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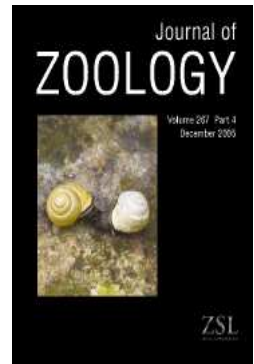
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Habitat use and diet of the American mink (*Mustela vison*) in Argentinian Patagonia

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DNA fingerprinting reveals high levels of genetic diversity within British populations of the introduced non-native grey squirrel (*Sciurus carolinensis*)

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INTRODUCTION

In general, if populations are founded by very small numbers of individuals, low levels of genetic diversity amongst subsequent generations known as founder effects, can be predicted to occur as a result of genetic drift (Franklin, 1980; Lacy, 1997). A loss of genetic variation has been reported in several species that have experienced genetic bottlenecks because of habitat fragmentation, geographic isolation or inbreeding depression (Gilbert *et al.*, 1990; Hoelzel & Dover, 1991; Ellegren *et al.*, 1993; Timms *et al.*, 1993; Wauters, Casale & Dhondt, 1994; Wauters, 1997). This loss of genetic diversity can have deleterious effects on reproductive output. For example, laboratory and captive breeding programmes provide extensive evidence of both decreased fecundity and reduced juvenile survival (Ralls & Ballon, 1982, 1986; Du Bois, Dhondt & Van Puijenbroek, 1990; Brock & White, 1992), and research conducted on natural populations of common shrews *Sorex araneus* has reported similar findings (Stockley *et al.*, 1994). However, genetic evidence from some wild populations shows that highly inbred populations can survive and thrive despite low levels of genetic variability (Gilbert *et al.*, 1990; Wayne *et al.*, 1991; Ellegren *et al.*, 1993). Grey squirrels *Sciurus carolinensis*, were introduced into Britain from eastern North America on several occasions between 1876 and 1910. Furthermore, between 1906 and 1937 grey squirrels were translocated to a variety of different locations within Britain (Middleton, 1931; Shorten, 1954). From the 1930s it rapidly expanded its range and is now ubiquitous to almost all of central and southern England, Wales and some lowland areas of Scotland (Lloyd, 1962, 1983; Gurnell & Pepper, 1993). In view of this highly successful colonization by an invading species the grey squirrel appears to have been unaffected by any loss of

genetic diversity as a result of recent population bottlenecks. We have used DNA fingerprinting (Jeffreys, Wilson & Thein, 1985a), a technique which provides a good indication of genome variability (Jeffreys *et al.*, 1985b; Kuhnlein *et al.*, 1990; Kunieda *et al.*, 1993) to assess overall levels of genetic diversity in two British grey squirrel populations; Alice Holt Forest on the borders of Hampshire and Surrey in southern England and Thetford Forest in East Anglia.

METHODS

Between January and August 1993, tissue samples were obtained from 14 squirrels from each population (see David-Gray, 1995). DNA was extracted from tail tips and 10 µg of DNA was digested with *Hinf*I (Pharmacia) for DNA fingerprinting. For details of electrophoresis, Southern blotting, probe labelling and hybridization conditions, see David-Gray (1995). We used the band-sharing coefficient, x (the probability that a band in an individual is in a second random individual) and the individual specificity of the DNA fingerprints, P (the probability that two unrelated individuals would have an identical fingerprint) for assessing genetic variability (after Jeffreys *et al.*, 1985b; Burke & Bruford, 1987). Band scoring was carried out under the assumptions that shared bands were always (1) identical alleles from the same locus, (2) were in linkage equilibrium and (3) had equal population frequencies. We were unable to carry out a segregation analysis to test these assumptions and therefore we are aware that the possibility of linkage disequilibrium among fragments cannot be discounted (Brock & White, 1991; Hanotte, Bruford & Burke, 1992).

RESULTS

Hybridization of Jeffreys' 33.15 probe to *Hinf*I digested squirrel DNA samples revealed complex individual banding patterns indicating that high levels of genetic

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Table 1. Comparative DNA fingerprint data for the Alice Holt and Thetford squirrel populations. Average number of DNA fragments scored (\pm SD) for each animal, the approximate size range of scored bands, allele frequency, and mean background band-sharing coefficient between unrelated individuals (\pm SD) are given. The probability of two unrelated individuals sharing the same banding pattern (individual specificity) is also shown

	Alice Holt	Thetford
No. bands/individual (n)	22.9 (\pm 3.90) $n = 14$	19.6 (2.60) $n = 14$
Size range (kb)	3–23	3–23
Allele frequency (q)	0.12	0.14
Mean background band-sharing (x)	0.22 (\pm 0.093) $n = 91$	0.26 (\pm 0.089) $n = 91$
Individual specific fingerprint pattern (P)	8.7×10^{-16}	3.4×10^{-12}

diversity existed in both populations. Band-sharing coefficients between individuals from Alice Holt ranged from 0.08 to 0.52 and between individuals from Thetford Forest from 0.11 to 0.51. The mean background band-sharing coefficient (x) was 0.22 ($n = 91$, $sd = 0.093$) for the Alice Holt population and 0.26 ($n = 91$, $sd = 0.089$) for the Thetford Forest population. The probability (P) that two unrelated individuals would have an identical fingerprint was calculated as 8.7×10^{-16} and 3.4×10^{-12} , respectively (Table 1). These results show that there was a significant regional difference in the levels of genetic variation between the two study sites ($t = 3.12$, $d.f. = 178.3$, $P < 0.01$), but overall the mean background band-sharing levels found in the two populations are similar to the studies from outbred genetically diverse small mammal populations, e.g. 0.16 in *Peromyscus californicus* (Ribble, 1991), 0.28 in *Dipodomys spectabilis* (Keane *et al.*, 1991) and 0.10 in *Sorex araneus* (Stockley *et al.*, 1993).

DISCUSSION

The results reported here demonstrate that populations of grey squirrels *S. carolinensis* in south-eastern England are genetically diverse despite their relatively recent arrival into this country. We believe that this is because the grey squirrel populations now found in Britain were not established from a small single introduction but from repeated introductions over several years of individuals from different source populations. Shorten (1954, after Middleton, 1931) lists nine introductions from the U.S.A. and two from Canada between 1876 and 1910, and 21 translocations within Britain (eight from Woburn in Bedfordshire) between 1892 and 1929. This combination of independent introductions has mediated against any founder effects and accounts for the high levels of genetic diversity found. The significantly higher level of background band-sharing in the Thetford Forest squirrel population may result from their relatively recent arrival into this area of

forest. Grey squirrels were not recorded in this area until the late 1960s. In contrast, the Alice Holt population was established in the early 1900s (Middleton, 1931; Lloyd, 1962, 1983). The differences in the levels of genetic diversity therefore may reflect genetic differences in the founder populations and/or the time period that has elapsed since colonization of the particular area.

Interestingly, the high levels of genetic variability are in direct contrast to that found in the European red squirrel *Sciurus vulgaris* by Wauters *et al.* (1994). Although red squirrel populations living in fragmented habitats showed lower levels of genetic variation in comparison to populations living in large continuous habitats, both had significantly increased levels of background band-sharing than that reported here. However, there was a negative correlation between band-sharing and immigration rate and it was concluded that the immigration rate per generation was the main factor in maintaining genetic diversity rather than total population size. Moreover, it appears that genetic diversity can be maintained by very low levels of gene flow. Theoretical models suggest that as little as one or two reproductively successful migrants can maintain genetic variability in subdivided populations (e.g. Allendorf, 1983; Boecklen, 1986; Varvio, Chakraborty & Nei, 1986; Gilpin, 1987; Lande & Barrowclough, 1987). Our results imply that the introduced British grey squirrel population has not experienced any loss of genetic diversity due to a genetic bottleneck. Although our sample size is small, the high levels of genetic diversity exhibited in the two squirrel populations today implies that the original populations were dynamic, with immigration and dispersal between subpopulations occurring regularly.

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Do emerging pipistrelle bats lose control of their timing due to 'crowd pressure'?

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INTRODUCTION

When bats emerge from colonies to feed and drink their emergence patterns deviate systematically from those expected at random (Kunz, 1974; Swift, 1980; Bullock *et al.*, 1987; Brigham & Fenton, 1986). In particular, many bats appear to group together as they emerge, and form into 'clusters' or 'outbursts' (but see McAney & Fairley, 1988; Kunz & Anthony, 1995 for exceptions). The function of this clustering behaviour has been the

topic of recent debate, with some authors favouring the hypothesis that the behaviour is an artefact of large numbers of animals moving through a restricted space (Kalcounis & Brigham, 1994) and others suggesting the behaviour has a more significant biological function such as protection from predation (Leen & Novick, 1977; Speakman, Stone & Kerslake, 1995) or information transfer (Wilkinson, 1992).

Separating between these hypotheses has proved difficult. Kalcounis & Brigham (1994) noted that a

goodness-of-fit statistic (χ^2), derived from software program for the analysis of clustering in emergence behaviour (Speakman, Bullock *et al.*, 1992; Speakman 1993) increased with colony size. They suggested that this effect was consistent with the bottleneck hypothesis. More recently, we have shown that although this goodness-of-fit statistic increased in relation to the extent of clustering it also increased as a function of sample size, even when the pattern of emergence remained constant. Thus the increase in the statistic as a function of emergence size might not necessarily reflect increased clustering (J. R. Speakman *et al.*, unpubl. obs.). In emergences of pipistrelle bats *Pipistrellus pipistrellus* we have shown that if the statistical artefact effect of emergence size is removed larger emergences are actually less clustered than smaller ones (J. R. Speakman *et al.*, pers. obs.). This does not mean that there is no effect of a bottleneck on clustering, but that the direction of the effect may be opposite that previously considered most likely. That is a bottleneck may disrupt clustering rather than promote it.

We have previously suggested (J. R. Speakman *et al.*, pers. obs.) a mechanism for this disruption. In larger emergences the large number of bats crowding to get out through the bottleneck may literally push bats out of the roost at times they would not otherwise choose, thus interfering with their ability to co-ordinate their behaviour with other individuals. In contrast, when fewer bats are emerging there may be no 'crowd pressure' effect and the bats may be able to synchronise their behaviour and produce clusters. Analysis of the extent of clustering throughout seven large emergences (> 400 individuals) supported this interpretation. At the start and end of emergences, when fewer bats were emerging, the pattern of emergence was significantly more clustered than in the middle of the emergence, when more bats were trying to get out. Indeed at the peak of emergence the pattern did not differ significantly from random on six of seven nights analysed. These observations are also consistent with observations made inside roosts of little brown bats *Myotis lucifugus* during emergences that suggest there is intense competition at the exit holes during peak emergence (Davidson & T. H. Kunz, pers. comm.).

In the present study we aimed to assess whether bats at the peak of emergence are forced to exit at times they might not wish to, in comparison to earlier and later in the emergence when they might exercise more control over their emergence behaviour. To investigate this possibility we exposed emerging bats to an aversive light stimulus for intermittent periods throughout emergences. We predicted that bats would avoid this stimulus more effectively when fewer were emerging, than under conditions of 'crowd pressure'.

METHODS

Observations were made at two roosts of pipistrelle bats (55 kHz phonotype: Jones & van Parijs, 1993) in north-

east Scotland during summer 1995. At each roost we made observations of the emergence behaviour on 12 unmanipulated nights to establish the usual pattern of emergence behaviour. On 5 further nights at one site, and four at the other, we performed manipulations using an aversive light stimulus. Bats are known to avoid daylight, probably because of increased risks of predation associated with flying in the light (Speakman, 1991; Jones & Rydell, 1994), and light intensity is well established to be the most important factor influencing the overall time that a colony leaves the day roost site. We thus expected that by shining a bright light on the roost exit we would provide a potent aversive stimulus likely to inhibit emergence.

On nights when manipulations were performed observations were started about 15 min before sunset. Average time of emergence of the first bat at these colonies is about 5–10 min after sunset. Immediately the first bat emerged a bright spotlight (Mazda 100 W car headlight linked to a 12 V car battery) was directed at the roost exit from a distance of about 5 m away. The light was left on for 30 s, and then switched off for 1 min. This cycle was repeated throughout the entire emergence. Throughout observations the emergence times of all bats was recorded by speaking into a dictaphone. The timing of events was analysed later using a timing program running. The on/off cycle of manipulations was continued until the emergence appeared to be over, i.e. no emergences recorded for 5 min. The light was then switched off and observations continued for another 10 min, in case any bats had failed to emerge during the period of manipulation. We assessed firstly whether bats avoided the light, and secondly whether their avoidance was contingent on the rate at which bats were emerging from the colony. The numbers of bats emerging at site one averaged about 500 (range 257–764) and at site two averaged about 250 (range 109–326).

RESULTS

A typical pattern of emergence (numbers emerging at 30-s intervals throughout the emergence) for each of the colonies, selected from the nights when no manipulations were made, is shown in Fig. 1a and b. At both sites the emergence was roughly normally distributed with low rates of emergence at the start and ends of the period and a peak of emergence in the middle. Typical manipulated emergences are illustrated in Fig. 1c and d. At roost one (Fig. 1c) the emergence was still normally distributed but was more fragmented and the total duration for the emergence (time from first to last bat) was increased by on average 12 min on manipulated nights. At roost two the effects of manipulation on the pattern of emergence were more profound (Fig. 1d) and the emergences became skewed with more bats emerging later.

The spotlight significantly inhibited emergence of bats (Table 1) on all but one of the nine manipulated nights

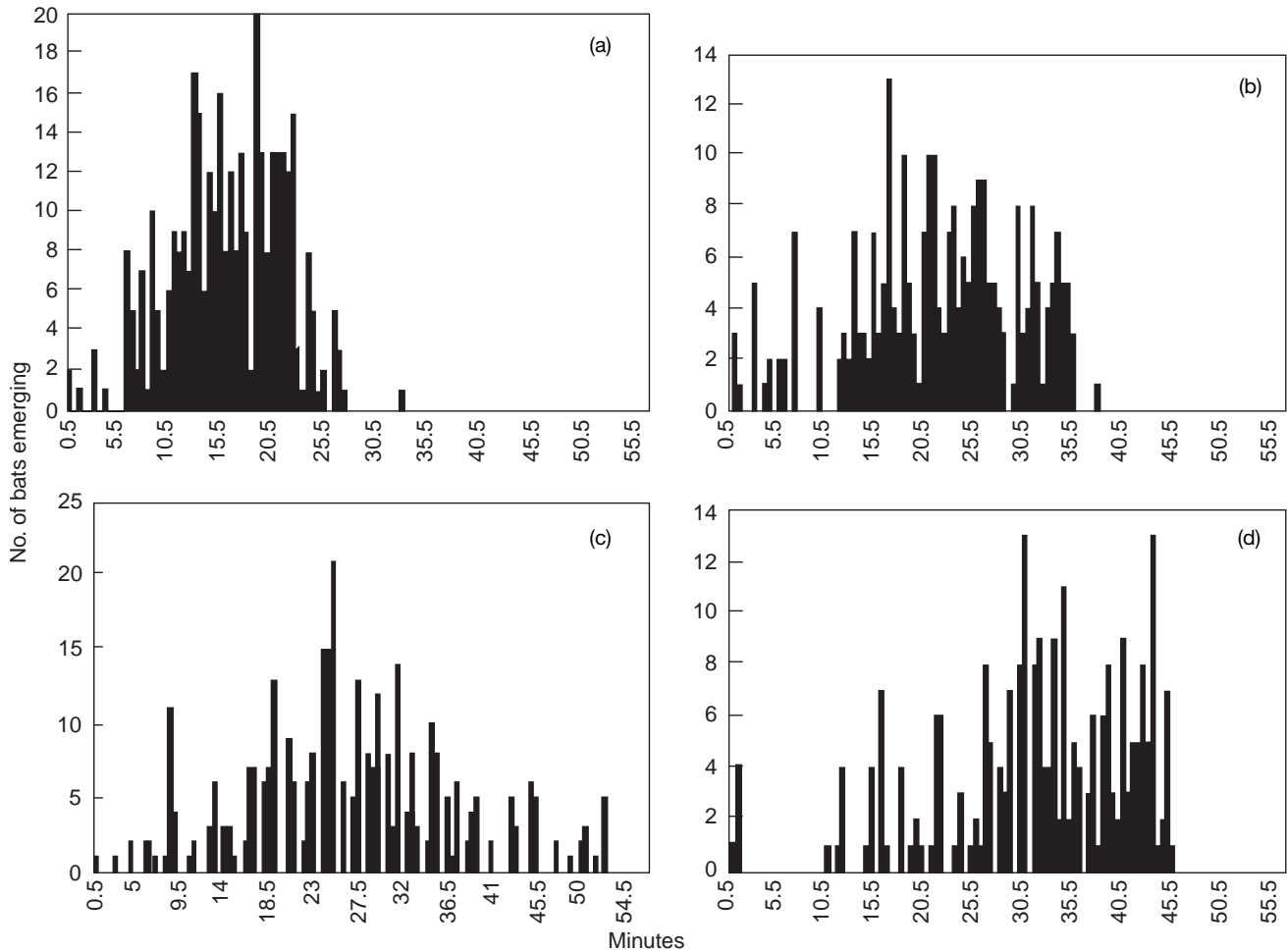


Fig. 1. Patterns of emergence at the two roosts on typical nights which were not manipulated (a, b) and nights which were manipulated (c, d). All four panels show the numbers of bats emerging at 30-s intervals throughout the entire emergence period.

Table 1. Median numbers of bats emerging during 30-s periods when light was shining on the exit hole, and during the following minute when no light was shining on the exit hole (separated into two 30-s periods : Dark 1 and Dark 2). Data are presented for nine emergences observed across two roosts. The significance (*P*) of the differences for each roost (Kruskal–Wallis ANOVA) are also presented

Roost	Light	Dark 1	Dark 2	<i>P</i>
1	1	3	5	0.007
1	1	6	8	0.001
1	1	2	3	0.003
1	1	3	3	0.21
2	0	2	4	0.001
2	0	5	3	0.001
2	0	2	6	0.001
2	1	1	3	0.005
2	1	2	4	0.001

(Kruskal–Wallis ANOVA, Table 1). There was no significant difference in the number of bats which emerged during the first 30 s after the spotlight was switched off and the number which emerged in the second 30 s after it was switched off. This suggests the

light was inhibitory but its effects did not carry over significantly into the immediately following dark period.

To assess whether bats avoided the light more effectively when fewer bats were emerging we related the numbers of bats emerging when the light was on to the number which emerged in the following 1 min dark period. The median number of bats emerging in the dark period was nine. When less than nine bats emerged in the dark period (mean = 4.5) the mean number of bats emerging in the preceding light period was 0.68 (*SD* = 1.25). However, when more than nine bats emerged in the dark period (mean = 16.9) the mean number of bats emerging in the immediately preceding light period was almost five times greater at 3.22 (*SD* = 3.63). The difference in numbers of bats emerging in the light between the times when many (> 9 in the following minute) and few bats (< 9 in the following minute)

were exiting was highly significant (ANOVA: $F = 10.9$, $P < 0.002$).

Despite the numbers of bats exiting in the light being much greater when more bats were exiting, this was not disproportionately so. Expressing the numbers emerging

in the light as a proportion of the numbers in the immediately following dark period revealed a proportion of 0.15 (SD=0.24), when few bats were emerging (< 9) and 0.19 (SD=0.18) when many (> 9) bats were emerging ($F = 0.55$, $P = 0.463$). A 2×2 (2 contingency table confirmed that summed across all manipulated emergences the numbers emerging in the light, when few bats were emerging, was not disproportionately lower than had emerged in the light when many bats were emerging ($\chi^2 = 0.99$, $P < .05$, d.f. = 1).

DISCUSSION

The aversion of light by emerging bats (Fig 1, Table 1) was not surprising given the wealth of data which indicate bats are probably nocturnal because of the risks of predation from diurnal birds (Speakman, 1991), and the many studies which have indicated that light levels are a primary stimulus triggering the onset of emergence behaviour (reviewed in Erkert, 1982). The function of these spotlight manipulations was to assess whether bats during the peak emergence are forced through the emergence holes by the 'crowd pressure' of bats pushing behind them, and thus have less control over the precise timing of their emergence behaviour than bats emerging when relatively few others are leaving the colony. If this was the case it would explain the decrease in the amount of clustering as colony size increases (J. R. Speakman *et al.*, pers. obs.) and the reduction in clustering around the period of peak emergence.

