}$$

Furthermore, Nei's unbiased genetic distance (Nei 1972) was computed by BIOSYS-2 software (Swofford and Selander 1997) between all subpopulation pairs.

Multilocus F-statistic was calculated by GENEPOP, estimating the F_{ST} coefficient for each pair of samples and for all Italian samples, according to Weir and Cockerham (1984). In order to evaluate gene flow among subpoputations, the same program allowed the effective number of migrants per generation (Nm) to be estimated on the basis of the private allele model (Slatkin 1985; Barton and Slatkin 1986). Thereafter a statistical analysis was carried out using the ISOLDE program, in the GENEPOP package, performing Mantel's tests (1 000 permutations) to highlight the possible presence of isolation by distance in the Italian population. For this purpose, D'_{AS}, Nei's unbiased distance, and F_{ST} were chosen as measures of genetic divergence and compared with geographic distance.

Results

A total of 51 wolves was genotyped at six microsatellite loci. All the loci showed polymorphism in the four Italian subpopulations investigated, except for locus 377 in the Alpine sample where allele A was fixed. Allele frequencies are given in table 1. Average H_e ranged from 0.505 ± 0.106 to 0.680 ± 0.038, while the probability of identity varied from 1/1 700 for the Alpine sample to less than 1/100 000 for the central-southern Apennines subpopulation (Tab. 2). In three out of four Italian samples, average H_e had a lower value than the observed one (Tab. 3), possibly due to limited outbreeding. Negative F_{is} values confirm this possibility (mean F_{is} over 6

Table 1. Allele frequency distributions at 6 microsatellite loci in wolf samples (AR – Tuscan Apennines; AB – Central-southern Apennines; VC – Alta Maremma: FR – Alpes Maritimes: SP – Spain; SL – Slovakia).

	AR	AB	VC	FR	SP	SL
Locus 109						
A	0.115	0.000	0.000	0.000	0.100	0.000
B	0.538	0.618	0.750	0.500	0.350	0.500
C	0.038	0.059	0.125	0.000	0.000	0.000
D	0.038	0.176	0.000	0.375	0.400	0.000
E	0.269	0.147	0.125	0.125	0.000	0.000
F	0.000	0.000	0.000	0.000	0.000	0.500
G	0.000	0.000	0.000	0.000	0.150	0.000
Locus 123						
A	0.240	0.353	0.000	0.000	0.000	0.000
B	0.000	0.059	0.125	0.125	0.000	0.000
C	0.160	0.206	0.375	0.000	0.278	0.667
D	0.080	0.000	0.000	0.250	0.056	0.000
E	0.000	0.029	0.000	0.250	0.389	0.333
F	0.520	0.324	0.500	0.375	0.167	0.000
G	0.000	0.000	0.000	0.000	0.111	0.000
H	0.000	0.029	0.000	0.000	0.000	0.000
Locus 204						
A	0.000	0.000	0.000	0.000	0.350	0.000
B	0.038	0.000	0.000	0.000	0.250	1.000
C	0.308	0.529	0.375	0.375	0.300	0.000
D	0.000	0.088	0.000	0.000	0.000	0.000
E	0.654	0.382	0.500	0.625	0.050	0.000
G	0.000	0.000	0.000	0.000	0.050	0.000
H	0.000	0.000	0.125	0.000	0.000	0.000
Locus 250						
A	0.077	0.206	0.000	0.286	0.500	0.667
B	0.115	0.147	0.375	0.286	0.150	0.000
C	0.000	0.029	0.000	0.000	0.000	0.000
D	0.692	0.324	0.500	0.429	0.150	0.000
E	0.000	0.000	0.000	0.000	0.000	0.333
F	0.077	0.294	0.125	0.000	0.150	0.000
G	0.000	0.000	0.000	0.000	0.050	0.000
H	0.038	0.000	0.000	0.000	0.000	0.000
Locus 377						
A	0.846	0.471	0.500	1.000	0.050	0.333
E	0.115	0.176	0.500	0.000	0.050	0.000
F	0.038	0.088	0.000	0.000	0.200	0.167
J	0.000	0.000	0.000	0.000	0.000	0.333
K	0.000	0.088	0.000	0.000	0.000	0.000
N	0.000	0.000	0.000	0.000	0.050	0.000
O	0.000	0.176	0.000	0.000	0.400	0.167
P	0.000	0.000	0.000	0.000	0.050	0.000
Q	0.000	0.000	0.000	0.000	0.200	0.000
Locus 2158						
A	0.000	0.059	0.000	0.000	0.000	0.000
B	0.000	0.000	0.000	0.000	0.000	0.167
C	0.042	0.059	0.000	0.000	0.000	0.000
D	0.458	0.324	0.000	0.500	0.000	0.667
E	0.000	0.000	0.000	0.000	0.444	0.000
F	0.000	0.088	0.250	0.000	0.111	0.000
G	0.083	0.265	0.375	0.375	0.000	0.000
H	0.083	0.000	0.000	0.000	0.000	0.167
I	0.333	0.147	0.375	0.000	0.000	0.000
J	0.000	0.059	0.000	0.000	0.000	0.000
L	0.000	0.000	0.000	0.125	0.444	0.000

Table 2. Expected heterozygosity (number of alleles in parentheses) and probability of identity in Italian wolf samples (AR – Tuscan Apennines; AB – Central-southern Apennines; VC – Alta Maremma; FR – Alpes Maritimes).

	Heterozygosity				Probability of Identity			
Locus	AR	AB	VC	FR	AR	AB	VC	FR
109	0.621 (5)	0.562 (4)	0.406 (3)	0.594 (3)	0.197	0.236	0.388	0.248
123	0.640 (4)	0.723 (6)	0.594 (3)	0.719 (4)	0.182	0.125	0.248	0.130
204	0.476 (3)	0.566 (3)	0.594 (3)	0.469 (2)	0.357	0.277	0.248	0.392
250	0.494 (5)	0.744 (5)	0.594 (3)	0.653 (3)	0.282	0.110	0.248	0.194
377	0.269 (3)	0.701 (5)	0.500 (2)	0.000 (1)	0.555	0.128	0.375	1.000
2 158	0.663 (5)	0.785 (7)	0.656 (3)	0.594 (3)	0.170	0.076	0.193	0.248
All Loci	0.527	0.680	0.557	0.505	3.4×10^{-4}	8.7×10^{-6}	4.3×10^{-4}	6.1×10^{-4}

Table 3. Genetic variation at 6 microsatellite loci and deviation from Hardy-Weinberg equilibrium. N, sample size; A, mean number of alleles per locus; H_o, observed heterozygosity (direct count); H_e, Hardy-Weinberg expected heterozygosity; HWE, significance of chi-square test for Hardy-Weinberg equilibrium without pooling; HWE_p, significance of chi-square test for Hardy-Weinberg equilibrium with pooling; SE, standard error; n. s., not significant.

Subpopulation/Population	N	A (SE)	H_o	H_e (SE)	HWE	HWE_p
AR – Tuscan Apennines	13	4.0 (0.4)	0.579	0.527 (0.061)	n. s.	n. s.
AB – Central-southern Apennines	17	5.0 (0.6)	0.676	0.680 (0.038)	n. s.	n. s.
VC – Alta Maremma	4	2.8 (0.2)	0.792	0.557 (0.036)	n. s.	n. s.
FR – Alpes Maritimes	4	2.7 (0.4)	0.652	0.505 (0.106)	n. s.	n. s.
Total (Italian population)	38	6.0 (0.7)	0.664	0.644 (0.040)	n. s.	n. s.
SP – Spain	10	4.8 (0.5)	0.683	0.693 (0.023)	n. s.	n. s.
SL – Slovakia	3	2.3 (0.4)	0.389	0.435 (0.097)	n. s.	n. s.

Table 4. Comparison of genetic variation at 5 microsatellite loci among different wolf populations and related canid species (N, sample size; A, mean number of alleles per locus ± standard error; H_e, Hardy-Weinberg expected heterozygosity ± standard error).
[a] recomputed from single locus frequencies data.

Species/Population	N	A	H_e	Reference
Canis lupus				
Italy	38	5.4 ± 0.4	0.619 ± 0.039	this study
Spain (Asturias)	10	5.2 ± 0.5	0.713 ± 0.013	this study
Canada (Northwest Territories)	24	6.0 ± 1.2	0.714 ± 0.063	ROY et al. (1994)[a]
Canada (Alberta)	20	5.2 ± 0.6	0.709 ± 0.027	ROY et al. (1994)[a]
USA (Montana)	66	5.0 ± 0.4	0.659 ± 0.055	FORBES and BOYD (1997)[a]
USA (Yellowstone National Park)	31	5.4 ± 0.7	0.686 ± 0.074	FORBES and BOYD (1997)[a]
Canis simensis	42	2.6 ± 0.7	0.167 ± 0.011	GOTTELLI et al. (1994)[a]
Canis lupus f. familiaris	40	6.8 ± 0.8	0.714 ± 0.075	GOTTELLI et al. (1994)[a]

loci for the overall Italian population equals –0.039), indicating breeding among non-relatives. Departures from the Hardy-Weinberg equilibrium for the different samples proved not significant at all loci. However, as shown in table 3, a recent colonized area (FR) and a strongly fluctuating population (VC) showed a marked excess of heterozygotes, although statistically not significant. Linkage disequilibrium for each pair of loci was confirmed by a probability test analysis in GENEPOP.

Referring to the restricted analysis (over 5 loci), mean H_e for the Italian sample was 0.619 ± 0.039, with a mean number of alleles per locus (A) of 5.4 ± 0.4. A comparison with other wolf populations and with two canid species (Ethiopian wolf, *Canis simensis*, and domestic dog, *Canis lupus* f. *familiaris*) is shown in table 4.

Levels of differentiation among subpopulations and populations were detected by comparing allelic and genotypic frequency distributions across loci. Significant levels of divergence within the Italian range were obtained only from the comparison between AR and AB samples (allelic data: Fisher exact test, $p = 0.00044$; genotypic data: G-test $p = 0.00042$). On the other hand, the whole Italian population showed both a genic and a genotypic statistically significant divergence from the Spanish and the Slovakian samples (allelic data: Fisher exact test, $p < 0.001$; genotypic data: G-test $p < 0.001$). Single-locus comparisons allow discrimination of subpopulations due to the presence of private alleles. Both AR and AB subpopulations showed exclusive alleles at different loci. All the alleles but one (allele H at locus 204) present in the VC sample belong to the AB subpopulation also. On the other hand, the FR sample has alleles present in both AR and AB populations, except for three alleles at locus 123, one exclusive to AR and two to AB, respectively, and for allele L at locus 2158, absent in other Italian samples. Mean D_{AS} (proportion of alleles not shared) within the Italian population was 0.466, whereas the mean values of derived D'_{AS} for subpopulation pairs ranged between 0.049 and 0.162 (Tab. 5).

Nei's unbiased distances were lower than 0.2 for all the comparisons among Italian samples (Tab. 6 a, below diagonal), and higher than 0.6 for all inter-population pairwise comparisons (Tab. 6 b, below diagonal). In the former case, the minimum values were obtained between AB and VC samples (0.051) and between AR and FR samples (0.054). On the basis of Nei's unbiased distance, a cophenetic tree may be plotted (Fig. 2).

F_{ST} values accounted for the proportion of total variation due to diversity between samples. Overall, F_{ST} for the whole Italian population was 0.053, a low value considering that a value of zero expresses the iden-

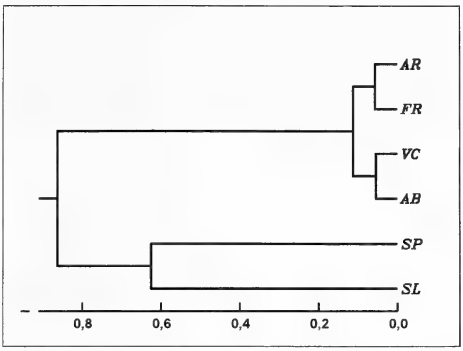

Fig. 2. Upgma phenogram of wolf populations based on Nei's unbiased genetic distances.

Table 5. Pairwise genetic distances by Shared Alleles (D'_{AS})

Subpopulation	AR	AB	VC
AR – Tuscan Apennines	*	*	*
AB – Central-southern Apennines	0.049	*	*
VC – Alta Maremma	0.070	0.061	*
FR – Alpes Maritimes	0.062	0.089	0.162

Table 6. Nei's unbiased genetic distance (below diagonal) and pairwise F_{ST}-values (above diagonal) among Italian subpopulations (a) and among European wolf populations (b).

a)

Subpopulation	AR	AB	VC	FR
AR – Tuscan Apennines		0.058	0.071	0.051
AB – Central-southern Apennines	0.094		0.022	0.042
VC – Alta Maremma	0.081	0.051		0.121
FR – Alpes Maritimes	0.054	0.093	0.162	

b)

Population	IT	SP	SL
IT – Italy		0.199	0.262
SP – Spain	0.764		0.181
SL – Slovakia		0.851	0.610

tity of allele frequencies among all subpopulations. F_{ST} values obtained for each subpopulation and population pair are shown in table 6 a and 6 b, respectively (above diagonal). The multilocus estimate of Nm for the overall Italian population gave a number of about 2.0 migrants per generation, which suggests a relevant amount of gene flow among subpopulations. When calculating Nm between the two most representative subpopulations, AR and AB, a value of 1.7 was obtained.

A positive correlation was found, using Mantel's test, only between D'_{AS} and geographical distance (Spearman rank correlation coefficient, $p = 0.038$), suggesting the presence of moderate isolation by distance. No significant correlation was found for Nei's distance and F_{ST}.

Discussion

Italian population samples showed a high intra-group diversity, as both H_e and P_{id} were relevant within each subpopulation. Although the standard error was sometimes considerable, due to the small sample size, the A was high for most loci even in small samples. Mean heterozygosity over 5 loci proved very close to the values obtained for North American populations (Roy et al. 1994; Forbes and Boyd 1997), and also the mean number of alleles per locus was completely comparable. This agrees with allozymic data, whose level of heterozygosity for the Italian population was found to be relatively high (Randi et al. 1993).

Comparing Italian wolf with a related species population, Ethiopian wolf (Gottelli et al. 1994), which went through prolonged isolation, a vast difference in heterozygosity calculated over the same loci is evident.

All samples fitted Hardy-Weinberg expectations, whether the χ^2-test was performed with or without pooling. Excess of heterozygotes in strongly fluctuating or recently colonized subpopulations, VC and FR, proved high but not significant. This may be due to random assembling of founder genotypes occupying new territories.

High Hardy-Weinberg expected heterozygosity, in comparison with the one observed in Italian samples, may arise from limited outbreeding, as confirmed by the negative F_{is} value. Breeding between unrelated individuals is a common trend in natural wolf populations (Smith et al. 1996), nevertheless high levels of induced mortality may enhance the natural turnover of pack members and favour outbreeding.

The most immediate indicator of genetic differentiation is allele frequency distribution. A significant level of divergence among Italian samples was found over all 6 loci only for the AB–AR pair, comparing both allelic and genotypic frequencies. As microsatellites are particularly sensitive to allele frequency differentiation, such differences may not be considered on their own a proof of genetic isolation.

Looking at allele frequency distribution, generally, the highest was the frequency across populations, and the widest was spatial diffusion. Several rare alleles were present, with occasional local specificity.

Examining the presence of single alleles, AR and AB samples showed a moderate level of diversity due to the presence of private alleles (5 for AR and 10 for AB). VC and FR samples appear compatible with a possible derivation from the other two subpopulations, but they also have exclusive alleles. The allele H at locus 204, present in the VC sample, was never found before in wolf individuals, whereas it proved the prevalent allele in dog samples (data not shown). A possible wolf dog hybridization event among the ancestors of the female individual presenting such an allele cannot be excluded. On the contrary, allele L at locus 2158 in the Alpine sample was found in other European wolves (e. g. in Spain) and might be present also at low frequency in the Italian population, but it was not detected in this work as a consequence of the limited sample size.

Both D_{AS} and Nei's unbiased distance values confirm the expected origin of the Alpine subpopulation from the northern Apennines. The allelic pattern of the VC sample, combined with measures of dis-

tance, is compatible with colonization from southern regions (AB). The area represents the most northern tail of the Tyrrhenian coast subpopulation, which is supposed to have maintained links up to the first half of the last century with the central-southern subpopulation and possibly have restored them in the last few decades. Data obtained in the present study seem to confirm this hypothesis. The overall F_{ST} value was small (0.053), suggesting very limited structuring of the Italian population.

Gene flow is relevant as, with more than 1 migrant per generation, differences among subpopulations are reduced, balancing the effect of genetic drift (Slatkin 1987). A value of 1.7, derived from the AR and AB subpopulations, is more reliable with respect to the estimate for the whole Italian population. This is because these subpopulations represent areas where the species was probably never eradicated, and they are close enough to maintain a sufficient level of gene flow. These aspects make the assumption of migration-drift equilibrium (Slatkin 1993) a plausible one.

Evidence for isolation by distance throughout the Italian population was found comparing D'_{AS} with geographic distances between different subpopulations. Historical factors and the geographic shape of the region played a key role in establishing a continuous and directional gene flow across the peninsula.

Summarizing, we have pointed out that the Italian wolf population constitutes a well-defined and viable natural population, where a high gene flow guarantees a sufficient genetic exchange among different areas. The origin of the nuclei settling in Alpes Maritimes should be attributed to movements of dispersing individuals from the northern Apennines, as suggested by the similarity between Alpine samples and specimens from the Tuscan Apennines. The Tyrrhenian subpopulation may have restored its continuity with the central Apennines, but human-caused mortality continuously threatens its stability, favouring high turnover and eventually outbreeding, at least in the peripheral zones of the wolf range.

Overall microsatellite diversity is substantial and comparable to that in North American populations. Inbreeding depression seems to be far from threatening Italian wolves. However demographic factors, difficult to predict, may affect population viability more than genetic aspects, producing dramatic changes especially in local situations. Therefore it would be advisable to maintain the genetic flow high across the peninsula, in order to balance the effect of local bottlenecks.

A long-term differentiation between Alpine and southern subpopulations may be expected as consequence of isolation by distance, while a progressive enlargement of the northern range along the Alps will progressively bring the Italian wolf closer to the Balkan populations.

The set of six polymorphic microsatellite loci used in this work represented an effective tool for investigating the actual genetic status of wild wolf populations. The low probability of identity between individuals (in the order of 10^{-4} to 10^{-6}) reveals a high resolution power in resolving pedigrees, i. e., for kinship analysis.

Acknowledgements

We would like to thank the Provincial Administration of Arezzo for institutional and financial support in setting up the laboratory and bearing the costs of analysis, and for having provided wolf samples. Additional support for M. S. was provided by a "G. Guelfi" grant from the Accademia Nazionale dei Lincei. We are also grateful to the staff of the Comunità Montana Val di Cecina and the staff of the Veterinary Service U. S. L. 5 in Volterra (Pisa), and to F. Baldassarri of the C. T. A. of the Foreste Casentinesi National Park. We also thank S. Cappelli and D. Del Chiaro for help in genetic analysis, P. Varuzza and E. Avanzinelli for technical assistance, G. B. Hartl, V. Nathaniel, M. Nores-Quesada, and P. Helle for having supplied samples, U. Baisch and J. Burge for linguistic support.

Zusammenfassung

Neues Anwachsen der italienischen Wolfspopulation: eine genetische Untersuchung mittels Mikrosatelliten.

