

Population density of the greater mouse-eared bat (*Myotis myotis*), local diet composition and availability of foraging habitats

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Abstract

We studied the regional variation in population density of *Myotis myotis* (Borkhausen 1797) in south-eastern Bavaria, Germany, and its relations to diet composition and the availability of potential foraging habitats. We monitored colony size and juvenile mortality from 1991 to 2003, conducted faecal analyses in 1993 and determined land-use patterns around colonies. The numbers of individuals counted in the nursery colonies showed only small fluctuations over the years. However, data on colony size demonstrated a pronounced regional variation. Epigeic arthropods, mainly Carabidae, were the most important prey. The diet included prey taxa of forest as well as grassland habitats. The percentage of those prey taxa in the diet that originated in grassland managed with different intensity varied according to the availability of these potential foraging habitats around the nursery roosts. The calculated population density of the bats was positively correlated to forest area and especially to the area of mixed forest around the nursery roosts. Our results indicate that the availability of foraging habitats is a limiting factor for local population densities in the greater mouse-eared bat.

Introduction

Bats are long-living, slowly reproducing mammals that maintain relatively stable populations and therefore are considered to be *K*-selected (Gaisler, 1989; Findley, 1993). The population density of *K*-selected species is expected to be near the carrying capacity of the environment, and density-dependent factors as food or roost availability are important for the regulation of the population (Krebs, 1985). Little is known about the factors determining the population density of bats, mainly because the density of most species is difficult to estimate. One exception is the greater mouse-eared bat (*Myotis myotis*, Borkhausen 1797) in Central Europe, females of which can be counted in the very conspicuous nurseries in attics of churches and castles. Census data from many areas demonstrate that large variations of population densities occur (Horáček, 1985; Güttinger *et al.*, 2001). However, as greater mouse-eared bats may forage further than 10 km away from their roost (Arlettaz, 1996; Güttinger, 1997), only a few roosts suitable for reproduction (e.g. warm attics in valleys) are necessary for inhabiting a large region. Rudolph & Liegl (1990) suggest that the availability of suitable foraging habitats may be an important factor to explain the observed population density patterns in northern Bavaria. They found only

a few colonies in areas where pine forests *Pinus sylvestris* with dense ground vegetation were dominant but many large colonies in areas where beech *Fagus sylvatica* and oak forests (*Quercus* sp.) with sparse ground vegetation were abundant. *Myotis myotis* is able to use only forest habitats with open ground to hunt carabid beetles, its main prey (Audet, 1990; Arlettaz, Perrin & Hausser, 1997; Güttinger, 1997). However, the studies of Arlettaz (1996) and Güttinger (1997) in Switzerland show that greater mouse-eared bats also forage on freshly mown meadows, short-grazed pastures or bare fields where the bats can easily catch their prey on the ground. It is therefore still an open question whether and how the availability of suitable foraging habitats could act as a limiting factor for the regulation of the population density in the greater mouse-eared bat.

If foraging areas are a limiting resource, a correlation between the regional variation in population density and the availability of potential foraging habitats should exist. Moreover, we expected that the diet composition reflects the composition of foraging habitat types around colonies.

To test these hypotheses, we studied a population of *M. myotis* in south-eastern Bavaria (south of Germany) for over 10 years, visited all potential roosts in buildings and monitored all nursery sites.

Methods

Study area and estimation of population size

We conducted the study from 1991 to 2003 in an area of c. 4000 km² located at the northern border of the Alps in south-eastern Bavaria. Forests and permanent pastures cover the mountainous parts in the southern quarter of the area, where the terrain makes agriculture difficult. Meadows are dominant in the lowlands close to the Alps where rainfall is high. Fields are the prevailing use of land in the drier northern half of the area.