Despite five times more bats emerging in the light periods during periods when many bats were emerging this was not more than would have been expected if the numbers coming out in the light reflected only a constant proportion of those emerging in the following dark period. Disproportionately more bats did not come out in the light during intense periods of emergence. There are several possible explanations for these observations which at present we cannot separate. First, we may have demonstrated that there is no loss of timing control during the periods of peak emergence. Another possibility, however, was that the aversive stimulus somehow affected not only the bats immediately at the entrance, but also at times of intense emergence the bats which were presumed to be pushing from behind. In which case the extent of 'crowd pressure' by these bats may have abated when the light was on, resulting in no greater emergence than anticipated from the increased numbers passing through the holes. Given the orientation and size of the exit holes at the current study roosts it seems unlikely that even the bright lights we used were shining directly into the holes onto the crowd of bats pushing to get out. However, this latter interpretation does not necessarily depend on a direct effect of the light on the bats behind, since information that it was light outside could perhaps be communicated backwards from those bats at the front experiencing the stimulus. At present we can only state that the current findings are not consistent with the

hypothesized loss of timing control at peak emergence due to 'crowd pressure'.

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Use of artificial water supplies by captive-born mountain gazelles (*Gazella gazella*) released in central Arabia

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Abstract

Tagged, captive-bred mountain gazelles were released into Hawtah Reserve, Saudi Arabia. More than 1 year after they were freed, their drinking behaviour at two water troughs was recorded for 2.5 months during late summer /autumn, using automatic cameras and monitors triggered when an infra-red beam was broken. Only 30% of gazelles ($n = 40$) were recorded drinking and only individuals which lived close to troughs drank. No gazelles visited the one natural water point. Among gazelles which lived close to the troughs, older individuals were more likely to drink than younger animals. The noise of the cameras as they took a photograph frightened some gazelles and may have influenced their frequency of drinking after they were photographed for the first time.

INTRODUCTION

Reintroductions are often used to restore populations of Arabian ungulates (Stanley Price, 1989; Dunham, 1995; Haque & Smith, 1996). Some ungulates are common in captivity and captive-born mountain gazelles *Gazella gazella* were released in Saudi Arabia (Dunham, 1997). Mountain gazelles are small antelopes, formerly common on the Arabian peninsula (Harrison & Bates, 1991).

When gazelles are captive, their food is often dried and they drink water daily. After they are freed into the wild, their diet changes to a natural one, which has a greater moisture content than the food which they ate when captive. The volume of water drunk probably decreases, because water consumption depends on the moisture content of their food (Williamson & Delima, 1991). The higher moisture content of a natural diet probably supplies most or all of their water requirement (Carlisle & Ghobrial, 1968; Ghobrial, 1974) and access to drinking water may not be essential for survival. For instance, wild mountain gazelles on the Farasan Islands (Red Sea) breed year-round without access to fresh-water for drinking, except temporarily after rain (Habibi, 1992).

The purpose of this study was to monitor the use of artificial water supplies by captive-bred gazelles more than 1 year after release. The study started during late summer when all natural water points, except one which could easily be checked for signs of use, were dry. The study was ended prematurely, because monitoring equipment at troughs sometimes malfunctioned, causing gaps in the records, and because operation of this

equipment may have influenced whether some gazelles revisited troughs after being photographed at them.

STUDY AREA

Hawtah Reserve is 150 km south of Riyadh in central Saudi Arabia (23°30'N, 46°30'E). Annual rainfall (July–June) averages about 50 mm (Habibi & Grainger, 1990), but varied from 18 mm to 149 mm during the 5 years 1991–96. Precipitation is mainly confined to winter and spring, and summer is dry and very hot (mean daily maximum temperature > 40 °C). Rainfall was 99 mm during July 1992–June 1993 (the climate year which ended shortly before the start of this study), including 24 mm which fell on 12 May 1993. No further rain fell before or during the study period (20 August–6 November 1993).

The reserve covers about 2000 km² and comprises a limestone plateau incised by wadis. Plant standing crop is low on the plateau, but greater in the wadis. Domestic camels *Camelus dromedarius* feed in the reserve, but receive water and supplementary food from their owners. Wadis Ghaba and Ghafar form part of the Matham wadi system (Fig. 1) and are fenced to exclude camels, but the fences permit the free movement of gazelles. Gazelles may travel between Ghaba and Ghafar via the wadi floor, but often steep cliffs in the upper wadis restrict movement directly from the wadi to the plateau. Heavy rainfall causes flooding in the wadis, but water is found in the river beds for only the few days following rain. There is a perennial spring in Ghaba and there are seeps with surface water for several months after rain in both Ghaba and Ghafar. Both seeps were dry at the start of this study.

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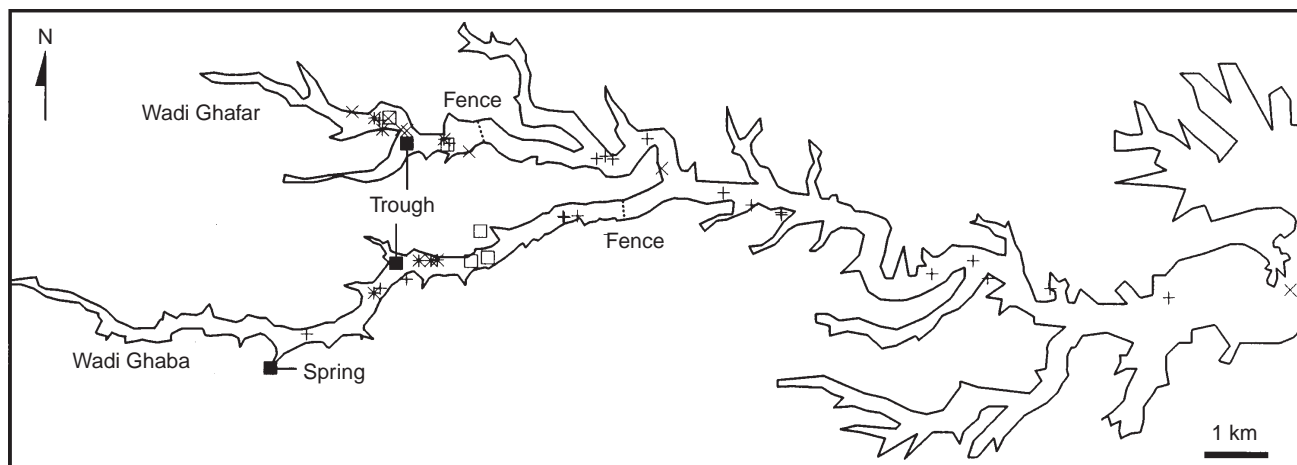


Fig. 1. The Matham wadi system in Hawtah Reserve, showing wadis Ghaba and Ghafar where gazelles were released, the camel-exclusion fences and the potential sources of drinking water (■). Each wadi contained a water trough and there was a perennial spring in Wadi Ghaba. The centre of the individual range of each released gazelle during August–November 1993 is shown: □, male which drank from a trough; + male which did not drink; * female which drank from a trough; × female which did not drink.

METHODS

Gazelle reintroduction in Hawtah Reserve

Mountain gazelles were freed in wadis Ghaba and Ghafar during 1991 and 1992 (Dunham, 1997). By August 1993, the population derived from these animals numbered about 97, including 40 (12 males and 28 females) that had been released and that were still alive at the end of this study. Released gazelles were captive-born at the King Khalid Wildlife Research Centre (KKWRC), where they ate concentrate pellets and dried alfalfa *Medicago sativa*, and had permanent access to water. Their dates-of-birth, or for the oldest animals their minimum ages, were known. Before release, all were fitted with a plastic ear tag, whose colour, shape, size and position permitted each individual to be identified. Some were also fitted with a metal tag and 11 wore a radiocollar. Wild-born gazelles were not tagged. Released gazelles are identified by the record number allocated to them while captive.

Before release into the wild, mountain gazelles were held for up to 1 month in a pen sited in their new environment (Dunham *et al.*, 1993). Here they had access to natural food plants, as well as the diet which they were used to eating in captivity and drinking water. They could change from their captive-diet to a natural one in their own time. After the releases, a water trough was provided in both Ghaba and Ghafar, close to the site of each pre-release pen, and the resident rangers of the National Commission for Wildlife Conservation and Development filled the troughs regularly.

Drinking behaviour

The 2 water troughs (1–2 m × 0.5 m), one each in wadis Ghaba and Ghafar, were partly surrounded by wire

netting so that gazelles could drink only from one long side. An infrared beam (Trailmaster TM1500 Active Infrared Trail Monitor; Goodson & Associates, Kansas, U.S.A.) and an automatic autofocus camera with flash (modified Olympus AF-1 Twin) were aligned along this side of each trough, with the beam approximately 50 cm above the ground. A gazelle approaching a trough broke the beam, causing the monitor to record the date and time and the camera to take a colour photograph. The monitor prompted the camera to take a photograph only if at least 2 min had lapsed since the previous photograph. The gazelles shown in the photographs could be recognized from their tag or collar. The beams operated from 20 August (Ghafar) or 21 August (Ghaba) to 6 November 1993. Ghaba spring was checked monthly for gazelle footprints.

Data analysis

The home ranges of freed gazelles and the territorial status of the males were known from a separate study (Dunham, 1998). Data from this were used to calculate the centre of the individual range of each gazelle. The range is defined here as the minimum-area convex polygon calculated with RANGES V (Kenward & Holder, 1996), using all sightings of an individual during August–November 1993.

In the absence of detailed meteorological data for the study area, data for air temperature and irradiance at the KKWRC, 200 km north of the study area but with a similar climate, are used for illustrative purposes.

Logistic regression (Cox, 1970) was used to determine which factors or variables affected whether individual gazelles drank and regression models were fitted with SYSTAT 4.1 (Wilkinson, 1988). The variables considered were: age on release (equal to the time spent in captivity, in years); age on 1 August 1993 (i.e. at the

beginning of the first month of the study, in years); and the distance from the centre of an individual's range to the nearest water trough (in km). These continuous variables were log-transformed before entry into the regression. The factors (i.e. binary variables) were sex (0 for male, 1 for female) and release site (0 for Wadi Ghaba and 1 for Wadi Ghafar).

Logistic regression models including different combinations of these variables were built by forward selection, using the procedure detailed by Green (1997). Initially, each variable was included in a 1-variable model and the significance of the effect of each variable was determined with a likelihood-ratio test. The variable with the highest significance was selected. Then the procedure was repeated, adding each remaining variable to 2-variable models, each of which included the selected variable. Incorporation of variables into the model continued until inclusion of any of those remaining did not cause a significant (at the 5% level) reduction in the deviance. At each step, the effect on the deviance of removing each included variable from the model was tested and only those whose effect was significant were retained in the final model. The entire model selection procedure was then repeated using the Bonferroni-adjusted significance level, which, with 5 variables, was $0.05/5 = 0.01$.

RESULTS

Use of water supplies

No gazelle footprints were found at the Ghaba spring, although water was present throughout this study, and it is presumed that gazelles never or rarely drank there. Of the 40 released gazelles in the population, 12 (30%) were photographed at one or other of the troughs. Three gazelles visited a trough once during the study, four visited on 2 days, two visited on 3 days and one each visited on 4, 17 and 52 days. All of these animals which drank (five males and seven females) had a home range which was centred < 1.5 km from a trough (Fig. 1).

The sample size was too small (12 released males) to determine if territoriality affected whether males drank, but both drinkers and non-drinkers included territorial males, non-territorial males and males which changed their status during the study.

Factors influencing which individuals drank

Data for 40 gazelles (12 which drank at least once and 28 non-drinkers) were included in the logistic regression analysis, to determine which factors influenced the probability that an individual drank (disregarding its frequency of drinking). When the effect of each variable on its own was considered, the distance from range centre to trough, the gazelle's age on 1 August 1993 (Fig. 2) and its age on release all had a significant effect on this probability (Table 1a). The effect of age on

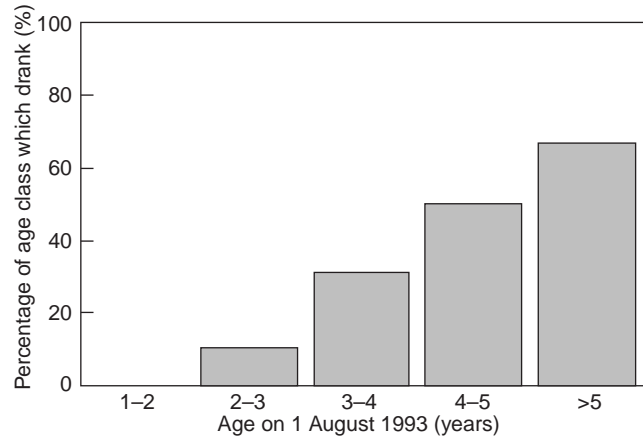


Fig. 2. The proportion of released mountain gazelles in each age-class which drank from the troughs at least once during the study increased with the age of the animals. $n = 4, 10, 16, 4$ and 6 , from left to right. There were no released gazelles < 1 year-old.

release was not significant when the Bonferroni-adjusted significance level was used. After the model selection procedure was applied (Table 1b, c & d), whether an individual drank was found not to be significantly related to its sex or the wadi where it was freed (Table 1d). The final model included the distance to the trough (negative effect), the age on 1 August 1993 (positive effect) and the age on release (negative effect). The effects of age on 1 August 1993 and distance were highly significant, while the effect of age on release was less so (Table 1c). When the Bonferroni-adjusted significance level was used, only the effects of the distance to trough and age on 1 August 1993 were significant. The final model was:

$\text{logit}(\text{prob}(\text{drank})) =$

$$5.0058 \times \log_e(1 + \text{age}_{1 \text{ Aug } 93}) - 3.0067 \times \log_e(1 + \text{distance to trough}) - 6.0857$$

Time of day when gazelles drank

Most gazelles (67%, $n = 12$) which drank made their first visit to a trough during 33% of the day, namely the two 4-h periods 04:00 to 08:00 and 16:00 to 20:00, i.e. the 2 h before and after dawn and dusk (Fig. 3). The timing of subsequent visits by some gazelles may have been influenced by the monitoring equipment (see below), but two females were photographed often enough to suggest that their behaviour was probably not affected. Female 135 (6.6 years-old) showed the same pattern as that for all drinkers, with 55% of her visits ($n = 20$ visits on 17 days) during the 2 h before and after dawn or dusk. Female 419 (aged 5.6 years) drank daily (at least during periods when the camera functioned) at the Ghaba trough, drinking once on 41 days and twice on 11 days, and most of her visits (68%, $n = 63$) were between dawn and noon, with a peak between 09:00 and 10:00.

Table 1. Logistic regression analysis of the variables which influenced the probability that individual gazelles drank from water troughs. Variables were: distance (from individual's range centre to the nearest trough, in km, log transformed); age on 1 August 1993 (in years, log transformed); age on release (in years, log transformed); sex (0 = male, 1 = female); and Wadi where released (0 = Ghaba, 1 = Ghafar). Data from five males and seven females which drank and seven males and 21 females which did not. For χ^2 , d.f. = 1

(a) One-variable models. The deviance associated with them and the significance of the effect of including the variable

Variable	Deviance	Significance of effect of including variable in model	
		χ^2	P
Distance	35.61	13.263	< 0.001
Age on 1 Aug 93	38.29	10.577	< 0.005
Age on release	44.50	4.364	< 0.05
Sex	47.79	1.078	NS
Wadi	48.16	0.707	NS

(b) Two-variable models, with distance as the first variable. The deviance associated with the models and the significance of the effect of including the second variable. For models in which including the second variable had a significant effect, the significance of the effect of removing the first variable is given

Second variable	Deviance	Significance of effect of including second variable in model		Significance of effect of removing first variable from model	
		χ^2	P	χ^2	P
Age on 1 Aug 93	27.41	8.192	< 0.005	10.878	< 0.001
Wadi	31.31	4.292	< 0.05	16.847	< 0.001
Age on release	33.35	2.256	NS	–	–
Sex	35.57	0.037	NS	–	–

(c) Three-variable models, with distance and age on 1 August 1993 as the first and second variables. The deviance associated with the models and the significance of the effect of including the third variable. For models in which including the third variable had a significant effect, the significance of the effect of removing the first or second variable is given

Third Variable	Deviance	Significance of effect of including third variable in model		Significance of effect of removing second variable from model		Significance of effect of removing first variable from model	
		χ^2	P	χ^2	P	χ^2	P
Age on release	21.60	5.814	< 0.025	11.750	< 0.001	17.556	< 0.001
Wadi	24.91	2.504	NS	–	–	–	–
Sex	26.72	0.693	NS	–	–	–	–

(d) Four-variable models, with distance, age on 1 August 1993 and age on release as three variables. The deviance associated with the models and the significance of the effect of including the fourth variable

Fourth variable	Deviance	Significance of effect of including fourth variable in model	
		χ^2	P
Sex	19.28	2.316	NS
Wadi	19.58	2.020	NS

The data set

Some photographs showed gazelles which were obviously frightened (probably by the noise of the motor which focused the camera lens immediately prior to a photograph being taken). The drinking behaviour of these animals may have altered after they were photographed for the first time. Thus, data on the frequency of drinking may be biased for some animals, although data relating to the first visit by individuals was unbiased.

An additional problem was that the cameras sometimes failed. Sometimes this was for unknown reasons, or because the flash failed to fire, and occasionally a film ended sooner than expected. The monitors showed that the cameras functioned properly on 75% of days ($n = 153$ camera days in total) and for some of the 24 h on a further 13% of days, which means that they worked correctly about 81.5% ($75 + (0.5 \times 13)$) of the time. Most individuals (75%, $n = 12$) recorded at a trough visited on two or more

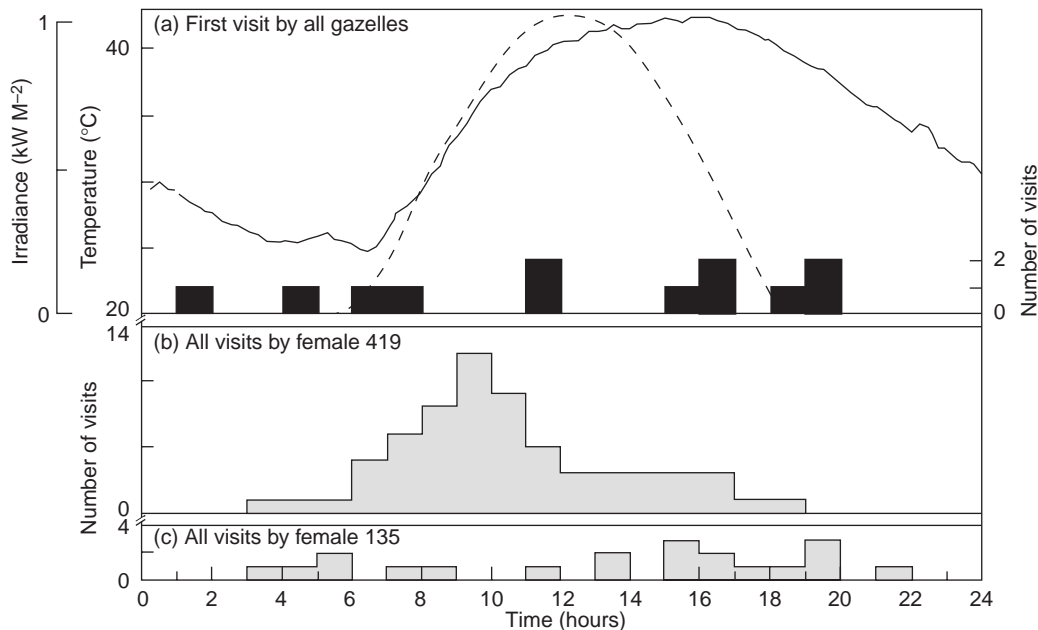


Fig. 3. The time of day when gazelles drank. (a) The time when 12 individuals first visited a trough (histogram) in relation to the diurnal variation in air temperature (solid line) and irradiance (dashed line) at KKWRC on 22 August 1993, the first full day of the study. (b) The time when female 419 drank ($n = 63$ visits = 41 days with one visit + 11 days with two visits). (c) The time when female 135 drank ($n = 20$ visits = 14 days with one visit + 3 days with two visits).

days and were photographed three or more times (twice during one visit).