Um die genetische Differenzierung innerhalb der anwachsenden italienischen Wolfspopulation (*Canis lupus*) zu untersuchen, wurden 38 Individuen von 4 verschiedenen Stellen des derzeitigen Verbreitungsgebietes mittels Mikrosatelliten analysiert. Die 6 betrachteten Mikrosatellitenloci zeigten einen hohen Grad an Polymorphismus und die kombinierte Identitätswahrscheinlichkeit reichte von 10^{-4} bis 10^{-6}. Insgesamt war die gefundene DNA-Variation beträchtlich und kaum niedriger als jene beim nordamerikanischen Grauwolf. Die beiden ältesten italienischen Teilpopulationen, jene in der Toskana und jene im zentralen bis südlichen Apennin, zeigten nur eine mäßige Divergenz. Die gefundenen Werte stimmten mit einer Abstammung der ersteren von der Westalpen-Subpopulation überein, während die letztere Ähnlichkeit zur Subpopulation der Westküste zeigte. Der Genfluß innerhalb des italienischen Wolfsbestandes war hoch. Die geographische Verteilung der Probengebiete stimmte mit den genetischen Abständen überein, was auf das Vorliegen von ‚Isolation durch Distanz' hindeutet. Hohe Divergenzniveaus wurden zwischen den italienischen Proben und jenen aus anderen europäischen Gebieten gefunden. Insgesamt deuten die Ergebnisse darauf hin, daß, trotz der Einförmigkeit im Bereich der mtDNA, der italienische Wolf noch immer einen hohen Grad an Kern-DNA-Variabilität und eine ausgeprägte genetische Identität besitzt. Eine weitere Vergrößerung des Wolfsareals, wie sie aufgrund der hohen Dispersionsrate zu erwarten ist, könnte in einigen Jahrzehnten dazu führen, daß die historische Isolation von einem genetischen Austausch mit dem osteuropäischen Genpool abgelöst wird.

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Mamm. biol. **66** (2001) 332–344
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

The phylogenetic position of southern relictual species of *Microtus* (Muridae: Rodentia) in North America

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Receipt of Ms. 14. 02. 2001
Acceptance of Ms. 03. 05. 2001

Abstract

Climatic fluctuation led to isolation of some populations of temperate species on southern mountaintops during warming trends. The most southern species of arvicoline rodents (*Microtus guatemalensis, M. oaxacensis, M. quasiater,* and *M. umbrosus*) in North America may be relicts, isolated in the mountains of Mexico and Guatemala at the end of the Pleistocene. We used parsimony and likelihood analyses of complete mitochondrial cytochrome b gene sequences of 28 species of *Microtus*, including eight Eurasian species, holarctic *M. oeconomus*, and all extant North American species except the island endemic *M. breweri*. North American species of *Microtus* were monophyletic under the maximum-likelihood criterion, but polyphyletic under parsimony. Likelihood ratio tests and bootstrapping indicated a rapid basal radiation with short intervals between cladogenic events. However, several sister taxon relationships were robust to bootstrapping or consistent between methods. We found that *M. quasiater* was sister to *M. pinetorum*, and these taxa were sister to a clade of *M. oaxacensis* and *M. guatemalensis*. The phylogenetic position of *M. umbrosus*, however, was unclear. Monophyly of the relicts was rejected by a likelihood ratio test, suggesting multiple southern invasions by arvicoline rodents. Phylogenetic data for these and other co-distributed taxa should be used in conservation efforts for these remote areas.

Key words: *Microtus*, Arvicolinae, historical biogeography, conservation, molecular systematics, Mexico

Introduction

Climatic fluctuations have been linked to the spatial expansion and contraction of species (Graham and Grimm 1990; Graham et al. 1996). Isolation during contraction phases may have stimulated allopatric diversification, particularly at the southern edge of ranges. For example, the mountains of Mexico and Guatemala host a highly endemic flora and fauna (Ramamoorthy et al. 1993) that includes a diverse set of organisms associated with mesic environments. These organisms apparently invaded the region during cooler periods and then became isolated at higher elevations as conditions at lower elevations became drier and warmer. This invasion and isolation

1616-5047/01/66/06-332 $ 15.00/0.

cycle may have occurred numerous times during the Pleistocene and has contributed to the complex biogeographic history of the region (Sullivan et al. 1997).

The genus *Microtus* is holarctic and north temperate in distribution and in the New World reaches its southern limit in Central America. At higher latitudes, up to five species (e. g. *M. longicaudus, M. miurus, M. oeconomus, M. pennsylvanicus*, and *M. xanthognathus* in Yukon Territory) may be found in close proximity. However, species tend to be more allopatrically distributed at southern latitudes. For example, *M. guatemalensis, M. oaxacensis, M. quasiater*, and *M. umbrosus* are endemic to separate mountains in the cloud and pine forests of Mexico and Guatemala (Fig. 1). *M. quasiater*, the Jalapan vole, is found in the southern Sierra Madre Oriental in Central Mexico. *M. oaxacensis*, the Tarabundi vole, is isolated in the Sierra de Juarez of Oaxaca, and occurs at elevations of 1,600 (Sanchez et al. 1996) to 2,499 m (Jones and Genoways 1967). *M. umbrosus*, the Zempoaltepec vole, is restricted to approximately 80 km^2 at elevations ranging from 1,829 to 3,000 m (Frey and Cervantes 1997) around Mt. Zempoaltepec in Oaxaca. *M. guatemalensis*, the most southern species, occurs from the mountains of central Chiapas south to central Guatemala. These species may be the result of peripheral isolation of ancestors that were more widely distributed during cool periods of the early to middle Pleistocene (Hoffmann and Koeppl 1985).

In contrast to these four disjunct species, *M. mexicanus* is widespread in Mexico and occurs in limited sympatry or parapatry with *M. oaxacensis, M. quasiater*, and *M. umbrosus* with a discontinuous distribution extending from New Mexico and Arizona to southern Mexico (Hall 1981). Its fossil record is limited to the late Wisconsinan from San Josecito in northeastern Mexico and localities farther north (Zakrzewski 1985). Phylogenetic relationships between *M. mexicanus* and other species of *Microtus* are unclear, but there is little indication that this species shares a common ancestor with other Mesoamerican species. Thus, its presence in Mexico probably reflects an independent colonization.

The aim of our study therefore is to investigate the phylogenetic relationships of the southern species of *Microtus* in order to test hypotheses regarding their ancestry in North America and their taxonomic relationships to other species.

Material and methods

DNA was extracted from ethanol-preserved tissues of these four southern *Microtus* (Tab. 1) with methods described in Conroy and Cook (1999). The cytochrome b gene (hereafter cyt b) was amplified in two or three sections and sequenced in

Table 1. Specimens of Meso-American species of *Microtus* examined in this study (in addition to those reported in Conroy and Cook [2000]) including location from which each specimen was collected, and CNMA (Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México) catalog number.

Species	Collection location	CNMA Catalog Number
M. umbrosus	Mexico: Oaxaca Cerro Zempoaltepetl, 5 km N Sta Ma. Yacochi. Mpio. Tlahuitoltepec, 2450 m.	34890, 34894
M. guatemalensis	Mexico: Chiapas: Cerro Tzontehuitz, 13 km NE San Cristobal de las Casas, Mpio. Chamula, 2880 m.	35262
	Mexico: Oaxaca: 11 km SW La Esperanza, Mpio. Santiago	
M. oaxacensis	Comaltepec, 2000 m.; Oaxaca: 11 km SE La Esperanza, Mpio. Santiago Comaltepec, 2000 m.	27415, 33815
M. quasiater	Mexico: Veracruz: 5 km W Naolinco, Mpio. Naolinco, 1650 m.	35282, 35274

both directions (Perkin-Elmer Prism® dye terminator kit; Fst-RR, 402119) on an ABI 373a automated sequencer. We included cyt b sequences from 24 species of *Microtus* and two species of *Clethrionomys* (Conroy and Cook 2000). In the phylogenetic analysis we represented each species

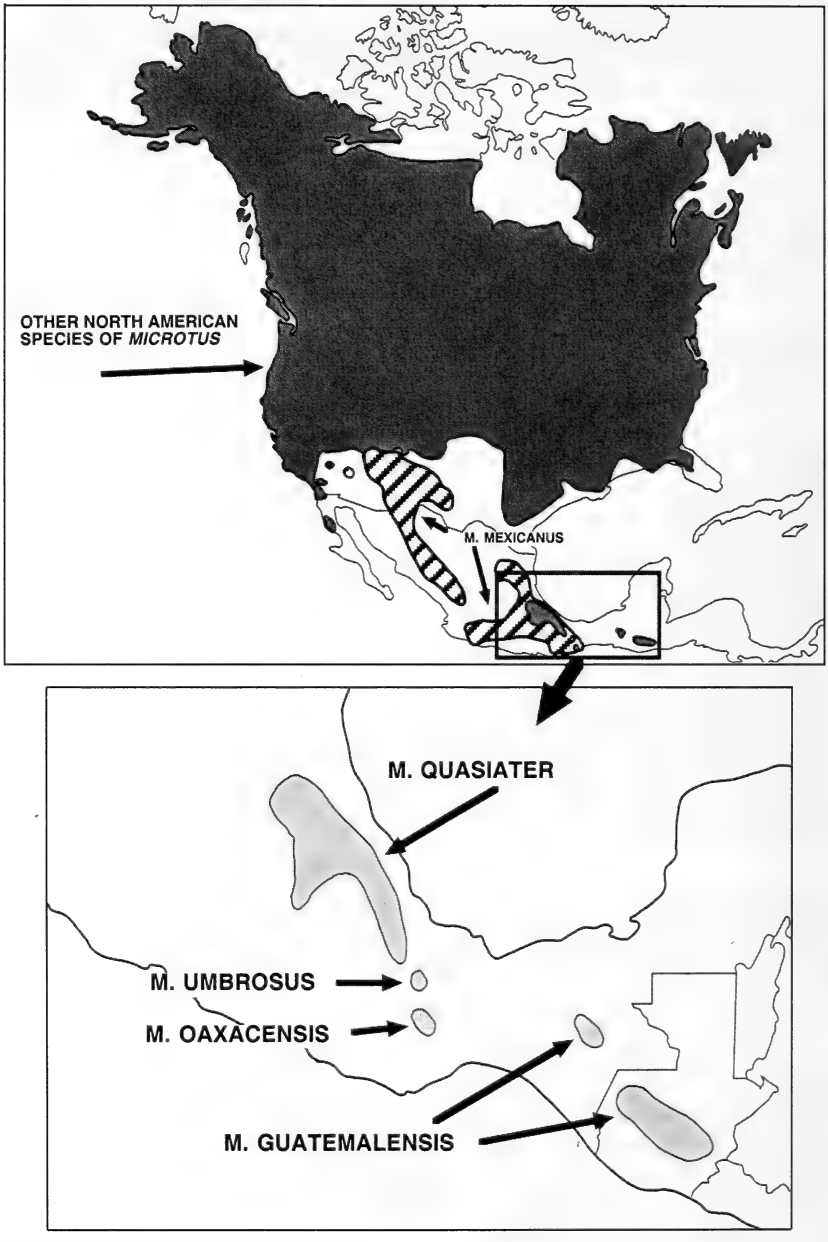

Fig. 1. Map of the distribution of species of *Microtus* in North America and south into Guatemala (redrawn from Hoffmann and Koeppl 1985).

with a single individual, but we examined intraspecific variation where possible by including multiple representatives for 24 of the 28 species. We used unweighted parsimony (MP) and maximum likelihood (ML) with the software PAUP*, version 4.0d64 (Swofford 1998). We estimated parameters for likelihood models of increasing complexity (JC: Jukes and Cantor 1969; HKY85: Hasegawa et al. 1985; and GTR: Yang 1994a; HKY85 + Γ, and GTR + Γ: Yang 1994b). We tested these with likelihood ratio tests to determine significant differences among their likelihood scores. We used 1,000 random addition sequences to locate multiple tree islands in the heuristic MP searches. As tests of node strength, we bootstrapped the parsimony analysis 1,000 times and bootstrapped the final ML analysis 100 times. We tested several alternative phylogenetic topologies against the ML tree by forcing likelihood searches to find the ML topology with particular constraints and then comparing scores (Kishino and Hasegawa 1989). We tested monophyly of the four relictual Mesoamerican species, and the four shortest maximum parsimony trees. Besides examining relationships among these southern latitude taxa, several tests were conducted to ascertain the effects of adding these four species to more general hypotheses concerning the systematics of *Microtus* previously conducted (Conroy and Cook 2000). We tested the monophyly of subgenus *Stenocranius* (Rausch 1964). This subgenus includes the Asiatic species *M. gregalis* and the North American *M. miurus* and *M. abbreviatus*. It has been hypothesized that the species in this subgenus diverged relatively recently. Secondly, we tested the monophyly of a clade of taiga adapted voles (*M. richardsoni, M. xanthognathus, M. chrotorrhinus*) that was not supported in our previous study (Conroy and Cook 2000). And, third, we tested the monophyly of all North American taiga voles (Hoffmann and Koeppl 1985), because previously we were able to reject this hypothesis with the Kishino-Hasegawa test. By including these tests, our investigation explores whether the addition of four southern taxa changes our interpretation of arvicoline history in North America. Prior to this study, the relationships of southern species to other North American species was unclear.

Results

Base composition and distribution of variable sites of the cyt b gene was similar to other *Microtus* (Conroy and Cook 2000) as well as other mammals (Irwin et al. 1991). Of the 1143 base pairs, 472 were variable across 28 species of *Microtus* and two species of *Clethrionomys*. When outgroups were excluded, 460 sites were variable. Of these, 100 were in the first position, 23 in the second position, and 337 in the third position of codons. Of the 381 amino acids, 76 (20%) were variable across species of *Microtus* and the replacement pattern was consistent with structural models (e.g. Irwin et al. 1991). There were 351 parsimony informative nucleotide sites and g_1 statistics ($g_1 = -0.325$) indicated phylogenetic signal in the data.

Maximum parsimony searches recovered four equally parsimonious trees (Fig. 2), each including a basal clade of the North American *M. ochrogaster* and Asian *M. gregalis*. A clade of *M. oeconomus, M. middendorffi, M. montebelli, M. kikuchii*, and *M. fortis* (hereafter the "Asian clade"), and the *M. pennsylvanicus* clade (i.e. *M. pennsylvanicus, M. montanus, M. townsendii*, and *M. canicaudus*) were present in the four trees. *M. pinetorum* and *M. quasiater* were sister in all trees, had high bootstrap support in MP and ML analyses (99%) and relatively high decay values (12). *M. oaxacensis* and *M. guatemalensis* were sister taxa in three of four MP trees, but the branch leading to this pair had weak bootstrap support (< 50%). Other clades were found in three or four of these shortest trees, but bootstrap support was generally low across basal relationships. *M. umbrosus* stemmed from the polytomy at the base of the European and North American species. Random addition of taxa uncovered these four shortest trees, but simple addition (i.e. alphabetical by species name) led to an island of longer length trees.

In the ML analysis, the HKY85 + Γ likelihood model (transition/transversion ratio = 3.43, $\alpha = 0.213$) was chosen since more complex models (e.g. GTR + Γ) were not significantly more likely and produced the same topology (not shown). As in other studies of cytochrome b (e.g. Sullivan et al. 1997), the addition of the gamma-distributed rate parameter, allowing among-site rate variation, contributed significantly to

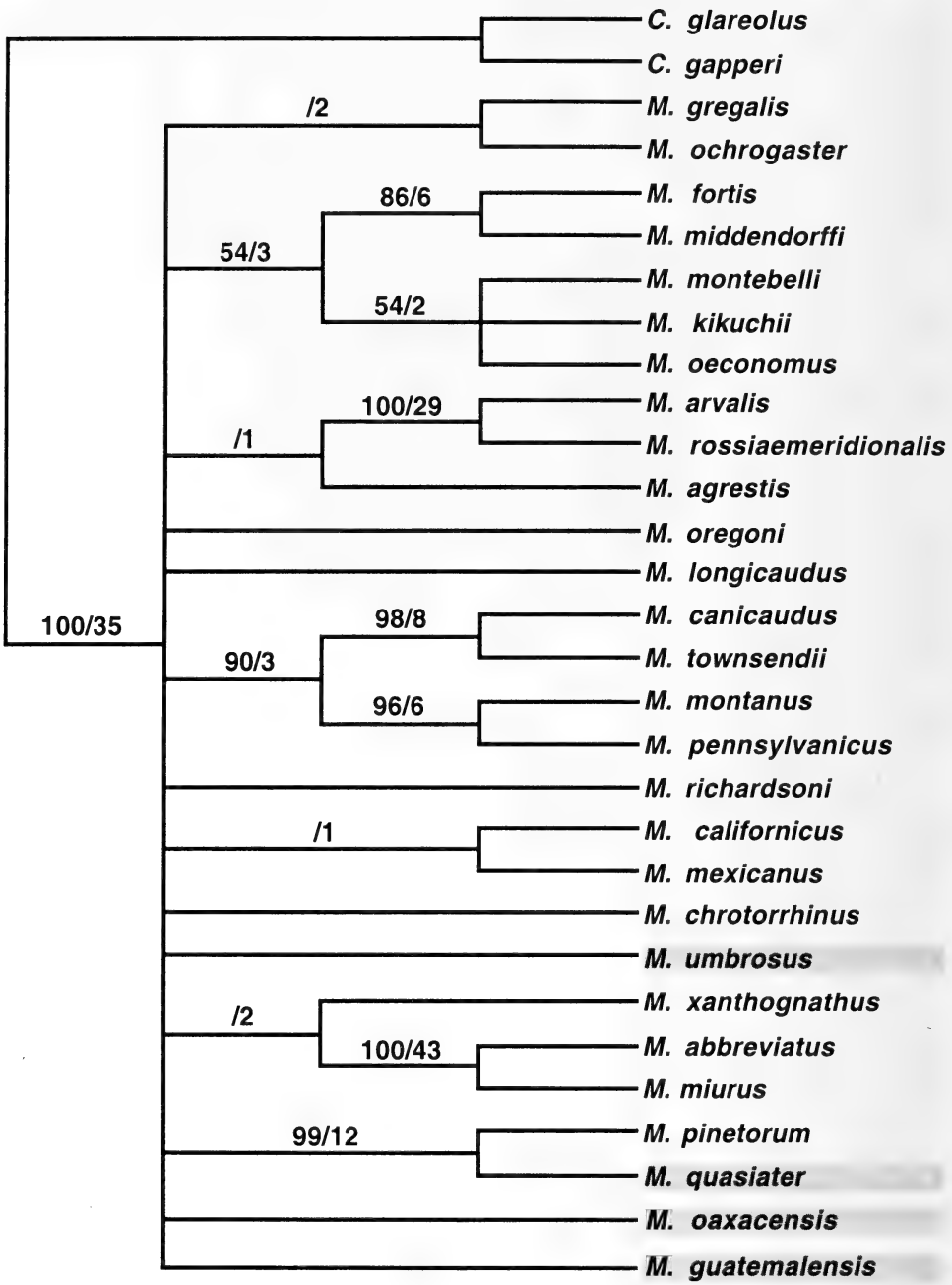

Fig. 2. Strict consensus of four trees from the MP search. Each tree had a length of 2038, a consistency index of 0.331, and retention index of 0.360. Values to the left of slash are bootstraps percentages greater than 50% from 1,000 searches with simple addition of taxa; values to the right of slash indicate decay indices calculated with 10 random-addition replicates for each search.

the likelihood. This model produded one tree (Fig. 3) in which *M. gregalis* was basal, followed by the Asian clade. North American endemic species formed a clade and the European species formed a sister clade to North American species. The Mesoamerican endemics were not basal within the clade of North American species. Three Mesoamerican species (*Microtus guatemalensis, M. oaxacensis*, and *M. quasiater*) displayed the same branching pattern as three of the parsimony trees, while *M. umbrosus* was sister to *M. chrotorrhinus*. Other relationships were similar to previous analyses (Conroy and Cook 2000). For example, the *M. pennsylvanicus* and Asian clades were