To determine the abundance of bats and the distribution pattern of roosts in the area, we visited 360 buildings (churches and castles) where nursery colonies could potentially exist. To eventually find roosts in other types of buildings, we contacted local bat conservation groups and carried out surveys in newspapers. Nursery roosts were recognized by the presence of females with juveniles during the nursery period in June and July. Roosts of solitary males were identified by sightings or by the presence of fresh faeces and dark-coloured marking areas around the roosting place, which indicate male roosts also if no individual is present (Zahn & Dippel, 1997). Between the end of May and the end of July, we checked all nursery colonies ($n = 22$) one to three times to count adults, living and dead juveniles.

Definitions of population parameters

On the basis of mean number of adults counted in each colony during the study period, we defined a 'relative population size'. The true population size is higher because the adults in the colonies are mainly females (Zahn & Dippel, 1997). Males, which are solitary during summer, are excluded as their numbers could not be determined accurately. To compare the relative population size in different parts of the study area, we could not use the colony sizes as an index of bat density because large and small colonies were often located in close proximity. Instead we used a 'calculated population density' which was determined for a radius of 10 km around each nursery roost. According to Güttinger *et al.* (2001) and Zahn, Haselbach & Güttinger (2005), most of the foraging sites are supposed to be located within this area. As closely neighbouring colonies were expected to share their 10-km range to a large extent (Rudolph, Zahn & Liegl, 2004), we used only those 12 colony sites for correlation analyses that shared less than one-third of the range with each other to prevent autocorrelations. For each of the 12 colony sites, the calculated population density was determined by adding the percentage of the size of each neighbouring colony according to the extent of radius overlap, for example if the 10-km radius of a colony overlapped to an extent of 20, 40 and 70% with three neighbouring colonies, 20, 40 and 70% of the size of the neighbouring colonies were added to the size of the colony under consideration.

This method allowed us to compare estimated densities of foraging bats instead of absolute colony sizes.

We used Spearman's rank correlation to analyse the statistical relation between the calculated population density and the percentage area of potential foraging habitats within the 10-km radius.

Estimation of availability of potential foraging habitats

To evaluate the composition and availability of potential foraging habitats, we determined human land-use patterns in a radius of 10 km (see above) around each colony. We obtained the percentage area of grassland and fields from the statistical reports (1987, 1989) of the Bavarian 'Landesamt für Statistik und Datenverarbeitung', the percentage area of coniferous forests and mixed deciduous-coniferous forests from a satellite photograph (11 July 1987; FO, colour, TM 192-27; 1:125 000). These data reflect the situation shortly before the beginning of our study in 1991. Forests with a percentage area of coniferous trees (mainly spruce *Picea abies*) of more than 70% were regarded as 'coniferous forests', and those where the percentage area of deciduous trees (mainly beech) exceeded 30% were regarded as 'mixed forests'. Pure deciduous forests were very rare and therefore included in 'mixed forests'. Grassland habitats were divided into two groups: meadows with high offtake (3–6 cuts per year, 'high farming intensity') and grassland with relatively low offtake (mainly permanent pastures, 'low farming intensity').

Faecal analyses

In 13 colonies, samples of fresh droppings were collected every 2 weeks in 1993 (eight samples; 18 May–13 September). Of every colony, 120 pellets (15 per sample) were analysed. The pellets were soaked in ethanol and then completely dissected using a binocular microscope. Using a needle and tweezers, we searched for taxonomically ascertainable fragments (Whitaker, 1988; McAney *et al.*, 1991; Wolz, 1993). Proportions of various prey taxa in the diet were quantified by the frequency of occurrence. We determined in each sample the percentage number of pellets in which a certain type of prey was found and calculated the mean for each colony. On the basis of these frequency values for each colony, we calculated the mean frequency of each colony group formed by cluster analyses.