DISCUSSION

The gazelles at Hawtah did not use the natural water point, a perennial spring, during this study. The logistic regression analysis revealed that the probability that a gazelle drank from a trough was high if the individual was old and if its home range was centred close to a trough. None of the 19 gazelles with a range centred > 1.5 km from a trough drank, regardless of their age (age range of these gazelles was 1.3–6.6 years at start of study). Amongst gazelles living close to a trough, the probability that an individual drank increased with its age: only one of the five gazelles younger than 3 years-of-age drank, but all four of those > 5 years-old drank. The territorial status of males did not obviously influence whether they drank.

Most gazelles (70%) did not drink, which suggests that supplies of drinking water were not essential for the survival of captive-born gazelles, at least not during the late summer and autumn study period. Possibly more gazelles drank during mid-summer.

Gazelles which drank during this study probably did so simply because water was available and close-by. An abundant supply of drinking water would reduce thermal stress (Williamson *et al.*, 1992) as water evaporates through the skin to reduce the body temperature (Ghobrial, 1970). This would permit gazelles to spend

more time feeding in the direct sun (Tatwany & Goldspink, 1996). Also, when drinking water was available, gazelles would need to obtain less water with their food and thus could eat relatively dry food (Ghobrial, 1974), perhaps permitting them to consume a wider range of food items than that eaten by gazelles without drinking water.

Some gazelles living close to troughs did not drink and these were usually younger animals (nine of 10 were < 4 years-of-age). The reason why a greater proportion of older gazelles drank is unclear. Possibly, kidney efficiency declined in older animals, so that they were unable to concentrate urine to the same extent as when young, thus requiring them to compensate by increasing water intake, which was most easily done by drinking.

The times of first visits by all drinkers and those for all visits by female 135 show that the hours around dawn and dusk, particularly dusk, were the preferred times of day to drink. Nonetheless, female 419 showed a different pattern, preferring to drink during the late morning.

Female 419 was also unusual in the frequency with which she visited a trough, drinking once or sometimes twice daily. Female 135 visited the same trough as 419, but drank on only one-third as many days, and so, on average, she visited the trough on one day in every three. But even this drinking frequency was relatively high, because about half of the gazelles which drank visited a trough on only 1 or 2 days during the entire study.

The cameras sometimes frightened gazelles. Therefore it is impossible to tell if the rare records of visits by

some animals were a genuine measure of the infrequency with which they preferred to drink, or if these animals were discouraged from drinking again after having been photographed once or twice. While the data on the frequency of visits may be biased, the photographs do show which individuals approached the troughs at least once and the time of that visit.

Records of which gazelles drank and when were interrupted by various problems: birds perching on a camera knocked it out of alignment; sometimes a flash failed to fire; occasionally a film ended sooner than expected. Sometimes gazelles could not be identified because only one ear was visible in a photograph. Possibly some gazelles visited a trough only at a time when a camera failed and therefore were wrongly regarded as non-drinkers. In practice, the combination of the high camera success rate (> 80% overall) and the low percentage (25%) of single-visit animals amongst the known drinkers suggests that few if any gazelles are likely to have drunk unrecorded.

An active transponder system (Hutchings & Harris, 1996) would be a better alternative method to use. Drinking by gazelles, each tagged before release with a unique transponder, could be detected by an aerial buried close to a trough and recorded by a controller. Gazelles would be unaware of the system, which would record only tagged animals drinking and not other untagged species.

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Estimating the population density of *Galemys pyrenaicus* in four Spanish rivers

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INTRODUCTION

In spite of the studies carried out for several decades on *Galemys pyrenaicus*, no paper has specifically estimated

desman densities, although indirect information can be inferred from the studies in the French Pyrenees on the use of space by Stone & Gorman (1985) and Stone (1987a).

The present work examines the density of Iberian desman in four mountain streams in northern Spain, the most favourable area for the species in the Iberian Peninsula (Queiroz *et al.*, 1994).

STUDY AREA

Four search campaigns were carried out in mountain rivers during summer 1991. Two searches took place in the Cantabrian mountain range in July, the first in the Autonomous Community of El Principado de Asturias, in the Pigüena River, near the village of Pigüena (Natural Park of Somiedo) and the second in the Muniellos River, near Tablizas (Biological Reservation of Muniellos). Two more trapping sites were selected in August on the Spanish side of the Pyrenees, one in Navarra (National Game Reserve of Quinto Real), in the Arga River, near the village of Eugui and one in the Urrobi River, near the town of Burguete.

Both Cantabrian trapping sessions were carried out in streams with similar features: 5–8 m width, near 1 m/s of current velocity and a discharge of over 1 m³/s. In both cases a dam was located around net number 10. In Somiedo the use of a small hydroelectric power station brought about a notable decrease of the water flow downstream, and, in Muniellos, the dam has been neglected since 1975 so a continuous water flow exists.

Pyrenean streams present some different features from those of the sampled Cantabrian streams. Their width was similar but their current velocity and their discharge were lower (around 0.2 m/s and 0.1–0.2 m³/s), the summer water temperature was between 1 °C and 3 °C degrees higher, and the wooded canopy of the riverbanks was less dense.

MATERIAL AND METHODS

For trapping purposes, 3 m long unbaited nets were used close to the river banks and were partially submerged to allow the survival of captured desmans, according to the method described by Peyre (1962) and Richard (1973).

In every sample station, 15 nets were set at intervals of 100 m, for 4 nights. Each net was checked day and night, at least 4 times every 24 h to avoid deaths resulting from starvation or cooling.

Since the average home range lengths for males and mated females are 429 m and 301 m, respectively, and they take 2 days to explore the complete territory (Stone, 1987a), the distance of 100 m between nets guarantees that the minimum requirement of a distance between nets being a quarter of the longest axis of the average home range (Spitz, 1969), is fulfilled. With this distance between nets, we guessed that during the 96 h of every trapping session, each individual should come close to some net at least 6 times. According to these home range sizes and with the spatial organization showed by Stone & Gorman (1985), a transect of

1400 m could allow, theoretically, a catch of 6 individuals of stable residence, if the occupation of the territory by fixed couples were complete, plus other vagrant or juvenile individuals.

Given the short trapping period, animals were marked only by cutting a fingernail, using Twigg's (1975) coded system, so that this slight marking should allow identification of the individuals and avoid injuries due to amputations during the trapping session.

In this study recaptures have been scarce. From a total of 23 specimens caught, only 3 were recaptured, at 170–269 m away from the point of release.

Because of the low rate of recaptures of *Galemys pyrenaicus* we estimated their density using a removal sampling method that considers only animals caught for the first time. Thus, density was obtained using the Zippin method of successive removals based on the constant catch probability during the trap period, in such a way that, having a constant catch effort, the number of animals caught per night diminishes noticeably over time (Zippin, 1956).

To verify whether the catches fitted the condition of significant reduction during the 4 nights, we used the criteria recommended by Smith *et al.* (1975), which state that the significance level of the linear correlation coefficient between daily catches and the cumulative previous catches should be lower than 0.05.

Specimens were weighed and measured in order to obtain the biometrical values for distinguishing juveniles from adults. We found no specimens under 50 g, a value given by Peyre (1962) and Stone (1987b) to identify both age categories.

Specimens were sexed by feeling of the pubic symphysis externally as described by Richard & Vallete Vaillard (1969) and by measuring the distance between the anal and urinary papillae, which is longer in males.

RESULTS

In three cases, the recommended condition of a the daily catch decrease was attained. The Muniellos River sample only reached a marginally significant value ($P = 0.72$), but was considered suitable owing to the difficulty of using the low figures obtained over only 4 days and the small error showed by the density estimation.

In our study, the densities obtained vary between 2.8 and 7.3 individuals/km and its estimations bear an acceptable degree of accuracy (Table 1). Only at the Pigüena River is the confidence interval very wide, even though the correlation coefficient, as a value of the decreasing catches, is adequate ($P < 0.02$); the confidence limits may become larger because of the slow decrease of daily catches.

The catches were not homogeneously located along the sampled streams. In all the samplings, catches were concentrated in a part of the transect, other portions remaining empty of desmans, since neither desmans nor spraints were found. The average density of spraints

Table 1. Number caught and densities of desman, with a confidence interval of 95%

Rivers	Catches	Individuals/km	% occupied by desmans	Individuals/km adjusted
Pigüena	7	7.3 (\pm 5.5)	50	14.6
Muniellos	7	5.0 (\pm 1.3)	65	7
Arga	4	2.9 (\pm 0.1)	62	4.7
Urrobi	3	2.8 (\pm 0.2)	70	4.1

was 13.3/km in the stretches of river where the catches took place, and 3.3/km in the no-catch areas. Somiedo catches and spraints were limited to the stretch located upstream of the dam, with no signs of their presence downstream where the water flow was low. In the remaining streams, desmans were also caught only in part of the sampled stretches, but there are no apparent habitat differences to explain their absence elsewhere. In the Muniellos and Urrobi Rivers desmans were taken in the first half the transect while in the Arga River animals were taken around the central area. Between 30 and 50% of the sampled river lengths had no desmans, i.e. approx. 40% of the checked areas seemed to lack desmans. This apparent void could be interpreted as areas of low probability of capture, filled, in the best of cases by non-resident individuals.

If we adjust the densities to refer only to the occupied areas (Table 1) their values are almost double.

There were 10 males to 12 females, figures which do not differ from the expected sex ratio of 1:1 ($\chi^2 = 0.045$; d.f. = 1; $P = 0.5$).

Most of the specimens ($n = 16$) were caught at sunset or in the first night hours, fewer were caught before sunrise ($n = 8$) and a small number ($n = 2$) came into the nets during daytime.

DISCUSSION

Although the density values obtained are precarious because of the low number of desmans captured, they are quite similar for the different locations and probably represent adequate values.

Our results agree closely with those obtained by Stone & Gorman (1985) for an Artillac stream (French Pyrenees), although they used different methods. Thus, the presence of a couple of desmans every 429 m (the male territory is the limiting factor for the settling of other resident couples) means the existence of 4.7 individuals/km, practically the average of our densities. If desmans are only present in 60% of the sampled stream lengths, the adjusted densities (Table 1) for the Spanish Pyrenean side are very close to the ones expected from French Pyrenean data. In the Cantabrian streams the density is higher and this could be due either to more vagrant individuals or to territories being shorter; our trapping system does not allow us to tell which.

Peyre (1956) also noted river stretches lacking desmans and he considered them to be unfavourable

areas within suitable habitats. Similarly, Richard (1973a) has noted that some tracts of river always give good trapping results, but in other seemingly similar tracts of river no captures are made. In most of our sampling areas, there were no appreciable habitat changes between occupied and unoccupied areas, the only exception being the severe reduction of the water flow downstream caused by the dam in the Pigüena River, where no desmans were caught and no dipper *Cinclus cinclus* were observed. The presence of *G. pyrenaeicus* is very closely related to that of *C. cinclus* because their foraging strategies are the same, especially during the breeding season (Bertrand, 1993).

The desman densities we obtained were from areas where the environmental conditions seem to be optimal for the species. In any case, our trapping results show a lower density of desmans from the Pyrenees than from the Cantabrian range, although it is impossible to establish any reason for this difference. In the Mediterranean mountains where the desman is present, density will foreseeably be much lower. Qualitative trapping in the Sistema Central gave very poor results (J. Gisbert, pers. comm.). This suggests large unoccupied zones between demes of animals concentrated in the most favourable points.

The time distribution of catches through the day also shows evidence of intensive nocturnal activity greater than that expected from the timing activity pattern given by Stone (1987b). A main nocturnal activity is clear but it appears to be divided into two peaks: the most intensive activity being around 23:00 and less activity between 4:00 and 5:00. Diurnal catches did not reach 8% of the total and occurred between 10:00 and 14:00 (official summer time).

Several improvements could be made to our methods for future studies. Moving the trapping season to a later date will probably cause a larger number of juveniles to be caught and allow for easier identification of adults. In this study it was not possible to get authorization for trapping until the end of the fishing season and, starting in July, we did find individuals weighing under 50 g while 18% of desmans captured by Stone (1987a) from May to July weighed under 45 g. The distance between traps seems to be adequate given the home range of the species, so to increase the catch number and therefore the reliability of the results, the length of the trapping line could be increased to 2–3 km. In practice, it could prove difficult to maintain a constant catch effort using many nets because the large size of the nets makes them

obvious and vulnerable. In our survey, the theft of several nets nullified the results of two other desman trapping sessions.

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Summer foods of the Andean hog-nosed skunk (*Conepatus chinga*) in Patagonia

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INTRODUCTION

The Andean hog-nosed skunk *Conepatus chinga* inhabits South America from Bolivia in the north to as far south as Neuquén province in Argentina (Redford & Eisenberg, 1992). In spite of its wide distribution and its value as a furbearer in Argentina (Fujita & Calvo, 1982), little is known about Andean hog-nosed skunk ecology, including its foods. It seems to forage solitarily during the night in open savannas and in arid and shrubby areas (Cabrera & Yepes, 1960; Mares *et al.*, 1996), capturing arthropods (mainly beetles and arachnids) and occasionally small mammals and preying on eggs and fledling birds (Cabrera & Yepes, 1960; Redford &

Eisenberg, 1992; Mares *et al.*, 1996). Here we present the first quantitative study on the diet of this species, based on the analysis of faeces collected during the summer season in two localities in Argentinean Patagonia.

STUDY AREA AND METHODS

Faecal droppings were mainly collected during January–February 1995 in two areas, 22 km apart, called Sañicó and Puesto Alamo. Sañicó is a high, rocky, flat and dry area 700 m above sea level, whereas Puesto Alamo is a more rainy grassy area in the bottom of a river valley, 800 m above sea level. Both sampling plots were in the Andean Precordillera, in north-western Patagonia (70°30'–71°30'W; 39°30'–40°20'S), which includes steep elevational (from 600 to 1400 m above

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Table 1. Foods of the Andean hog-nosed skunk *Conepatus chinga* in north-western Argentinean Patagonia during summer. Diet is expressed as percent occurrence in scats and percent biomass ingested for two different localities. *N*, number of faeces; figures in parentheses, values of large taxonomic groups

Localities	Percentage occurrence in faeces			Percentage biomass ingested		
	Puesto Álamo (<i>n</i> = 56)	Sañicó (<i>n</i> = 33)	Total (<i>n</i> = 89)	Puesto Álamo	Sañicó	Total
Vertebrates	(16.1)	(45.5)	(30.3)	(46.1)	(69.8)	(55.0)
Mammals	(12.5)	(9.1)	(12.4)	(34.0)	(24.5)	(30.4)
Rodents						
Long-haired field mouse <i>Akodon longipilis</i>		3.0	1.1		7.8	2.9
Yellow-nosed field mouse <i>A. xanthorhynchus</i>	1.8		1.1	4.9		3.0
Olivaceous field mouse <i>A. olivaceous Akodon</i> spp.	1.8		1.1	1.3		0.8
Darwin's leaf-eared mouse <i>Phyllotis darwini</i>	1.8		1.1	1.3		0.8
Unidentified	3.6		2.2	0.3		0.2
Lagomorphs						
European hare <i>Lepus europeus</i>	1.8		1.1	5.9		3.7
Carnivores						
Andean hog-nosed skunk <i>Conepatus chinga</i>		6.1	2.2		16.3	6.1
Ungulates						
Guanaco <i>Lama guanicoe</i>	1.9		1.1	11.7		7.4
Amphibians	(1.8)	(3.0)	(2.2)	(0.5)	(5.7)	(2.5)
Unidentified						
Reptiles	(3.6)	(39.4)	(16.9)	(11.2)	(37.5)	(21.1)
Sauria		24.2	9.0		31.6	11.9
Ophidia	1.8		1.1	11.0		6.8
Eggs	1.8	18.2	7.9	0.2	1.4	0.7
Unidentified		3.0	1.1		4.5	1.7
Birds	(1.8)	(3.0)	(2.2)	(0.4)	(2.0)	(1.0)
Birds		3.0	1.1		2.0	0.8
Eggs	1.8		1.1	0.4		0.2
Invertebrates	(94.6)	(90.9)	(93.9)	(51.3)	(26.0)	(41.7)
Arthropods	(94.6)	(90.9)	(93.9)	(44.8)	(21.4)	(36.0)
Insects						
Formicidae	1.8		1.1	0.5		0.3
Orthoptera	28.6	9.1	21.3	8.5	0.9	5.6
Orthoptera eggs	7.1		4.5	1.6		1.0
Coleoptera	82.1	75.8	79.8	27.2	19.8	24.2
Coleoptera larvae	3.6		2.2	4.4		2.7
Lepidoptera pupae	1.8		1.1	0.4		0.3
Lepidoptera larvae	3.6		2.2	0.7		0.4
Unidentified		3.0	1.1			0.1
Chelicerata						
Scorpiones	14.3	6.1	11.2	1.0	0.6	0.9
Aranae	12.5	3.0	9.0	0.7	0.2	0.5
Annelids	(17.9)	(30.3)	(22.5)	(6.4)	(4.6)	(5.7)
Unidentified						
Vegetal matter	(3.6)	(6.1)	(4.5)	(2.6)	(4.3)	(3.3)
Fruits	3.6		2.2	2.6		1.7
Unidentified		6.1	2.2		4.3	1.6

sea level) and rainfall (from 300 to 1000 mm) gradients (Pearson & Pearson, 1982). The climate is cold, with frosts throughout most of the year and frequent snowfall in winter. Topographically, the area consists of plains at 700–900 m above sea level dissected by steep rugged valleys and large rivers. The habitat is dominated by scattered low bushes (e.g. *Mulinum spinosum*, *Schinus molle*) usually <1 m tall, and mixed with bunchgrass (e.g. *Festuca palescens*, *Poa* spp., *Senecio* spp.).

Although we recognized and collected faeces of several species of mammalian carnivores in the area,

including pumas *Felis concolor*, South American wildcats *Felis* spp., South American foxes *Pseudoalopex* spp. and grisons *Galictis cuja*, we were unable to find faeces of skunks. Almost by chance, we discovered the tip of a mass of insect remains emerging from the sand close to a rock and near skunk tracks. By scratching in a small zone where the sand was flattened, we found a buried dropping rather similar, but smaller, to those of the European badger *Meles meles* made of arthropods. Since then, we recognized this kind of smoothed sandy soils in small caves at the base of rock piles and cliffs and successfully collected skunk faeces by scratching

there. The aspect and the placement of the skunk faeces make it impossible to confuse them with those of other carnivores from the area. The collected faeces were dried and weighed before separating their components by hand. Mammals were identified to the species level based on their hair and bone remains, by using a collection of reference and the keys by Pearson (1986). Birds and amphibians were identified to the class level, reptiles to the subclass level and invertebrates to the order or family level.

To make our results comparable with most descriptions of carnivore diets, we expressed them in terms of percent occurrence for each prey type. Additionally, we estimated the ingested biomass, because this is a more realistic way to express the diet of any predatory species. We calculated the mass of the undigested matter from each prey type. Next, conversion factors were applied to correct biases caused by differential ingestion and digestion. A conversion factor is the consumed weight of the prey item divided by the dry weight of undigested matter of this prey in the faeces and can be estimated by feeding tests. We used those developed by Lockie (1959) for red foxes *Vulpes vulpes* and afterwards used them for different carnivore species, such as the pine marten *Martes martes* (Lockie, 1961) and the European badger *Meles meles* (Martín, Rodríguez & Delibes, 1995).

