



Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*

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Abstract. This paper describes the feeding behaviour and foraging strategy of the sibling mouse-eared bat species *Myotis myotis* and *M. blythii* under natural conditions. In the Swiss Alps, the main prey of *M. myotis* consisted of carabid beetles (46% by volume), whereas bush crickets contributed most to *M. blythii*'s diet (60%). However, the diet varied seasonally in both species: although they were probably a predictable food source throughout the season, carabids were under-represented in the diet of *M. myotis* in May and September; and when bush crickets were unavailable in May and June, they were replaced by cockchafer in *M. blythii*'s diet. The bats selected alternative, more abundant and/or more profitable prey at certain times of the year, mostly by switching from their traditional feeding habitats to secondary (usually temporary) foraging grounds. Direct visual observations in temporary food patches showed that mouse-eared bats gleaned most prey on the soil surface while flying, but cockchafers were usually caught in flight; foraging behaviour was highly flexible. The results suggest that mouse-eared bats are opportunistic predators that maximize their average rate of food intake by balancing habitat selection.

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Recent studies on the diet and foraging behaviour of insectivorous bats have confirmed Norberg & Rayner's (1987) predictions based on wing morphology that a large proportion of species are able to catch prey from surfaces (Bauerova 1978, 1986; Fenton & Bell 1979; Bell 1982; Swift & Racey 1983; Jones & Rayner 1988; Rydell 1989; Barclay 1991; Beck 1991, 1994–1995; Kalko 1991; Krull et al. 1991; Shiel et al. 1991; Faure & Barclay 1992; Taake 1992; Wolz 1993). For instance, among the 25 species presently occurring in Switzerland, at least nine (36%) are considered to be gleaning bats, all of them belonging to the genera *Myotis* and *Plecotus* (Beck 1994–1995). Microchiroptera have been reported to glean prey from all types of surfaces: water, ground, grass, cliff walls, tree bark, branches or leaves (Fenton 1982). However, gleaning bats may also switch from gleaning to aerial-hawking foraging strategies (Anderson & Racey 1991; Barclay 1991;

Krull et al. 1991; Faure & Barclay 1992; Krull 1992).

In Central Europe, the greater mouse-eared bat, *Myotis myotis*, preys mainly on flightless carabid beetles (Carabidae; Kolb 1958; Bauerova 1978; Gebhard & Hirschi 1985), and is thus believed to be an exclusive ground-gleaning predator (e.g. Rudolph 1989; Audet 1990). Radio-tracking studies carried out on *M. myotis* in Germany (Liegl & Helversen 1987; Rudolph 1989; Audet 1990) have failed to provide a detailed description of its foraging behaviour under natural conditions (Krull et al. 1991); as this species was foraging exclusively in woodland (Rudolph 1989; Audet 1990), the vegetation probably precluded any direct visual observations.

The ecology of the lesser mouse-eared bat, *M. blythii*, is poorly documented, owing both to its southern distribution (most ecological studies on European bats have concerned species of the northern latitudes) and to the difficulty of distinguishing it from *M. myotis* (Ruedi et al. 1990; Arlettaz et al. 1991). Preliminary dietary studies showed that *M. blythii* feeds mainly on bush crickets (Tettigoniidae) gleaned from grass

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(Arlettaz et al. 1993; Arlettaz & Perrin 1995). However, as for *M. myotis*, no field observations of *M. blythii*'s foraging behaviour have been reported so far.

I have dealt with resource partitioning (trophic niche segregation and habitat selection) and interspecific competition between these two sympatric sibling species of bats elsewhere (Arlettaz et al. 1993; Arlettaz 1995; Arlettaz & Perrin 1995). In the present paper I describe how free-living mouse-eared bats forage under natural conditions, and compare diet composition with food supply, establishing how the two species respond to seasonal variations in trophic resources.

METHODS

I studied bats in the Alps of Valais (southwestern Switzerland; 46°15'N, 7°30'E) in 1990–1992.

The diets of *M. myotis* and *M. blythii* were investigated by analysing, respectively, 152 and 169 faecal samples. I collected faecal pellets in May–September from individuals returning to their nursery after foraging, or from bats mist-netted within temporary food patches. A blood sample (50–70 µl from the brachial vein) was taken from each bat and stored in an Ependorf tube in liquid nitrogen. I identified species by electrophoretic analysis of these blood samples in the laboratory (Ruedi et al. 1990). Prey fragments were identified to the order or family level under a binocular microscope. The proportion (% volume) of prey categories was estimated for each individual faecal sample to the nearest 5–10%.