Variation of diet and composition of potential foraging habitat

To address the question of whether regional differences in the diet correlate with the availability of different habitat types around the colonies, we grouped the 13 colonies by means of a cluster analysis (within-groups linkage, Euclidean distance), using the frequencies of only those prey taxa which (1) could be related to a certain habitat type and (2) showed an average frequency in the faeces (mean of all colonies) of at least 4%. The carabid beetles *Carabus auronitens* and *Pterostichus burmeisteri* are typical forest-

dwelling species (Thiele, 1977; Wachmann, Platen & Barndt, 1995); Acrididae and many large common species of Tipulidae (e.g. *Tipula paludosa*, *Tipula oleracera*) prefer grassland habitats. High population densities of Acrididae can be usually found in grasslands with low farming intensity (Schlumprecht & Waerber, 2003). Several large Tipulidae species normally occur in very high densities in rather humid meadows and pastures (Sellke, 1936; Lauenstein, 1986; Ramsell, Malloch & Whittaker, 1993; Wöllecke, Ispas & Bölscher, 1996). Seasonal peak abundance of tipulids in the diet of the bats during August and September were according to the abundance patterns observed in eastern Switzerland by Güttinger (1997). There large tipulids (mainly *T. paludosa*) can be regularly found in very high densities in cultivated grassland habitats in certain regions during late summer. Therefore, we regarded the frequencies of Tipulidae in the faeces collected in August and September as an indicator of foraging activity in grassland habitats.

As one cluster contained only a single colony, it was excluded from this statistical comparison. We used the Mann–Whitney *U*-test to detect statistical differences between the other two clusters (including seven and five colonies) with respect to the habitat specific prey taxa (frequencies of occurrence of forest-dwelling carabid beetles, large Tipulidae, Acrididae) and the availability of potential foraging habitats (percentages of forests, meadows, fields) in the 10-km radius of the colonies. Consequently, unsuitable habitat types as settlements or streams were excluded from the analyses.

Results

Distribution of nursery colonies and relative population size

Roosts of *M. myotis* were found in 83% of all 360 buildings investigated (churches and castles). In most cases only roosts of solitary males were found. Nursery colonies settled only at 22 locations (6.1%).

The location and size (adults) of nursery colonies and the distribution of male roosts in the study area is shown in Fig. 1. The colony roosts were located in altitudes from 391 to 634 m. The size of the colonies did not correlate with altitude ($r = 0.29$, $P = 0.19$, $n = 22$). Although the observed distribution patterns and colony sizes of nursery roosts were regarded to represent the relative population size during summer in different parts of the study area, the location of the detected male roosts depended on the distribution of the buildings investigated. The total number of male roosts was unknown, as solitary bats also roost in bat boxes and tree cavities, which were not considered.

Nursery colony sizes varied between four and 960 adults. The three colonies that contained less than 18 adults in 1991 declined progressively during the study period and became extinct in 1999.

In spite of considerable variations in the colony sizes, the overall population size remained rather constant during the study period. The relative population size in the whole area

varied between 3461 in 1992 and 2993 in 1997 (mean over the years: 3185; SD: ± 151). The difference of the relative population size between two consecutive years never exceeded 11% and could be partly explained by juvenile mortality. In 5 of 6 years when the juvenile mortality was less than 5%, the relative population size was higher in the following year. In 4 out of 6 years when juvenile mortality exceeded 5%, the relative population size was lower in the consecutive year.

Regional variation of diet composition

The diet composition of different nursery colonies showed a remarkable variation (Table 1). Carabidae, Scarabaeidae, Tipulidae, Araneae and Opiliones were found in the faeces of all 13 colonies, whereby Coleoptera (especially carabids) were the most important prey in all cases. Chilopoda, Acrididae, Gryllotalpidae, Ichneumonidae and Lepidoptera were represented in the diet of more than five colonies. Tettigoniidae, Sylphidae, Staphylinidae, Chrysomelidae, Dermaptera, Chironomidae and Syrphidae were found in the diet of less than five colonies.

The presence of several prey categories revealed a geographic pattern in the diet (Table 1). Acrididae were regularly found in the six most southern colonies (mean frequency 10.2%) and only rarely in the seven northern sites (mean frequency 0.5%). The same pattern could be observed in the case of *Gryllotalpa gryllotalpa*, which was part of the diet in all six southern colonies (mean frequency 2.1%) but only in three of the seven northern colonies. In Tipulidae, an opposite pattern was found: this prey was rarer in the south (mean frequency 13.3%) than in the north (mean frequency 21.3%).