RESULTS

We analysed 89 faecal droppings: 56 from Puesto Alamo and 33 from Sañicó. A wide variety of food types, ranging from berries to vertebrates and carrion, were represented in the whole sample (Table 1). Arthropods occurred in >90% of each sample. The best represented group was Coleoptera, including imagos as well as larvae, followed by Orthoptera. Chelicerata were also important. Vertebrates occurred in a lower proportion of faecal samples (<45%). Main differences in vertebrate occurrences between Puesto Alamo and Sañicó were among reptiles (Table 1). Other prey were earthworms, which occurred in 18–30% of samples, and berries (3–6%) (Table 1).

When the results were expressed as estimated ingested biomass, vertebrates predominate over invertebrates in the Sañicó sample (70% and 26%), but were of similar importance in the Puesto Alamo sample (46% and 51%). Foods of vegetal origin were unimportant everywhere (3% and 4% of biomass in Puesto Alamo and Sañicó, respectively).

The occurrence of some large mammal remains in faeces, such as guanacos *Lama guanicoe* and probably hares *Lepus europaeus*, strongly suggests that the skunks occasionally consume carrion. Also, we found in two faeces an abundance of skunk hairs suggesting cannibalism, maybe through the consumption of carrion (hare and skunk carcasses are frequently found on the roads).

DISCUSSION

Skunks (Mephitinae, Mustelidae, Carnivora) are usually described as opportunistic omnivorous feeders (Rosatte, 1987). Striped skunks *Mephitis mephitis* rely heavily on easily procured food materials such as birds' eggs, nestlings, frogs, insects, voles and carrion (Aleksiuk & Stewart, 1977). This can probably be applied to most skunk species, including Andean hog-nosed skunk, which preys seem to be easy to capture, the species being more a 'harvester' than a hunter.

Hog-nosed skunks *Conepatus* spp. are reported as primarily insectivorous, their peculiar long and flexible nose adapted for capturing ground beetles in shallow burrows, grasshoppers, crickets and fruit (Howard & Marsh, 1982). Also, their long claws and well-developed forelimbs suggest that these skunks usually dig to locate prey.

In our study site and period the Andean hog-nosed skunk fitted this general description, because it consumed vertebrates, invertebrates and fruits, but insect remains composed the bulk of its faeces. Also, the habit of digging was confirmed by the relative high frequency of remains of insect larvae and reptile eggs in the faeces. However, vertebrate prey contributed to the diet in a much greater quantity, judging by prey biomass rather than judging by percent occurrence. The same was observed for the burrowing owl *Speotyto cunicularia* in Chile, which was rather considered 'carnivorous' instead of 'insectivorous' as previously proposed (Silva *et al.*, 1995). It is likely that the importance of vertebrates to the diet of *Conepatus chinga* will be even higher in winter, when invertebrates are less abundant, as reported for other hog-nosed skunks (Bailey, 1931 in Howard & Marsh, 1982).

High trophic diversity of the Andean hog-nosed skunk results both from intra and intersite prey variation. We can speculate that the high frequency of occurrence of reptiles in Sañicó could be related to the rocky habitat, while in the grassy Puesto Alamo rodents should be more abundant. Dietary changes can be expected in opportunistic foragers such as skunks with season and geographic location.

Some aspects of the ecology of the close relative and rather smaller (Fuller *et al.*, 1987) Patagonian hog-nosed skunk *Conepatus humboldtii* have been studied in Torres del Paine National Park in southern Chile, where a grassland-shrubland steppe similar to that found in our study area prevails (Johnson, Franklin & Iriarte, 1990). Skunks in Torres del Paine were found foraging in open grassy habitats and feeding primarily on insect imagos and larvae, roots and small vertebrates (Fuller *et al.*, 1987; Johnson, Fuller *et al.*, 1988; Johnson, Franklin *et al.*, 1990). The ecological similarity of *Conepatus chinga* and *Conepatus humboldtii* could explain their strong interspecific geographical segregation, as the former is present mainly north of 40°S latitude and the second one south of there, although their ranges overlap in a narrow strip in northern Patagonia (Redford & Eisenberg, 1992).

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Fraser's dolphin (*Lagenodelphis hosei*) stranded in South Uist: first record in U.K. waters

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On 3 September 1996, B. Neill, investigating the peculiar behaviour of three ravens, found them disputing over a freshly dead dolphin stranded on the shore at Bornish, South Uist, Western Isles, Scotland (National Grid ref: NF 721 300). Neither he nor M. Bones, who collected the skeleton, could immediately identify the dolphin, despite having seen most of the species recorded around the Western Isles, although we suggested that it might be an Atlantic white-sided dolphin *Lagenorhynchus acutus* with an aberrant colour pattern.

The dolphin was 2.47 m long and was male, with a slim body, short beak, small dorsal fin and flippers, and a definite angle on the keel just behind the anus. The left eye had been pecked out; there was superficial grazing to the left side of the thorax but otherwise no sign of damage and no indication of the cause of death.

Figure 1 shows the colour pattern observed. The upper part of the dolphin was dark grey, and the under-part white with a pinkish tinge. The tip of the lower jaw was grey, the edge between grey and white running back from a point near the front of the jaw to the anterior

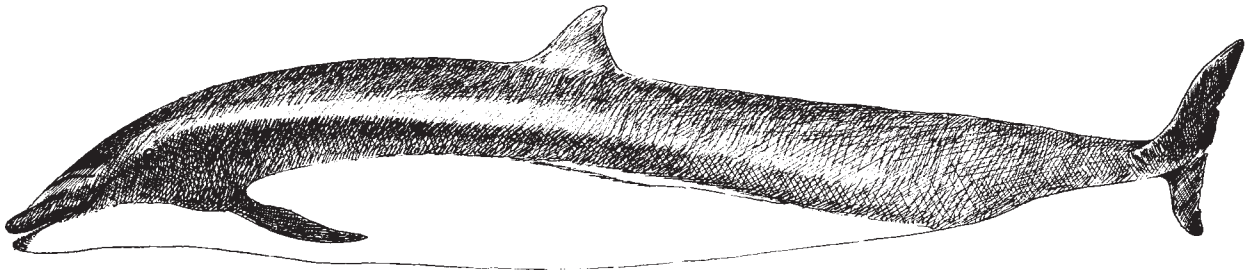


Fig. 1. Pattern of grey and white on the Bornish dolphin. Drawing by Bill Neill.

edge of the flipper, which was dark grey. Above the flipper, the line between grey and white curved forward slightly, then ran back almost in a straight line to a point between the genital slit and the anus, the tail being all grey. Within the dark grey upper part there was a long pale band above and roughly parallel to the edge of the grey, running from just above the inner end of the mouth, over the eye and back towards the anus. A thin irregular grey line ran just below the edge of the grey from a point below the dorsal fin to a point above the genital slit. There were two parallel pale grey stripes along the edge of the melon just above the beak.

While filleting the dolphin to retrieve the skeleton, parasitic cysts were seen in the blubber in the posterior half of the body, especially in the genital area. The stomach was empty. A piece of skin and two teeth were sent to the Scottish Agricultural College Veterinary Centre in Inverness for further investigation, the results of which will be included in future reports from the Scottish Strandings Scheme.

The return of the photographs prompted a reconsideration of the suggested identification: we were unable to assign the dolphin to any species previously recorded in British waters. A brief survey of popular literature suggested that the colour pattern of the Bornish dolphin matched that of Fraser's dolphin *Lagenodelphis hosei*. This was supported by the increasing frequency of sightings of this species in the Atlantic, and the group stranding of 11 dolphins in Brittany in 1984 (van Bree *et al.*, 1986). It was helpful to see photographs showing variations in the detail of the pigmentation pattern (Perrin, Leatherwood & Collet 1994; Perrin, Best *et al.*, 1973).

The only Fraser's dolphin skeleton known in Britain is the type specimen in the Natural History Museum, London, collected in Sarawak in 1895 and described as a new species by F. C. Fraser in 1956. The skull from Bornish was taken to London, and found to be essentially the same as that of the type specimen. Fraser noted two features in particular which distinguish this species from *Lagenorhynchus*: fusion of the premaxillae in the middle line and pronounced grooving of the palate. Skulls from the French stranding show that fusion of the premaxillae is related to age, and in the Bornish skull, while the mesial margins of the premaxillae are contiguous, they are not fused. They are of similar width along the whole length of the beak, as in *Lagenodelphis*, rather

than converging slightly, as in *Lagenorhynchus acutus*, and there is distinct grooving on the palate. There are sockets for 41 and 42 teeth in the right and left maxillae respectively, and 40 and 42 in the right and left sides of the mandible respectively: these figures fall within the range recorded for *Lagenodelphis* but are greater than generally recorded in *Lagenorhynchus*. Minor differences between the Bornish skull and the type specimen can be attributed to individual variation and, perhaps, a difference in the age of the dolphins.

Since the features of the skull confirm the identification of the dolphin from the external appearance as Fraser's dolphin, this stranding becomes the first record for this species in the British Isles, and, to the best of our belief, the second in Europe. It is, however, only within recent years that the majority of British strandings have been examined in any detail. In Scotland, this has been encouraged by the Scottish Strandings Scheme, funded by the Department of the Environment since it began in January 1992. This underlines the importance of increasing public awareness regarding the reporting of strandings.

The skeleton will be deposited with Museum nan Eilean, the Western Isles Council Museum Service.

Acknowledgements

We would like to thank Theya Molleson and Ian Stevenson for help in obtaining copies of relevant articles, and Drs Richard Sabin and P. Jenkins for giving access to the Fraser's dolphin skeleton (BMNH 1895.5.9.1) at the Natural History Museum.

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Wing shape in New Zealand lesser short-tailed bats (*Mystacina tuberculata*)

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INTRODUCTION

The theoretically optimal shape of a bat's wing changes with flight mode (Norberg, 1987; Norberg & Rayner, 1987) and several studies have shown this theory to be largely born out in practice (Aldridge & Rautenbach, 1987; Norberg & Rayner, 1987; Crome & Richards, 1988). For instance, bats with wings of relatively low surface area (high wing loading) that are also relatively long and thin (high aspect ratio) tend to be fast, straight fliers spending most of their flying time foraging or commuting in open areas such as pasture or above the forest canopy (Norberg & Rayner, 1987). In such bats manoeuvrability is improved by the possession of small, pointed wing tips to reduce drag. In contrast bats with wings of relatively high surface area that are also relatively short and wide with large, rounded wing tips tend to be slow, highly manoeuvrable fliers foraging in cluttered habitats such as woodland (Norberg & Rayner, 1987).

The New Zealand lesser short-tailed bat *Mystacina tuberculata* is one of only two species of bat currently recognized in New Zealand, both of which are endemic. At present three populations of *M. t. tuberculata* are recognized: one from the north of the North Island (*M. t. aupourica*), one from the central plateau of North Island (*M. t. rhyacobia*) and one producing geographically discontinuous records ranging from the south of North Island to Codfish Island off the south coast of South Island (*M. t. tuberculata*) (Daniel, 1990).

Mystacina tuberculata is an omnivorous bat restricted to indigenous forest habitat. It roosts primarily in tree holes and feeds mainly on arthropods but also on fruit, nectar and pollen (Daniel, 1976, 1979). That much of the arthropod prey of *M. t. tuberculata* is caught either on the ground or on the trunks of trees is implied by the high proportion of undigested fragments of non-flighted species found during faecal analysis. For instance, of a sample of 325 droppings from Codfish Island, 24% contained spider remains, 11% weta and 9% weevils (Arkins, 1996a; see also Arkins, 1996b for diet of *M. t. aupourica* from Little Barrier Island). Daniel (1979) tentatively estimated the proportion of foraging by *M. tuberculata* accounted for by ground, foliage and tree-trunk gleanings to be 0.3, while that accounted for by aerial insectivory, frugivory and nectarivory was 0.3, 0.2 and 0.2, respectively. If bats spend a large pro-

portion of time foraging on the ground, we might expect there to be adaptive pressure for the development of wings that facilitate vertical take off (i.e. wings of relatively high surface area = low wing loading).

Similarly, if most of the flighted arthropod prey is caught by aerial hawking within the forest itself then we might expect to find wings adapted for slow (by necessity), highly manoeuvrable flight in a cluttered environment. Based on general observations of flight in free-living individuals of both New Zealand bat species (*M. tuberculata* and *Chalinolobus tuberculatus*) Stead (1936; quoted in Daniel, 1979) suggested that *M. tuberculata* was the less agile of the two species while Daniel (1979) suggested that *M. tuberculata* was the slowest flier.

In this study we determined various measures of wing shape in *M. t. tuberculata* from Codfish Island and compared them with previously published measures for other bat species (as reviewed by Norberg & Rayner, 1987). We were interested in establishing whether wing morphology in this species agreed with what we might predict for a bat that flies in a highly cluttered environment (relatively short wings = low aspect ratio) and that could benefit from low speed agility for hawking around vegetation (small, short, rounded wing tips) and an ability to take off easily and efficiently from the ground (low wing loading) (see Norberg & Rayner, 1987 for a detailed discussion).

METHODS

We trapped 26 male and 9 female short-tailed bats at night below the forest canopy using mist nets set to trap bats flying at 1–3 m above the ground (Dilks, Elliot & O'Donnell, 1995). Captured individuals were immediately weighed (+ 0.1 g), fitted with metal bands around the forearm to permit future identification and then retained in captivity (as part of a separate trial on short-term captive management of *M. t. tuberculata* – see Sedgely, 1996) in communal wooden roost boxes within a free-flight aviary. Captive bats were provided with an *ad libitum* supply of water and mealworms and weighed at regular intervals to ensure body mass was maintained. Over the following few days individuals were removed from the communal roost box and the length of their right forearms (+ 0.05 mm) determined using callipers. For each individual the right wing was

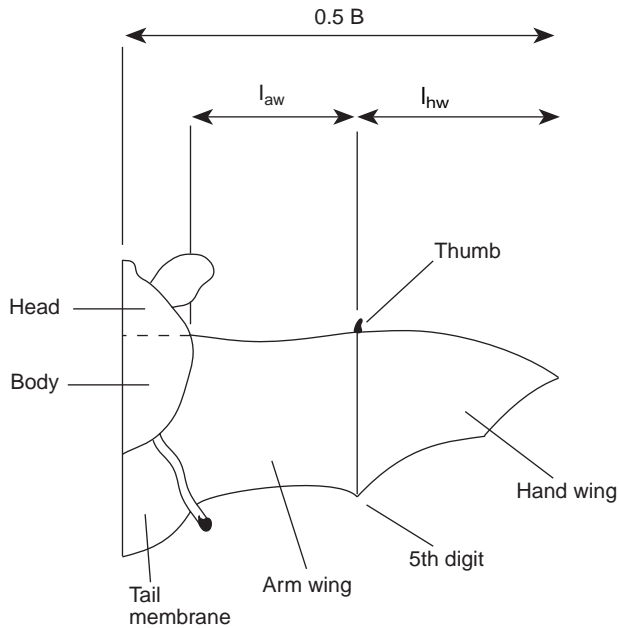


Fig. 1. Important features for the determination of wing shape. See text for a detailed description of measurements.

then opened fully and its outline together with that of the head and the unfurled tail were traced onto white paper. The position of the thumb, the free ends of the digits of the hand, the shoulder, the foot and the tip of the tail were marked on the trace (Fig. 1). From this trace were calculated the wing span (B = the distance between the wing tips when the leading edge is as straight as possible), the area of the right hand-wing (S_{hw}), the area of the right arm-wing (S_{aw}), the length of the right hand-wing (l_{hw}), the length of the right arm-wing (l_{aw}) and half the total wing area ($0.5 S$ = the combined area of the right hand wing, the right arm wing, the tail membrane between the right leg and the tail and half the area of the body between the wings) (see Fig. 1).

The following morphological ratios were then calculated:

- i. Wing-loading (WL) = Body mass at capture / S
- ii. Aspect ratio (AR) = B^2/S
- iii. Tip-length ratio (T_1) = l_{hw} / l_{aw}
- iv. Tip-area ratio (T_s) = S_{hw} / S_{aw}
- v. Tip-shape index (I) = $T_s / (T_1 - T_s)$

The calculated ratios were compared with expected ratios for an 'average' microchiropteran bat of the same body mass calculated from previously published values for other species as reviewed by Norberg & Rayner (1987). Expected ratios were calculated either as the mean value across all species where the ratio was independent of body mass, or as the ratio predicted from least squares linear regression analysis of log transformed data where the ratio was mass dependent. A ratio was considered to be significantly different to that expected for a microchiropteran bat of the same

body mass if it fell outside the 95% confidence limits for the expected ratio.

RESULTS

There was no significant affect of sex on any of the measures although the difference in forearm length was close to significant (two sample t -test; Table 1). Mean \log_{10} wing loading, aspect ratio, tip length index, tip area index and tip shape index all fell within the 95% confidence intervals of expected values for a microchiropteran bat of similar body mass (Table 1; Fig. 2a–e). Even if a subjective case were to be argued only mean \log_{10} tip shape index could be said to be different (in this case higher) to the predicted mean value (Fig. 2d).

DISCUSSION

We expected *M. tuberculata* from Codfish Island to possess wings of relatively low aspect ratio and relatively low wing loading, which they did not. Neither did they have especially rounded, short or small wing tips. The wings of *M. t. tuberculata* do not therefore appear to be especially well adapted for slow, agile flight in a cluttered environment or for ease of take off from the ground (Norberg & Rayner, 1987). Perhaps then these bats are not the specialists in highly manoeuvrable flight within the crowded forest understorey that we might initially suspect in a deep-forest dwelling species. We do not know how much time *M. tuberculata* spend flying nor where most flight occurs (e.g. below, within or above the forest canopy), nor the relative contribution of aerial hawking, gleaning and terrestrial foraging to prey capture.

Analysis of dietary remains in the faeces of *M. tuberculata* (Arkins, 1996a,b) implies that at least a proportion of time is spent foraging on the ground or on the trunks of trees. At least some of the arthropod prey is flighted, however (Arkins, 1996a,b) and could in theory be caught either on the ground or during flight in the air. *Mystacina tuberculata* are certainly adept at terrestrial locomotion and scuttle around in leaf litter and on the trunks of trees (with an 'astonishing rodent-like agility'; Daniel, 1979) using the hind feet and wrists as points of contact. The strong, stocky hind legs are presumably an advantage in this form of locomotion. Rather than initiating take off from the ground by flapping the wings, however, individuals seem rather to launch themselves into the air from all fours (P. I. Webb, unpubl. obs.). Perhaps such a mechanism for take off circumvents the necessity for low wing loading.

