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Original investigation

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

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Abstract

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

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

Introduction

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

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

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

Material and methods

The study area ranges from Garmisch-Partenkirchen (11°06′ O, 47°29′ N) in the west to Berchtesgaden (13°0′ O, 47°37′ N) in the east and includes altitudes from approximately 800 m to 2 963 m above sea level (Zugspitze). About 50% of the area is covered with forest (mostly *Fagus sylvatica*, mixed with *Picea abies*, *Abies alba* and *Acer pseudoplatanus*). The remaining area consists of extensively used mountain pastures and, over about 1 800 m above sea level, of unused alpine meadows, dwarfpines and rocky outcrops.
Five hundred buildings (from small wooden mountain cabins to hotel-sized stone houses) at altitudes between 800 m and 1 800 m were surveyed between May and September 1997. Of these, 451 provided potential roosts for bats. As potential roosts we regarded all kinds of crevices if they were dry, narrow (< 5 cm wide), dark and without a strong airflow (< 15 cm deep). As described below, these crevices were roughly divided into five categories. Shutters, which are frequently used by bats (RICHARZ 1986) in spite of that fact that they offer less shelter from wind and rain than the other types, were also included. Large accessible attics, which are common roost sites for bats in the lowlands, were rarely present in the investigated buildings and are therefore not included in the list of potential roosts.
Faeces and dead or living animals were taken as evidence for site use. Substantial accumulation of faeces was taken as evidence for colonies. Site use inferred from faeces' presence is referred to as "indirect proof", whereas alive animals were taken as "direct proof". When possible, living animals were caught for species identification. With the exception of *Myotis myotis* whose droppings reliably could be identified through size and structure, no species identification was attempted using faeces. During the study we did not distinguish between *Pipistrellus pipistrellus* and the "new species" *Pipistrellus "pygmaeus/mediterraneus"* (HÄUSSLER et al. 2000).
For comparison with the lowland bat population, data of the ASK Bavaria (database "Arten- und Biotopschutzkartierung" of the Bavarian State Office of Environmental Protection) were called upon. These data were obtained as well by systematic controls of churches, castles and other buildings that offer suitable attics as by roost controls conducted after house owners informed the relevant authorities about bat presence. These roost controls (visits of attics, inspection of crevices) were conducted in the same way as in the present study.

Results

Species composition and abundance of roosting bats

At 189 (41.9%) of the 451 potentially suitable buildings evidence of site use by bats was obtained. In 100 of these cases, the animals' presence was indicated by faeces alone. A total of 203 roosting animals (excluding nursery colonies) was found. Of these, 110 were identified to the following nine species: Greater mouse eared bat (*Myotis myotis*, 4%), Geoffroy's bat (*M. emarginatus*, 1%), whiskered bat (*M. mystacinus*, 50%), Brandt's bat (*M. brandti*, 13%), common pipistrelle (*Pipistrellus pipistrellus*, 13%), Nathusius' pipistrelle (*Pipistrellus nathusii*, 1%), northern bat (*Eptesicus nilssonii*, 13%), common long eared bat (*Plecotus auritus*, 5%) and parti-coloured bat (*Vespertilio murinus*, 2%). With 29 animals, no reliable differentiation between *M. mystacinus* and *M. brandti* could be made. We assumed that the relative fraction of the two species was the same as that determined reliably, i. e. *M. mystacinus* about 80%, *M. brandti* about 20%. In the following, these two species are mostly combined and referred to as *M. my./br.* 64 animals remained unidentified but certainly belonged to smaller species (i. e. larger species like *M. myotis*, *Eptesicus spec.*, *V. murinus* or *Plecotus spec.* could be excluded). Species dwelling in buildings which occur in adjacent areas but were not found in buildings at higher altitudes included barbastelle (*Barbastella barbastellus*), noctule bat (*Nyctalus noctula*), serotine bat (*Eptesicus serotinus*) and lesser horseshoe bat (*Rhinolophus hipposideros*).

Altitudinal distribution

Bats preferred roosts in buildings at lower altitudes. Figure 1 shows that the percentage of buildings with traces of bats – either alive animals or faeces – decreased significantly at altitudes higher than 1300 m above sea level ($X^2 = 26.6$, $p < 0.01$).