On the basis of the frequencies of the forest-dwelling *C. auronitens* and *Pt. burmeisteri* and of the grassland-dwelling Acrididae and Tipulidae in the diet of the different colonies, a cluster analysis revealed three groups of colonies that were geographically separated in the study area. Cluster 1 included all seven colonies outside the Alps in the northern part of the study area. The five colonies of cluster 2, located in the southern half of the area, settled in valleys or on slopes of the most northern foothills of the Alps. Cluster 3 contained only the most southern colony of the study area, located in a valley of the northern limestone Alps. Cluster 1 was characterized by relatively high frequencies of *Pt. burmeisteri* and large Tipulidae, and cluster 2 by higher frequencies of *C. auronitens*, and Acrididae (means: Fig. 2). Except in *C. auronitens* these differences between the two clusters were significant (*U*-test, $P < 0.05$; values per site see Table 1). The single colony of cluster 3 had the highest value for *C. auronitens*, medium values for Acrididae and *Pt. burmeisteri*, and lowest values for Tipulidae.

Regional variation of potential foraging habitats

We found considerable differences concerning the availability of potential foraging habitats between the three colony

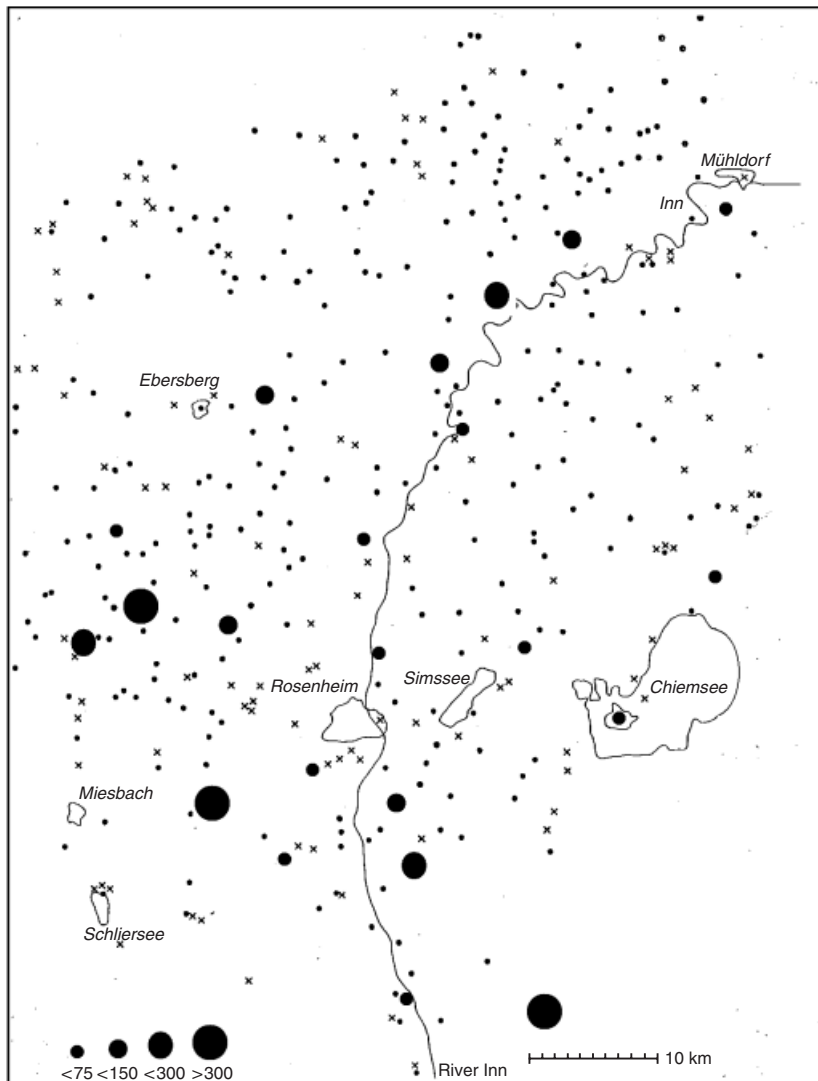


Figure 1 Spatial distribution of the roosts of nursery colonies and single males in the study area. Black circle, nursery colony; black dot, male roost; cross, suitable building without roost. Colony sizes: <75, average size during the study period <75 adults; <150, average size during the study period 75–144 adults; <300, average size during the study period 145–299 adults; >300, average size during the study period >300 adults.