Also, although most of our observations of *M. t. tuberculata* in flight have been within the forest understorey, this may simply be because this is where we have spent most of our time looking. We have not, for instance, made any attempt to locate *M. t. tuberculata*

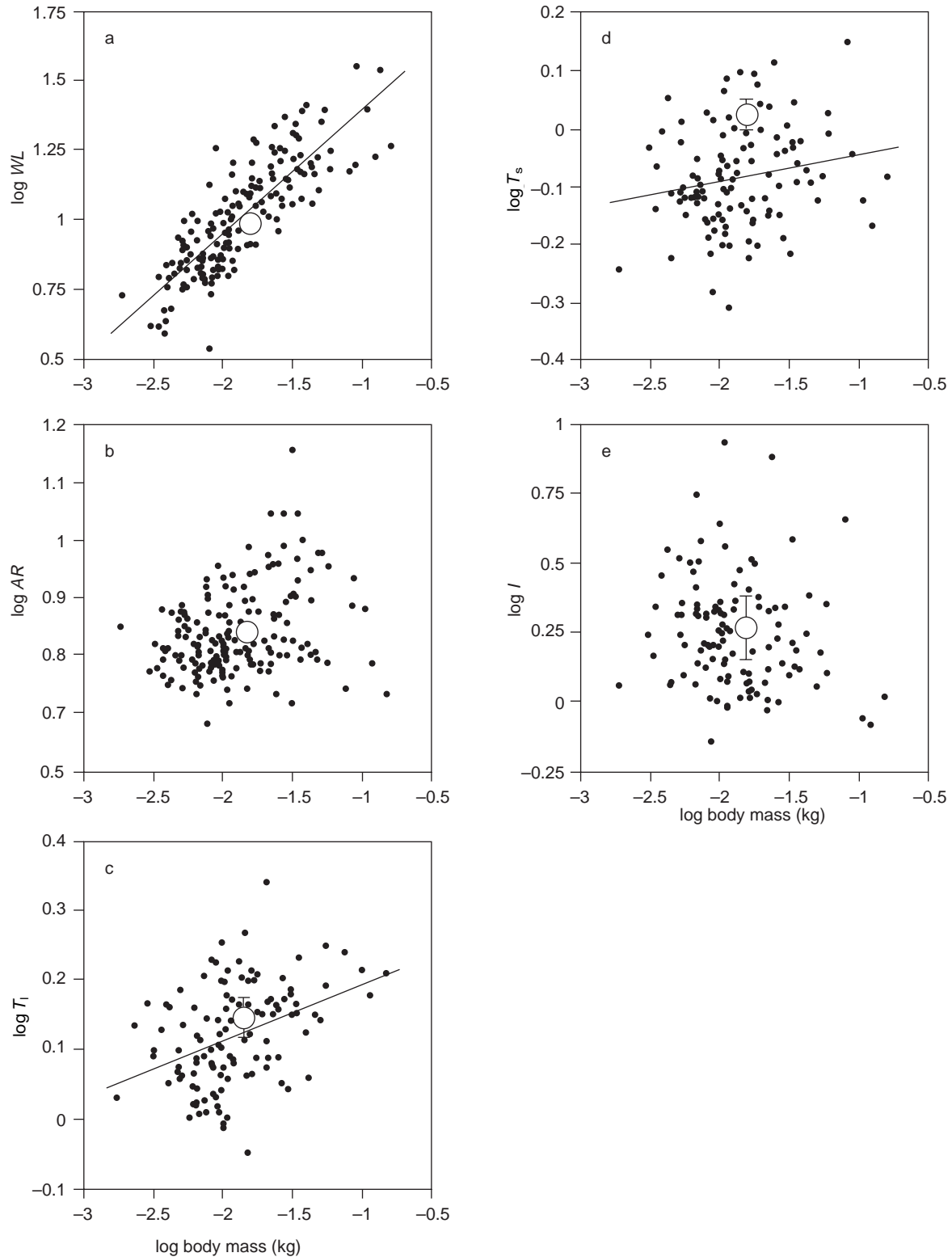


Fig. 2. The log–log relationship between (a) wing loading ($n = 186$ species), (b) aspect ratio ($n = 177$ species), (c) wing-tip length ratio ($n = 117$ species), (d) wing tip area ratio ($n = 116$ species) and (e) wing tip shape index ($n = 115$ species) on body mass in microchiropteran bats. \bigcirc , mean values (± 1 SD) for *M. t. tuberculata* in the present study (Table). Solid lines, least squares regression equations for data for all species (except *M. t. tuberculata*) in those cases where the regression was significant (< 0.05): (a) $y = 1.85 - 0.45x$, $r^2 = 0.70$, $F_{1,185} = 426$, $P < 0.001$; (c) $y = 0.27 + 0.08x$, $r^2 = 0.16$, $F_{1,115} = 21.5$, $P < 0.001$; (d) $y = 0.005 + 0.048x$, $r^2 = 0.04$, $F_{1,114} = 4.6$, $P = 0.03$.

Table I. Mean body mass and wing shape measures in male and female *M. t. tuberculata* caught at night on Codfish Island during late June and early July. *P* values are for inter-sex differences (two-sample *t*-test). Errors are \pm 1 s.d. Predicted 95% CIs (confidence intervals) are those for an 'average' microchiropteran bat of the same body mass (see text for details)

	Male	Female	<i>P</i>	All	Mean log ₁₀	Predicted 95% CI log ₁₀
<i>n</i>	26	9	35			
Body mass (g)	15.7 \pm 0.8	15.5 \pm 0.9	0.7	15.7 \pm 0.8	–	–
Forearm length (mm)	41.9 \pm 0.7	42.4 \pm 0.8	0.07	42.1 \pm 0.8	–	–
Wing loading (<i>WL</i> in N.m ⁻²)	9.63 \pm 0.77	9.82 \pm 0.82	0.7	9.68 \pm 0.76	0.985	0.823–1.242
Aspect Ratio (<i>AR</i>)	5.55 \pm 0.25	5.62 \pm 0.22	0.4	5.57 \pm 0.24	0.745	0.693–0.982
Tip-length ratio (<i>T</i> _l)	1.40 \pm 0.09	1.39 \pm 0.10	0.8	1.40 \pm 0.09	0.144	–0.066–0.258
Tip-area ratio (<i>T</i> _s)	0.90 \pm 0.06	0.91 \pm 0.06	0.8	0.90 \pm 0.06	–0.046	–0.249–0.086
Tip-shape index (<i>I</i>)	1.90 \pm 0.56	2.01 \pm 0.68	0.7	1.93 \pm 0.59	0.270	–0.140–0.635

above the forest canopy on Codfish Island. Preliminary radio-tracking of a limited number of individuals from a recently discovered population of *M. tuberculata* in Fiordland suggests that short-tailed bats may actually commute relatively large distances and do not shirk from crossing open ground (O'Donnell *et al.*, 1997). Individuals from the Fiordland population flew directly across 1–2 km stretches of open grassland, were clocked during commuting flights at speeds of around 60 km.h⁻¹ and made commuting flights of up to 15 km at a time (O'Donnell *et al.*, 1997). The theoretically optimal wing shape for direct, fast, long distance flight is quite different to that for short, slow, agile flight. For instance, speed during direct flight is improved by high wing loading, the energetic cost of fast flight is reduced by high aspect ratio while manoeuvrability at high speed is improved by the possession of pointed wing tips (thus reducing drag; Norberg & Rayner, 1987). It may be that wing shape in *M. tuberculata* represents a compromise between different adaptive pressures (for instance fast, direct commuting flight and slow, manoeuvrable foraging flight). More information on the general ecology and behaviour of this species is required before more precise conclusions can be made.

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The difficulty of estimating population densities of nocturnal forest mammals from transect counts of animals

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INTRODUCTION

Many nocturnal small- to medium-sized forest mammals can be surveyed only by directly sighting or hearing each individual. This is particularly so in tropical regions. Signs (footprints, dung scratch-marks, etc.) are often not identifiable to species (similar species frequently occur together); villagers' identifications are rarely clear enough for research purposes, and the provenance of specimens in markets can rarely be established to satisfactory precision. Assessments of animal status from brief surveys are becoming increasingly important for many conservation purposes. A repeatable methodology for field assessment of the status of nocturnal mammals is needed to allow comparisons, particularly between sites.

Nocturnal forest mammals are commonly surveyed by an observer walking slowly through the area, continuously searching all vegetation storeys with a head-torch for animals' reflecting eyes or body shapes whilst remaining alert for the sounds of dropping fruit, vegetation displacement and calls. Results may be expressed by dividing the survey time by the total number of contacts (e.g. Duckworth, 1992a); population densities are sometimes calculated (e.g. Walker & Cant, 1977; Charles-Dominique, 1978; Glanz, 1982). A contact frequency has no intrinsic meaning, but an accurate population density is a feature of biological value; therefore it is clearly desirable to calculate the latter if it is possible to do so. The use of line transect surveys to estimate animal population densities has greatly advanced recently and this paper discusses the possibilities of performing these calculations for nocturnal mammals by assessing whether the assumptions made explicit by Buckland *et al.* (1993) for DISTANCE sampling theory are upheld.

THE DIFFICULTY OF DETECTING ALL INDIVIDUALS ON THE TRANSECT MIDLINE

If detection of mammals on the transect midline falls below 100%, the detectability function starts at an unknown point and densities are underestimated. Many individual nocturnal forest mammals of many species are missed for reasons other than their distance from the transect midline, and so this assumption is not met. Animals can be detected by eye-shine only if they have a

reflective tapetum to the eye, are unobscured and look towards the torch. Sighting of the body shape rarely reveals animals unless they are in the open, close to the observer, silhouetted, large or gliding. Detection by ear (of calls, rustles or dropping fruit) is only usual for noisy species, which are calling, moving or feeding when the observer passes. Mammal species vary in their ease of detection. Four classes of mammals linked by their detectability reveal that these three methods do not allow a complete census of mammals on the transect midline.

1. Partially nocturnal primates with weak eye-shine who alarm call at the observer, e.g. baboons *Papio* spp., colobus monkeys *Colobus* spp. and brown lemur *Eulemur fulvus*. The calling animals are extremely difficult to see, even from directly underneath because they are obscured by the vegetation and their eye-shine is so weak. Detection depends almost entirely on their calling. Although these mammals would not be surveyed by night, they are an instructive group for comparing with fully nocturnal species.

2. Mammals with bright eye-shine that move quietly and call rarely (at least seasonally), e.g. lorises *Nycticebus* spp., lemurs *Cheirogaleus* spp. and *Avahi* spp., common palm civet *Paradoxurus hermaphroditus* and colugo *Cynocephalus variegatus*. Even though their bright eye-shine aids detection, many animals are missed as they are obscured by vegetation: this is demonstrated as some escape detection until the observer has passed and looks behind; at a pause, animals are found several minutes (and scans) after stopping; and the second of two adjacent observers invariably finds animals the first observer has overlooked. Animals can be missed even in the open: a slow loris *Nycticebus coucang* observed in a leafless tree for 55 min was invisible for many periods of several minutes simply because it was not looking at the torch. A passing observer could easily have overlooked it.

3. Noisy mammals with bright eye-shine, e.g. kinkajou *Potos flavus*, small-toothed palm civet *Arctogalidia trivirgata* and bushbabies *Galago* spp. The two carnivores are usually detected by sound rather than eye-shine; when in the canopy they are easily overlooked visually (see category 1). At one site in Ethiopia, bushbabies in low bushland acacias were usually found by eye-shine, but those in adjacent dense forest were heard first (Duckworth, 1992b). Small-toothed palm civet and pygmy loris *Nycticebus pygmaeus* were two common

arboreal mammals at one site in Laos (Duckworth, 1994). Lorises, detected only by eye-shine, were never heard calling or rustling; civets called loudly and crashed through the canopy. Four pygmy lorises were found and nine civets; only one of the latter was detected by eye-shine, suggesting that a large number of pygmy lorises were passed over.

4. Quiet mammals with no eye-shine, e.g. sloths *Choloepus* spp. and neotropical porcupines *Coendou* spp. As there is no easy way of detecting the animals, sightings are disproportionately rare, although dung counts reveal that sloths are among the commonest forest mammals (Glanz, 1982). The proportion of animals on the midline that are overlooked defies easy estimation. The development of methodology to allow population estimation where many midline animals are missed is experimental (Buckland *et al.*, 1993) and has not addressed the specific problems with nocturnal forest mammals. Distance sampling techniques override problems of variation in cue production, observer ability and environment effects (Buckland *et al.*, 1993), but only when detection on the transect midline is not reduced. Detection of nocturnal mammals, including on the midline, is affected by patterns in activity or vocalization during the night or with season (e.g. Duckworth, 1992b), lunar cycles (e.g. Emmons, 1982), plant phenology (notably in deciduous forests; e.g. Laurance, 1990) and hunting pressure (leading to torch-shyness) in the area.

SAMPLE SIZES

For population to be derived meaningfully from distance surveys, a minimum of 60–80 contacts is needed (Buckland *et al.*, 1993). Over much of South East Asia, it is rare to find mammals (as a whole) more frequently than once per hour. Even frequently seen species are rarely found more often than once per 6–9 h (Duckworth, Timmins *et al.*, 1994). Thousands of hours would thus be needed per site to achieve adequate samples for a representative selection of species.

OTHER POINTS OF SURVEY DESIGN

The use of roads and paths

For unbiased results, survey lines should be placed randomly with respect to object distribution (Buckland *et al.*, 1993); this is most unlikely to be so if roads are walked (e.g. Duckworth, 1992). In practice, for rapid assessment surveys (as distinct from detailed study), roads offer excellent opportunities for high visibility and quiet passage. Walking within forest gives low sighting rates; being surrounded by vegetation, the observer cannot see much, and anyway has flushed many of the animals by making so much noise. In faunal surveys is usually imperative to maximize the number of encounters with respect to time, because many surveys are done under great time constraint.

Multiple use of trails

An important point often not discussed is the extent to which observations were made repeatedly along the same line. Roads are often scarce, so each may be used many times (Walker & Cant, 1977; Emmons, 1982; Glanz, 1982; Laurance, 1990; Duckworth, 1992a,b). Ideally, for any measure of the relative abundance of each mammal species, each route would be walked only once. Multiple counts require careful statistical testing as the independence of data may be compromised; Glanz (1982) discussed this problem for red spider monkeys *Ateles geoffroyi* on Barro Colorado Island and similar principles would apply to nocturnal species. This is often not too serious a problem, however, as a line walked 3 nights in a row often yields largely different species each time, with, furthermore, different individuals of a given species on different nights (Duckworth, 1992a), because encounters so depend on chance that one detects a different subset of the population every night. Logically, therefore, unstructured multiple trail use is incompatible with estimating population densities: such trail use is acceptable if only a small proportion of the animals available are in fact detected, while the calculation assumes much more complete coverage. In theory, because even the crudest contact frequencies assume the principle of statistical independence (the sampled subsection should represent the whole area), the survey area should be divided up into sections of line. Within each section, the entire length should be walked the same number of times. For each section, a separate encounter rate should be calculated, and these rates combined, weighted according to the length of section, to produce an overall rate representing the whole area. Laurance (1990) did this. This low proportion of species where individual animals are seen repeatedly includes indolent sub-canopy species such as common palm civet and sportive lemurs *Lepilemur* spp. and crepuscular species with regular resting sites (e.g. canids and deer). The observer is likely to notice in the field any error strong enough to be of biological importance, and make allowance.

RECOMMENDATIONS

For most nocturnal forest mammals it is not possible to use direct contact transect data to calculate population densities because major assumptions of distance theory are not met. However, for many purposes, the most pressing need is a rough estimate of the status of a species in an area. Population estimates may not be the best use of available time: comparable data from further areas are often more useful in assessing conservation priorities for species and areas. Laurance (1990) presented many conclusions of high relevance to forest mammal conservation based entirely on sighting frequencies: no population densities were estimated. Brockelman & Ali (1987) deplored the presentation of population density estimates for diurnal primates with little indication of

how they were derived (making it impossible for others to try alternative calculations), in place of raw data.

Until theory and technique for calculating populations has addressed the problems of low detectability of animals on the midline, information from nocturnal transect surveys is best presented as contact frequencies accompanied by some contextual information:

1. Contacts are more usefully related to time than to distance because a paused observer detects new animals after several stationary minutes: no new distance is traversed, but time has elapsed. An observer cannot double the number of contacts per hour simply by covering twice as much ground, because less conspicuous animals are then overlooked. However, the balance of species recorded may change with speed: preliminary results from Borneo showed that walking faster produced more mouse-deer and fewer canopy flying squirrels (Duckworth, in press).

2. Calculations, including statistical tests, should use the number of contacts rather than the number of individuals (each group of more than one animal being a single contact) since the animals within a group are not statistically independent. Information showing the total number of animals must also be presented.

3. Visibility in the habitat should be indicated, since animals are detected at greater distances in more open habitats; results should indicate the typical sighting distance of animals.

4. Main methods of detection should be given for each species; contacts of those detected by ear are relatively unaffected by vegetation thickness.

5. Hunting pressure in the area should be indicated as this may affect both the population and its detectability.

6. Whether observations were made from roads, paths, or across the habitat at random should be stated; results should be presented separately for each category.

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Cached fungi in non-native conifer forests and their importance for red squirrels (*Sciurus vulgaris* L.)

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Abstract

The caching of fungi by red squirrels *Sciurus vulgaris* was investigated in commercial conifer plantations by walking transects in Kielder Forest, Cumbria and Wauchope Forest, Scotland. In 11 transects, a total of 58 fungal fruiting bodies were observed on branches in trees, consisting of four different species (49

Russula ochroleuca, seven *R. metica*, one *R. vesca*, one *Colybia maculata*). Fungal stores were found to be short lived and most fruiting bodies cached were gone after 2 weeks. Based on the survey findings we estimate that within an average red squirrel home range there would be a minimum of 42 cached fruiting bodies, constituting a food store of approx. 525–714 kJ.

Key words: *Sciurus vulgaris*, hoarding behaviour

INTRODUCTION

Fungi are considered to be an important food source for red squirrels in both deciduous and coniferous woodlands (Gurnell, 1987). This includes subterranean fungi, fruiting bodies from the forest floor and fungi growing under bark on trees (Moller, 1983). Fungi have been found in the stomachs of red squirrels in all months of the year, but were most prevalent in the autumn (Rajala & Lampio, 1963; Tittensor, 1970; Grönwall, 1982) and at times when tree seed crops failed (Gurnell, 1987). They are relatively rich in nitrogen and contain a number of important minerals such as calcium, magnesium and potassium (Grönwall & Pherson, 1984). Fungi are also relatively easy to digest (Grönwall & Pherson, 1984) and energy intake has been estimated to be up to five times larger per unit feeding time compared to lodgepole pine seeds (Smith, 1968). Red squirrels have been observed to store fruiting bodies on branches in trees in Finland (Sulkava & Nieholm, 1987) and it has been estimated that an individual squirrel could cover up to half its daily energetic requirement by feeding on fungi alone (Grönwall & Pherson, 1984).

Commercial conifer forests in the north of England and southern Scotland support low density red squirrel populations. This type of habitat is characterised by large single species plantations of Sitka spruce *Picea sitchensis*, Norway spruce *Picea abies* and lodgepole pine *Pinus contorta* and squirrels are subject to large temporal and spatial variations in tree seed supply (Lurz, Garson & Rushton, 1995; MacIntosh, 1995; Lurz, Garson & Wauters, 1997). There is no understorey of shrubs or ground cover present and fungi provide one of the few alternative sources of food. In this paper we investigated the occurrence and abundance of cached fungi in trees and discuss their importance as a food source for red squirrels in these resource limited conifer habitats.

METHODS

We selected 11 study sites in plantations in the Border Forest, Scotland (Wauchope Forest) and Kielder Forest, Cumbria (Spadeadam Forest). The forests consist of plantations of Sitka spruce or mixtures of Sitka spruce with Norway spruce lodgepole pine or Japanese larch *Larix japonica* (Table 1). All sites were known to contain red squirrels based on previous surveys (Garson & Lurz, 1996) and the presence of squirrel feeding signs (stripped cones).

In each of the 11 sites a transect (≤ 1800 m long, Table 1) was walked twice during October–November 1997 and the branches of 2 rows of trees on either side were scanned for fungi. The number and species of fungi seen on branches were recorded. Where possible the fungi were collected and examined for tooth marks to verify that red squirrels had indeed placed them there. The wet weights of a small sample of fungi was measured.

RESULTS

Fungi were found to be placed on branches next to the trunk at heights ranging from 0.6 m to approx. 8 m. We observed single mushrooms or groups of three to six placed individually at different heights on different branches of the same and adjacent trees. Four different species were found cached: common yellow russula *Russula ochroleuca*, sickener *Russula emetica*, bare-toothed russula *Russula vesca* and spotted tough-shank *Colybia maculata*. On the 11 transects we found a total of 58 fruiting bodies that showed squirrel teeth marks and had been placed on branches near the trunk of trees (49 *R. ochroleuca*, seven *R. metica*, one *R. vesca*, one *C. maculata*). This is a minimum estimate as more fruiting bodies may have been cached higher up in the crown of the trees out of view. The common yellow russula and the sickener were the most abundant fungi in the plantations and commonly associated with stands of Sitka spruce and lodgepole pine (*R. emetica* in particular), although we also observed a variety of other species (Table 2) none of which were found cached. A sample of 10 fruiting bodies indicated a mean (± 1 SD) wet weight of 8.15 ± 3.85 g.