I investigated the phenology of some of the main prey categories, carabid beetles (Carabidae), mole crickets, *Gryllotalpa gryllotalpa*, and bush crickets (Tettigoniidae), by pitfall trapping and hand-netting of the ground and/or grass arthropod fauna from early May to late July 1992. I sampled three habitat types: woodland, orchards and steppe (climatic xeric grassland found in the Central Alps). These habitats were chosen from the hunting grounds (delimited by radio-tracking; Arlettaz 1995) of individuals from the roosts that yielded faecal pellets. Each site was set up with three separate (150–600 m distant) groups of five pitfall traps. I collected the trapped arthropods every 10 days. In addition, I performed hand-netting with a net 45 cm in diameter in the steppe grass on a transect 15–30 m long along rows of

traps, on the same dates when trap collecting took place. Samples were stored in 70% ethanol. In the laboratory, I sorted the content of samples and estimated the frequency of the different categories for each sample. Insects were dried in an oven for 72 h at 65°C. The dry weight of each category within a sample was measured to the nearest 0.001 g. For steppe, items from pitfall traps and hand-netting were pooled for analysis. Data on the phenology of cockchafers, *Melolontha melolontha*, were obtained from the agriculture service of State Valais. I estimated the mean item biomass of the main prey categories from the same samples.

I observed foraging bats between May and August 1990–1992 (i.e. during the period of pregnancy and lactation). I fitted 24 individuals (12 *M. myotis* and 12 *M. blythii*) with transmitters fixed around the neck with a silicone collar (TSW, Telemetrie-Systeme für die Wildbiologie, Dr F. Kronwitter, Glonnerstrasse 22, D-8011 Oberpframmern, Germany). A piece of reflector tape (Scotchlite) glued on the upper side of the transmitter enabled me to locate and identify tracked individuals in the field through direct visual observation with the help of a night scope (light amplifier, Big III, Wild-Leitz, Leica SA, rue de Lausanne 60, CH-1020 Renens, Switzerland). A chemiluminescent capsule (Buchler 1976) glued on the mid-dorsal hairs with Skin-Bond surgical adhesive (Smith and Nephew United, Largo, FL 34643, U.S.A.) enhanced my chances of locating a tagged individual during the 3–5 h after its release. At the end of each radio-tracking session, individuals were recaptured at the roost or mist-netted on their feeding grounds, and the transmitters were removed. No more than two individuals were radio-tracked simultaneously. Bats were followed between dusk and dawn, from a car or on foot by one or two observers equipped with radioreceivers and H-antennas (Telonics, Telemetry-electrical consultants, 932 E. Impala av., Mesa, AZ 85204-6699, U.S.A.; Yaesu FT-290RII adapted by Karl Wagener, HS+NF-Technik-Telemetrie, Herwarthstrasse 22, D-5000 Köln 1, Germany), and a Walkman tape-recorder with a tie-microphone for data collecting. The foraging bats were watched with the night scope, and occasionally with a 100-W spotlight mounted with a red filter. Among the 24 tagged individuals, 11 (six *M. myotis* and five *M. blythii*) were observed visually at least once during their foraging activity.