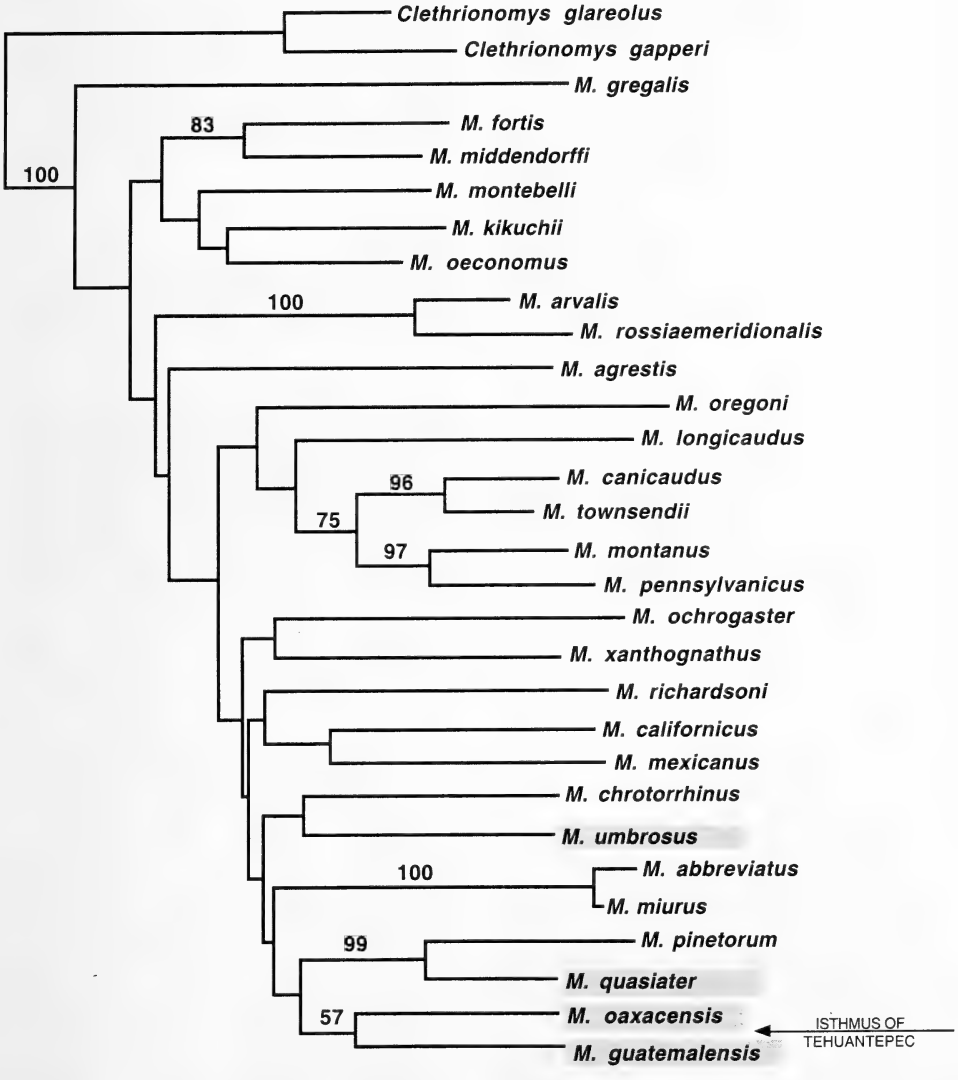

Fig. 3. Maximum likelihood phylogenetic tree based on the HKY85 + Γ model (see text for parameter values). Values above branches are bootstrap percentages greater than 50% from 100 bootstraps.

supported and *M. mexicanus* was sister to *M. californicus*. In Kishino-Hasegawa tests (Tab. 2), few of the alternate topologies could be rejected. Those that were rejected were one of the MP trees and two ML trees constrained to monophyly of the four southern species.

Relative depth of divergence was estimated with pairwise likelihood distances between taxa estimated under the same model used for the ML phylogeny. *M. abbreviatus* and *M. miurus*, which differ by only 0.015, probably separated at the end of the Pleistocene when rising sea levels isolated *M. abbreviatus* on islands in the Bering Strait. Another late Pleistocene divergence may be *M. canicaudus* and *M. townsendii* which differ by 0.058. Other pairs that were relatively closely related included *M. arvalis* and *M. rossiaemeridionalis* (0.072) and *M. montanus* and *M. pennsylvanicus* (0.086). Divergence values between the southern species (*M. quasiater* and *M. pinetorum* [0.094], *M. guatemalensis* and *M. oaxacensis* [0.113], and *M. chrotorrhinus* and *M. umbrosus* [0.137]) are greater than any of the preceding examples, suggesting older speciation events. These comparisons should be interpreted with caution. Demographic and historical differences among species can alter rates of evolution and species of *Microtus* probably have evolved at different rates. Also, genetic differentiation may not necessarily coincide with vicariant events, such as the rise of the Bering Sea. Finally, molecular estimates of divergence, particularly for a single locus, have substantial amounts of stochastic variation (Ayala 1999).

Discussion

Previous investigations into the history of North American species of *Microtus* sug-

Table 2. Kishino-Hasegawa tests of tree topologies. The "*Stenocranius*" constraint forced *M. miurus*, *M. gregalis*, and *M. abbreviatus* to be monophylyetic. The "Second taiga vole" constraint enforced *M. xanthognathus*, *M. chrotonrhinus*, and *M. richardsoni* monophyly. The "All taiga voles" constraint enforced the monophyly of the "Second taiga vole" species with a clade of *M. pennsylvanicus*, *M. montanus*, *M. townsendii*, and *M. canicaudus*. The "Meso-Americans" constraint enforced *M. guatemalensis*, *M. oaxacensis*, *M. quasiater*, and *M. umbrosus* monophyly. Two trees were obtained from the ML search under this last constraint. The parsimony trees were derived from unweighted heuristic searches with ten random-addition replicates. Columns below indicate, from left to right, 1) -log likelihood score of that tree, 2) difference in score between that tree and the best tree, 3) the standard deviation of that comparison, 4) the associated T test statistic, and 4) the associated p value.

Tree	Constraint	-log likelihood	Diff-lnL	s. d. (diff)	T	P*
1	None	9868.811	(best)			
2	Stenocranius Monophyletic	9891.258	22.447	16.723	1.342	0.180
3	Second taiga vole clade	9879.176	10.365	9.080	1.142	0.254
4	All Taiga voles Monophyletic	9897.044	28.233	18.904	1.494	0.136
5	Meso-Americans monophyletic I	9910.346	41.535	11.613	3.577	0.0004*
6	Meso-Americans monophyletic II	9910.346	41.535	11.613	3.577	0.0004*
7	Parsimony Tree 1	9908.109	39.298	22.586	1.740	0.082
8	ParsimonyTree 2	9908.743	39.932	20.492	1.949	0.052
9	ParsimonyTree 3	9908.493	39.682	20.581	1.928	0.054
10	ParsimonyTree 4	9919.839	51.027	20.528	2.486	0.013*

*Significant at $P < 0.05$

gested an evolutionary history closely tied to fluctuating boreal ecosystems (Hoffmann and Koeppl 1985). The elevational distribution of species of *Microtus* in Mexico and Guatemala indicates Holocene isolation due to the contraction of cool, moist forests. The paucity of synapomorphic morphologic characters, but apparent abundance of autapomorphic characters has led to their characterization as ancient, highly divergent species; however, their biogeographic history has been enigmatic. This study reconsiders the biogeographic and evolutionary history of the southern relicts in light of molecular characters examined within a wider taxonomic sampling (28 species) for the genus.

Biogeography

The Mesoamerican species of *Microtus* were not basal in the North American clade, nor were they monophyletic. *M. quasiater* is closely related to *M. pinetorum*, and *M. oaxacensis* and *M. guatemalensis* are sister to this pair, while the fourth (*M. umbrosus*) is a weakly-supported sister taxon to *M. chrotorrhinus*. Our data do not support the hypothesis of Hoffmann and Koeppl (1985) that these southern species of *Microtus* may be relicts of an early colonization of North America prior to the arrival of the ancestors of the other species that are endemic to the higher latitudes of North America. Interspecific distances do, however, suggest they began to diverge earlier than suspected late-Pleistocene peripheral isolates such as *M. abbreviatus* and *M. miurus*. Assuming an equivalent rate of cyt b evolution across species of *Microtus* and *Clethrionomys*, Mesoamerican *Microtus* apparently fragmented into isolated populations prior to the colonization of North America by *Clethrionomys*, which is thought to have occurred during the early Pleistocene (Repenning et al. 1990). The split between North American *Clethrionomys gapperi* and Eurasian *C. glareolus* (Tamura-Nei D = 0.079) occurred about the time their common ancestor invaded North America. However, disparate levels of ancestral polymorphism and histories of population fluctuation in these independent colonizers, among other variables, would impact estimates of ages of differentiation. Two topologies that constrained ML searches for monophyly of these southern species were significantly less likely than the best ML topology, refuting common ancestry of Mesoamerican species of *Microtus*.

Sullivan et al. (1997) and Sullivan et al. (2000) found that the Isthmus of Tehuantepec was a significant geographic barrier for other mesic rodents such as *Reithrodontomys* and the *Peromyscus aztecus* group in Mexico and Guatemala. They summarized divergence patterns in other co-distributed organisms (see Ramamoorthy et al. 1993) and recommended that the significance of the isthmus as a biogeographic barrier be tested with other mesic taxa. *M. guatemalensis* occurs east of the isthmus and is sister to *M. oaxacensis*, found west of the isthmus, suggesting that their common ancestor may have been distributed across the isthmus when conditions were cooler. Western and eastern populations subsequently diverged. *Microtus, Reithrodontomys*, and *Peromyscus* are widely sympatric in this region, and levels of genetic differentiation across the isthmus are surprisingly similar with D = 0.075–0.091 in *Peromyscus* (Sullivan et al. 1997), D = 0.063–0.085 in *Reithrodontomys* (Sullivan et al. 2000), and D = 0.100 between *M. guatemalensis* and *M. oaxacensis*. If we assume similar rates of molecular evolution, these three clades may have diverged across the Isthmus of Tehuantepec at roughly the same time. High levels of biotic diversity in the region provide ample material to further test hypotheses regarding the timing and number of mammalian colonizations of the region. The biogeography of other organisms, such as reptiles (e. g. Campbell 1984; Campbell et al. 1989), may also suggest former connections across the Isthmus of Tehuantepec.

Systematics

Microtus quasiater is a member of the subgenus *Pitymys* (Musser and Carleton

1993) and shares dental morphology with extinct *Microtus* (*Pitymys*) *meadensis*, a widespread species of mid-Pleistocene North America and Mexico (Repenning 1983). *M. pinetorum* has often been classified as a member of *Pitymys* based on shared dental morphology (Zakrzewski 1985). Thus, it is not surprising that morphological characters (Musser and Carleton 1993) and these DNA sequences place *M. quasiater* sister to *M. pinetorum*. *M. quasiater* previously was considered sister to *M. ochrogaster* (Moore and Janecek 1990) in an allozyme study, but only nine of 19 North American species and no Palearctic species were examined.

The evolutionary relationships of *M. guatemalensis* and *M. oaxacensis* have not been addressed in detail, although they have not been suspected to be closely related (Musser and Carleton 1993). *Microtus guatemalensis* is in the monotypic subgenus *Herpetomys*, but may have affinities with *Pitymys* (Martin 1987). Our analyses contradict its placement in *Herpetomys*, or suggestions that it is related to *Phenacomys* (Hinton 1926). The relationship between *M. oaxacensis* and other species has also been obscure (Musser and Carleton 1993), but it also was considered a part of an early pitymyine invasion (Hoffmann and Koeppl 1985; Martin 1974). A widespread ancestor (e.g. *M. meadensis*) may have given rise to *M. pinetorum*, *M. guatemalensis*, *M. quasiater*, and *M. oaxacensis*, prior to peripheral isolation in the eastern deciduous forests and southern cloud forests (Hoffmann and Koeppl 1985). The mitochondrial phylogeny suggests isolation occurred first between an ancestor of *M. pinetorurn–M. quasiater* and an ancestor of *M. guatemalensis–M. oaxacensis* although the branching order among these clades is weakly supported. The latter pair may have diverged after invasion across the Isthmus of Tehuantepec, while the former pair diverged following an episode of range retraction induced by climatic warming. Significant portions of the temperate flora on mountain tops in Mesoamerica are as old as the late Cenozoic (Graham 1999), however, we do not know of a comparable phylogenetic assessment of vegetation.

A sister relationship between *M. umbrosus* and *M. chrotorrhinus* was weakly supported in the ML tree and was unexpected because they differ morphologically. *Microtus umbrosus* is the sole member of the subgenus *Orthriomys* (Musser and Carleton 1993) and has been considered a relict from an early invasion from Asia during the mid-Pleistocene by the extinct *Phaiomys* (Martin 1987). Though previously considered closely related to *M. xanthognathus* (Hall and Kelson 1959), *M. chrotorrhinus* was later distinguished based on chromosomal complement (Rausch and Rausch 1974). The lack of similarity between *M. chrotorrhinus* and *M. umbrosus* and the "pitymyine" species suggests an independent invasion of the southern latitudes by a common ancestor of *M. umbrosus* and *M. chrotorrhinus*.

North American monophyly and other phylogenetic hypotheses

Our assessment of *Microtus* includes 28 of approximately 65 species of *Microtus* (Musser and Carleton 1993), with the addition of Mesoamerican taxa potentially contributing to more accurate estimations of relationships (Hillis 1996). This larger study did not significantly alter the ML topology previously obtained based on 24 species of *Microtus* (Conroy and Cook 2000). Monophyly of all North American species included in this study and of the *M. pennsylvanicus* clades was supported. The expanded analysis suggested two differences based on Kishino-Hasegawa tests. Without Mesoamerican species, we rejected the topology ($p = 0.026$; Conroy and Cook 2000) which constrained all North American taiga voles as monophyletic (sensu Hoffmann and Koeppl 1985). However, with the inclusion of Mesoamerican species, this hypothesis was not rejected ($p = 0.136$). The expanded analysis also rejected a topology placing *M. chrotorrhinus* basal to all species of *Microtus* sampled and *M. gre-*

galis (Russia) within a clade of North American species ($p = 0.013$).

Morphological material for interspecific comparison is abundant, but the phylogenetic utility of some morphological characters for arvicolines (e. g. tooth pattern) has been criticized due to high variation within and between species (Guthrie 1965; Zakrzewski 1985). Despite the availability of standard karyotypes for many species of *Microtus*, non-differentially stained chromosomes have minimal phylogenetic information because the rate of chromosomal evolution varies greatly among species (Cervantes et al. 1997; Modi 1987). Indeed, our phylogeny suggests a complicated series of events are needed to explain chromosomal rearrangements in *Microtus*. Species with low diploid numbers are not sister to each other. For example, the mitochondrial data indicate *M. oaxacensis* ($2N = 30$) is sister to *M. guatemalensis* ($2N = 52$), and *M. canicaudus* ($2N = 24$) is sister to *M. townsendii* ($2N = 50$). These relationships support *Cervantes* et al.'s (1997) contention that the interpretation of chromosomal evolution based only on standard karyotypes will be difficult.

Conservation

Mexico has one of the richest mammalian faunas due partially to an overlap of neotropical and nearctic biomes (Fa and Morales 1993). Conservation efforts are complicated by this high diversity and a variety of threats (Ceballos and Navarro 1991). Species of *Microtus* in the region are nearctic relicts that are dependent on high elevation, mesic habitats. Protection of habitat in the mountains of Oaxaca, a region of high mammalian diversity (Arita et al. 1997), could help conserve three endemics, *M. oaxacensis*, *M. umbrosus*, and *M. quasiater*. Whether conservation criteria focus on rarity, diversity, or degree of endemism, these southern relicts warrant conservation concern.

Molecular systematic studies of other endemic taxa should be considered in planning conservation efforts in this region (Baker et al. 1995; Cook et al. 2001). Our analysis suggests that temporal scale may be a crucial component to interpreting the significance of biogeographic barriers. Detection of patterns at different temporal scales could help resolve shared histories of taxa in the region (Avise 1994) and be used to conserve historical associations of flora and fauna.

Species of *Microtus* in Mexico and Guatemala are not monophyletic but instead are the result of at least three colonizations of this region during the Pleistocene: one by the ancestors of *M. oaxacensis*, *M. quasiater*, and *M. guatemalensis*, a second by the ancestor of *M. umbrosus*, and a third colonization apparently gave rise to *M. mexicanus*. A lack of fossils inhibits the dating of cladogenic events among these species; however, depth of divergence relative to other splits within *Microtus* suggest mid-Pleistocene divergence. Morphological similarity between extant species (e.g. *M. pinetorum* and *M. quasiater*) and formerly widespread (mid to late Pleistocene) taxa that are now extinct (e.g. *M. meadensis*) suggest isolation by range retraction is a viable hypothesis. Morphological studies also support the shared history of several of the pitymyine species. The weakly-supported sister relationship between *M. umbrosus* and *M. chrotorrhinus* has not been predicted previously and should be tested further. Phylogenetic analysis of other Mesoamerican organisms may help identify regions of shared evolutionary history and the role of significant biogeographic barriers in promoting diversification in this biologically rich region.

Acknowledgements

This work was supported by grants from the UAF graduate school, Hayward Fund (UA Museum), National Science Foundation, U.S. Fish and Wildlife Service, and the Consejo Nacional de Ciencia y Tecnologia, Mexico, to CJC, JAC, and FAC. E. Hadly, J. Sullivan, B. Riddle, K. Winker and several anonymous reviewers provided critical comments. M. van Tuinen and S. Pyott prepared the German summary.

Zusammenfassung

Die phylogenetische Stellung südlicher Reliktarten von *Microtus* (Muridae Rodentia) in Nordamerika.

Klimatische Fluktuationen führten in Zeiten der Erwärmung zur Isolation einiger Populationen von Arten aus gemäßigten Zonen auf südlichen Bergen. Die südlichsten Arten arvicoliner Nager (*Microtus guatemalensis, M. oaxacensis, M. quasiater* und *M. umbrosus*) in Nordamerika mögen Relikte darstellen, die am Ende des Pleistozäns in den Bergen von Mexico und Guatemala isoliert wurden. Wir untersuchten mittels Parsimony- und Likelihood-Analysen die kompletten mitochondrialen Cytochrom b-Gen-Sequenzen von 28 Arten der Gattung *Microtus*. Darunter befanden sich acht eurasische Arten, holarktische *M. oeconomus* und alle heute lebenden Arten Nordamerikas außer der inselendemischen *M. breweri*. Die nordamerikanischen Arten waren in der Maximum-Likelihood-Analyse monophyletisch, in der Maximum-Parsimony-Analyse jedoch polyphyletisch. Likelihood-Ratio-Tests und Bootstrap-Analysen wiesen auf eine rasche adaptive Radiation mit kurzen Intervallen zwischen Kladogenese-Ereignissen hin. Die Analysen von Schwestertaxa zeigten jedoch Konstanz in Bootstrap-Analysen oder unterschiedlichen phylogenetischen Auswertemethoden. Nach unseren Ergebnissen war *M. quasiater* die Schwestergruppe von *M. pinetorum* und beide bildeten eine Schwestergruppe zu einer Klade aus *M. oaxacensis* und *M. guatemalensis*. Die phylogenetische Stellung von *M. umbrosus* blieb unklar. Die Monophylie der Relikte erwies sich nach Likelihood-Ratio-Tests als unhaltbar, was auf multiple südliche Invasionen arvicoliner Nager hinweist. Die phylogenetischen Daten für 17 diese und andere Taxa sollten in Arbeiten zur Arterhaltung in diesen abgelegenen Gebieten berücksichtigt werden.