A comparison between the number of fruiting bodies found and the location of trees in relation to forest edge (including forest rides) and the inside of plantations suggests that more fruiting bodies are cached in trees next to rides and on the forest edge (Table 1; chi-square test $\chi^2 = 25.12$, $P < 0.001$, d.f. = 1). Based on the survey results (Table 1) we calculated a minimum estimate of the number of fruiting bodies stored by a squirrel within an average sized home range:

$$\text{Estimated number of cached fungi} = (\text{number found/transect area}) * \text{mean home range area}$$

Within a mean home range of 9.13 ha, typical for this type of habitat (minimum convex polygon; Kenward, 1987; Lurz, 1995), one would expect to find an estimated 42.23 cached fruiting bodies.

Table 1. Transect length (nearest 100 m), composition (Sitka spruce SS, Norway spruce NS, Lodgepole pine LP, Larch L) and the number of fungi stored on branches in the 11 surveyed sites. Sites 1–8 were located at Wauchope Forest and sites 9–11 at Spadeadam Forest

Site	Transect (m) Length	Inside	Edge	Tree species	Total	Fungi Inside	Edge
1	1800	1700	100	SS/LP	0	–	–
2	1700	1700	–	SS/LP	1	1	–
3	1400	1400	–	SS	8	8	–
4	1800	1800	–	SS	5	5	–
5	1800	1100	700	SS/L	0	–	–
6	900	500	400	SS/LP	6	1	5
7	500	900	400	SS/LP	8	3	5
8	1600	–	1600	SS/LP	11	3	8
9	1700	1200	500	SS	17	2	14
10	1500	1100	400	SS/NS/LP	2	2	–
11	1700	1300	400	SS/NS/LP	1	1	–

Table 2. Other species of fungi found in different conifer plantations (Sitka spruce SS, Norway spruce NS, Lodgepole pine LP)

Species of fungi	Plantation type
<i>Clitocybe nebularis</i>	NS
<i>Cystoderma amanthinum</i>	NS, SS, LP
<i>Hygrocybe pustulatus</i>	NS
<i>Lactarius deterrimus</i>	NS, SS
<i>Lactarius rufus</i>	NS, SS, LP
<i>Lycoperdon perlatum</i>	NS
<i>Marasmius androsaceus</i>	NS
<i>Russula atropurpurea</i>	NS
<i>Russula queleti</i>	NS
<i>Tricholomopsis rutilans</i>	NS

DISCUSSION

Red squirrels in Sitka spruce dominated conifer plantations typical of Kielder and the Border Forest Park live in a system shaped by marked seasonal and annual changes in tree seed availability. Their flexible home range behaviour, patterns of habitat use, low levels of site fidelity and the occurrence of breeding dispersal (Greenwood, 1980; Lurz, 1995; Lurz, Garson & Wauters, 1997) all appear to be a response to the variability of food resources in space and time.

The caching of food items is thought to be a strategy to increase food availability during periods of scarcity (Anderson & Krebs, 1978). Hoarding behaviour is observed in a number of mammal and bird species (Smith & Reichman, 1984) and is well documented in tree squirrels (Thompson & Thompson, 1980; Gurnell, 1987; Rice-Oxley, 1993). In red squirrels it has been suggested that caching is an adaptive strategy to preserve temporarily abundant food resources and individuals that hoarded were found to be more likely to survive and reproduce (Wauters, Suhonen & Dhondt, 1995).

The large number of *Russula* fruiting bodies found cached at Spadeadam and Wauchope Forest (57 out of 58) is most likely a reflection of the great abundance of these species at this time of year. During our survey most of these were found in trees next to rides or the

forest edge. Given the observed occurrence of fruiting bodies throughout the forest, possible explanations are better drying conditions and more squirrel activity near the edge of plantations. Edge trees are known to produce larger cone crops relative to trees growing inside (Phillipson, 1987) and it is therefore possible that squirrels spend more time there foraging.

A large proportion of the caches found during the study appeared short lived and the majority of fruiting bodies observed on the transects had disappeared after 2 weeks. As a food store these caches are clearly vulnerable to intra- and interspecific competitors as well as weather conditions (e.g. heavy wind, frost) and cache recovery rates may therefore vary.

The minimum estimate of 42.23 fruiting bodies cached within an average home range would constitute approximately 525–714 kJ (using a mean wet weight of 8.15 g, an estimate of 90% water content and 15.96–21.84 kJ/g dry weight; Grönwall & Pherson, 1984). This is equivalent to the energetic requirements of a red squirrel (330–420 kJ) for 1–2 days (Grönwall, 1982). A more detailed study is required to determine the relative importance of fungi in the diet of red squirrels and the ecological relationship between fungi and squirrels, such as their possible role as spore dispersal agents (Kotter & Farentinos, 1984).

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The denning behaviour of feral ferrets (*Mustela furo*) in a pastoral habitat, South Island, New Zealand

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Abstract

This paper describes the denning behaviour of 24 feral ferrets *Mustela furo* on farmland, East Otago, South Island, New Zealand. One hundred and ninety seven dens were located and radio-collared ferrets were found to share dens simultaneously with other ferrets on 7.4% of 706 radio-tracking events and used dens that had been previously used by other ferrets (sequential den sharing) on 44.3% of occasions. In this particular study, ferrets were exhibiting a higher degree of sociality than has been recorded in other solitary mustelid species and therefore may not be adhering to the model of intrasexual territoriality thought to apply to other mustelid species. Den sharing may be a mechanism by which bovine tuberculosis *Mycobacterium bovis* is transmitted within ferret populations. Over 80% of the sequential den sharing occurred within 14 days, well within the survival span of *M. bovis* bacilli. Denning of infected ferrets in haybarns may pose a risk of transmission of *M. bovis* to livestock from hay.

INTRODUCTION

Little is known about the biology and ecology of the feral ferret *Mustela furo* in New Zealand even though it supports the largest population in the world (Nowak & Paradiso, 1983). Ferrets have been implicated in the decline of some endemic species (Murphy, 1996). and recently there has been debate

about the role and importance of ferrets as vectors of bovine tuberculosis (Tb; *Mycobacterium bovis*) to livestock in New Zealand. High prevalences of infection have been found in ferret populations, tuberculous ferrets have been found throughout Tb-infected areas and in association with infected livestock, and the observed pathology suggest that ferrets are potentially infectious to other animals (Walker, Reid & Crews,

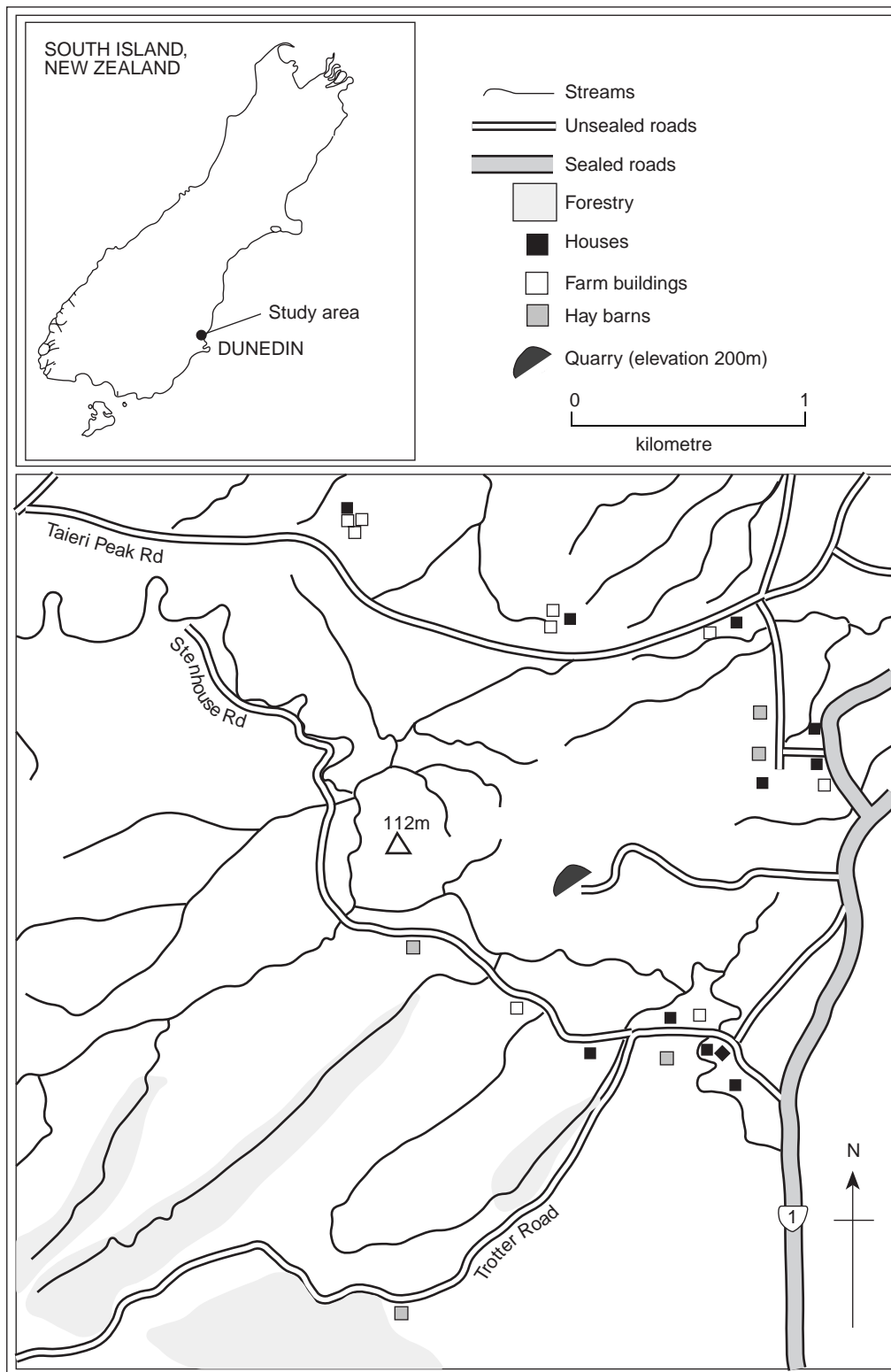


Fig. 1. Location and habitat details of the study site, South Island, New Zealand.

1993; Ragg, Moller & Waldrup, 1995; Lugton *et al.*, 1997).

Tuberculosis is thought to be transmitted by two main routes: behavioural interactions (where infection is passed between animals through direct contact) and contamination of pasture or food. In Ireland and the U.K., the badger *Meles meles*, another mustelid, is thought to be the wildlife species responsible for infecting domestic stock with Tb (O'Connor & O'Malley, 1989; Nolan & Wilesmith, 1994). The badger typically exhibits a high degree of sociality, living in social groups and denning underground in setts. It is unclear what role denning behaviour has on Tb transmission between badgers; it has been theorized that the sett provides an ideal situation for aerosol transmission to occur (Nolan & Wilesmith, 1994), although some researchers have expressed surprise that given this lifestyle, many badger groups have a low prevalence of Tb (Neal & Cheeseman, 1996).

In New Zealand, Tb transmission among adult possums has been found to occur in areas that have a high concentration of den sites suggesting that some aspect of denning behaviour is involved (Morris & Pfeiffer, 1995). The current Tb control programme in New Zealand is guided by predictions from a model that assumes that transmission within possum populations is closely associated with infected den sites (Barlow, 1993).

The basic mustelid spacing pattern is thought to be intrasexual territoriality (Lockie, 1966; Erlinge, 1977; Powell, 1979, 1993; Sandell, 1989); where males are territorial against males, females against females, but the territory of one sex may overlap the territory of a member of the other sex. Even though a female territory may lie completely within a male territory it has been hypothesized that there is little contact except during the breeding season. A mark-recapture study of feral ferrets at Pukepuke Lagoon in New Zealand concluded that ferrets were exhibiting intrasexual territoriality (Moors & Lavers, 1981). However, home range estimates were based on trap locations, there were few captures for some individuals and there was no demonstration that the ranges depicted were fully described.

The denning behaviour of feral ferrets has not been described before. Instances of ferrets denning together have been found when ferrets have been radio-collared for other reasons. Alterio & Moller (unpubl. data) found three instances of ferrets denning together at Boulder Beach on the Otago Peninsula, New Zealand. In the semi-arid grasslands of Central Otago, J. L. Norbury, D. C. Norbury & R. P. Heyward (pers. comm.) found two instances of den sharing when excavating 41 dens containing radio-collared ferrets.

This paper describes the use of dens by ferrets in order to examine their degree of sociality. If intrasexual territoriality is indeed a feature of ferret ecology then presumably the occurrence of den sharing would be infrequent. As den sharing could be a potential mechanism by which Tb is transmitted within ferret populations' describing its occurrence may help to define the probability of intraspecific transmission.

MATERIALS AND METHODS

Feral ferrets were radio-tracked on farmland near Palmerston (45°S, 170°E), 51 km north of Dunedin, New Zealand (Fig. 1). The study area was grazed by cattle and sheep and had a mixture of developed pastureland, grazed tussock grassland *Chionochloa* spp., oak *Quercus* spp. and pine *Pinus radiata* plantation. Gorse *Ulex europaeus*, broom *Cytisus scoparius* and matagouri *Discaria toumatou* were predominant in some gullies and over some semi-developed areas. A part of the study area bordered the outskirts of Palmerston township.

Ferrets were trapped as part of a monthly mark-recapture study which started in January 1996. Ferrets were immobilized by a 0.2 ml intramuscular injection of ketamine (20 mg) with xylazine (2 mg), and sexed, ear-tagged and released. Age class (juvenile or adult) was determined at first capture in the January–March trap sessions; juveniles were obviously smaller, reproductively immature with minimal tooth wear and poor sagittal crest development. Adult females showed signs of recent lactation and adult males often had scars from fight wounds and frequently supported bald tails.

Ferrets were fitted with stage 2 transmitters with brass loop aerials (SirTrack Ltd, Havelock North, New Zealand) in the February and March trap sessions. Some preliminary radio-tracking began in late February. Regular radio-tracking began in April 1996 and finished in early July 1996. Ferrets were radio-tracked to den site using hand-held yagi antennae with Merlin 48 or Telonics TR4 receivers. Ferrets were only located during daylight hours (09:00–18:00); when they were normally inactive. All other radio-collar frequencies were scanned to check for den sharing. Goodness-of-fit tests (χ^2) were used to determine whether ferrets showed a preference for denning in human-derived dens (hay-barns, woolsheds, houses) compared to natural dens.

Simultaneous den sharing was defined as 2 or more ferrets sharing the same den site at the same time. The rate of individual simultaneous den sharing was calculated from the number of times an individual was found with another ferret and the population rate of simultaneous den sharing was the total of all the individual simultaneous den sharing divided by 2 (so that when 2 ferrets were found together it counted as one event). Sequential den sharing was defined as 2 or more ferrets using the same den site over the study period. The individual and population rates of sequential den sharing were calculated from the number of occasions ferrets used dens that had been previously used by other ferrets.

RESULTS

Thirteen females (eight adults and five juveniles) and 11 males (two adults and nine juveniles) were radio-tracked (Table 1) from March 1996 until July 1996. Almost every attempt to radio-track particular animals were

Table 1. The denning behaviour of 13 female and 11 male ferrets in a pastoral habitat, South Island, New Zealand. The number of sequential and simultaneous fixes are given in parentheses

Ferret id	Sex (M or F), Age (J or A)	Radio-tracking period ^b	Total no. of fixes	No. of dens used	No. of 'multiple ferret' dens	No. of ferrets who used same den	Percentage of sequential den sharing	Percentage of simultaneous den sharing
1	M, J	7/3–11/7	47	13	5	5	76.1, (35)	23.9, (11)
2	M,	22/4–28/6	22	6	2	5	9.5, (2)	0
3	M, A	26/3–12/7	41	19	6	8	51.2, (21)	12.2, (5)
4	M, J	26/3–12/7	34	13	6	7	64.7, (22)	14.7, (5)
6	F, A	7/3–11/7	43	20	7	3	38.2, (13)	0
8 ^a	F, J	4/6–28/6	18	4	3	6	88.8, (16)	61.1, (11)
9	M, J	17/4–12/7	33	18	7	5	53.1, (17)	18.8, (6)
10	F, A	8/3–3/7	37	17	6	4	35.1, (13)	0
27	M, J	7/3–17/4	5	5	0	0	0	0
33	M, J	13/6–11/7	12	6	4	2	69.2, (9)	0,
45	F, J	16/4–10/7	34	10	4	2	69.2, (18)	7.7, (2)
48	M, J	12/4–12/7	36	6	4	5	80.5, (29)	41.6, (15)
49 ^a	M, J	26/3–8/6	24	4	1	4	83.3, (20)	62.5, (15)
52	F, A	28/3–11/7	44	11	3	2	11.9, (5)	2.4, (1)
54	F, A	8/3–12/7	47	19	1	4	11.1, (5)	6.7, (3)
55	F, A	16/4–11/7	35	15	5	3	29, (9)	3.2, (1)
56	M, J	15/4–12/7	35	19	12	10	78.8, (26)	24.2, (8)
68 ^a	F, J	7/3–22/4	4	3	2	3	50, (2)	25, (1)
72	F, A	6/3–11/7	49	15	2	2	28.6, (12)	7.1, (3)
108 ^a	M, A	12/3–14/5	10	7	4	5	70, (7)	20, (2)
109	F, J	13/3–11/7	42	8	4	6	71.4, (30)	35.7, (15)
113 ^a	F, A	14/3–21/5	17	7	2	1	56.3, (1)	18.8, (3)

^a Died.^b all 1996.

successful and there were no difficulties detecting animals underground. Only four adult males were trapped in the immediate study area. Four ferrets (one adult male, two juvenile males and one juvenile female) were not relocated or recaptured and so probably left the study area soon after collaring. Seven radio-collared ferrets died during the course of the study. Radio-collars were then fitted to new ferrets as soon as possible. At any one time there were usually 18 radio-collared ferrets to locate. Two ferrets (AF52 and JM2) denned outside the study area although some initial fixes were within the study area. Sixty-six other ferrets were trapped in the monthly mark-recapture sessions from January 1996 until July 1996.

A total of 197 different dens were identified from 706 telemetry occasions. Thirty-eight of the 197 dens (19.3%) were used by more than one ferret (termed 'multiple ferret' dens). The population rate of sequential den sharing was 44.3% ($n=313$). Six buildings (one house, two woolsheds and three haybarns) that were used by more than one ferret accounted for 151 fixes.

Simultaneous den sharing occurred in 14 of these 38 multiple-ferret dens on 49 occasions (7.4% rate of simultaneous den sharing). There were 74 combinations of ferrets denning together as more than two ferrets were sometimes found denning together (Table 2). Simultaneous den sharing was found to occur amongst females ($n=13$), males ($n=28$) and males and females ($n=33$). Juveniles of both sexes shared dens with each

other and with adults of both sexes. Some juveniles (i.e. JM56, JF45 and JM9) often denned together or used the same dens. Two adult females shared a den on one occasion.

Twenty-one multiple-ferret dens had instances of sequential den sharing within 2 days. Sequential den sharing over a period of time occurred in all but two of the multiple-ferret dens. Ferrets denned together on 37.6% of all occasions that multiple-ferret dens were used and 80% of all multiple-ferret dens were used again by another ferret within 14 days (Fig. 2). When occurrences of simultaneous den sharing were removed from the calculations of the usage of multiple-ferret dens, 30.1% of occasions had another ferret reusing the den within 1 day; and another ferret used the same den site within 14 days in 80% of occasions (Fig. 2).

The actual den site was not determined for 58 den sites because they were either inaccessible (often the case when the ferrets denned in gorse or dense scrub) or when identifying the actual position would have required too much disturbance. Rabbit holes were the most common den site comprising 53% of all identified den sites (Table 3). Even though only 10% of dens were human-derived (buildings, rubbish piles, etc.), ferrets used these den sites significantly more than the natural den sites (Chi $\chi^2=272$, 1 d.f., $P=0.0001$). As significance ($P<0.05$) occurred for 17 of the 21 ferrets (with the deviations from the expected in the same direction) the data were pooled.