groups. The mean percentage area of fields within the 10-km range of each colony site was highest for colonies of cluster 1, low for colonies of cluster 2 and extremely low for the single colony of cluster 3 (Table 2). Mean percentage areas of forests were very high for colonies of clusters 2 and 3 and indicated a pronounced dominance of this habitat type. In the 10-km ranges of the northern colonies (cluster 1), forest covered only one-third of the area (Table 2). The mean extension of grassland with high farming intensity was highest in cluster 1 and lowest in cluster 3. The percentage area of grassland with low farming intensity was lowest in cluster 1 and comparatively high in clusters 2 and 3. The proportions of all open habitat types differed significantly between the seven colonies of cluster 1 and the five colonies of cluster 2 (U -test $P < 0.05$; means: Table 2), whereas no statistical difference was found for the proportion of forest area.

These differences in land-use patterns can widely explain the regional dietary variations (Fig. 2). In colonies of

cluster 1, which were located in areas with the highest proportion of intensively farmed grassland, Tipulidae occurred most frequently in the faeces. In colonies of cluster 2, which were located in areas with the highest proportion of grassland with low farming intensity, Acrididae were most often found in the diet. The low values of Tipulidae in the single colony of cluster 3 were in agreement with the comparatively low proportion of intensively farmed grassland, whereas the high frequencies of forest-dwelling carabids corresponded to the large forested areas around the colony site.

Calculated population density and availability of potential foraging habitats

In spite of the fact that the observed variation in diet composition could be explained by the land-use pattern of the potential foraging habitats, the calculated population density correlated only with the proportion of forest area

Table 1 Prey categories found in the faeces of the different colonies (frequency of occurrence)