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Mamm. biol. **66** (2001) 345–356
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Assessing competition between forest rodents in a fragmented landscape of midwestern USA

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Receipt of Ms. 04. 12. 2000
Acceptance of Ms. 13. 06. 2001

Abstract

Forests of the agricultural midwestern United States are highly fragmented, and species of small mammals that rely on the remaining forest fragments exhibit non-random distributions. We tested the extent to which interspecific competition between pairs of five species of granivorous forest rodents has influenced the structure of local assemblages occupying forest patches. We used a regression technique and incorporated patch and landscape variables in addition to local habitat variables. After accounting for variation in focal species density explained solely by local habitat variables, significant levels of interspecific competition were implicated for *Sciurus niger–Tamias striatus*. *T. striatus* also had a negative effect on densities of *Peromyscus leucopus* in forest patches > 10 ha. Inclusion of patch and landscape variables increased the explanatory power of regressions for *T. striatus* and *S. carolinensis*, two species generally regarded as sensitive to agriculturally induced fragmentation of forest habitat. Even when allowing for habitat selection at larger spatial scales, our results indicated competitive effects comparable to the analysis incorporating only local habitat variables. One difference was a marginal negative effect of *S. carolinensis* on *Tamiasciurus hudsonicus* after accounting for multi-scale selection. Overall, interspecific competition explained a significant proportion of the variation in densities for only three of the 24 potential interactions. In contrast, habitat and landscape features explained 0.37–0.71 of the variation in densities for all species except *S. niger* (0.09–0.20). We discuss the roles of competition and habitat fragmentation in mediating the coexistence of forest granivores.

Key words: Rodents, competition, fragmentation, habitat selection

Introduction

Numerous studies have examined the degree to which interspecific competition influences the composition of communities (Abrams 1988; Bengtsson 1991; reviewed by Connell 1983; Drake 1990; Hallett et al. 1983; McIntosh 1995; Minot and Perrins 1986; Nee and May 1992; Rosenzweig et al. 1984). In addition, studies of island biogeography (MacArthur and Wilson 1967) have shown that groups of insular faunas, resulting from either geological or anthropological processes, typically exhibit highly ordered (i. e., nested) patterns of species distribution (Cutler 1994; McCoy and

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Mushinsky 1994; Patterson and Atmar 1986; Patterson 1990; Wright et al. 1998). Nested patterns of distribution often result from differential colonization and/or extinction probabilities among species (Atmar and Patterson 1993; Patterson 1990). Factors influencing these colonization or extinction probabilities may include intrinsic characteristics of species such as minimum-area requirements, vagility, specific habitat affinities, and population stability (Patterson 1990; Peltonen and Hanski 1991).

In the absence of habitat fragmentation, differential habitat affinities of species can ameliorate competitive interactions, thus emphasizing the importance of considering local habitat effects in analyses of interspecific competition (Abramsky et al. 1979; Crowell and Pimm 1976; Hallett et al. 1983). Theoretical models predict that habitat fragmentation may promote coexistence of competing species by permitting inferior competitors to escape spatially, even in the absence of differences in habitat affinities (Abrams 1988; Holmes and Wilson 1998; Huxel and Hastings 1998; Moilanen and Hanski, 1995; Nee and May 1992). Moreover, empirical evidence suggests that mammalian species select habitat at multiple spatial scales rather than just at local scales, and patch- and landscape-level selection can have important influences on community composition (Lindenmayer et al. 1999, 2000; Schweiger et al. 2000). In at least some instances local competition interacts with landscape-level habitat selection, influencing community structure (Gabor and Hellgren 2000). Habitat selection by species at the local, patch and landscape-level may be a major mechanism structuring communities in fragmented landscapes; thus, it would be prudent to examine the importance of habitat structure measured at multiple spatial scales on populations before invoking competitive interactions as mechanisms structuring a community.

Our aim in the present study is to test for competition after incorporating habitat selection at multiple spatial scales rather than only at a single spatial scale. We focus our tests on five species of granivorous forest rodents that occur syntopically in our study area in west-central Indiana, USA: white-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*), red squirrels (*Tamiasciurus hudsonicus*), gray squirrels (*Sciurus carolinensis*), and fox squirrels (*S. niger*). These species exhibit a highly nested distribution among forest patches in agricultural landscapes (Nupp and Swihart 2000), but they vary considerably in the degree to which local, patch, and landscape features influence their density or distribution (Nupp 1997). In addition to our general tests for competition, we tested the hypothesis (Nupp and Swihart 1996, 1998) that white-footed mice mice occupying smaller patches are released from interspecific competition in fragmented landscapes due to the absence of larger granivores. This test was accomplished by conducting separate analyses for mice in forest patches < 10 ha and ≥ 10 ha.

Material and methods

Study area

Our study was conducted on the Indian Pine Natural Resources Area in west-central Indiana. This 259 km^2 area encompasses two major watersheds in Tippecanoe and Warren counties; 82% of the landscape is subjected to cultivation, principally for production of corn and soybeans. Within this agricultural landscape, woodlands comprise 16% of the area and consist of small, more or less isolated farmland woodlots and larger wooded riparian strips (Sheperd and Swihart 1995). Thirty-five woodlots (0.1–150 ha) and two sites representative of more extensive wooded areas (~1500 ha) were selected for study based on the criteria of relatively mature, deciduous woody vegetation. These study sites were 30–870 m from their nearest neighboring forest patch.

Determination of density

Each study site was sampled at least once during spring of 1992 to 1996 by live-trapping. Sherman^{tm} live-traps ($7.5 \times 9.0 \times 30$ cm) were placed at 15-m intervals and Tomahawk^{tm} live-traps

(15×15×60 cm) at 30-m intervals on sampling grids established at each study site. All traps were pre-baited for 2 days and followed by 5 days of trapping. Sherman traps were baited with a mixture of rolled oats, sunflower seeds and peanut butter, and Tomahawk traps were baited with English walnuts.

Abundance estimates of adult mice (> 18 g) (Cummings and Vessey 1994) were calculated using program CAPTURE (Otis et al. 1978), and abundance of other adult small mammals (eastern chipmunks > 80 g, red squirrels > 200 g, gray squirrels > 400 g, and fox squirrels > 600 g) was estimated using minimum number known alive (MNA; Krebs 1966). Density estimates were calculated subsequently using either the entire area of woodlots (when the entire area was trapped) or the area of the trapping grid plus a 7.5-m buffer on all sides (for areas that were too large to cover completely, in which case a grid of ~2 ha was used).

Quantification of habitat features

We used standard line transect and point-count sampling to quantify structural characteristics of the local habitat in each forest patch with 24 variables (Tab. 1). Parallel transects were spaced at 15-m intervals on trapping grids. Diameter at breast height (dbh) was measured for all trees > 10 cm and ≤ 1.5 m from a transect line. Trees also were classified as hard-mast (i. e., nut) producers, soft-mast (i. e., samara, fruit) producers, conifers, or other. Basal area, average dbh, and frequency were computed for all trees, snags, hard-mast producers (further separated into *Quercus*, *Carya*, and *Juglans*), soft-mast producers, and conifers. Counts of stumps, logs, grapevines, and burrows were obtained along transects and expressed in terms of their frequency per 100 m. At 30-m intervals along each transect, we measured vertical vegetative cover from 0–1 m, 1–2 m, and 2–3 m above ground using a modified density

Table 1. Habitat, patch, and landscape variables used in principal components analysis for detecting variation in granivorous rodent density as a function of habitat measured at multiple spatial scales. The acronym dbh refers to diameter at breast height. Total and sound mast production, as well as mast production excluding walnuts were used only in the analysis with 37 trapping episodes. Except for fractal dimension, patch and landscape variables were transformed using square roots (core area index) or natural logarithms (all other variables) before analysis. Squared terms, centered on mean values, also were included for patch area, proximity, and nearest neighbor distance. See text for details related to each variable.

Local Habitat Variables	Patch and Landscape Variables
Basal area of all trees	Area of forest patch
Basal area of hard-mast trees	Perimeter of forest patch
Basal area of oaks (*Quercus*)	Core area index of patch
Basal area of hickories (*Carya*)	Fractal dimension of patch
Basal area of walnuts (*Juglans*)	Proximity of focal patch to other patches
Basal area of soft-mast trees	Distance to nearest neighboring patch
Basal area of conifers	
Basal area of snags	
Average dbh of hard-mast trees	
Average dbh of soft-mast trees	
Average dbh of snags	
Number of hard-mast trees	
Number of soft-mast trees	
Number of grapevines	
Number of snags	
Number of stumps	
Number of logs	
Vertical cover, 0–1 m	
Vertical cover, 1–2 m	
Vertical cover, 2–3 m	
Percent canopy cover	
Total mast production (kg/ha)	
Sound mast production (kg/ha)	
Mast production excluding walnuts (kg/ha)	

board (Nudds 1977). Percent canopy closure was measured at 30-m intervals using a spherical densiometer (Lemmon 1957).

Previous studies have documented the importance of production of hard mast on population dynamics of white-footed mice, eastern chipmunks, and tree squirrels (e. g., McShea 2000; Nixon et al. 1975; Wolff 1996). Production of hard mast was estimated using seed traps placed at 30-m intervals within the trapping grids. Seed traps were constructed of circular plastic bags (1 m^2 area) elevated off the ground. Traps were placed before mast began to fall, in late August or early September of 1993, 1994, or 1995. Mast was collected from the traps in October, sorted by species and soundness, oven-dried, and weighed. Unfortunately, it was not possible to estimate production of hard mast in each forest patch in the fall preceding trapping. We collected corresponding data on hard mast production for 37 of 61 spring trapping episodes.

To quantify patch and landscape characteristics, forest patches within the Indian Pine landscape were digitized from aerial photographs (1 : 15 000) and the digital map was analyzed. We calculated patch area and perimeter, proximity, nearest-neighbor distance, core area index, and fractal dimension (Tab. 1). Proximity is inversely related to isolation of a forest patch and is the sum of patch area divided by the nearest squared edge-to-edge distances between a neighboring patch and the focal patch, for all neighboring patches within a specified radius of the focal patch. A radius of 1 km was used in our analysis. Core area index is a measure of the ratio of interior to edge habitat, calculated as the percent of the total patch area > 50 m from the patch's edge. Fractal dimension is a measure of shape complexity and is equal to two times the logarithm of patch perimeter divided by the logarithm of patch area. Squared terms for patch area, proximity, and nearest-neighbor distance also were included in the analyses, after centering on mean values to reduce collinearity (Neter et al. 1990). In all analyses, patch and landscape variables were logarithmically transformed to stabilize variances. Two exceptions were core area index, which was square-root transformed, and fractal dimension, which required no transformation.

Computation of interaction coefficients

The technique of determining competition coefficients from census data using regression techniques was developed by Schoener (1974) and Crowell and Pimm (1976) and has been the subject of considerable debate (Abramsky et al. 1986; Hastings 1987; Pimm 1985; Rosenzweig et al. 1985). Recently, Fox and Luo (1996) addressed a shortcoming of the original technique and used perturbation experiments to demonstrate the validity of a modified Schoener-Pimm analysis. Luo et al. (1998) also have applied the technique to identify seasonal fluxes in the intensity of competition between *Rattus luteolus* and *Pseudomys higginsi* in Tasmania. We briefly outline the pertinent statistical procedures below.

The equilibrium population size for species i, N_i^*, can be expressed using the Lotka-Volterra equations for competition, $N_i^* = K_i + \Sigma\alpha_{ij}N_j^*$, where K_i is the carrying capacity of species i in the absence of competitors, N_j^* is the equilibrium population size of species j, and α_{ij} is the per capita effect of species j on the growth rate of species i ($i \neq j$). For a community at equilibrium, interaction coefficients (α_{ij}) can be estimated from population censuses using linear regression.

Under conditions of heterogeneous habitat, variation in density could be due to differences in habitat selection among species. Incorporating the potential effects of M local habitat variables, H_m, into a model for predicting the equilibrium density of species i yields (after Hallett 1982) $N_i^* = \beta_0 + \Sigma\alpha_{ij}N_j^* + \Sigma\beta_{im}H_m$. Several methods for computing estimates of α_{ij} have been proposed for this model. Crowell and Pimm (1976) used stepwise multiple linear regression performed on principal components for habitat. After habitat components entered the model, densities of other species were allowed to enter the equation. Rosenzweig et al. (1984) also used a stepwise regression performed on habitat components as explanatory variables, with density as the response variable. Residuals were saved from each regression, and then a series of regressions were conducted on the residuals, with each species taking its turn as the dependent variable. Both the Crowell-Pimm method and the residual analysis method attempt to estimate interaction coefficients between species after accounting for variation in species densities that can be explained by habitat variables. This is a conservative approach, because some segregation due to habitat may be a result of competitive interactions. Rosenzweig et al. (1985) proposed a "free" regression approach in which stepwise regression is conducted on habitat variables and species densities simultaneously, thus permitting species interaction terms to enter the model before habitat components.

Dependence of α_{ij} estimates on the variances of species densities is a problem of all of the above methods for estimating interaction coefficients. Fox and Luo (1996) addressed this problem by

standardizing density estimates for each species so that mean standardized density equalled 0 and variance equalled 1. They applied this approach to estimate interaction coefficients for a small mammal assemblage in which field removal experiments also were conducted. Interaction coefficients estimated using standardized densities matched coefficients computed from removal experiments quite well (Fox and Luo 1996). Luo et al. (1998) also used standardized densities to obtain reasonable estimates of interaction coefficients for a pair of small mammal species censused across three seasons in Tasmania. Thus, standardized densities should be used instead of unstandardized densities when estimating competitive effects.

In our analysis, we standardized the density estimates so that each species' density had a mean of 0 and a standard deviation of 1. We then used these standardized densities as response variables in stepwise linear regressions ($F > 2.0$ to enter the model) adhering to the Crowell-Pimm, residual analysis, and free regression methods.

A second problem not addressed by published methods for estimating interaction coefficients is their focus on local habitat selection by species. In light of recent evidence indicating the occurrence of habitat selection at larger spatial scales (Lindenmayer et al. 1999, 2000; Schweiger et al. 2000), we modified the model of Hallett (1982) to incorporate the effects of Q patch effects, P_q, and R landscape-level effects, L_r, on the density of species i:

$$N_i^* = \beta_0 + \Sigma\alpha_{ij}N_j^* + \Sigma\beta_{im}H_m + \Sigma\gamma_{iq}P_q + \Sigma\varphi_{ir}L_r.$$

We conducted a separate analysis for the complete set of 61 censuses, and for the subset of 37 censuses for which data on hard-mast production also were available. To reduce dimensionality, local habitat, patch, and landscape-level variables were subjected to principal components analysis (PCA). Only scores for principal components with eigenvalues > 1 were used in regression models. In each analysis, we estimated interaction coefficients in the following manner: Two separate regressions were performed for each species of sciurid. In one regression we used as explanatory variables principal components derived only from local habitat variables. In the other regression we used principal components derived from local habitat variables and principal components derived from pooled patch and landscape variables. Our motivation for partitioning the explanatory variables was to determine whether variation in species densities could be explained by variables operating at multiple spatial scales, and to assess the degree to which inclusion of patch and landscape metrics affected estimates of interspecific interaction.

Results

The 61 spring trapping episodes yielded captures of 1669 white-footed mice, with mice captured in all trapping episodes. In addition, we captured 207 fox squirrels in 43 episodes, 264 eastern chipmunks in 47 episodes, 78 gray squirrels in 14 episodes, and 31 red squirrels in 12 episodes. Trapping in the spring following estimation of hard-mast production at 37 sites yielded captures of 961 white-footed mice at 37 sites, 148 fox squirrels at 29 sites, 147 eastern chipmunks at 28 sites, 46 gray squirrels at 7 sites, and 18 red squirrels at 6 sites. The number of sites at which we caught gray and red squirrels was marginal for use in subsequent regression analysis. Southern flying squirrels (*Glaucomys volans*) were excluded from analysis, as they were captured only in the 2 extensive woodlands and 3 of the largest forest patches.

When all 61 episodes were considered, PCA on the local habitat variables yielded seven usable principal components (i. e., eigenvalues > 1), and these components explained 80.2% of the total variation of the original variables. PCA on the patch and landscape-level variables yielded three usable components that together explained 90.3% of the total variation. When the 37 sites with data on mast production were considered separately, PCA on the local habitat variables yielded eight usable components, and these components explained 83.4% of the total variation. PCA on the patch and landscape-level variables yielded three usable components that together explained 84.3% of the total variation.

For each species, we obtained significant regression models relating standardized densities to the principal components derived from local habitat variables. These models explained 9–64% of the variance in standardized density estimates when all trapping episodes were used and 20–60% of the variance when only the 37 episodes with data on hard-mast production were used (Tab. 2). When we constructed regression models using principal components from both local habitat variables and patch and

Table 2. Coefficients of multiple determination (adusted R^2) and P values (in parentheses) for regressions relating standardized density to principal components of either local habitat variables alone or in combination with principal components of patch and landscape variables. Separate analyses were conducted for all spring trapping episodes (n = 61) and for those episodes for which hard-mast production was estimated the preceding fall (n = 37). For white-footed mice, too few trapping episodes occurred at sites ≥ 10 ha to permit analysis.

	Crowell-Pimm and Residual Analysis Methods		Free Regression Method	
Species	Local Habitat Only	Local + Patch + Landscape	Local Habitat Only	Local + Patch + Landscape
All Trapping Episodes				
White-footed mice, < 10 ha	0.41 (0.001)	0.41 (0.001)	0.41 (0.001)	0.41 (0.001)
White-footed mice, ≥ 10 ha	0.64 (0.004)	0.61 (0.012)	0.64 (0.004)	0.61 (0.012)
Eastern chipmunks	0.34 (0.001)	0.46 (0.001)	0.36 (0.001)	0.46 (0.001)
Fox squirrels	0.09 (0.030)	0.09 (0.030)	0.09 (0.030)	0.09 (0.030)
Gray squirrels	0.34 (0.001)	0.45 (0.001)	0.37 (0.001)	0.45 (0.001)
Red squirrels	0.37 (0.001)	0.45 (0.001)	0.37 (0.001)	0.45 (0.001)
Episodes with Mast Data				
White-footed mice, < 10 ha	0.42 (0.005)	0.42 (0.003)	0.42 (0.005)	0.42 (0.003)
Eastern chipmunks	0.35 (0.002)	0.46 (0.001)	0.37 (0.001)	0.46 (0.001)
Fox squirrels	0.20 (0.025)	0.20 (0.025)	0.27 (0.006)	0.30 (0.006)
Gray squirrels	0.54 (0.001)	0.71 (0.001)	0.55 (0.001)	0.74 (0.001)
Red squirrels	0.60 (0.001)	0.63 (0.001)	0.60 (0.001)	0.64 (0.001)

landscape-level variables, substantial increases in adjusted R^2 values occurred for eastern chipmunks (increases of 0.09–0.12) and gray squirrels (increases of 0.08–0.19), moderate improvements in R^2 values were noted for red squirrels (increases of 0.03–0.08), and little or no change in R^2 values occurred for fox squirrels (0.00–0.03) and white-footed mice (–0.03–0.00) (Tab. 2).

Estimates of interaction coefficients generally were similar within a given set of data, irrespective of the regression method used. Generalized community matrices (Hallett 1982) for interaction coefficients estimated after accounting for components of local habitat indicated significant negative effects of eastern chipmunks on densities of white-footed mice in forest patches ≥ 10 ha and reciprocal negative effects between chipmunks and fox squirrels (Tab. 3). When the effects of patch and landscape-level variables were incorporated into the estimation procedure, the negative interactions noted previously with the local habitat variables were retained (Tab. 4). In addition, we noted significant positive effects of mice and fox squirrels, and a negative effect of gray squirrels, on density of red squirrels (Tab. 4).