Species composition did not change significantly with altitude. At all altitudes, *M. my./br.* were by far the most abundant species (Fig. 2). Together they made up 70.5% of all reliably identified individuals. Assuming a relation of 20% *M. brandti* in all *M. my./br.* individuals, also Brandt's bat was more abundant than any other species except the whiskered bat. It is also apparent that, within the studied range of altitude, no species showed any preference for particular elevations. The only exception was *M. myotis*, which was found exclusively below 1200 m. However, with *M. brandti* and *E. nilsonii* two species were present which are only rarely found in the adjacent lowland areas.

The highest site where roosting bats were found was at 1670 m in a group of cabins near Königssee (Berchtesgaden). In five different cabins, a total of 10 animals, including *M. mystacinus*, *Pl. auritus* and *V. murinus* was found.

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

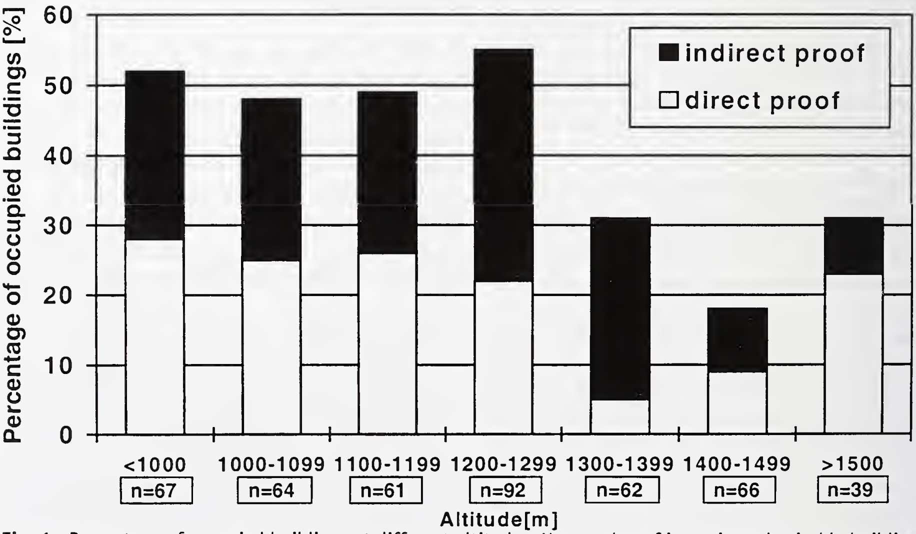

Fig. 1. Percentage of occupied buildings at different altitudes. N = number of investigated suitable buildings.

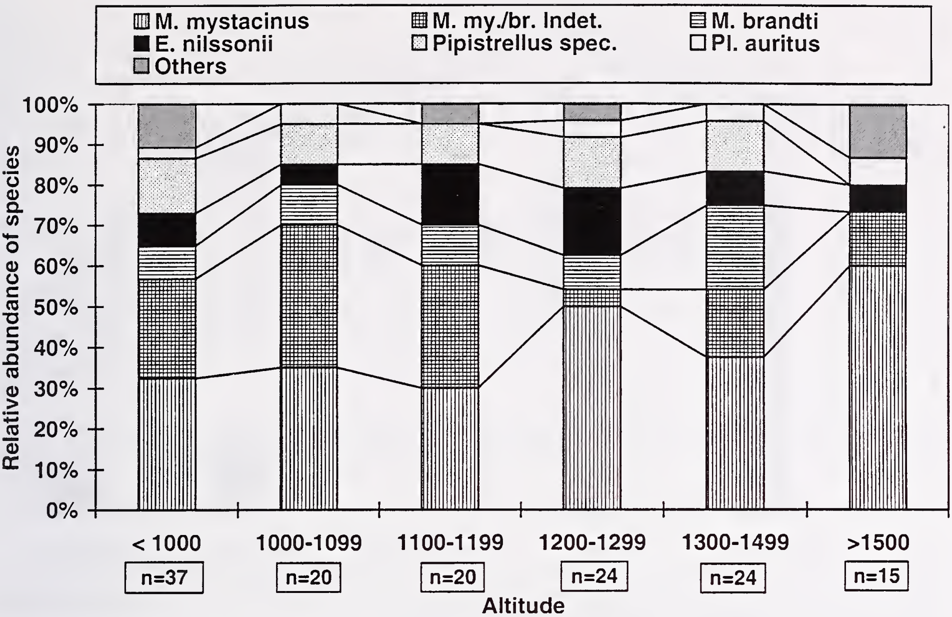

Fig. 2. Relative abundance and altitudinal distribution of reliably identified species. N = number of bats. The altitudes 1 300 m–1 499 m are drawn together because of only two direct observations between 1 300 m and 1 399 m.