Table 2. Instances of simultaneous den sharing between 13 female and 11 male ferrets in a pastoral habitat, South Island, New Zealand. Numbers indicate the number of days found denning together

Ferret identification number (see Table 1)																						
1	2	3	4	6	8	9	10	27	33	39	45	48	49	52	54	55	56	68	72	108	109	113
-	2	2	-	*	6	-	*	-	-	-	*	*	*	*	*	*	*	*	-	1	9	-
2	-	-	-	*	-	*	*	*	*	*	*	*	*	*	*	*	*	*	-	-	-	*
		3	1	*	2	*	-	-	1	-	*	*	*	*	*	*	*	-	-	-	1	-
			4	*	-	*	*	*	*	*	*	*	*	*	*	*	*	-	3	1	-	-
				6	*	*	-	*	-	-	*	*	*	*	*	*	*	*	*	-	*	*
					8	*	*	*	*	*	*	*	*	*	*	*	*	*	*	-	9	-
						9	*	*	*	*	2	1	-	-	-	-	5	-	*	*	*	*
							10	*	-	-	-	*	*	*	*	*	*	-	*	-	-	*
								27	*	*	-	*	*	*	*	*	*	-	-	*	*	*
									33	1	*	*	*	*	*	*	-	*	-	-	-	*
										39	*	*	*	*	*	*	*	*	-	-	-	*
											45	-	-	-	-	-	1	-	*	*	*	*
												48	14	-	3	-	1	-	*	*	*	*
													49	-	3	-	1	-	*	*	*	*
														52	-	1	-	-	*	*	*	*
															54	-	-	-	*	*	*	*
																55	-	-	*	*	*	*
																	56	1	*	*	*	*
																		68	-	-	*	*
																			72	-	*	*
																				108	-	-
																					109	3
																						113

* = no overlap in home range; - overlap in home range but no den sharing found. Home range overlap data from Ragg (submitted). Note; on one occasion each, unidentified ferrets were also observed denning with 9, 48 and 49.

DISCUSSION

Den sharing has been underestimated

There were many other uncollared ferrets present in the study area. A portion of the ferrets caught in the monthly trap sessions would have been transients and others would have died, or dispersed from the area during the study. It is not possible to check ferret dens for other occupants other than radio-collared individuals because ferrets tend to den underground or in inaccessible places. These two factors mean that the rates of simultaneous and sequential den sharing are likely to be underestimated in this study. Another compounding factor was that some radio-collared ferrets moved outside the study area (i.e. AF54 and JM2), lowering encounter rates with radio-collared ferrets. In studies of possum denning behaviour (Cowan, 1989; Pfeiffer & Morris, 1991; Cole, 1993) it is possible to determine den sharing more accurately by direct observation.

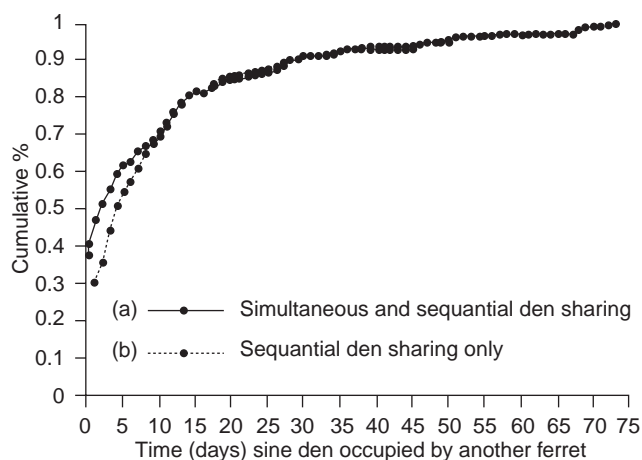


Fig. 2. Cumulative frequency plot of the usage of the 'multiple-ferret' dens where (a) both simultaneous and sequential den sharing occasions are counted as a contact (simultaneous den sharing fixes = 0) and (b) simultaneous den sharing fixes are excluded as a contact. Time is expressed as days since the den was last occupied by another ferret.

Den sharing as an expression of sociality

Den sharing within the solitary mustelid species has received little research attention. Most studies of sociality of mustelids have relied on trapping or visual and snow tracking (e.g. Erlinge, 1974; Moors & Lavers,

Table 3. Classification of the different den types ($n = 197$ dens) used by 24 radio-collared ferrets in pastoral farmland, South Island, New Zealand

Den type	Number
Rabbit holes	104
Unknown	58
Dead branches	12
Under-runners	6
Hay (including haysheds)	6
Buildings	5
Holes in rocks	4
Miscellaneous holes	4
Woodpiles	3
Tree trunks	1
Rubbish piles	2
Piles of corrugated-iron sheets	2
Offal pit	1

1981). Indications from the present study point to a higher degree of sociality than is consistent with the intrasexual territoriality social system proposed for other solitary mustelids. In particular it is the sharing of dens with individuals of the same sex that casts suspicion on the proposed model of intrasexual territoriality applying to feral ferrets in this study. In addition, on one occasion each, two adult female ferrets and two adult male ferrets were trapped in the same trap which also does not support the same sex avoidance hypothesis.

The expression of territoriality will vary among populations, across a species range and through time as limited resources vary (Powell, 1993). The frequency and opportunity for contact will be influenced by population density. This particular study site has a ferret population density of 6.3 ferrets per km² (Cross *et al.*, in press), higher than any other recorded estimates of ferret density. The amount of den sharing could vary seasonally and may be influenced by the population biology, especially the numbers of juveniles. Juvenile ferrets were involved in the vast majority of den sharing. Some juveniles were often closely associated and could have been littermates. Juveniles may also associate with their mothers after they are functionally capable of being independent. The majority of den sharing observed between adults of the same sex involved sequential den sharing indicating that home ranges were not exclusive.

Den attributes

A study of polecats *Mustela putorius* in Wales found that 22.7% of telemetry fixes were associated with agricultural premises. Rats may have been the reason polecats were attracted to these premises as scats showed that rats *Rattus* spp. dominated polecat diet (J. D. S. Birks, unpubl. obs.). What attracts ferrets to use buildings in the present study is unknown. Like polecats, ferrets may be attracted by prey or possibly because haybarns and farm buildings offer sheltered and dry den sites. The presence of animal remains at

one particular wool shed would have certainly attracted ferrets. Rabbit holes were the most common type of ferret den which were often associated with vegetation cover.

It was observed that some den sites were used only once and for a reasonably short period of time and during that time often more than one individual used the den site. On these occasions, ferrets may be using these den sites because they contain dead prey or carrion, or they could be attracted to them for some unexplained social reason.

The significance of den sharing on the transmission of tuberculosis

In New Zealand, transmission of Tb in possums is thought to be associated with denning. Cowan (1989) found that possums in the Orongorongo valley shared the same tree on 3.4% of 1987 occasions but noted that in 70% of these cases it appeared that the possums were not actually sharing the same den site. The rate of sequential den sharing was much higher at 49% (Cowan, 1989). A rate of 20% simultaneous den sharing and 34% sequential den sharing was recorded by Cole (1993) for a high density possum population in Otago. Paterson *et al.* (1995) reported that in a 20 day study at Castlepoint, no simultaneous or sequential den sharing was observed in three tuberculous possums. One case of simultaneous den sharing (apart from mother–joey pairs) was recorded in 332 occasions and 9% of dens were used sequentially in an earlier study at Castlepoint (Pfeiffer & Morris, 1991). The rates of sequential and simultaneous den sharing observed in the present study are therefore comparable to those found in some possum populations.

As it is presently unclear how Tb is spread through ferret populations, it is difficult to determine the significance of social contact like den sharing in the transmission of Tb. Infection indicative of a percutaneous route was found in approx. one-quarter of ferrets (Ragg, Waldrup & Moller, 1995; Lugton *et al.*, 1997) suggesting that ferrets are capable of transmitting infection to one another. It has been hypothesized that ferrets are infected from scavenging tuberculous carrion such as dead possums (Lugton *et al.*, 1997) and that the disease levels are a function of the amount of tuberculous carrion available. Even if tuberculous carrion is the underlying source of infection, it is too simplistic to propose that social organization and behaviour has no role in the spread of disease. For example; ferrets will carry prey and carrion to their den sites and while this behaviour may exclude access to other ferrets, when den sharing occurs this would result in more ferrets having exposure to infection. Bacilli survival is undoubtedly enhanced by the relocation of carcasses down dens which may further increase the transmission risk. Therefore at low ferret population densities, Tb prevalence may be a direct function of the availability of tuberculous carrion whereas at moderate to high population densities, social

interaction may have a more important role in the intraspecific transmission of Tb.

It is obvious that the probability of disease transmission when sharing dens depends on the survival of *M. bovis* and the magnitude of the challenge dose, especially in cases of sequential den sharing. A study looking at the environmental survival rates of *M. bovis* found that survival was enhanced in possum dens compared to pasture and forest floor situations (Jackson, de Lisle & Morris, 1995). In the present study in 80% of den sharing events there was reuse of the same space by different ferrets within 14 days which would be well within the survival time of *M. bovis* bacilli in damp, dark conditions (Jackson *et al.*, 1995). In cases of simultaneous den sharing, the route of transmission may be related to direct social contact (aerosol or bite wounding) rather than infection from contaminated den sites.

In this study ferrets often denned in haybarns. Tuberculous ferrets have been found to excrete bacilli in faeces, sputum and urine (Lugton *et al.*, 1997) so it is possible that they could contaminate their immediate environment. If ferrets are contaminating hay that is subsequently fed out to cattle then it is possible that cattle could become infected with Tb by this means. A similar parallel has been observed in Britain, where tuberculous badgers have been found associated with farm buildings and have defecated amongst feed (Cheeseman & Mallison, 1981).

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The influence of public access and sett visibility on badger (*Meles meles*) sett disturbance and persistence

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Abstract

The impact of public rights of way on badger setts was examined in the Bradford area of West Yorkshire using comparisons of 38 setts surveyed in 1985–1996 and again in 1992–1993. Badger setts were compared on the basis of whether they were still in use or not, and on the number of illegal disturbance events recorded over the study period. The number of, and distance from, public accesses did not influence sett persistence, and the least frequently disturbed setts (i.e. those with an average of one or less disturbance incidents every 2 years) were closer to a larger number of accesses. Frequency of poaching was high near to heavily disturbed setts and those no longer occupied at the later survey. Less frequently disturbed setts were associated with landowners who were unsupportive of badger conservation: it is possible that such landowners are highly protective of their land and thus incidentally reduce the frequency of poaching and other forms of disturbance. Setts in areas with formal authorized shooting were less disturbed. Setts still in use tended to be in open habitats and visible from roads and nearby dwellings. Setts in open areas were less often disturbed than those in wooded sites. Since public access may not reduce sett persistence and may even be beneficial in an area of high wilful persecution, there are implications for the management of public access.

INTRODUCTION

Although the badger *Meles meles* (L.) is protected in Britain by legislation (primarily the Badgers Act 1992: H.M.S.O., 1992) disturbance to setts is widespread, with an estimated 9000 being dug each year (Cresswell, Harris & Jeffries, 1990). Badgers are also wilfully persecuted by some landowners and during game management. Between 1979 and 1989, 554 people were charged with offences contrary to the Badgers Act 1973, with one individual having committed 152 offences within a 6 year period (Griffiths, 1992). Persecution is particularly prevalent in northern England (Cresswell *et al.*, 1990; Griffiths, 1992). Historically, badger baiting has been common in the north of England, being recorded in Yorkshire from the 17th century. Despite this, in 1956 Taylor noted that badgers in Yorkshire were less local and more abundant than in 1881. However, in the early 1970s there was a national increase in sett digging (Cresswell *et al.*, 1990) and the number of setts in use by badgers in West Yorkshire fell from 91% in the period 1970–1976 to 34% in 1977–1978 (Paget & Patchett, 1978). This led the then Nature Conservancy Council to conclude that badgers in West Yorkshire were in serious jeopardy (Patchett, 1979) and the Home Office designated the county as a Special

Protection Area under the 1973 Act (Home Office, 1979). Badgers may also be sensitive to disturbance from public access. Whilst badger protection laws are now stronger than ever, they do not override the demands of long standing public access legislation, which concentrates on asserting the rights of walkers and thus provides few opportunities for accommodating concerns about wildlife conservation. Human disturbance is known to affect species richness in urban and urban fringe areas (Dickman, 1987). In an area of Denmark, human disturbance and/or loose dogs were thought to contribute to a 33% decline in badger numbers over a 10 year period (Aaris-Sørensen, 1987). Moreover, in woods where pet dogs are permitted, badgers are absent; badgers were found to have moved to quieter areas (J. Aaris-Sørensen, pers. comm.). Consequently, habitats may be made more favourable by zoning public access (Lankester *et al.*, 1991). In Britain, although increased ease of access (Harris & Cresswell, 1988) and walkers with dogs (S. Harris, pers. comm; D. Yalden, pers. comm.) have been suggested to be detrimental to badgers, successful setts do exist in severely disturbed areas (e.g. Teagle, 1969). It is far from certain whether public access is detrimental, and there may even be benefits if access deters persecution; for example, setts near roads in good view of the public may be less frequently disturbed by digging and gassing (Paget & Patchett, 1978). However, as yet little, if any, work has investigated the impact of public access on badgers.

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The Bradford Metropolitan District covers 36 235 ha, with a human population of 474 000, most of whom live in the south-eastern quarter. The high concentration of residents, in addition to seasonal visitors, leads to heavy usage of the district's 900 km of public footpaths and bridleways. The public rights of way density is 534 people/km, compared to 231/km for England and Wales and 298/km for Yorkshire and Humberside (Survey Research Associates, 1993). Increasing public use of rights of way is likely to continue. It is therefore important to understand the effects of public access on local badger populations. Here we investigate the influence of public access on badger sett persistence and disturbance in the Bradford area, an urban borough in the north of England.

METHODS

We examined the disturbance history of, and environmental influences on, 38 setts (comprising 25 main, 12 subsidiary and one annexe sett following Cresswell *et al.*, 1990) in the Bradford area which had been previously surveyed by local sett monitors in 1985–1986 and found to be in use at that time. Data were collected in 1992–1993 from the local badger group's records supplemented by interviews with sett monitors, site visits and aerial photographs, and compared with the previous survey. Setts were recorded as still in use if there was any evidence of occupation at any time during 1992–1993. The number of illegal disturbance events, either accidental or malicious, between 1985–1996 and 1992–1993 were collated from sett monitor records. These included disturbance by digging, obstruction, gassing and dogs entering the sett.

The following potentially relevant factors, identified from previous studies (e.g. Skinner, Skinner & Harris, 1991a,b; Thornton, 1988; Aaris-Sørensen, 1987), were assessed:

(1) the physical ease of sett digging by humans (ranked from 0 – very difficult, to 4 – easy); (2) whether the site was wardened, gamekeepered, alarmed or under formal surveillance; (3) the frequency of poaching (from 0 – none, to 3 – very frequent) and of authorized shooting (0 – none, 1 – informal vermin control, 2 – rough shooting, 3 – driven shooting); (4) the attitude of the landowner to badger conservation (0 – very unsupportive, to 2 – very supportive); (5) whether the sett was visible from the nearest dwelling and whether in a wooded or open landscape; (6) likelihood of a person on the sett being observed by passing motorists (1 – impossible, to 6 – certain); (7) the distance to the nearest public access and the number of such within 400 m of the sett; (8) whether an access near the sett was used by children or for localized recreation (e.g. for picnicking).

Setts were compared on the basis of badger usage (those still in use in 1992–1993 compared to those disused) and level of disturbance (low or high: low being those with fewer than five disturbance incidents between

Table 1. Densities of sett types examined in the 232 km² study area

	Main setts	Subsidiary setts
Density over all land classes (per km ²)	0.1078	0.0517
Density over rural land classes (per km ²) ^a	0.1445	0.0694
Mean number of holes per sett (SE)	6.6 (1.01)	2.3 (0.41)

^a Calculated over 173 km² for those rural land classes identified by Cresswell *et al.* (1990).

1985–1996 and 1992–1993, i.e. an average of one or less disturbance events every 2 years). Data were analysed using StatView (version 4.5, Abacus Concepts). Where nominal data were recorded, *G* tests were employed, all other analyses used Mann–Whitney *U* tests (with *Z* corrected for ties where necessary).

RESULTS

Of the 38 original setts recorded, 18 (47.4%) were no longer in use. Overall, there was a mean of 10.7 (± 2.72 SE) disturbance incidents per sett over the period. The densities of the setts investigated are given in Table 1 for the whole study area and, following Cresswell *et al.* (1990), the areas classified as rural land. Nine setts were undisturbed during the period, with 16 having fewer than five incidents, and 13 with five or more incidents. The majority (10) of the highly disturbed setts were particularly near to major conurbations (<10 km). Digging (19.6%) and putting dogs into setts (49.6%) accounted for the majority of incidents, while wilful persecution by game or land-owning interests accounted for <15%. Only one conviction was recorded from the 118 incidents listed in badger group records. There was no association between setts disturbed five or more times and those which were no longer used in 1992–1993 (*G* = 0.33, d.f. = 1, *P* = 0.564).

No setts were alarmed and very few were wardened (3), formally surveyed (2) or in areas which were gamekeepered (4). These low numbers preclude further analysis. Two factors were significant in comparisons between those setts still in use and those disused in 1992/3 (Table 2). Frequency of poaching was higher around abandoned setts, while the visibility of a person on the sett to a passing motorist was higher at setts still in use. Ease of digging, level of shooting, attitude of the landowner, and the distance to and number of accesses near to the sett did not significantly differ between disused setts and those still in use. Six factors were significant in comparisons between heavily and less heavily disturbed sites (Table 2). Ease of digging, level of authorized shooting and the number of public accesses within 400m of the sett were higher in less disturbed areas. Increased frequency of poaching, supportive attitude of the landowner to badger conservation, and the distance of the sett from the nearest public access were higher around

Table 2. Factors influencing sett usage and frequency of disturbance Mann–Whitney U tests. * $P < 0.05$, ** $P < 0.01$

Factor	Effects on sett usage			Effects on disturbance		
	Z	n	Interpretation	Z	n	Interpretation
Ease of digging	0.84	38	–	2.10*	38	Highly disturbed setts are harder to dig
Frequency of poaching	2.85**	37	Setts no longer in use have higher levels of poaching	2.62**	37	Highly disturbed setts have higher levels of poaching
Level of authorized shooting	1.63	37	–	2.15*	37	Less disturbed setts have higher levels of authorized shooting
Attitude of landowner to badger conservation	0.86	32	–	2.37*	32	Less disturbed setts have land-owners who are unsupportive of badger conservation
Visibility of a person on the sett to passing motorists	2.10*	38	Setts still in use are more	–	–	–
Distance of nearest public from setts	0.59	34	–	2.95**	34	Less disturbed setts are nearer to public accesses
Number of public accesses within 400m of sett	1.35	38	–	2.08*	38	Less disturbed setts are nearer to more public accesses

Table 3. Effects of the frequency of selected factors on sett usage and level of disturbance G Tests with 1 degree of freedom

Factor	Effects on sett usage			Effects on disturbance		
	G	P	Interpretation	G	P	Interpretation
Whether visible from the nearest building	4.39	0.036	Setts still in use are more visible	2.32	0.128	–
Whether in a wooded or open landscape	4.07	0.044	Setts still in use are more often in open habitats	3.92	0.048	Highly disturbed setts are more often in wooded areas
Whether used by children/ localized recreation	2.10	0.148	–	0.01	0.928	–

setts with more disturbance incidents. Setts associated with more formalized shooting were more likely to have a low frequency of poaching ($r_s = -0.42$, $n = 36$, $P = 0.014$) and land occupiers who were unsupportive of badger conservation ($r_s = -0.46$, $n = 32$, $P = 0.010$). However, no relationship was found between land occupier attitude to badger conservation and frequency of poaching ($r_s = -0.19$, $n = 31$, $P = 0.295$).

Setts still in use in 1992–1993 tended to be visible from the nearest dwelling and in open landscapes (Table 3). Those in wooded areas were the most disturbed, although visibility appeared to have little effect on disturbance. There was no association between use of the area by children or for localized recreation and sett usage or level of disturbance (Table 3).