Discussion

Because of the importance of patch and landscape features to density of some of the species in our assemblage, estimation of competitive interactions should account for variation in density due to habitat features measured at multiple spatial scales. Of the five species we examined, gray squirrels and eastern chipmunks are the most sensitive with respect to habitat fragmentation (Nupp and Swihart 1998, 2000), whereas red squirrels, fox squirrels, and white-footed mice appear to be progressively less sensitive (Bayne and Hobson 2000; Nupp and Swihart 1998, 2000; Swihart and Nupp 1998; Goheen and Swihart unpubl. data). In accord with these differences, models for gray squirrels and eastern chipmunks exhibited the greatest increase in variation explained when patch and land-

Table 3. Generalized community matrices for five species of granivorous forest rodents in west-central Indiana, U.S.A. Entries indicate the per capita effect of the column species on the row species, taking into account the effects of local habitat on species density. For a given species pair, interaction coefficients are listed in the following order: Crowell-Pimm, residual analysis, free regression. All interaction coefficients in the table exhibited P values < 0.05.

	White-footed mice	Eastern chipmunks	Fox squirrels	Gray squirrels	Red squirrels
All Trapping Episodes					
White-footed mice					
< 10 ha		–	–	–	–
≥ 10 ha		–0.22 ns –0.22	–	–	–
Eastern chipmunks			–0.27 –0.27 –0.28	–	–
Fox squirrels	–	–0.26 –0.37 –0.26		–	–
Gray squirrels	–	–	–		–
Red squirrels	–	–	–	–	–
Episodes with Mast Data					
White-footed-mice					
< 10 ha		–	–	–	–
Eastern chipmunks	–		–0.37 –0.38 –0.41	–	–
Fox squirrels	–	ns –0.44 –0.45		–	–
Gray squirrels	–	–	–		–
Red squirrels	–	–	–	–	

scape components were included in regressions. Smaller increases in explanatory power were evident for red squirrels when patch and landscape components were included in regression models. For fox squirrels and mice, inclusion of patch and landscape components contributed virtually nothing to the models' explanatory power. Density of white-footed mice actually is inversely related to patch area (Nupp and Swihart 1996, 2000), indicating a positive response to habitat fragmentation.

Habitat factors measured at multiple spatial scales explained a substantial amount of the total variation in species abundances. In contrast, evidence of strong competitive effects among species of small mammals in our study was relatively sparse; only three out of 24 possible species interactions were consistently significant for each type of model constructed (local habitat variables only; habitat, patch and landscape variables combined). Local habitat affinities and larger-scale responses to agriculturally induced fragmentation of habitat appear to be the principal determinants of community structure in forest patches, with interspecific interactions relegated to a secondary role. Swihart and Nupp (1998) drew the same conclusion based on spatially explicit simulation models of gray squirrel, fox squirrel, and red squirrel populations.

Table 4. Generalized community matrices for five species of granivorous forest rodents in west-central Indiana, U.S.A. Entries indicate the per capita effect of the column species on the row species, taking into account the effects of local habitat, patch, and landscape-level variables on species density. For a given species pair, interaction coefficients are listed in the following order: Crowell-Pimm, residual analysis, free regression. All interaction coefficients in the table exhibited P values < 0.05 except red-gray, which was 0.06.

	White-footed mice	Eastern chipmunks	Fox squirrels	Gray squirrels	Red squirrels
All Trapping Episodes					
White-footed mice					
< 10 ha		–	–	–	–
≥ 10 ha		−0.26 −0.18 −0.22	–	–	–
Eastern chipmunks	–		−0.24 −0.28 −0.24	–	–
Fox squirrels		−0.26 −0.46 −0.26			
Gray squirrels	–	–	–		–
Red squirrels	0.23 ns 0.23	–	0.22 0.24 0.22	–	
Episodes with Mast Data					
White-footed-mice					
< 10 ha		–	–	–	–
Eastern chipmunks	–		−0.33 −0.33 −0.36	–	–
Fox squirrels	–	ns −0.50 −0.52		–	–
Gray squirrels	–	–	–		–
Red squirrels	–	–	–	ns ns −0.20	

A possible exception to secondary effects of competition was the mutually negative interaction observed between fox squirrels and eastern chipmunks. Both eastern chipmunks and fox squirrels inhabit woodlands throughout the study area (Nupp and Swihart 2000). This pattern of co-occurrence places them in potential conflict for a common food source, namely hard mast (Koprowski 1994 a; Snyder 1982). Consistent with this hypothesis, densities of fox squirrels and eastern chipmunks increase in response to principal components of habitat variables characterizing basal area of hard mast trees and mast production, respectively (Nupp 1997).

A negative effect of eastern chipmunks also was noted on densities of white-footed mice in large (≥ 10 ha) forest tracts. Both of these species occur syntopically throughout the study area (Nupp and Swihart 2000). However, previous studies have demonstrated that eastern chipmunks are sensitive to fragmentation and exhibit lower survival in small forest fragments than in continuous tracts of forest (Henein et al. 1998; Nupp

and Swihart 1998), potentially leading to local extinctions from fragments (Henderson et al. 1985). Thus, competitive effects of eastern chipmunks on white-footed mice may be dependent on patch attributes and landscape context. We observed a negative effect of chipmunks on mice in large forest patches but not in small (< 10 ha) forest patches, a finding consistent with the hypothesis that mice experience release from competition with larger granivores in small forest patches (Nupp and Swihart 1998, 2000). Competitive release in fragments appears to be common for small mammals with generalist habitat requirements, although social structure may regulate a species' ability to respond to the absence of competing species (Debinski and Holt 2000).

The relatively minor role of interspecific interactions in determining current population densities does not imply that competition was unimportant in the relatively continuous forest that characterized presettlement Indiana. Historical influences often are represented in current distributions of species and are difficult to identify using current observational data (Connell 1983; Drake 1990; Kelt et al. 1995). Local competition also can influence geographic ranges and the composition of regional biotas (Brown et al. 2000). Fragmentation of Indiana's forest began approximately 150 years ago (Petty and Jackson 1966). Competition could have played an important role in structuring the distribution and abundance of granivorous rodents in the previously unfragmented forest, but it seems likely that deforestation and concomitant reductions in area and increases in isolation of the remaining forest patches have played an increasingly important role in the last century. Our results thus support the notion that observed interactions between two species may be a function of properties intrinsic to the species and, perhaps more importantly, of properties of the landscape in which they co-occur (Danielson 1991; Debinski and Holt 2000).

Acknowledgements

We thank the numerous landowners in west-central Indiana who graciously permitted us to use work in their woodlots. Also, we thank S. Ayers, T. Bowman, R. Chapman, D. Cuddy, L. Curts, G. Dahle, J. Davis, T. Fairchild, R. Gehl, L. Hughes, J. Hunt, J. Ivan, D. Lotter, R. Miller, J. Parslow, R. Ritchey, R. Rodts, S. Smallidge, C. Webster, R. Williams, and J. Winters for field assistance. G. R. Parker, P. M. Waser, H. P. Weeks, Jr., and two anonymous reviewers provided helpful comments on drafts of the manuscript. Financial support was provided by Purdue University and by National Research Initiative Competitive Grants Program/USDA award 93-37101-8702. This is contribution 16411 to Purdue University Agricultural Research Programs.

Zusammenfassung

Abschätzungen zur Konkurrenz von im Wald lebenden Rodentiaspecies in einer fragmentierten Landschaft im mittleren Westen der USA

Viele Wälder im landwirtschaftlich intensiv genutzten mittleren Westen der USA sind stark fragmentiert, und die Kleinsäugerarten der Habitatinseln zeigen eine nicht zufällige Verteilung. Wir haben den Grad der Konkurrenz zwischen fünf Arten von Samen fressenden Waldnagetieren untersucht, um den Einfluß auf die Struktur des lokalen Vorkommens in Waldinseln abzuschätzen. Dazu wurde die Technik der Regressionskalkulationen erweitert, um Landschaftsvariablen zusätzlich zu den Habitatvariablen einzubeziehen. Nachdem die Varianz der Dichte von interessierenden Arten durch lokale Habitatvariablen erklärt wurde, sind signifikante Konkurrenzeffekte für das Artenpaar *Sciurus niger-Tamias striatus* gefunden worden. *T. striatus* hat außerdem eine negative Wirkung auf die Dichte von *Peromyscus leucopus* in Waldinseln, die größer sind als 10 ha. Die Einbeziehung von Patch-Fläche und Landschaftsvariablen erhöht den Erklärungswert der Regression von *T. striatus*

und *S. carolinensis*, zwei Arten, die als sensibel gegenüber Fragmentierung angesehen werden. Auch wenn die Habitatwahl in einem größeren Maßstab einbezogen wurde, zeigten unsere Ergebnisse Konkurrenzeffekte, die vergleichbar waren mit der Analyse, die nur lokale Habitatvariablen beinhaltete. Eine Ausnahme war eine geringe negative Wirkung von *S. carolinensis* auf *Tamiasciurus hudsonicus* nachdem die Habitatwahl auf unterschdiedlicher räumlicher Skala einbezogen wurde. Insgesamt hat die interspezifische Konkurrenz nur für drei von den 24 möglichen Interaktionen einen signifikanten Einfluß auf die Dichte. Im Gegensatz dazu haben Habitat und Landschaftsstruktur 0.37–0.71 der Dichtevarianz für alle Arten außer *S. niger* (0.02–0.20) erklärt. Wir diskutieren die Rolle von Konkurrenz und Habitatfragmentierung auf die Koexistenz von Waldsamenfressern.

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Mamm. biol. **66** (2001) 357–364
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

The daily activity period of the brown hare (*Lepus europaeus*)

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Receipt of Ms. 17. 10. 2000
Acceptance of Ms. 15. 05. 2001

Abstract

The times of 241 entries into and 573 exits by brown hares from their forms on a 65 ha area of the Somerset Levels, South West England, were recorded over a ten year period to reveal the variation during the year of the duration of the daily activity period. In December when nightlength was 16 h, activity was exclusively nocturnal; intervals between entry and sunrise were longer and less consistent than those between sunset and exit. In June with nightlength down to 7.4 h, activity was part diurnal, post-sunrise and pre-sunset, for a total of 6 h. From a peak duration of 14.5 h in December, the activity period declined to 12 h in the third week of March, mirroring night time duration. It then increased to 13.5 h in late midsummer before again reducing in the autumn. It is suggested that the proximate cause of this circannual cyclicity is an aversion to daylight activity.

Key words: *Lepus europaeus*, brown hare, activity period

Introduction

Research on the circadian and circannual activity of the brown hare (*Lepus europaeus* Pallas, 1778) has hitherto been effected either by direct observation of hares on their foraging grounds (Homolka 1986) and travelling to and from them (Matuszweski 1981) or by radiotelemetrical monitoring of their movements (Pepin and Cargnelutti 1994), the one exception being Holley and Greenwood (1984) where, for part of the year, hares were timed exiting their forms in the evening. Such studies all suggest an annual cycle in the circadian activity period.

The brown hare's day and that of some other leporids is divided into two distinct periods. One, comprising all or a large part of the daylight hours, is spent crouched in its form or resting place. During much of the other, comprising mostly the night hours, the hare travels, feeds and interacts socially with conspecifics. These activities are, however, interspersed with shorter and less formal periods of rest. The combination of the clear-cut distinction between active and inactive periods and the exclusively above-ground lifestyle of the brown hare make it one of the best candidates of the smaller mammals for direct observational field studies of its circadian rhythm. The objects of this study were, by monitoring the times of entry into and exit from forms throughout the year, to define any annual cycle in the duration of the daily activity period and to consider the reason or reasons for it.

1616-5047/01/66/06-357 $ 15.00/0.

Material and methods

The observations reported here were part of a larger study of behaviour of the brown hare (Holley 1992) on approx. 65 ha, divided between 17 fields in the north western sector of the Somerset Levels, close to Brent Knoll, Somerset, U.K. (51°16′ N, 2°58′ W). Fields were predominantly permanent pastures with a minority being ploughed in rotation for cereal growing. There were few hedges, fields being divided by drainage channels. Observations were made from September 1977 to September 1987 from windows 9 m above ground level in the roof space of my house within the study area. Optical equipment employed consisted of 7×50 and 15×80 binoculars, a Zeiss Jena 20/40×80 binocular telescope and a Celestron 11 catadioptic astronomical telescope, giving magnifications in excess of 100×. The latter could be coupled to a Canon F1 camera as a telephoto lens with a focal length of 2 800 mm. With the equipment it was possible to identify and sex individual animals. Occupied forms were under observation over distances up to 400 m.

I recorded the times (Greenwich Mean Time throughout the year) of entry into or departure from forms. All entries and departures, except temporary departures, were included whenever observed although most were obtained during observation periods conducted for the purpose, commencing at least an hour before the earliest or closing at least an hour after the latest expected entry or departure, as the case might be. Usually, hares were noted either entering or departing their forms but not both on the same day. These will be referred to as once-a-day (OD) observations. In some cases, which will be referred to as twice-a-day (TD) observations, I recorded both the time a hare entered its form and the time it departed. Preliminary observation having confirmed the popular notion that hares become more noticeable in March, TD data were collected particularly intensively in March of each year. The OD data were collected throughout the study, the TD data being collected during the second five-year period. The population of the study area was thought to be between 5 and 15 adult hares each year. No individual hare was seen in more than four successive years.

At some times of the year it was possible to record six or more entries or departures in one observation period. In cases of doubt, when a hare appeared to be entering a new form but might merely be taking a rest before moving on, I only counted an entry if the hare was still in occupation after all other visible hares were also in their forms. For departures, where in doubt, I only included hares previously observed in occupation of the same form before noon on the day. Temporary departures caused, for example, by disturbance from humans, cattle or other hares were disregarded. Apart from such temporary exits, hares remained in their forms until the normal departure time, the only exception being when a doe was very close to, or in, oestrus; bucks could then be active throughout daylight. The interval between departing and entering forms is defined as the activity period although it may include within it periods of rest. Likewise, the interval between entering and departing forms is defined as the inactive period.

Employing standard optical equipment, it was possible by sweeping the study area to observe departures throughout the year but in December and early January, when the nights were longest, it was not normally possible to detect entries more than 40 mins before sunrise. Because of this problem, I mounted special watch, between 15 December 1985 and 6 January 1986, on one form occupied regularly by the same hare with the principal object of recording entry times.

The observed times of entries and exits were differenced from the day's sunrise/sunset values, averaged for each day and then averaged over the pertinent week. These weekly differentials indicate the time in relation to sunrise/sunset at which activity usually started or stopped. Those results having indicated a cyclic behaviour, harmonic functions were fitted to the a. m. and p. m. weekly mean differentials.

The fitted seasonal curves have the form

$$y = A.\cos(wx - \varnothing) + C$$

Where $w = 2\pi/T$, $T = 52$, the period in weeks of the function, y, and $x = 1,2,3, \ldots 52$, the weekly independent variable. A, C, ∅, are constants determined by an Ordinary Least Squares fit to the weekly averages, A being the amplitude, C the long run average of the variable y, and ∅ the phase of the cosine function. The phase can be expressed in terms of the week, P. marking the peak of the cosine function

$$P = \varnothing.T/2\pi$$

A test of statistical significance of the computed function, y, can be carried out on the constant A by an approximate F test with 2 and N-3 degrees of freedom, (N = number of weekly observations, somewhat less than 52). Likewise, the significance of the displacement of one cyclic seasonal from the other can be determined by an approximate z test of the difference between the two values of

P. The choice of positive and negative for the differentials was arbitrary.

Results

Altogether 241 entries into forms and 573 exits from forms were observed; 178 were from TD observations, leaving 152 entries and 484 exits from OD observations. The number and relative frequency of these records spread over the year is shown in table 1, which also shows in relation to sunrise and sunset the average weekly differentials of entries and exits of OD and TD observations, with the pattern of records appearing in figure 1. Seasonal variation in the number of observations primarily reflects detectability of the forms, except for the peak of TD data in March which reflects application of additional observer time. The statistics and tests of significance for the fitted harmonic curves are given in table 2.

The divergence between entry and exit curves, which is significant (Tab. 2), justifies their separate treatment. As nights shorten in the early part of the year, hares begin to leave their forms before sunset on average about two weeks earlier than they begin to enter them after sunrise (Fig 1). There are insufficient data from which to make the same analysis for the equivalent period in the second half of the year. The fit between both sets of data (OD and TD observations) and the curves is clear but there are indications in mid-summer that activity at both ends of the day extends for longer than the curves predict and also that from week 31, the first in August, onwards and until the end of October it is shorter than predicted.

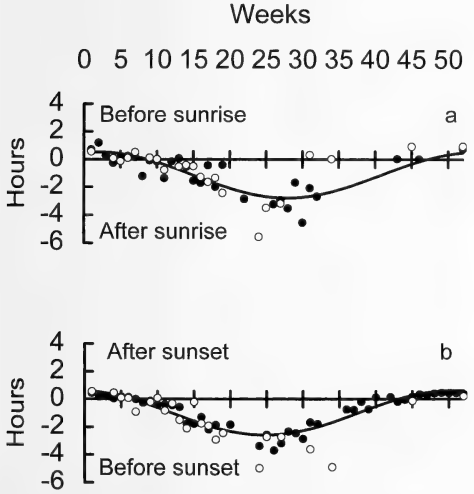

Fig. 1. Night duration differentials. The constants are respectively sunrise (a) and sunset (b) with the curves of the harmonic functions of entries into and exits from forms throughout the year. Observations of OD hares from which the curves have been constructed (•) and the excluded TD hares (○) are averages for each week.

In December and early January, when the nights are longest, hares are almost totally nocturnal, entering and leaving their forms in darkness. The time of exit is very consistent, being generally no more than 30 mins after sunset. For the reasons given in methods, quantitative data on the timing of entry were not obtained at this time of year. In figure 2 are the results of intensive daily observation of one form occupied by the same hare during December 1985 and January 1986. Exit times averaged 26.8 mins post-sunset (range = 19–36, n = 11 days). Entry time was only observed directly (by moonlight) twice (83 and 56 mins pre-sunrise), while on 6 occasions the hare was already in the form when first observed that day (range of 46-96 mins pre-sunrise). Intervals between entry and sunrise were therefore longer and less consistent than those between sunset and exit.