Table 1: Altitudinal distribution of nursery colonies

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

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

Age structure and composition of sexes

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

Preference of roosts and surrounding

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

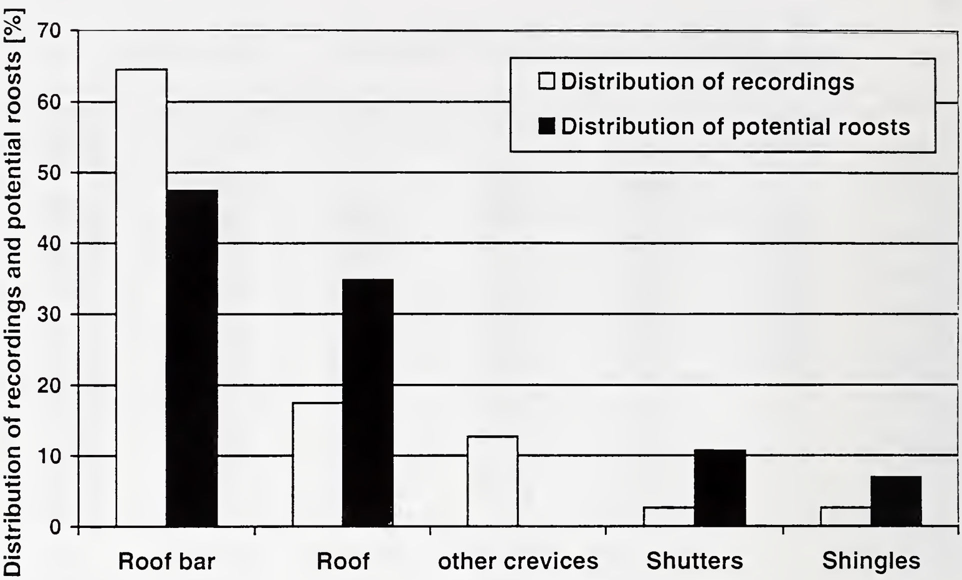

Fig. 3. Distribution of recordings compared to the distribution of potential roosts. As the number of "other crevices" can hardly be estimated, no value is given for this category.

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

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

Influence of seasons

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

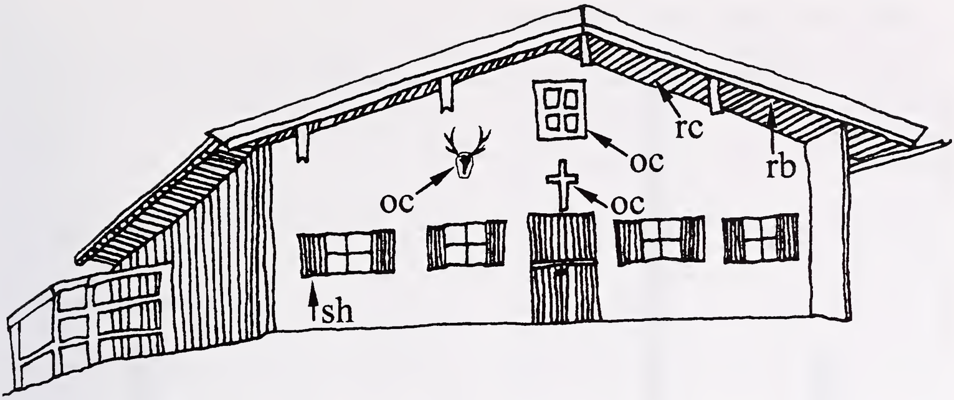

Fig. 4. Typical Bavarian mountain cabin with various roosting possibilities. rb = crevice behind ridge board, rc = roof crevice (i. e. crevices between tin covering and underlying roof bars), sh = crevice behind shutter, oc = other crevices.