Prey category	Mean	SE	Colonies												
			North			←→							South		
			1	2	3	4	5	6	7	8	9	10	11	12	13
Coleoptera	87.6	4.6	97.6	90.0	91.5	83.3	88.3	83.1	87.5	84.4	82.0	85.1	90.0	83.8	92.2
Coleoptera larvae	5.7	2.7	7.6	9.7	7.4	3.8	10.3	7.4	3.1	3.1	4.6	3.6	7.2	4.6	1.7
Carabidae	83.6	6.8	95.2	88.5	88.5	83.1	83.3	80.5	85.3	76.4	67.9	82.0	84.9	80.3	90.3
Carabus	55.4	9.8	74.8	55.6	59.7	51.5	65.0	55.1	55.0	45.0	41.7	64.1	55.4	39.2	58.6
<i>Carabus auronitens</i>	4.3	2.9	6.5	2.6	0.5	2.3	3.3	2.1	2.2	2.8	3.3	9.0	7.2	3.8	9.7
<i>Carabus granulatus</i>	1.2	1.5	5.1	1.0	0.5	3.1	2.5	0.0	0.6	0.0	0.8	1.0	0.5	0.5	0.0
<i>Cychrus</i>	4.0	3.2	1.8	1.8	2.1	1.0	3.1	3.3	5.8	1.1	5.1	4.6	5.4	4.1	13.1
Pterostichinae	66.5	5.4	66.7	74.3	70.5	65.4	60.0	64.9	67.8	69.2	54.9	60.3	70.5	67.9	72.2
<i>Pterostichus burmeisteri</i>	15.6	6.4	8.1	19.0	20.8	27.2	17.8	24.4	16.7	12.2	10.6	7.2	12.6	8.5	17.8
<i>Poecilus</i>	1.7	1.2	1.2	1.5	4.1	3.6	1.1	2.6	2.2	1.7	1.3	1.8	0.0	1.0	0.0
<i>Abax</i>	2.0	1.2	3.3	2.8	0.5	1.5	3.9	1.0	1.1	1.9	2.3	3.1	2.6	1.8	0.0
Scarabaeidae	5.8	3.8	4.8	1.3	4.9	2.8	5.6	5.1	6.1	3.6	17.2	5.1	7.1	6.7	4.6
<i>Aphodius</i>	4.5	4.2	3.6	0.5	0.5	2.8	3.9	3.6	6.1	3.1	17.2	4.6	6.4	4.3	1.9
<i>Melolontha</i>	1.3	1.3	1.2	0.8	4.6	0.0	1.7	1.5	0.0	0.6	0.0	0.5	0.8	2.3	2.5
Diptera	17.8	6.8	16.7	27.4	13.3	28.5	20.0	27.4	18.1	14.4	21.8	12.6	12.0	10.8	8.3
Tipulidae	17.6	6.6	16.1	26.1	13.3	28.5	19.4	27.4	18.1	14.4	21.8	12.6	12.0	10.8	8.3
<i>Saltatoria</i>	6.1	7.3	2.4	0.5	0.8	0.5	0.0	0.0	1.4	17.8	16.9	14.9	10.0	9.5	4.7
Acrididae	5.0	6.0	1.8	0.0	0.0	0.5	0.0	0.0	1.4	13.6	16.9	13.1	7.2	6.9	3.9
<i>Gryllotalpa gryllotalpa</i>	1.1	1.3	0.6	0.5	0.8	0.0	0.0	0.0	0.0	4.2	1.0	1.3	1.8	3.1	1.4
Arachnida	6.1	2.4	2.1	7.7	9.5	5.6	2.8	7.7	5.0	5.8	4.1	7.9	6.4	4.9	9.7
Araneae	3.6	1.6	1.5	2.6	5.9	4.4	1.7	3.1	1.4	4.7	2.8	6.9	4.4	3.6	3.9
Opiliones	2.6	1.9	0.6	5.1	3.6	1.3	1.1	5.1	3.6	1.1	1.3	1.0	2.1	1.3	6.4
Chilopoda	3.2	3.5	2.4	3.1	1.6	2.6	1.9	1.0	0.0	5.0	1.0	0.5	1.0	9.7	11.4

The colonies are listed geographically from north (left) to south (right). Cluster 1, colonies 1–7; cluster 2, colonies 8–12; cluster 3, colony 13. Not included are *Calathus spec.*, *Carabus cancellatus*, *Carabus monilis*, Chironomidae, Chrysomelidae, Dermaptera, Hymenoptera, Lepidoptera, *Molops spec.*, *Nebria spec.*, Silphidae, Staphylinidae, Syrphidae, Tettigoniidae, which were found in less than 1% of the faeces. Grey shading: prey categories used for cluster analyses.

within the 10-km range ($r = 0.69$; $P = 0.01$, $n = 12$; Fig. 3a). If coniferous and mixed forests were tested separately, a higher positive correlation exists between the calculated population density and the proportion of mixed forest around the colonies ($r = 0.80$, $P < 0.01$; Fig. 3b). The other correlations were not significant (fields: $r = -0.40$; grassland with high farming intensity: $r = 0.05$; coniferous forests: $r = 0.23$; grassland with low farming intensity: $r = 0.43$; in all cases $P > 0.3$).

Discussion

Our study is based on the assumptions that the bats forage in the habitat types included in the analyses and that the prey taxa used for the cluster analyses are typical for specific habitats. That *M. myotis* forages in forests, meadows and pastures when open floor is available was shown for several central European landscapes, including southern Bavaria (Audet, 1990; Arlettaz *et al.*, 1997; Güttinger, 1997; Zahn *et al.*, 2005). In all these cases the bats foraged in habitat types regarded as potential foraging areas in our study. In case of the prey taxa, we used only species or prey categories for the analysis that were habitat specific in central Europe according to the literature and to results of a study con-

ducted by one of us in Switzerland (Güttinger, 1997). Studies of Arlettaz (1996) and Arlettaz *et al.* (1997) show that prey composition obtained from faecal samples of mouse-eared bats depends indeed on foraging habitats and on the phenology of prey species in these habitats.