For the majority of entries and exits the identity and sex of the individual was not known. However, in a minority of cases individuals were recognised thereby providing additional information. Over a two year period, I obtained 17 exit times of a known buck, Bolingbroke, who at the time was the alpha male in the dominance hierarchy within the study area (Holley 1986). In 13 (76%) instances his exit from the form was before the mean time of exit by the study population. The exceptionally late entry and early exit TD data appearing in figure 1 and table 1 for week 24 refer to a study doe,

Table 1. The weekly means in hours for OD and TD hares of the differences between entries and sunrise (positive values before, negative values after) and exits and sunset (positive values after, negative values before). Also, nightime duration, sunrise to sunset, and the values of the fitted harmonic functions

Week	Nightlength	Entries am					Exits pm			
		OD hares	(n)	Fitted Function	TD hares	(n)	OD hares	(n)	Fitted Function	TD hares
1	15.983	0.70	6	0.517	0.56	4	0.43	21	0.591	0.57
2	15.817	1.19	2	0.526			0.18	19	0.528	
3	15.533	0.29	6	0.511			0.22	19	0.442	
4	15.233	−0.26	4	0.472	0.08	1	0.04	16	0.336	0.47
5	14.867	0.15	13	0.409	−0.12	4	0.18	36	0.211	0.09
6	14.483	0.24	16	0.325	0.10	5	0.14	23	0.069	0.22
7	14.050	0.15	2	0.219	0.51	2	−0.01	24	−0.088	−0.92
8	13.633	−1.22	1	0.093			−0.27	16	−0.258	
9	13.167	−0.07	1	−0.050	0.12	4	−0.14	40	−0.439	−0.22
10	12.717	−0.15	8	−0.209	0.02	1	−0.42	26	−0.627	0.08
11	12.267	−1.36	3	−0.382	−0.77	3	−0.39	17	−0.819	−0.83
12	11.800	−0.16	9	−0.565	0.12	17	−0.45	12	−1.014	−0.37
13	11.350	0.07	12	−0.756	−0.43	17	−0.58	20	−1.209	−1.62
14	10.883	−0.55	4	−0.953	−0.28	3	−1.78	20	−1.399	−2.22
15	10.450	−1.55	10	−1.153	−0.05	3	−1.77	13	−1.584	−0.22
16	10.000	−1.70	4	−1.352	−1.28	1	−1.30	4	−1.759	−1.75
17	9.550	−0.43	1	−1.548	−1.64	2	−2.17	7	−1.923	−1.92
18	9.150	−1.99	15	−1.738	−1.34	5	−1.86	8	−2.073	−2.92
19	8.767	−0.40	5	−1.919	−2.42	3			−2.206	−2.44
20	8.400			−2.088			−1.84	4	−2.322	
21	8.067			−2.243					−2.418	
22	7.817	−2.84	3	−2.382					−2.492	
23	7.617			−2.503					−2.545	
24	7.467			−2.604	−5.75	1	−3.38	1	−2.574	−4.97
25	7.417			−2.683	−3.48	1	−2.56	2	−2.580	−2.72
26	7.433	−3.22	1	−2.740			−3.70	3	−2.562	
27	7.533	−2.93	8	−2.773	−3.17	1	−3.18	1	−2.521	−2.72
28	7.733	−3.51	3	−2.782			−2.33	4	−2.457	
29	7.950	−1.68	5	−2.767			−2.45	2	−2.371	
30	8.267	−4.55	1	−2.728			−2.86	4	−2.265	
31	8.600	−2.08	4	−2.666	0.32	2*	−1.67	2	−2.140	−3.62
32	8.697	−2.68	1	−2.581			−1.79	3	−1.998	
33	9.367			−2.475					−1.841	
34	9.783			−2.349	0.02	1			−1.671	−4.90
35	10.217			−2.206					−1.491	
36	10.667			−2.047			−0.75	1	−3.303	
37	11.100			−1.875			−0.78	1	−1.110	
38	11.550			−1.691			−0.20	1	−0.915	
39	12.000			−1.500			−0.73	1	−0.721	
40	12.467			−1.303			0.12	1	−0.530	
41	12.917			−1.103					−0.346	
42	13.367			−0.904			0.14	2	−0.170	
43	13.850	0.040	2	−0.708			−0.18	6	−0.006	
44	14.217			−0.518			−0.05	4	0.143	
45	14.633			−0.338	0.92	1	0.17	7	0.277	−0.13
46	15.000	0.020	1	−0.168			0.35	1	0.393	
47	15.350			−0.013			0.30	9	0.488	
48	15.650			0.126			0.41	5	0.563	
49	15.867			0.247			0.47	5	0.615	
50	16.033			0.348			0.44	15	0.644	
51	16.117			0.427			0.44	15	0.650	
52	16.117	0.77	1	0.483	0.94	7	0.38	43	0.632	0.21
			152			89		484		

* A doe and mateguarding consort

Table 2. Statistics of the harmonic function (a) and tests of statistical significance (b).

(a) Differentials	A(Amplitude) hours	C hours	P Peak-week
Entries	1.65	−1.1281	1.875 (Jan.)
Exits	1.62	−0.9647	−1.255 (Dec.)
(b) Amplitude, A	F-statistic	Degrees/freedom	p-value
Entry differentials	45.77	2 & 27	<.001
Exit differentials	340.49	2 & 41	<.001
Seasonal Displacement			
Difference of Peaks, P (am) − P (pm)		Approximate z-statistic	p-value
	3.13 (weeks)	4.0	<.001

Bluebell, on the day of her parturition when she occupied her form for only six hours.

In mid-December, when night length in the study area exceeded 16 h, the activity period, all of it within those hours, occupied about 14.5 h (Tab. 1; Fig. 2). In mid-June when night length reduced to a minimum of 7.4 h, the activity period occupied about 13.5 h, six of them in daylight (Tab. 1). Is there, during the period of exclusively nocturnal activity, any relationship between night length and the length of the activity period? That question is addressed in figure 3 which is constructed exclusively from TD data, since these provide an accurate measurement of the activity period of the hare. From a peak of nearly 15 h in week 1, the activity period declined to a minimum of just over 12 h in week 12, the third full week in March, mirroring the decline in night duration. That decline was reversed in week 13 when the activity period increased to 13.4 h and exceeded night duration by two hours. By week 18 it was exceeding night duration by > 4 h. The results from this figure, supported by data in table 1, demonstrate a close correlation between respectively the lengths of the night hours and of the activity period between the start of the year and the latter part of March.

Discussion

The results of this study suggest that the brown hare is essentially a nocturnal animal. Given sufficient hours of darkness, all activity takes place within them. During the few weeks when there was a marked excess of the dark hours over the activity hours, hares consistently emerged from their forms and commenced activity within 30 mins after sunset, and the excess was reflected in the time they entered their forms and ceased activity, which was as early as one and a half hours before sunrise. However, it appears that when the night hours are insufficient, the activity period overlaps into daylight at either end of the day.

This annual activity pattern conforms closely to that appearing in the observational reports of hare activity on their foraging grounds by Matuszweski (1981) and Homolka (1986) and also the results of radiotracking analysis of individual activity by Pepin and Cargnelutti (1994). Limited evidence suggested, however, that certain individuals, such as pregnant and nursing does and alpha bucks, could be active for periods of up to 16 h or more. Such individual variation is also reported by Pepin and Cargnelutti (1994).

The daily activity period follows a seasonal cycle, getting shorter as the hours of day-

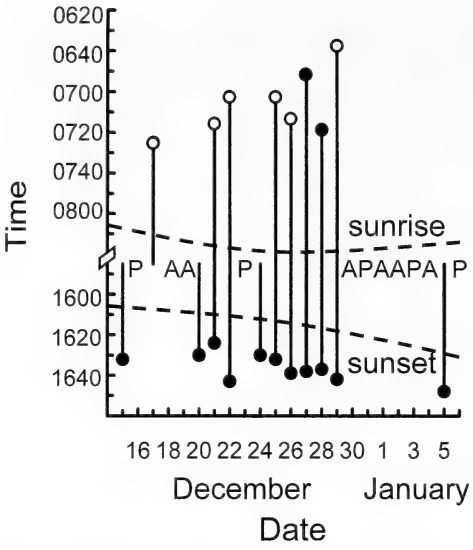

Fig. 2. Observed occupation (vertical lines) of one form by the same hare between 15 December 1985 and 6 January 1986. Symbols indicate observed entry or exit (•), earliest sighting of hare already in form (○), hare present in form on the day but entry and exit not observed (P) and hare absent that day (A).

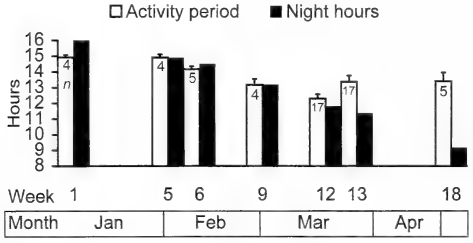

Fig. 3. The mean daily activity period (i. e. length of time out of forms (+SE) based on TD observations) compared with the average night length, sunset to sunrise, during the first 18 weeks of the year. Data only presented for weeks with four or more TD observations (sample size in histogram).

light increase. This produces the surprising outcome that it is substantially longer before the breeding season commences in late December (Tapper 1991) than it is in the peak reproductive months of February to June. Why should that be? Why does it cycle at all? The answer appears to lie in not just a nocturnal preference but an aversion to daylight activity on the part of the brown hare. Preference is shown by choice, aversion by withdrawal. Assuming an optimal activity period of over 14 h, it would be expected that the transition from a totally nocturnal activity period to a partially diurnal one, as the night hours drop below 14, would not affect the length of the period. That, however, is not the case, the duration of the period in fact declining from nearly 15 h in the first week of January to a minimum of just over 12 h in the third full week of March, mirroring the duration of the night hours. Then, towards the end of March the activity period begins to increase and takes in some of the daylight hours. Why does the duration of the activity period not remain constant instead of reducing substantially January to March and then increasing to mid summer? Perhaps hares might need longer hours feeding in winter to meet the higher energetic demand of lower ambient temperature and to allow for the lower calorific value of food. That possibility seems unlikely because there is no sign of any extension of the activity period following the onset at the end of December of the reproductive season with its dependent energetic demands. The pattern of events does seem to indicate, first, that some inhibitory factor is preventing easy transition from a totally nocturnal to a partially diurnal regime and, secondly, that there is a point, at roughly 12 h of duration, beyond which the activity period cannot easily be contracted. This suggests that the inhibitory factor is daylight itself: hares are shy of daylight activity. Another manifestation of the inhibitory factor is in the difference between the harmonic curves for the times of form entry and departure. In spring, the departure curve crosses the sunset line into daylight two weeks before the entry curve crosses the sunrise line. Daylight activity extending before sunset precedes daylight activity lasting after sunrise. In the evening, after spending the day in its form, a hungry hare will be less shy of daylight activity than a well fed one returning to its form in the morning. The results from this study show the difference to apply as well before as after commencement of the

breeding season and thus cannot be entirely connected to reproductive and agonistic interactions which in both nocturnal and diurnal mammals and birds often peak at activity onset (for review see Daan and Aschoff 1982). Although hares, once they are regularly active diurnally, rapidly extend the duration of daylight activity, none the less the inhibitory factor appears to be still operating to the extent that, in this study area, the duration of activity remains shorter than during the totally nocturnal regime. There are indications of a relatively sudden withdrawal from daylight activity at the end of the breeding season in August.

Of related species, studies using automatic activity recording of mountain hares (*Lepus timidus*) in Sweden by Cederlund and Lemnell (1980) and Lemnell and Lindlof (1981) showed a close relationship between sunset and onset of activity and sunrise and cessation of activity in winter. Daylight activity gradually increased up to 50% in summer when the nights were very short. The study of Mech et al. (1966) on five radio-collared snowshoe hares (*Lepus americanus*) in Minnesota, USA, also showed that seasonal changes from January to May in both onset and cessation of activity followed the trend of changing sunrise-sunset times, but with the difference that contraction of the activity period continued into May when it amounted to less than nine hours. I propose that the proximate cause of cyclicity in the activity period of brown hares is an aversion to daylight activity. It seems that this may be shared by a number of other leporid species.

The emergence of the brown hare from darkness on to the daylight arena in March, as demonstrated in this study, adds further clarification to the explanation of the "mad March hare" of literature (Carrol 1865) given by Holley and Greenwood (1984).

Acknowledgements

I am greatly indebted to my brother-in-law, Dr. Thomas Hayton, for valuable statistical analysis and advice and to Ruth Temple and Dr. Nancy Vaughan for discussions and preparation of the figures. My thanks go also to Dr. John Coulson and Dr. Neil Metcalfe and to anonymous referees for their very helpful comments on a previous draft and to Klaus Hackländer for translation into German. Sunrise and sunset values reproduced, with permission, from data supplied by the Science and Engineering Research Council.

Zusammenfassung

Die tägliche Aktivitätsperiode des Europäischen Feldhasen (*Lepus europaeus*)

Um die Veränderung der Länge der täglichen Aktivitätspenode im Laufe eines Jahres für Feldhasen zu bestimmen, wurde die Nutzung der Sassen auf einem 65 ha großen Gebiet in Südwestengland aufgezeichnet. Dabei wurde das Aufsuchen (n = 241) und das Verlassen der Sasse (n = 573) protokolliert. Im Dezember (Nachtlänge: 16 h) waren die Hasen ausschließlich nachtaktiv. Die Intervalle zwischen dem Aufsuchen einer Sasse und dem Sonnenaufgang waren länger und inkonsistenter als jene zwischen dem Verlassen der Sasse und dem Sonnenuntergang. Im Juni (Nachtlänge: 7,4 h) reichte die Aktivitätsperiode für insgesamt 6 h in den Tag hinein: Sie endete erst nach Sonnenaufgang und begann bereits vor Sonnenuntergang. Die Länge der Aktivitätsperiode verkürzte sich entsprechend der Nachtlänge von 14,5 h im Dezember auf 12 h in der dritten Märzwoche. Darauffolgend stieg die Aktivitätslänge auf 13,5 h im Spätsommer, um im Herbst wiederum zu sinken. Diese Ergebnisse weisen daraufhin, dass eine proximate Ursache für den circannuellen Rhythmus bei Feldhasen eine Vermeidung von Aktivität bei Tageslicht ist.

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Mamm. biol. **66** (2001) 365–370
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Home range size, movements, and habitat utilization of three male European wildcats (*Felis silvestris* Schreber, 1777) in Saarland and Rheinland-Pfalz (Germany)

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Receipt of Ms. 30. 01. 2001
Acceptance of Ms. 20. 04. 2001

Key words: *Felis silvestris*, home range, habitat utilization, nightly movements

Although several radio-telemetry studies of European wildcats have been conducted (e. g. Corbett 1979; Stahl et al. 1988; Liberek 1999), systematic investigations on European wildcats are lacking in Germany. Due to a population size of approximately 1000 individuals (F. Raimer pers. comm.) and the connection to wildcat populations in neighbouring France and Luxembourg, the population in Rheinland-Pfalz is of great importance for the conservation of wildcats in central and western Europe. Therefore, a radio-telemetry study was conducted in Saarland and adjacent parts of Rheinland-Pfalz, to assess home range size, movements and habitat utilization of European wildcats in this region.

The study area encompassed approximately 130 km^2 in northern Saarland and southern Rheinland-Pfalz, southwest Germany (6°55′ E, 49°36′ N). Elevation in the area ranges from 250 to 650 m. Precipitation is greatest at high elevations and ranges annually from 700 to 1000 mm and temperatures vary from –16.5 °C to over +30.0 °C (Fischer 1989). A mean snow depth of 10 cm is recorded for 10 to 80 days. Approximately 39% of the study area was forested. The dominate native tree was red beech (*Fagus sylvatica*), but spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*) were commonly planted. At lower elevations agriculture was common and forest climax consisted of submontane beech-oak-forests (*Quercus petrea*). Current agricultural practices result in many fallow fields and meadows.

Over the duration of the study, 3 male wildcats were caught in box traps, sedated with a Ketamin/Xylazin-mixture (Hatlapa and Wiesner 1982), weighed, measured, and radiocollared (50 g; K. Wagener Cologne, Germany) (Tab. 1). Approximate age was estimated based on tooth succession and condition.

Wildcats were primarily located continuously during their main active period at night resulting in successful locations approximately once every 50 minutes. Accuracy of radio locations was evaluated under different habitat conditions, consistent with literature standards (White and Garrott 1990) and allowed to evaluate a habitat-specific telemetry error of 100 m. For home range analysis, locations were filtered for 2 hour intervals to equally distribute the data. Adaptive Kernel (AK) estimates (Worton 1989) of annual and seasonal home ranges were estimated using the program Ranges V (Kenward 1995). In addi-

1616-5047/01/66/06-365 $ 15.00/0.

tion, minimum convex polygons (MCP) (Mohr 1947) were measured for comparison with previous research.

The area enclosed in the 95% AK contour was defined as the home range of an individual to exclude outliers. Core areas were defined as the area within the 50% contour. Seasonal delineations considered mating behaviour (Piechocki 1990) and prey availability (Sládek 1973) and included: winter mating season (January–March), spring (April–June), summer (July–September), and autumn (October–December). Over the duration of this study, M1 was monitored for 249 days, M2 for 49 days, and M3 for 266 days resulting in a total of 1276 relocations with 77% of the locations being recorded between 18.00 h and 07.00 h.

Minimum nightly movements were calculated by summing the distances between relocations of nights where cats were followed for ≥5 hours and both daily resting sites were recorded. The average observation time per night was 9.35 hours. (SD = 3.02) resulting in an average of 11 (SD = 4) successful locations per night.

Locations were imported into the Geographic Information System (GIS) MapGrafix (ComGrafix USA). Habitat use was determined using a circular buffer with a 100 m radius around the locations filtered for a 1 hour interval. Within this 3.14 ha buffer the extent of each habitat was recorded. When analyzing for seasonal habitat use, areas for each habitat category included in all locations were summed to equal the probability that a location was in a specific habitat category. Analysis of habitat utilization was restricted to M1 and M2 as digitized maps were unavailable for M3. Selection of habitat was assessed by comparing availability and use of habitat types within the total range (100% AK) of an individual following the method described by Neu et al. (1974). An $\alpha = 0.05$ was used to determine significance for tests of the null hypotheses.

Home range: The largest seasonal home range of 2515 ha was observed in winter 1996 for M2 (Tab. 1). Both M1 and M3 had their largest seasonal home ranges during spring. Seasonal home ranges during winter and spring were significantly larger than during summer and autumn (one tailed t-test, df = 6, p = 0.025). Accounting for the total number of relocations, annual home ranges were estimated to be 1407 ha for M1 and 1916 ha for M3, averaging 1662 ha. Core areas ranged from 92 to 460 ha. Spatial overlap between M1 and M2 during January and February 1996 was 224 ha. Therefore M1 shared 29% and M2 approximately 9% of its range. Core areas were used exclusively.

Nightly movements: The seasonal average of distances travelled per night ranged from 2.8 km during summer to 11.3 km during winter (Tab. 1). Over a period of 14 hours, the longest observed nightly movement was 13.3 km recorded for M2 in February 1996. Nightly movements during winter/spring averaged 5.5 km (SD = 2.6 km) and were significantly longer than movements during summer/autumn averaging 3.0 km (SD = 1.2 km) (one tailed t-test, df = 70, p < 0.001).

Habitat use and selection: More than 1 habitat category was found within the 100 m accuracy buffer around 74% of the locations of M1 and 65% of the locations of M2. Of these 85 and 79% included forest edge for M1 and M2 respectively. Of the locations encompassing only 1 habitat category, 96% were in forests. For both cats, 3 habitat types (forests, fields/meadows, riparian meadows) accounted for 86 to 91% of the relocations. Forests were used most intensively throughout the study period ranging from 50 to 55% of the locations. Fields/Meadows were used by M1 more intensively during winter and summer, riparian meadows were used most often in spring. Percentages of forested areas included in seasonal total ranges varied between 40 and 66%.