Comparison between higher altitudes and lowlands

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

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

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

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

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

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

Discussion

Roosts

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

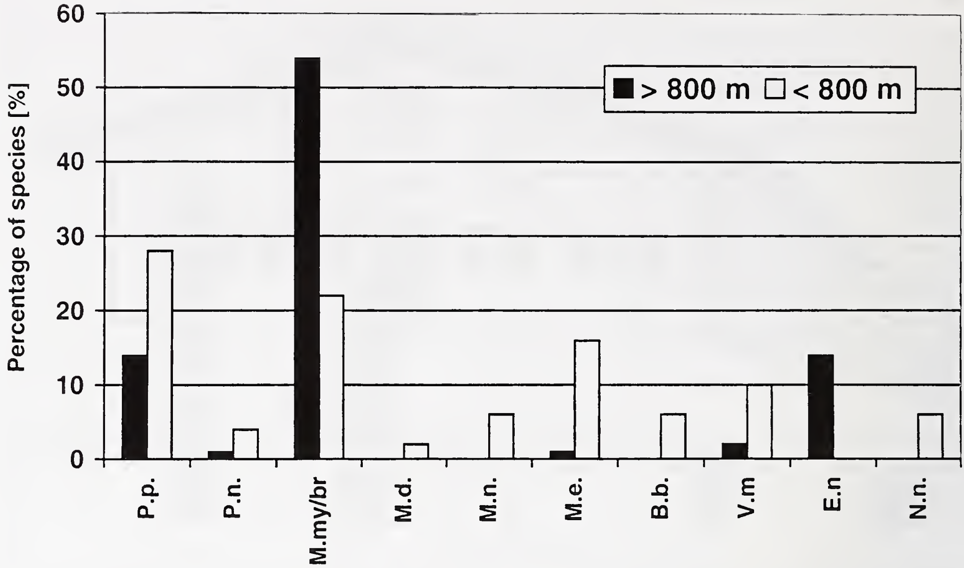

Fig. 5. Comparison of the species composition in solitary roosting bats at high (> 800 m, n = 101) and low (< 800 m, n = 50) altitudes. *M. myotis*, *Pl. auritus* and *R. hipposideros*, which probably find only few suitable buildings in higher regions, are excluded. P. p. = *Pipistrellus pipistrellus*;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

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

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

Species composition

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

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

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

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

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

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

The whiskered bat is the only species of this study for which every aspect of the life cycle (breeding, mating, hunting, hibernating) was observed to take place at higher altitudes. The distribution of whiskered bat and Brandt's bat in other countries show that they are indeed sturdy species in adverse climates: in Scandinavia they reach 64° of latitude (Schober and Grimmberger 1987), and in Switzerland nursery colonies of *M. mystacinus* occur up to 1 670 m (Zingg and Burkhard 1995). In a recent investigation of the National Park Hohe Tauern in Austria *M. my./br.* also make up almost two-thirds of the species composition at higher altitudes (Hüttmeir and Reiter 1999). *P. pipistrellus*, on the other hand, has quite similar habitat demands and roost preferences but reaches only 61° of latitude in Scandinavia (Schober and Grimmberger 1987) and seems to prefer the lower altitudes. In Canton Wallis (Switzerland), the number of roosts decreases continually over 400 m above sea level (Arlettaz et al. 1997).

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

It is still not quite clear whether a true preference for higher altitudes exists for *M. brandti*, although the virtual absence of this species in lowland areas and multiple records in the study area above 800 m encourage this suggestion. The low population density in the lowlands could partially be an artefact due to the difficulties in differentiating between *M. mystacinus* and *M. brandti*, especially concerning the females. It might well be that some *M. brandti* colonies in the lowlands have been mistaken for *M. mystacinus*. Still, its abundant occurrence at higher altitudes, especially of males, is apparent. Results from Canton Wallis in Switzerland, where *M. brandti* was found exclusively over 1200 m above sea level (Arlettaz et al. 1997), also support that *M. brandti* is indeed well adapted to the conditions in the mountains.

Also the northern bat seems to prefer the higher altitudes. While 14 solitary animals plus one nursery colony were found at the higher altitudes, neither solitary roosting animals nor nursery colonies are known from adjacent areas in the last 10 years. Also in Switzerland, the majority of *E. nilssonii* was found between 1200 m and 2000 m above sea level (Arlettaz et al. 1997).

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

Male dominance

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

Climatic chance and altitudinal distribution

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

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Zusammenfassung

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

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

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