DISCUSSION

The densities of the setts studied (Table 1) are similar to those found nationally by Cresswell *et al.* (1990) for rural land classes of the type that occur in the Bradford district. Of the original setts, 47% have subsequently become disused. However, this does not necessarily imply a corresponding reduction in the number of badger social groups. Here we only examined previously identified active setts: no systematic search was made for new setts in the 1990s. However, we did observe one

main and two subsidiary setts which had not been recorded in 1985–1996, and it is therefore possible that animals may have moved. Skinner *et al.* (1991b) found that, on re-surveying 790 setts in Essex, 36% had become derelict or unrecognizable after 20 years. The loss in Bradford in only 9 years is higher, but not exceptional; of 27 setts in 1969 in Cheshire, there was an abandonment rate of 96% over 4 years (Ratcliffe, 1974).

The Bradford setts frequently occur in rocks and fissures, possibly reducing the potential for extensive excavations. They were found to have about half the holes per sett than the national averages of 11.9 and 4.3 for main and subsidiary setts, respectively (Cresswell *et al.*, 1990). Neal (1972) found the percentage of setts in quarries, embankments, coal tips and mines in West Yorkshire was higher than the national average. The number of sett entrances may be physically limited in such habitats, and badger distribution in adjacent South Yorkshire is also now centred around similar artificial environments, possibly due to increased physical protection from sett diggers (Paget & Middleton, 1974). Paget & Patchett (1978) suggest that setts which are harder to dig in West and South Yorkshire have a natural means of defence. In the current study, no relationship was found between sett survival and ease of digging, although more frequently disturbed setts appeared to be harder to dig (Table 2). It is possible that badger diggers

encountering such setts return to make repeated attempts to gain access to the badgers. Some wilful persecution by game or landowning interests was noted, although this accounted for <15% of all disturbance incidents. Indeed, game management interests may be beneficial since less frequently disturbed setts were associated with more formalized authorized shooting (Table 2). More formalized authorized shooting was also associated with lower frequencies of poaching. A lower frequency of poaching is beneficial, being associated with low sett disturbance and high sett usage (Table 2).

Co-operation of the land occupier may be important for badger welfare. However, we found no relationship between land occupier attitude to badgers and sett survival. Furthermore, less frequently disturbed setts had unsupportive landowners. However, unsupportive landowners were associated with more formalized shooting. These findings may be explained by the enthusiasm with which landowners protect their land. Any trespasser (naturalist or potential badger digger) may be discouraged by a formidable land occupier who, although not an active supporter of badger conservation, may not directly persecute the animal.

Since sett visibility was associated with low levels of disturbance and high continued usage, the likelihood of being seen disturbing a sett may be an important and effective deterrent to persecution. For example, visibility from the nearest dwelling was a feature of setts which were still in use in 1992–1993 (Table 3). Visibility from roads is also a factor associated with sett usage (Table 2), supporting the anecdotal observation by Paget & Patchett (1978) that, in South and West Yorkshire, setts near roads in good view of the public are less frequently disturbed by digging. Visibility may also explain why setts still in use and less frequently disturbed were more often in open (non-wooded) rather than wooded landscapes (Table 3). This supports the view of Paget & Patchett (1978) that, in West and South Yorkshire, setts in open areas are safer than those in woodland. Thus, whilst Neal's (1972) opinion that badgers prefer cover around their setts may be true in areas of low persecution, in the Bradford area badgers may not survive as well in woodland setts. Conversely, in The Netherlands, where road deaths are regarded as the greatest threat, setts in open landscapes with a greater increase in road density were more likely to deteriorate than those in wooded areas (van der Zee *et al.*, 1992).

The presence of public access may delay badger emergence and available time for foraging (S. Harris, pers. comm.; D. Yalden, pers. comm), and may be important considerations in the success of populations. However, we found no relationship between the number of, and distance from, public accesses and continued sett usage by badgers. Less frequently disturbed setts were closer to a larger number of public accesses (Table 2). However, we also found that the frequency of disturbance did not correspond to sett survival. This may be because practices with a severe impact on badger survival, such as sett gassing, poisoning and

destruction, had a comparatively low occurrence (3% of all events). Consequently, public access may deter high frequency events such as setts being dug or dogs entered deliberately (69% of all events), but not all persecution types. More severe practices may be carried out by land managers who may be less conspicuous to members of the public.

We suggest that existing public access may be benign or even beneficial in areas of high wilful persecution. Work on other animals has shown that public access may be detrimental where it is associated with localized recreational activities. For example, the invasive use of woodland for orienteering caused significant disturbance to roe deer *Capreolus capreolus* (Jeppesen, 1987). However, non-deliberate disturbance to badgers may be easier to address through management, planning legislation and education, than wilful persecution, which still exists despite over 140 years of protective legislation.

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Habitat use and diet of the American mink (*Mustela vison*) in Argentinian Patagonia

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INTRODUCTION

Popularity as a fur-bearing species led to the American mink *Mustela vison* being transported far beyond its native range in North America (Dunstone, 1993). In many places the species was bred in fur farms, from which there were inevitably escapes, and in some areas it was deliberately released in large numbers with the intention of establishing harvestable populations. Both routes led to the widespread establishment of feral populations of this versatile semi-aquatic mustelid. Invariably, close scrutiny of the impact of feral American mink on native fauna has led at least to concern, and increasingly to proof, that they are inimical to the conservation of native species. Evidence of the impact of the American mink on native species falls into two categories. First, American mink may reduce significantly, and locally exterminate, certain vertebrate prey (Macdonald *et al.*, in press). Second, as versatile and seemingly aggressive competitors they may alter the competitive balance within the local guild of semi-aquatic predators, even ousting native mustelids.

A negative impact on native prey has been documented for avian prey, such as coot and moorhen in Britain (P. Ferreras & D. W. Macdonald, pers. obs.), and this can have economic costs, e.g. in the case of eider ducks in Iceland (Hersteinsson, pers. comm.). Regarding mammalian prey, suspicions that feral mink were associated with an accelerating decline of water

voles, *Arvicola terrestris*, in Britain (Strachan & Jeffries, 1993; Halliwell & Macdonald, 1996), have been locally confirmed by Barreto, Macdonald & Strachan. (in press) and Strachan *et al.* (in press). That the American mink can have an impact on sympatric mustelids can be inferred from character displacement (V. Sidorovich, H. Kruuk & D. W. Macdonald, pers. obs.) and associated shifts in diet (e.g. Clode & Macdonald, 1995; Maran, Kruuk *et al.*, in press). It is most dramatically illustrated by mounting evidence that the American mink is substantially responsible for the dramatic decline towards extinction of the European mink *Mustela lutreola* (Maran, Macdonald *et al.*, in press; Sidorovich *et al.*, in press).

There are therefore grounds for concern wherever American mink spread into areas where local endemics may be threatened. One such area is Patagonia. Local wildlife administrators attribute to mink the disappearance of several populations of water birds and semi-aquatic mammals (e.g. the endemic subspecies of coypu *Myocastor coypus coypus*) from several lakes of the Andean Patagonia (Erize *et al.*, 1981). The American mink was introduced into Argentinean Patagonia for commercial farming in the 1940s (Pagnoni, Garrido & Martin, 1986). Escapes and deliberate releases continued until the 1970s, during which time feral populations spread rapidly through the region's sub-Antarctic forests and adjacent Patagonian steppe. Currently, although the detail of its distribution is

Table 1. Results of life trap capturing at Bahía Anchorena, Puerto Gross and Puerto Totorá

Bay	Sampled shoreline (m)	Sampling periods	Trap-nights	Captures	Captures/trap-nights
Anchorena	3437	22/1–5/2	171	13	0.034
		18/3–31/3	215	7	
		4/4–17/4	288	3	
Gross	725	4/2–5/2	3	0	0.011
		22/4–24/4	7	1	
		27/4–30/4	36	1	
		3/5–11/53	129	0	
Totorá	342	21/5–26-5	38	3	0.079
Total	4504	22/1–26/5	887	28	0.032

unknown, the species is widespread in fluvial valleys throughout the Andean–Patagonian region (Pagnoni *et al.*, 1986).

Currently, nothing is known of the habitat preferences of American mink in this region. Here, we investigate this with a view to establishing which native prey are at greatest risk and to exploring the likelihood of interaction between these mink and one endangered native predator, the huillin or southern river otter, *Lutra provocax*. It is well established that the abundance of mink scats provides a useful index of their distribution (Strachan & Jefferies, 1993), and these can be used to evaluate their habitat preferences and those of their prey (e.g. Barreto, Rushton *et al.*, in press). A recent study of the huillin (Porro & Chehébar, 1995) provides data which we can re-analyse for comparison with our observations on mink.

STUDY AREA AND METHODS

We studied American mink in the Nahuel Huapi National Park, a mountainous area of 7800 km² with abundant glacial lakes. The largest is the 530 km² Nahuel Huapi Lake, in which is situated the 3710 ha Victoria Island (40°56'S, 71°33'W), which has maximum dimensions of 20 × 4 km. Mean temperatures in winter and summer are 2 °C and 18 °C, respectively. The dominant vegetation type is southern beech forest *Nothofagus* spp.

Population estimates

Between January and May 1997 we live-trapped mink using Tomahawk traps baited with fish, deer, cow fawn eggs (a widely used and effective technique, e.g. Halliwell & Macdonald, 1996). Traps were set in 3 bays on the east coast of Victoria Island: Bahía Anchorena, Puerto Gross, and Puerto Totorá. Trapping dates, length of sampled shoreline, and number of trap-nights are described in Table 1. Traps were checked daily. Captured mink were lightly anaesthetized with Ketamine (Upjohns, U.K.) and released, fully recovered, within 40 min at the site. Animals were individually recognizable on the basis of white marks on their

ventral pelage. Thirteen morphometric parameters were taken on each captured mink.

Habitat use

Mink and huillin scats were counted (and collected for diet analysis), and habitats characterized at 2 bays: Puerto Gross (12 January to 18 March 1997) and Bahía Anchorena (5–7 May 1997). At each, a total of 15 100 × 25 m transects was distributed at semi-random on accessible areas of the coast, with *c.* 75 m between them. The following habitat characteristics were recorded:

Shoreline type: presence of rock, sand, clay, mud, pebble

Shoreline width: average width (m)

Shoreline slope: average slope (degrees)

Water depth: average depth at 2 m from the shore

Herbaceous: estimated % herbaceous coverage in the transect

Shrub: estimated % shrub coverage in the transect

Tree coverage: estimated % shrub coverage in the transect

Perennial shrub: estimated % perennial shrub coverage in the transect

Perennial trees: estimated % perennial trees coverage in the transect

Emergent vegetation: % of shoreline fronted by emergent vegetation.

Overhanging shrubs: % of shoreline fronted by overhanging shrubs.

Overhanging trees: % of shoreline fronted by overhanging trees.

Trunks: number of tree trunks lying on the shoreline

Human settlements: presence of hotels, garden houses, or piers.

Dogs: presence of dogs

Visitors: high or low frequency.

A stepwise regression analysis was used to identify the environmental determinants of habitat use. The minimum tolerance for entry into the model was 0.01. Principal component analysis (PCA), based on a correlation matrix of the original habitat data, was used to ordinate the habitat variables in the regression analysis. Variables with component loadings higher than ± 0.5 ,

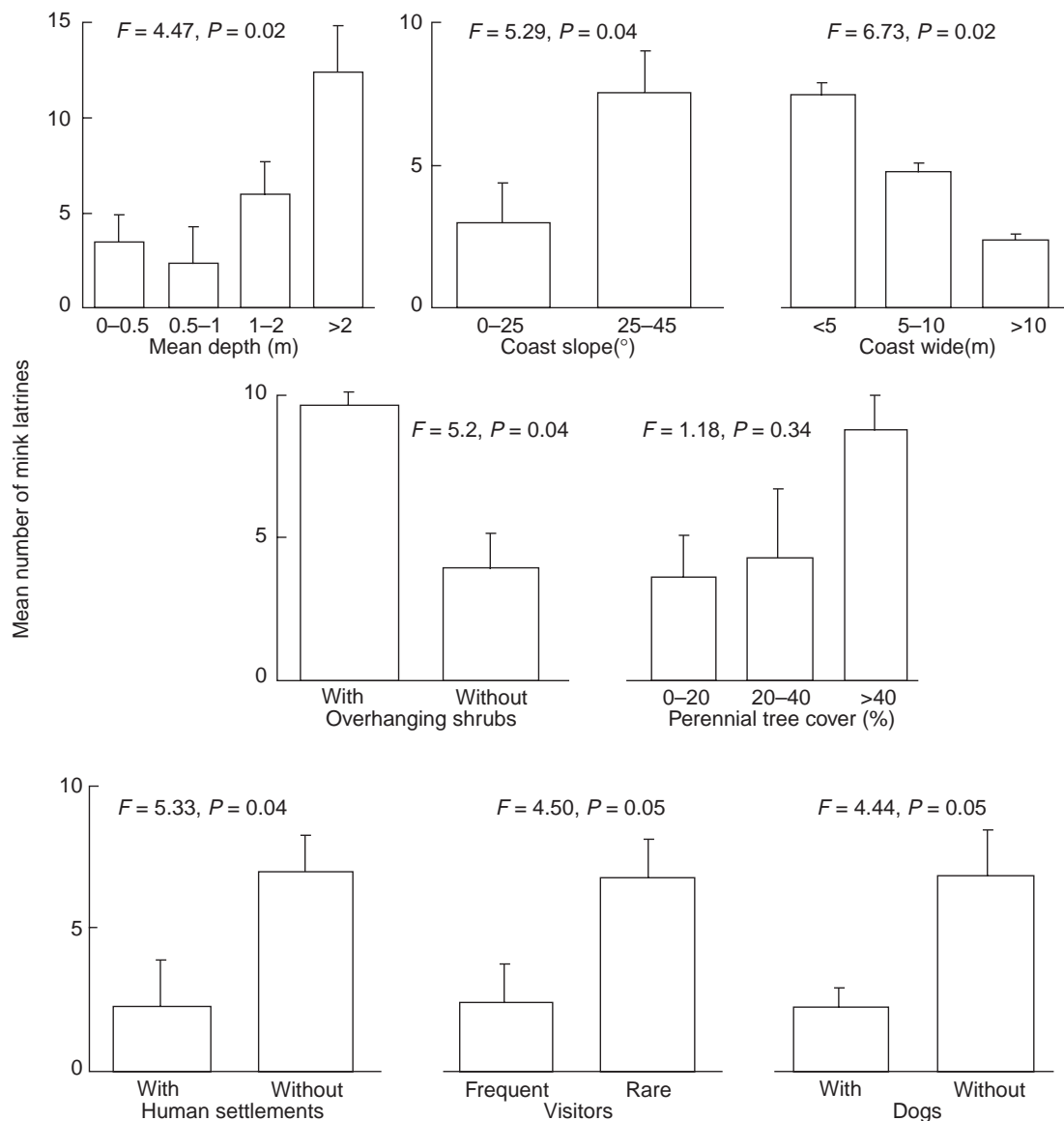


Fig. 1. The relationships between the mean numbers of mink latrines and the eight variables that provided high scores to the first principal component in the PCA. ANOVAs were conducted in order to validate the results of the PCA.

were considered to contribute high scores to the component.

Diet

To estimate the sample size needed to study the diet of mink, we followed the methods of Hanson & Graybill (1956). We distinguished mink's faeces based on a combination of size, appearance and the presence of stray hairs ingested while grooming (Chehébar & Bencit, 1988).

Contents of scats were classified into nine exclusive categories: mammal, bird, reptile, amphibian, fish, insect, crustacean, plant, and other. Diet content is presented as percentage frequency of occurrence (e.g. Racey & Euler, 1983).

RESULTS

Table 1 shows the length of coast that was sampled, the sampling periods, the number of captures, and the sampling effort in the three study sites.

Eight different mink were captured in 4.5 km of coast, of which seven were sub-adults (85.7%) and six were female (71.4%) (Table 2). Only mink GR was captured sufficiently often to reveal an approximate home range, traversing 950 m of coast and 400 m of land (from Bahía Anchorena to Puerto Gross) in 3 months (see Fig 1).

The first principal component of the PCA explained 23% of the variation in habitat variables. This was the only component that was significantly (negatively) related to the number of mink latrines ($a = 5.13$, $b = -2.95$, $r = 0.45$, $F_{1,13} = 10.71$, $P = 0.006$). High

Table 2. Characteristics of mink captured

Name	Sex	Captures	Date	Body length	Body weight
VA	F	4	23 Jan–31 Jan	43.5–43.5	400–315
GR	F	13	23 Jan–23 Apr	46–51.5	420–540
FL	M	1	23 Jan	43	315
MU	F	2	23 Jan–3 Feb	42	308
CO	M	1	3 Feb	55.5	790
CL	F	1	20 Mar	46.5	400
ES	F	1	9 Apr	–	500
CU	F	2	25/5–26/5	47	480

Table 3. Frequency and percentage of occurrence of prey types in 60 scats collected

Prey type	Frequency	Percentage
Mammals	25	41.7
Birds	18	30
Reptiles	2	3.3
Amphibians	0	0
Fish	22	36.7
Insects	38	63.3
Crustaceans	59	98.3
Vegetation	38	63.3
No identified	2	3.3

positive scores on PC1 were related to shoreline topography (slope, depth, and width), vegetation (tree coverage, and overhanging shrubs), and human disturbance (settlements, dogs, and visitors), whereas negative scores on this component were associated with narrow and steep shorelines with deep water, high coverage of perennial trees, abundant overhanging shrubs and isolation.

Simple ANOVAs were conducted to validate the results of the stepwise linear regression using PC1. Figure 1 shows the relationships of mean numbers of mink latrines per transect with the associated habitat characteristics that influenced PC1. All habitat variables that contributed highly to the first component of the PCA were significantly related to the mink abundance index, with the exception of 'tree cover'.

Table 3 shows the composition of mink diet. They preyed upon several categories of prey, including insects, mammals, fish, and birds. However, crustacea were the most frequent prey, occurring in almost all faeces analysed (59/60).

DISCUSSION

Our live-trapping yielded an estimated density of 1.5 mink/km of shoreline. This is within the estimates quoted elsewhere (e.g. Eagle & Whitman, 1987; Halliwell & Macdonald, 1996). On Victoria Island, scat distribution indicated that American mink favoured aquatic habitats adjoining wooded cover. This is also in accord with results elsewhere (review by Allen, 1986). In

our study area, deep water with overhanging vegetation was associated with complex shoreline environments, thought to be ideal habitat for the crustacea *Aegla* and *Sammastacus*. Crustaceans comprised c. 80% of the diet. Mink are widely reported to adapt their habitat use to the availability of prey (reviewed by Eagle & Whitman, 1987). The habitats selected by mink may also have been the least disturbed, and were characterized by minimal human presence and little disturbance by dogs, although opinions differ over whether mink are (e.g. Racey & Euler, 1983) or are not disturbed by people (e.g. Kauhala, 1996).

Habitat use and diet of huillin were studied in Nahuel Huapi National Park by Chehébar (1985) and Chehébar *et al.* (1986) before mink were established there. Scat surveys revealed that their habitat and food preferences closely paralleled those we report here for American mink. Huillin diet also was comprised largely of crustacea which occurred in 99% of huillin scats, a value almost identical to the 98.3% that we obtained for mink. Porro & Chehébar (1995) surveyed 11 lakes and rivers in Nahuel Huapi National Park for both huillin and mink. Considering the distribution of habitats between these survey sites, it is possible to estimate the probability of finding both species at any one site. Cassini (1997) re-analysed the data obtained by Porro & Chehébar (1995), and found a significant negative correlation between the distribution of both species ($r_s = -0.90$, $P < 0.002$).

These results are reminiscent of Clode & Macdonald's (1995) finding of diet shifts where American mink and European otters *Lutra lutra* co-exist on offshore Scottish islands. In the latter case the diets of the two species were very similar where they occurred separately, but the diet of the mink was shifted when it occurred sympatrically with otters. Clode & Macdonald (1995) concluded that the food niche of the two species was very similar, throwing them into competition with the result that the larger otter forced a shift in the mink's diet. In the case of our study, and the inferences we can thereby draw from Porro & Chehébar's (1995) survey, it seems that competition between the huillin and American mink is likely. Considering the conservation status of the huillin, this possibility merits urgent study.

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