Habitat use was significantly different from expected for M2 during winter, showing preference for fields/meadows and avoidance for clearings ($\chi^2 = 30.41$, df = 4, p < 0.001) (Fig. 1). During the same period M1 used habitats proportionately to their occurrence ($\chi^2 = 4.52$, df = 4, p = 0.34). M1

Table 1. Wildcats characteristics, home range sizes, and nightly movements

	Capture			Loss	Number of relocations		Home range in ha				Nightly movements in km		
							Adaptive Kernel			MCP			
	Collared	Age	Weight	Date/Status	Season	n	100%	95%	50% core area	95%	Complete nights (n)	Average	SD
M1	09. 01. 1995	adult,	5 250 g	29. 9. 1996	Winter	116	1 613	966	138	889	7	5.4	1.8
	24. 02. 1996	> 24	4 800 g	Unknown	Spring	208	3 475	1 806	457	1 744	25	4.1	1.6
		months			Summer	177	2 095	1 261	228	1 202	20	2.8	1.1
					Autumn	–	–	–	–	–	–	–	–
					Total	501	3 401	1 407	452	2 261	52	3.9	1.7
M2	12. 01. 1996	adult,	6 700 g	29. 2. 1996	Winter	99	3 343	2 515	177	1 718	4	11.3	1.8
		> 36		Starvation	Spring	–	–	–	–	–	–	–	–
		months			Summer	–	–	–	–	–	–	–	–
					Autumn	–	–	–	–	–	–	–	–
					Total	–	–	–	–	–	–	–	–
M3	22. 08. 1997	adult,	5 750 g	14. 5. 1998	Winter	113	3 513	1 779	231	1 453	6	4.8	3.0
		> 24		Unknown	Spring	68	2 536	2 342	460	1 764	4	6.6	1.4
		months			Summer	47	740	502	92	382	3	2.9	0.3
					Autumn	87	1 462	986	134	892	3	4.8	1.2
					Total	315	3 450	1 916	245	1 993	16	4.9	2.3

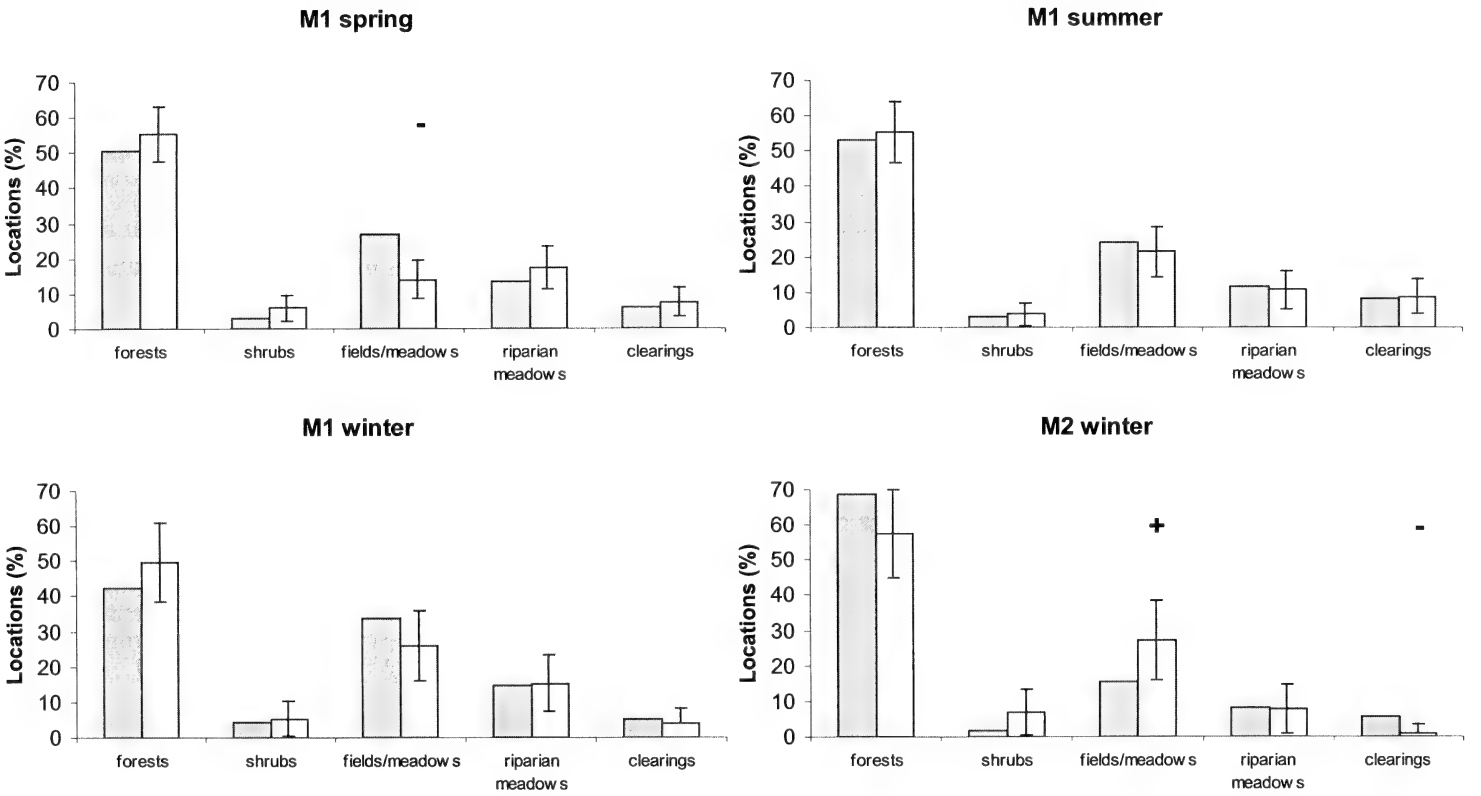

Fig. 1. Habitat selection M1 and M2; grey columns indicate avaibility within individual seasonal total range, white columns indicate habitat use, error bars indicate confidence intervals according NEU et al. (1974), ± = habitat use significantly different from expected.

showed avoidance of fields/meadows in spring ($\chi^2 = 28.63$, df = 4, $p < 0.001$) and used habitats in proportion to their availability during summer ($\chi^2 = 1.75$, df = 4, $p = 0.78$).

The average annual home range size of 1662 ha in this study was larger than ranges reported for radiocollared male wildcats in previous studies (Corbett 1979; Stahl et al. 1988). However, MCP seasonal range sizes in this study were smaller than seasonal MCP range sizes recorded for male wildcats in Switzerland (Liberek 1999), indicating that home range sizes in male European wildcats vary under different ecological conditions. Use of home ranges is believed to be exclusive in areas where lagomorphs dominate the diet as opposed to exclusiveness only for animals of the same sex in areas where rodents dominate the diet (Stahl et al. 1988). As the energetic requirements of wildcats increase with the number of prey items required to fulfil their energy demand (Hemmer 1993), the observed differences in range sizes may be explained by differences in availability and abundance of prey.

First order selection (Johnson 1980) of areas inhabited by European wildcats have highlighted the importance of large forested areas with clearings interspersed to increase the amount of edge (e. g. Vogt 1985; Hemmer 1993). First order selection would be strongly influenced by persecution by people and resulting extirpation from large areas of suitable habitat.

Third order selection using radio-telemetry has been studied in east central France (Stahl 1986). Results of this study are consistent with Stahl (1986) with seasonal total ranges including 40 to 66% of forested areas showing the importance of cover to wildcats. Because 65 to 74% of the locations encompass more than 1 habitat category, the importance of habitat boundaries, especially forest edge was indicated. The animals studied showed individual and seasonal variation in habitat selection. The flexibility of wildcat habitat use during this study indicates the ability of wildcats to live in forested landscapes altered by humans and suggests that habitat may not be preventing wildcat recovery from low population numbers.

Acknowledgements

The presented project was part of a study conducted at the Institute of Biogeography at the University of the Saarland, Germany. I thank Dr. P. Müller, Institute of Biogeography, University of the Saarland for financial support and added telemetry data and H. Carius for telemetry field work. I am thankful to Dr. Bruce McLellan, Dr. Urs Breitenmoser, and Roger Ramcharita for comments on earlier drafts of this manuscript. Dr. Anne Olson and Dr. Dan Weary provided helpful comments on statistical analyses.

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Mamm. biol. **66** (2001) 371–375
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Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

Genetic distinction of roe deer (*Capreolus pygargus* Pallas) sampled in Korea

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Receipt of Ms. 17. 01. 2001
Acceptance of Ms. 30. 05. 2001

Key words: *Capreolus pygargus*, mitochondrial DNA, molecular taxonomy

The roe deer (genus *Capreolus*, Artiodactyla, Cervidae) includes two species: the smaller European (*C. capreolus*) and the larger Siberian (*C. pygargus*) roe deer (Groves and Grubb 1987; Sokolov and Gromov 1990; Hewison and Danilkin 2001), which have widespread distributions in central-western Europe, and in Asia and east Europe, respectively. They show a number of diagnostic morphologic, chromosomal and DNA traits (Groves and Grubb 1987; Heptner et al. 1989; Douzery and Randi 1997; Randi et al. 1998 a). Populations of the two species occur in putative contact zones in the Caucasus, where *C. capreolus* is distributed at the southern slopes and *C. pygargus* at the northern slopes of the mountain ranges, and along the rivers Volga and Don (Heptner et al. 1989; Danilkin 1996). However, most probably European and Siberian roe deer populations do not hybridize in nature where they overlap in distribution (Danilkin 1996; Hewison and Danilkin 2001).

Populations of the Siberian roe deer show extensive body size and coat colour variability, and up to six subspecies were recognized (Grubb 1993). However, recently Danilkin (1996) and Hewison and Danilkin (2001) recognized only two subspecies: *C. p. pygargus*, from western and part of eastern Siberia, and *C. p. tianschanicus*, from Tian Shan and eastern Asia, including Korea. Other authors referred to roe deer populations from Korea as a distinct subspecies, e. g., *C. p. bedfordi* (Sokolov and Gromov 1990), or *C. p. ochracea* (Barclay 1935). The genetic basis and taxonomical significance of morphological variation among Siberian roe deer populations are still unclear. Aim of this study is to assess the genetic distinction and clarify the taxonomic status of the *C. pygargus* population from Cheju Island in Korea.

Three specimens of roe deer from Cheju Island in Korea were collected and muscle samples were stored in a deep-freezer. Total cellular DNA was extracted from muscle samples digested for 2 hours at 55 °C in 500 µl of STE buffer (0.1 M NaCl, 10 mM Tris-HCl, 1 mM EDTA, pH 8.0), 25 µl of 10 mg/ml Proteinase K stock solution, and 25 µl of 20% SDS solution. DNA was extracted with equal volumes of phenol-chloroform and chloroform, precipitated with 2 volumes of ethylalcohol, and resuspended in 50 µl of distilled water. The solution was incubated at 37 °C for 30 min with 5 µl of 10 mg/ml RNase stock solution, and DNA was extracted again.

The entire mtDNA CR was PCR-amplified using primers L-Pro and H-Phe (Douzery

1616-5047/01/66/06-371 $ 15.00/0.

and Randi 1997; Randi et al. 1998 b) and the following thermal cycle: 94 °C for 5 min; 94 °C for 1 min, 72 °C for 1 min, 54 °C for 1 min (32 cycles); 72 °C for 5 min. PCR-amplified products were purified using the DNA PrepMateTM kit (Bioneer Co., Cheongwon-gun, Korea), and sequenced using an automated DNA sequencer (Perkin Elmer 377) at the Korea Basic Science Institute (Daejeon).

The new mtDNA CR sequences were aligned with homologous complete (Douzery and Randi 1997) and partial (Randi et al. 1998 b) sequences, using the computer program ClustalX (Thompson et al. 1997). Phylogenetic analyses were performed by maximum parsimony (MP), using paup* 4.0b 2a (Swofford 1998), with unordered character states (uninformative nucleotide positions excluded), 10 replicates of random addition of terminal sequences and TBR branch swapping, and by neighbor-joining procedure (NJ; Saitou and Nei 1987), with Tamura and Nei (1993) DNA distances (TN93), using PAUP*. Majority-rule (50%) consensus trees were constructed when multiple equally parsimonious topologies resulted from MP analyses. Robustness of the phylogenies was assessed by bootstrap percentages (BP; Felsenstein 1985), with 1000 random resamplings. Clades can be considered significantly supported when BP values are ≥ 70%.

PCR products were clean single bands of the expected molecular weight, and the sequencing allowed unambiguous nucleotide identifications. Regional organization of the CR from *Capreolus* was concordant with data from other cervid CRs (Douzery and Randi 1997; Randi et al. 1998 b; Nagata et al. 1998; Cook et al. 1999; Randi et al. 2001), thus suggesting that they represent true mtDNA sequences and not nuclear copies. The CR of *Capreolus* includes a central conserved region (CR-II), a left domain (CR-I, on the tRNAs Thr and Pro side), and a right domain (CR-III, on the tRNA Phe side; not shown).

A complete alignment 926 nucleotide long was obtained (the new sequences are available from the GenBank with accession nos. AJ311188 and AJ311189). The average TN93 genetic distance between the Cheju samples and European or Siberian roe deer was 4.5%, and 2.5%, respectively. Roe deer from Cheju showed two distinct mtDNA CR haplotypes, which diverged at 0.2% of their sequences. Moreover, we have aligned partial mtDNA CR sequences, 679 nucleotide long, obtained from 23 samples of European, Siberian, and Korean roe deer. Equally weighted MP analysis of the CR alignment (with 47 parsimony-informative characters) produced 90 trees (length L = 81; consistency index CI = 0.617; retention index RI = 0.881). The 50% majority-rule consensus tree is equivalent to the NJ phylogenetic tree, which is shown in Fig. 1.

MP and NJ trees concordantly showed that: (1) European and Siberian roe deer sequences split into two divergent evolutionary lineages (BP = 100%); (2) Siberian roe deer sequences split into three significantly different evolutionary lineages (BP = 70%–100%), including roe deer from east Siberia (Amur Region), Korea, and west Siberia (Kurgan Region); and (3) roe deer sequences from Korean individuals joined into a monophyletic dade (supported by BP = 91%), which was nested within the Siberian roe deer clade which is the sister clade of the roe deer sampled in the Kurgan Region (west Siberia).

Thus, mtDNA sequences support a genetic distinction between west Siberian and far eastern roe deer, in accordance with both Sokolov and Gromov (1990) and Danilkin (1996) taxonomical listings. The new mtDNA sequences analysed in this study strongly suggest that roe deer from Cheju island are more closely related to populations sampled from the geographically distant Kurgan Region in west Siberia (*C. p. pygargus*) than to those from the geographically close Amur region in south-east Siberia (Fig. 1). The mtDNA sequences from Cheju Island form a significantly distinct clade within *C. pygargus*, thus indicating that roe deer from Korea belong to distinct populations, and supporting Sokolov and Gromov's (1990) view that roe deer from

the far east including Korea, should be kept distinct from the other Siberian roe deer populations. The Korean peninsula is a part of eastern Asia within the Palaearctic region, and it is bound on the north by northeastern China and far eastern Russia. Cheju Island, the largest of the southern Korea islands, originated by a series of volcanic ac-

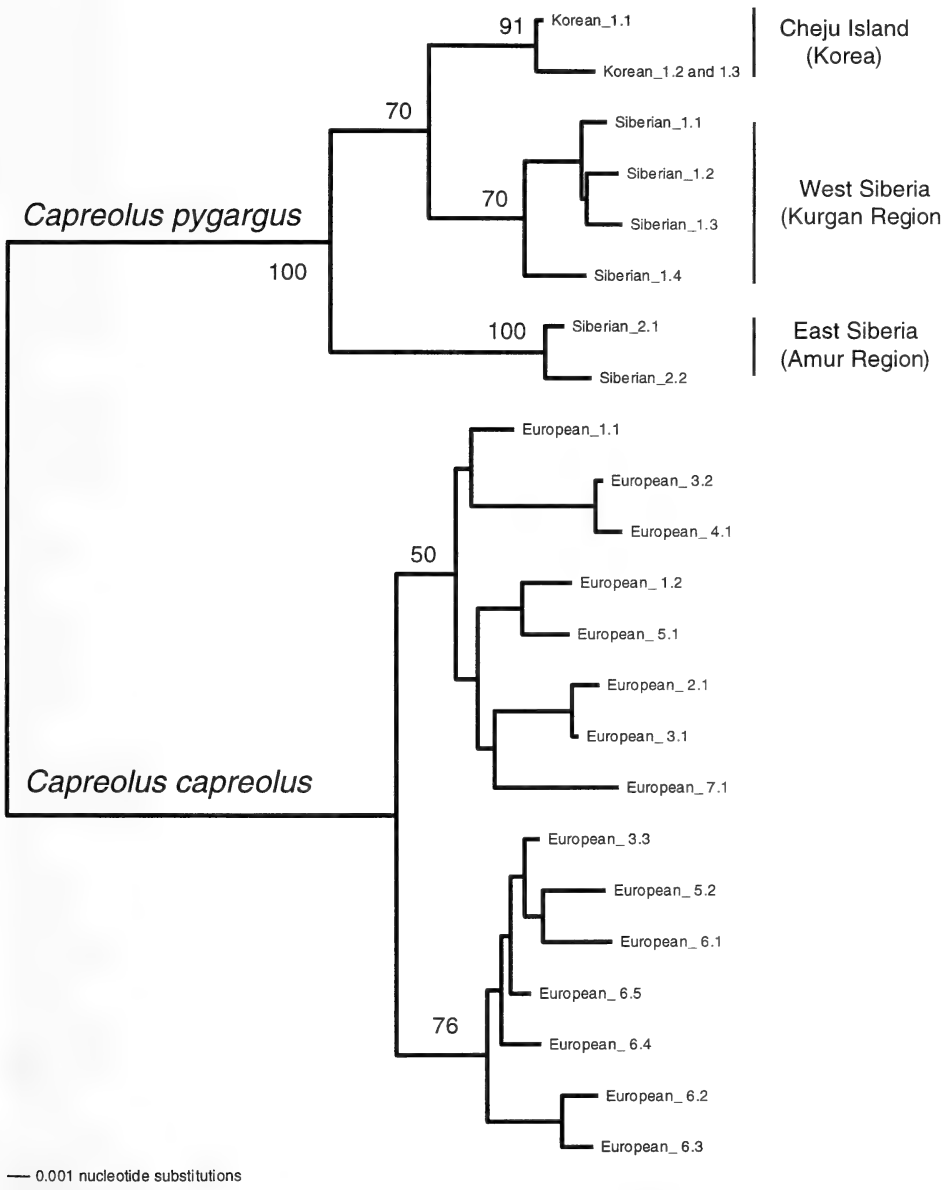

Fig. 1. Neighbor-joining tree (rooted using homologous *C. elaphus* mtDNA CR sequences as outgroups; not shown) clustering mtDNA CR haplotypes from *Capreolus*, computed using TAMURA and NEI (1993) DNA distances. At internodes are reported the bootstrap values ≥ 50%. For the identification of *C. pygargus* (Siberian) and *C. capreolus* (European) haplotypes, see: RANDI et al. 1998 b.

tivities at the end of the Tertiary (Park 1985). Cheju Island was connected to the Korean peninsula during the Pleistocene and separated again at the end of the last glaciation, about 10 000 years ago. Therefore, roe deer in Cheju could have evolved in isolation during the last 10 000 years. Koh et al. (1997) reported that roe deer from the Korean peninsula showed smaller body size and skull length than west and east Siberian roe deer subspecies. Thus, molecular and morphological data lend support to the view that roe deer from Korea do not belong neither to *C. p. tianschanicus* nor *C. p. mantschuricus* (= *bedfordi*), and might belong to a distinct subspecies, *C. p. ochracea*, as described by Barclay (1935).

Acknowledgements

This research was in part supported by the Korean Science Foundation (grant 97-0402-05-01-3 to Hung Sun Koh), and by the Italian Istituto Nazionale per la Fauna Selvatica (I.N.F.S.) and Consiglio Nazionale delle Ricerche (C.N.R.).

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Mamm. biol. **66** (2001) 376–378

http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

A new karyotype of *Heliophobius argenteocinereus* (Bathyergidae, Rodentia) from Zambia with field notes on the species

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Receipt of Ms. 05. 03. 2001
Acceptance of Ms. 11. 04. 2001

Key words: *Heliophobius argenteocinereus*, Bathyergidae, karyotype, field notes

The silvery mole-rat (*Heliophobius argenteocinereus*) is a little known member of the family Bathyergidae, endemic to east to central Africa eastern of the Great Rift Valley, south of Equator, and north of the Zambezi river, i. e., in Kenya, Tanzania, Zambia, Malawi, and Mozambique (Burda 2001). The only available information on the biology of *Heliophobius* is based on a few studies concerning physiology (McNab 1966) and burrowing and activity patterns (Jarvis and Sale 1971; Jarvis 1973). George (1979) described the karyotype of this species from Kenya. Since it resembled the karyotype of *Heterocephalus glaber* (both having 2 n = 60), she concluded that the whole family Bathyergidae is chromosomally rather conservative.