A problem in our analyses was that the data on land use and forest composition refer to the situation 6 years before the faecal samples were taken. However, between 1987 and 1993 the forest composition and the relation between fields and meadows did not change much in the study area, according to our personal observations.

Our study shows that populations of *M. myotis* are stable over years and that the availability of one type of foraging area, the mixed forest, can explain most of the variation of the population density in the study area. Alternative hypotheses are not convincing:

(1) The number of available roosts is unlikely to limit the distribution or the population density in the study area as only 7% of all roosts occupied by *M. myotis* contain nursery colonies. As most attics of churches and castles have a similar construction and as the colonies were found in all types of attic constructions including those with considerable differences in temperature (Zahn, 1999), it seems likely that many of the sites investigated, which were occupied

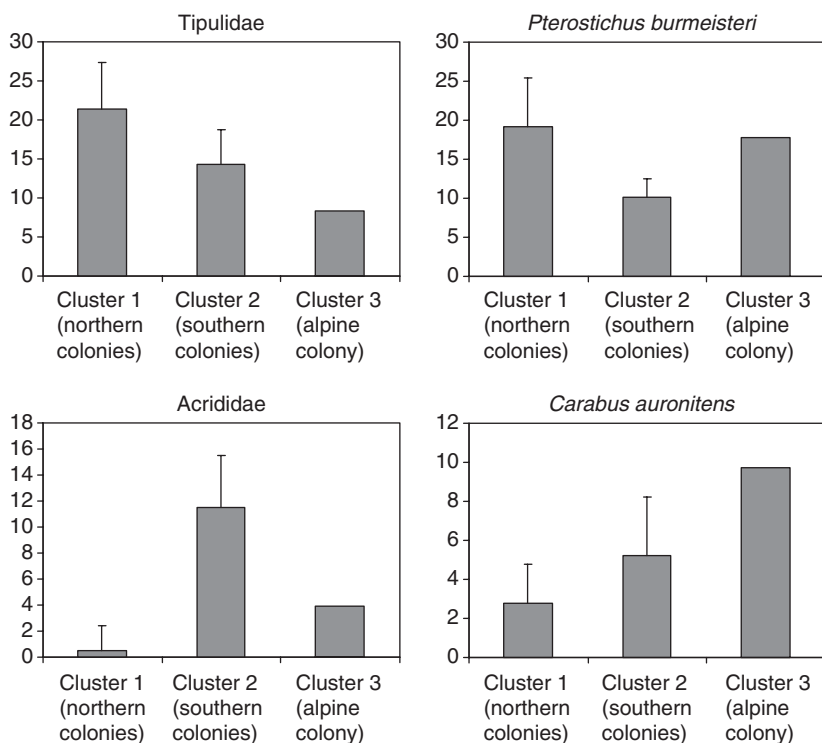


Figure 2 Frequency of selected prey taxa (percentage number of pellets in which a certain type of prey was found) in the diet of different clusters. The mean frequencies of the seven colonies of cluster 1, the five colonies of cluster 2 and the frequency of the one colony of cluster 3 are given.

Table 2 Composition of potential foraging areas (10-km radius of the colonies) in different clusters

Potential foraging habitat	Cluster 1 (seven colonies)	Cluster 2 (five colonies)	Cluster 3 (one colony)
Grassland with low farming intensity	6 (± 4.1)	16 (± 2.8)	14
Grassland with high farming intensity	34 (± 4.1)	25 (± 6.7)	15
Field	24 (± 11.2)	5 (± 1.8)	2
Forest	36 (± 6.4)	54 (± 5.1)	59

Areas that do not belong to the potential foraging areas as settlements, shrubs, riparian forests or lakes are excluded. The mean percentages (%) and standard deviations of the colonies belonging to clusters 1 and 2 and the percentages of the one colony of cluster 3 are given.