Regarding the fact that recently a large chromosomal variation (ranging from 2 n = 40 to 2 n = 78) has been found in *Cryptomys*, another bathyergid mole-rat (Scharff 1998; Burda 2001), the question arises in as much the karyotype established for a Kenyan population is representative for the whole genus *Heliophobius* which is distributed across at least 15 latitude degrees. To address this question we have examined karyotypes of *H. argenteocinereus* trom Zambia, i. e., close to the southern distributional limit.

Three silvery mole-rats (one male, two females), collected in August 1996 in the Lubalashi Area in the Central Province of Zambia (14°40′ S; 29°55′ E) about 160 km east of Lusaka, were examined.

Karyotypes were prepared from bone marrow following the splash method according to Ford and Hamerton (1956). Chromosomes were differentially stained with the C-banding (Sumner 1972) and G-banding (Seabright 1971) methods. Characterisation of chromosomes followed the nomenclature of Hsu and Benirschke (1967).

The diploid chromosome number in all the examined individuals of *Heliophobius argenteocinereus* from Zambia was 2 n = 62. The karyotype consisted of 27 pairs of metacentric and submetacentric chromosomes (autosomes) of decreasing size and 3 pairs of small acrocentrics (Nfa = 114). The X-chromosome was the second largest metacentric, while the Y-chromosome was dot-like (most probably metacentric).

The karyotype of *Heliophobius argenteocinereus* from Zambia (2 n = 62; Nfa = 114) is very similar to that of silvery mole-rats from Kenya (2 n = 60; Nfa = 114; George 1979). The difference between both karyotypes (one pair of metacentrics vs. two pairs

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of acrocentrics) is most probably due to a simple Robertsonian fusion or fission. Unfortunately, the poor quality of G-banding in both GEORGE's (1979) and our studies does not allow any detailed comparison and homologization of individual chromosomes. Although Robertsonian fusions are supposed to be more frequent than fissions in mammals (suggesting thus that the Zambian population would be more ancestral) (cf. also NEVO et al. 1986), the opposite process ot fission cannot be excluded (cf. NEVO 1999).

In view of the remarkable chromosome diversification of *Cryptomys* in the Zambezian region (i. e., in Zimbabwe, Zambia, and Malawi), yet its uniformity in the Southern African subregion (SCHARFF 1998; BURDA 2001), the relative constancy of the karyotype of *Heliophobius* is of particular interest. It can be assumed that, contrary to mole-rats in most of the Zambezian region, the populations of silvery mole-rats east of the Great Rift Valley have never been fragmented so that also isolation and speciation could not occur.

Regarding the paucity of data on silvery mole-rats, it is worth to mention observations which we made on the Zambian silvery mole-rats. Altogether eleven mole-rats (1 male and 6 female adults, 1 female and 3 male juveniles) were obtained in the Lubalashi Area, south of the Lunsemfa River in the Luano Valley, in miombo-woodland, mixed with few agricultural spots. The ground of the thin miombo forest was densely covered with tall grass which was partly burned by farmers. The adult male weighed 200 g, the average weight of the adult females was 146 ± 20 g (range 118–170 g; $n = 6$). Four females reared a single pup each. The male pups weighed 26 g, 34 g, and 48 g, whereas the weight of the single female pup was 37 g. At the time of capture (August 1996), the pups were haired and their eyes and ears were open. The high proportion of nursing females in the sample suggests a distinct breeding season, with (small) litters being delivered during the dry season (which lasts from April/May till October/November).

Burrow systems (identified by the presence of mounds) of silvery mole-rats were very unevenly distributed in the study area. The mounds measured about 30 cm (up to 50 cm) in diameter. Burrow systems consisted of a main straight tunnel with short side branches and reached about 50 m in length. Most parts of the main tunnels were only 10–20 cm deep but some parts went into depth of more than 150 cm. A few blind ending tunnels or "bolt holes" were found. Diameter of burrows was 8–9 cm on average. One breeding nest was hidden within the system of tree roots, 20–30 cm deep. *Heliophobius* has been observed in two occasions feeding on (undetermined) grass rhizomes. The grass also served as nesting material.

No macroscopic ectoparasites nor intestinal helminths have been found in any of the animals.

Although silvery mole-rats have been reported to be highly aggressive (JARVIS and SALE 1971; JARVIS 1973), our silvery mole-rats could be kept in pairs and have not engaged in serious fighting. Also, presence of juveniles was tolerated. One male offspring lived with its mother in a common cage for more than one year (three other juveniles died within three months of the capture). Furthermore, most of the adult silvery mole-rats were tame immediately after capture and did not try to bite.

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Mamm. biol. **66** (2001) 379–382
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Short communication

New distributional records of small mammals at Beni Biosphere Reserve, Bolivia

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Receipt of Ms. 29. 12. 2000
Acceptance of Ms. 30. 05. 2001

Key words: *Bolomys*, *Marmosops*, *Mycroryzomys*, *Oxymycterus*, Bolivia

The mammalian fauna of Bolivia is among the least known in South America (Pine 1982). Fortunately, the knowledge about the diversity and distribution of this fauna has been increasing in recent years (e. g., Anderson 1997; Eisenberg and Redford 1999). Currently, 316 species are recognized for Bolivia, 71% of which are small mammals. The geographic distribution of most species is based on a handful of records from a few sites (Anderson 1997). Consequently, new distributional records are needed to clarify further the biogeography of Bolivian mammals (e. g., Yensen et al. 1994; Tarifa and Anderson 1997).

Much sampling effort has been devoted to the northern highlands and La Paz valley (Ergueta and Sarmiento 1992). In the Amazonian region, the Beni Biosphere Reserve (EBB) has received considerable attention in recent years (Herrera-MacBryde et al. 2000), including sampling of bats, marsupials, and rodents (Cabbot et al. 1986; Wilson and Salazar 1989; Anderson 1997; Yáñez et al. 1998; Brace et al. 2000; see also Rumiz and Herrera 2000). The reserve lies in the Llanos de Moxos region, a center of high plant biodiversity. Furthermore, it is regarded as a key area for the conservation of threatened birds in the Neotropics (Brace et al. 2000; Moraes et al. 2000). Currently, only 11 species of small mammals have been registered, seven rodent and four marsupials (Cabot et al. 1986; Anderson 1997). However, despite the efforts allocated to inventorying mammals at the EBB, ongoing sampling of mammals at both a terra firme forest and forest fragments at El Porvenir ranch, EBB'headquarters, have revealed four new species for the region. Here we present these noteworthy records.

During 1996 a small live-trapping sampling bout was allocated to three forest fragments at El Porvenir (Yáñez al. 1998). Two others have been sampled since 1999. Forest fragments sampled during 1999 and 2000 are known as "Taita B" (2.2 ha) and "Airstrip B" (0.3 ha) (14°51′37″ S/66°19′68″ W 163; Brace et al. 2000). We also sampled the grassland neighboring a water course and marsh close to the forest fragment named "Porv A". The sampling site at the terra firme forest, known as "Campo Monos" is located roughly 45 km NW from El Porvenir (14°39′59″ S/66°04′60″ W and 130 m asl, see Moraes et al. 2000 for vegetation description). During 1999–2000, sampling consisted of live-trapping and collecting for four consecutive nights each time with 200 medium Sherman traps in linear transects, traps being 10 m apart. We have also examined prey remains

1616-5047/01/66/06-379 $ 15.00/0.

in 440 pellets of the barn owl (*Tyto alba*) collected at El Porvenir (VARGAS et al. unpubl.). All specimens collected have been deposited in the Coleccion Boliviana de Fauna (CBF), La Paz.

Marsupialia: Didelphidae

Marmosops dorothea (Thomas, 1912) is endemic to Bolivia and regarded as threatened by the IUCN (NOWAK 1999) This marsupial has a disjunct distribution with records in the humid Yungas of La Paz (840–2 300 m asl) as well as in the arid lowlands of Santa Cruz (250–620 m asl; ANDERSON and TARIFA 1996). Known from 23 localities and 46 specimens, the two areas of distribution are over 400 km apart (ANDERSON 1997). This broad disjunction led ANDERSON and TARIFA (1996) to suggest that two taxa could be involved. However, we collected it at Campo Monos, a record in the middle of the distribution gap challenging this contention.

A single subadult female (CBF 6442; TL 208, T 122, HF 15, E 18; 15 g) was captured (July 1999) in a seasonally flooded forest, close to the Curiraba river, the understory dominated by *Heliconia* sp, coinciding with known habitats of *M. dorothea* (EMMONS 1999). The single specimen represents 2% of small mammals captured in a total of 424 trap/nights. Besides *M. dorothea*, *Oecomys bicolor*, *Oryzomys capito*, *Philander opossum* and *Proechimys* sp. were also captured in the same habitat.

Rodentia: Muridae

Microryzomys minutus (Tomes, 1860): the pigmy rice rat is known from high elevations (2500–3000 m asl) in the Andes of Ecuador, Peru and Bolivia (EISENBERG and REDFORD 1999). lt has also been reported for the Monte Zerpa's cloud forest in Venezuela (DIAZ 1994). In Bolivia, it is known from 10 localities and 28 specimens of the Yungas from Cochabamba, La Paz and Santa Cruz (ANDERSON 1997). Despite being considered a highland species (e. g., NOWAK 1999), a subadult female (CBF 7078; TL 163 mm, T 90, E 14, HF 21, 12 g) was collected at Campo Monos in September 2000. It was captured in a forest tract with an understory dominated by *Heliconia* sp. In this habitat, *Marmosops dorothea*, *Oecomys bicolor*, *Oryzomys capito*, *Philander opossum* and *Proechimys* spec. were also captured. *Microryzomys minutus* represents 2% of the 52 individuals captured at Campo Monos, with a trapping success of 0.2% (one out of 424 trap/nights), suggesting it might be rare.

There were no records of *M. minutus* at the Department of Beni. This record extends its known distribution roughly 150 km NW of its previously recorded limits. Besides it biogeographical relevance, the record of *M. minutus* is of medical concern for EBB human populations, as this species might be a reservoir of human cutaneous leishmaniasis (ALEXANDER et al. 1998).

Oxymycterus spec. (Waterhouse, 1837): burrowing mice inhabit open grassland, marshes, swamps, and grasslands being rare in humid forests (EMMONS 1999). Three species including five subspecies are known from Bolivia, but their biology is unknown (ANDERSON, 1997). Of these species, *Oxymycterus inca iris* (Thomas, 1901), dwells in the humid forest of the Amazonian lowlands. In Bolivia it is known from 20 localities and 63 specimens from La Paz, Santa Cruz and the western portion of Beni. We recorded it as prey of *T. alba* at El Porvenir, extending its distribution 100 km NE. The single skull recovered represents 0.2% of the prey remains of *T. alba* over 1998–1999 (VARGAS et al. unpubl.).

Bolomys spec. (Thomas, 1916): a single skull of *Bolomys* spec. was found among the prey of *T. alba* (VARGAS et al. unpubl.). While the individual undoubtedly belongs to *Bolomys*, it was not possible to assign it to any of the three species known for Bolivia. *Bolomys amoenus* (Thomas, 1900) is known from four localities and just 13 specimens, being restricted to Cochabamba and Tarija at elevations from 3 800 to 4 000 m asl (ANDERSON 1997). However, ANDERSON (1997) includes the southeastern portion of Beni in its distribution with no further support. If our specimen represents *B. amoenus*, this record will increase its distribution 260 km NW denot-

ing also a notorious change of habitat. Another species, *B. lenguarurm* (Thomas, 1898) is widely distributed in the lowlands, including several records from western Beni (Anderson 1997; Anderson and Olds 1989). If the skull recovered at El Porvenir belongs to *B. lenguarum*, it would represent a further 120 km E expansion of its known distribution.

Twenty-two percent of Bolivian mammals are known from one to three localities (Anderson 1997). The four species reported here are hence comparatively better known regarding their geographic distribution. Even though and although EBB could be regarded as a relatively well known region (Herrera-MacBryde et al. 2000), these four new records clearly state that much field work needs to be done to assess fully the diversity and distribution of Bolivian mammals.

Acknowledgements

This work has been supported by Fondecyt 1981050 and 790003 to JAS. C. Miranda, EBB Director granted permit for collecting specimens. Support and encouragement of our collegues A. A. Grez, M. Moraes, and R. O. Bustamente is appreciated. We are indebted to I. Huareco for field assistance.

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Mamm. biol. **66** (2001) 383–384
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Mammalian Biology
Zeitschrift für Säugetierkunde

Book reviews

HOMES, V.: **On the Scent: Conserving Musk Deer – The Uses of Musk and Europe's Role in its Trade.** Brussels: Traffic Europe 1999. 57 pp. ISBN 90-9012795-X

As is commonly known the relationship between man and some wild mammalian species is extremely problematic. This holds true especially for those species whose bodily attributes are believed to be essential for human medical or cultural needs. Without doubt the musk deer belong to this group. In contrast to older assumptions of only one existing species in total four species of this small and primitive cervid genus are recognized in modern taxonomy (Himalayan musk deer – *Moschus chrysogaster*; black musk deer – *M. fuscus*; forest musk deer – *M. berezovskii*; Siberian musk deer – *M. moschifera*). These are distributed throughout a large region in Asia including certain parts of Afghanistan, Pakistan, Nepal, Bhutan, Myanmar, the Koreas, China, Mongolia, Kyrgystan, Kazakhstan, and Russia (eastern Siberia, far East, Sakhalin). Males of these species produce musk in an integumental gland and store this substance in the musk sac located between the navel and the sexual organ. Although some other mammalian species (i. e., muskrat – *Ondatra zibethica*; desman – *Desmana moschata*; musk oxen – *Ovibus moschatus*; suni – *Neotragus moschatus*) or plants (i. e., musk mallow – *Hibiscus abelmoschus*; musk rose – *Rosa moschata*; musk milfoil – *Achillea erba-rotta moschata*) are believed to produce similar aromas, these have nothing in common with the chemical substance of musk or with its odour and characteristics. Original musk exceeds most other natural constituents in smell intensity, persistence and fixative properties. In Asiatic and Arabic cultures it has been used by man for over 5000 years as a fragrance, fixative for other fragrances or in medicine as a tonic for the heart and mind, for chronic headache and, of course, as an aphrodisiac. In ancient times musk was introduced to the western world by Arabic doctors and since then increasingly has been in demand worldwide. Today, it is one of the most expensive substances derived from any animal. In Europe, for example, the price for musk per g during the 1990s reached three to five times that of gold. Consequently moschus deer males have been extensively pursued and hunted by native people with the aim to remove the entire gland (pod) and thus obtain musk. An adult deer male produces approximately 18 to 32 g of musk and by selling 2 musk pods (about 50 g) a Nepalese family in remote mountain regions is reported to have acquired at least a year's income. This situation has led to a serious decrease in numbers of deer. All musk deer species, therefore, have been included in the Appendices I or II of the Convention on International Trade in Endangered Species (CITES) since 1979 and the IUCN Red List of Threatened Animals from 1996 classifies these species as vulnerable or at least as nearly threatened. In Russia, e. g., between 1989–1993 a total of 90 to 100 thousand individuals was killed and the population size was estimated to be 53–60 thousand in 1996. However, poaching of deer and illegal trade with musk most probably still exists in vast regions of remote areas although musk deer farms have been established since 1958 in China and methods were developed to remove musk from live individuals without injuries. The brochure in hand is a thorough research report on the international trade and use of musk from musk deer carried out by TRAFFIC Europe-Germany between January and July 1998. It contains much information on the biology of these cervids, on their status as well as on the effects of conservation efforts.

D. KRUSKA, Kiel

1616-5047/01/66/06-383 $ 15.00/0.

YALDEN, D.: **The history of British mammals.** London: T. and A. D. Poyser Ltd. 1999. Hardcover, 305 pp., numerous black and white pictures, numerous maps and tables. £ 29.95. ISBN 0-85661-110-7.

In this time of specialisation and over-specialisation, when many authors seem to avoid overviews, it is wonderful to experience a book like that from DEREK YALDEN, the managing editor of the British "Mammal Review"! The author presents a broad approach to the problems related to "The history of British mammals". His presentation is based on own mammological investigations, publications dealing with questions of general zoology, as well as on information concerning domestic mammals, palaeontology, archaeology, biogeography and history. From these sources Dr. YALDEN has produced an authorative text that offers delightful and informative reading on up-to-date knowledge.

Short remarks on Mesozoic and Tertiary mammals introduce the reader to the subject at hand. A section on Pleistocene mammals follows; it is illustrated with instructive maps and tables. The second chapter deals with "the beginning of history" during the late Pleistocene, but also comparisons with mammalian faunas of continental Europe can be found. However, the "splendid isolation" of Britain since, at least, about 7 000 years before present, forms a biological "laboratory" with scientific problems different from those on the European continent. For the Roman, Saxon, Norse and Norman and later mediaeval periods of British history and for modern times, introductions of mammals, as well as extinctions of other species are described – once again illustrated by diagrams, maps and tables. In these paragraphs detailed information on surviving species is also supplied. The author also takes a look at the twentieth century and beyond. In a special chapter problems confronting mammals on large (Ireland) and small islands, such as Shetland, Orkney, Hebrides, Man, Scilly and Jersey, are addressed.

It is impossible in deal here with the multitude of stimulating ideas presented in this book. A very detailed list of references (24 pages) and an index of ten pages concludes this remarkable publication. As the author draws information from a wide range of sources, this is an outstanding reference source also for readers with specialised fields of interest. The present reviewer hopes that the book from DEREK YALDEN will find a wide distribution and can thus be appreciated by a wide range of mammalogists and lay persons!

P. LANGER, Giessen

ELTRINGHAM, S. K.: **The Hippos. Natural History and Conservation.** London: T. and A. D. Poyser Ltd. (1999). Hardcover, 184 pp., numerous black and white pictures and 8 black and white plates. £ 27.95. ISBN 0-85661-131-X.

This book gives detailed information on *Hippopotamus amphibius*, the river hippo. The data supplied for *Hexaprotodon* (*Choeropsis*) *liberiensis* (*pygmy hippo*), however, are still limited. For example, while eleven pages deal with reproduction in *Hippopotamus amphibius*, less than two pages deal with respective data in the pygmy hippo. Similar relationships can also be found in the chapters on behaviour and on diet and feeding habitals. These statements do by no means indicate criticism of KEITH ELTRINGHAM'S accomplishments, but they make obvious where the gaps in our knowledge are and where research efforts are necessary. Observations, not to speak of field experiments, of *Hexaprotodon liberiensis* will become increasingly difficult: Most pygmy hippos live in countries – Liberia and Sierra Leone – with practically no means of law enforcement and a wide distribution of firearms because of civil wars and social unrest. For the larger species, the river hippo, one "can conclude... that, over the whole of Africa, there is no immediate threat to the hippo as a species although some of the constituent populations are certainly at risk" (page 171).

The book deals with anatomy and physiology of both species, their palaeontological origins, their social life and reproduction, with diet and feeding habits, ecology, as well as diseases, parasites and commensals and with the relationships between the hippo species and man. Finally, the distribution of the two species is discussed. The origin of the wealth of information that is woven into the text is documented on six pages of references. Special questions can be easily accessed with the help of an index of six pages. The text is clear and direct and sometimes also humorous. It is obvious that the author often draws on his own profound research experience with both species!

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Mammalian Biology
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Mammalian Biology

Zeitschrift für Säugetierkunde

URBAN & FISCHER Verlag
Jena/Germany

ISSN 1616-5047
Mamm. biol. · 66(2001)6 · 321-384

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