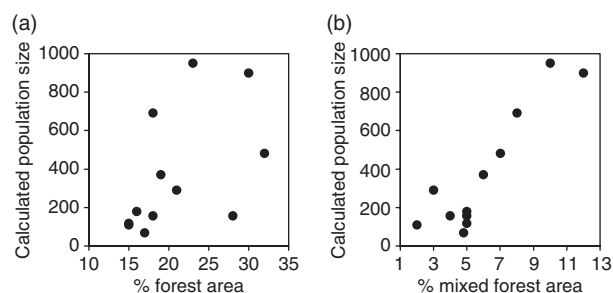


Figure 3 Correlation between the calculated population density and (a) the percentage of forest ($r=0.69$) and (b) the percentage of mixed forest ($r=0.80$) in the 10-km radius.

only by males, would also be suitable for maternity colonies. This is especially the case in warmer areas at lower altitudes, where colonies are usually concentrated (Spitzenberger, 1988; Rudolph & Liegl, 1990; Güttinger, 1994) and where many potentially suitable roost sites were found.

(2) Cold and wet weather generally influences juvenile mortality (Roer, 1973), which contributed to the small interannual variations of the relative population size in the area, but this mortality did not regulate the population as it was not a density-dependent factor. The percentage of dead juveniles did not correlate with the bat density in different parts of the study area (Zahn, 1999).

However, results of the faecal analyses seem to contradict the assumption that the foraging area 'forest' is a limiting resource for the studied population of *M. myotis*. The remains in the faeces demonstrate that foraging outside of forests must be common because prey of open habitats such as grasshoppers were frequently found in the faeces. Moreover, the cluster analyses indicate that the prey composition at the colony sites depends on the prevailing foraging habitats because the frequency of Tipulidae and Acrididae in the faeces varied according to the human land-use patterns around the colony sites.

An explanation could be that in a seasonal structured environment, a resource influencing the population density may act as a limiting factor for only a critical period of the

year. In the case of *M. myotis*, spring could be such a critical period. Bats show the lowest weights of the year in April after hibernation and in cold springs the weights are still decreasing (Güttinger *et al.*, 2001). Forests are the most important foraging areas in that period (Güttinger, 1997). They have a more temperate climate than habitats in open landscape, which favours arthropods and therefore offers better conditions for foraging bats than meadows and alpine pastures, especially during cool weather. Additionally, pit-fall trap samples indicate that carabid activity is greatest in south Bavarian forests at this time (Audet, 1992).

The climatic advantages of forests could also be important in autumn, when juvenile bats have to gain much weight for hibernation. Therefore, forests probably offer better conditions for hunting mouse-eared bats during critical periods than foraging areas in open habitats. That food supply is indeed scarce in spring and autumn was already shown by Bauerova (1978), who found less profitable prey such as spiders mainly in these periods when he studied prey composition in digestive tracts of *M. myotis*.

The correlation between population density and percentage area of mixed forest (Fig. 3) indicates that mixed forests mainly dominated by beech *F. sylvatica* and spruce *Pic. abies* are more important foraging areas than pure spruce-dominated coniferous forests. However, there is no evidence for a strong selection against spruce forests from radio-tracking studies in Bavaria and Switzerland (Güttinger, 1997; Zahn *et al.*, 2005). A reason for the importance of mixed forests for *M. myotis* might be the density of the undergrowth in this habitat compared with spruce forest (Güttinger, 1997). When spruce forests age, a decline in crown density favours the growth of herbs and shrubs, making old stands unsuitable for foraging. In beech and beech-mixed forests, even old stands have a dense canopy that prevents dense undergrowth. Given forests of the same size and age composition, in beech and mixed forests a higher percentage of the area is suitable as foraging habitat for *M. myotis* than in spruce forests. This could explain the correlation between mixed forest area and population density of *M. myotis*.

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