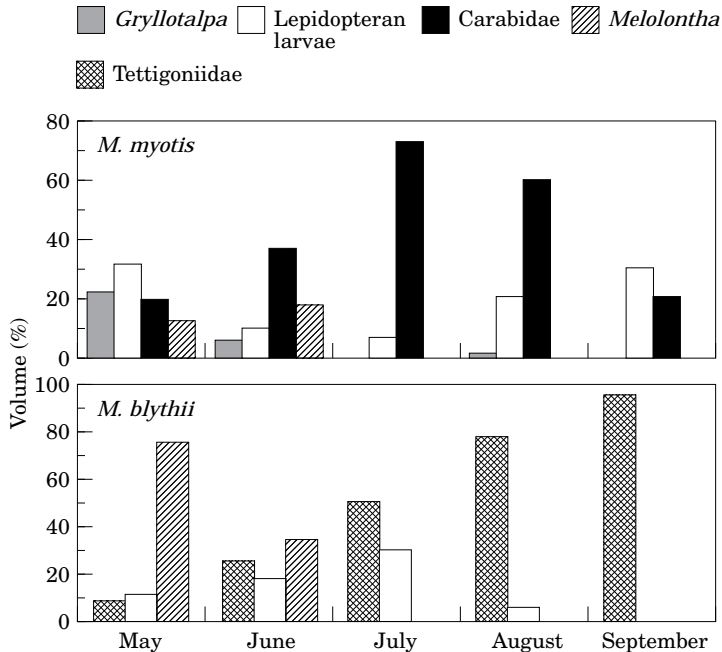


Figure 1. Seasonal variation of the main prey found in the diets of *M. myotis* and *M. blythii*.

Temporary food patches where bats aggregated were discovered through radio-tracking. They could be distinguished from their normal foraging grounds because (1) they were exploited on a few nights only, (2) they were much smaller, and/or (3) the composition of their prey supply, as revealed by subsequent faecal analysis, was different (see below). This distinction corresponds to the definitions of a patch proposed by Stephens & Krebs (1986).

Within a patch, the foraging behaviour of a tagged individual was first observed in detail; then, data on the other foragers that aggregated at the same place were also collected. At a given site, the overall bat feeding activity was monitored visually during at least 10 periods of 5 min each per night. As far as possible, the same individual was followed continuously for a full 5 min; but if it happened to leave the patch another hunting bat was immediately selected. It cannot be excluded that the same individual may have been recorded more than once. Quantitative data about foraging activity and feeding rate were collected by direct visual observation with the night scope as follows: (1) average bat density (N/ha) at a given site between 2300 and 0200 hours (i.e. during peak activity); (2) average number of capture attempts

per bat per min (i.e. number of landings on the ground, see below); (3) number of successful captures per bat per min (i.e. number of circular up-flights immediately subsequent to landing actions, see below).

Proportions of either species foraging within the patches were assessed through mist-netting. For each patch, the dates of grass mowing and hay removal were also noted.

All radio-tracking experiments were carried out under licence from the Nature Conservancy Service of State Valais.

Data are presented as $\bar{X} \pm SD$; where shown, range and sample size are given in parentheses.

RESULTS

Seasonal Variation in Diets

Myotis myotis fed predominantly on carabid beetles (46%), lepidopteran larvae (19%) and mole crickets (10%), whereas *M. blythii* preyed upon bush crickets (61%), cockchafers (14%) and lepidopteran larvae (10%). The three commonest prey types thus contributed, respectively, 75% and 85% of the total diet of each species.

There were seasonal differences in species-specific patterns (Fig. 1). Carabids predominated

Table I. Number of individual *M. myotis* and *M. blythii* mist-netted in temporary food patches where bats aggregated

Date	Habitat type	Dominant prey (%)	<i>M. myotis</i>	<i>M. blythii</i>
30 July 1990	Freshly cut meadow	? Carabidae (88)	2 (2)	—
5 July 1991	Freshly cut meadow	Lepidopteran larvae (46)	1 (1)	—
15 July 1991	Freshly cut meadow	Scarabaeidae (50)	2 (2)	—
17 July 1991	Freshly cut meadow	Scarabaeidae (78)	7 (6)	1 (1)
2 August 1991	Freshly cut meadow	? Carabidae (37) Lepidopteran larvae (28)	8 (7)	1 (1)
6 June 1991	Freshly cut meadow	? Carabidae (84)	1 (1)	—
14 August 1991	Freshly cut meadow	Acrididae (53)	1 (1)	—
5 September 1991	Intensive orchard	Tipulidae (83)	10 (10)	1 (1)
12 June 1992	Grassland with hedges	<i>M. melolontha</i> (100)	1 (1)	2 (2)
26 June 1992	Freshly cut meadow	Lepidopteran larvae (26)	5 (4)	1 (1)
29 June 1992	Freshly cut meadow	Scarabaeidae (75)	7 (4)	—
5 July 1992	Freshly cut meadow	Staphylinidae (70)	1 (1)	—
15 July 1992	Freshly cut meadow	Lepidopteran larvae (48)	8 (7)	3 (2)
Total	13 habitats		54 (47)	9 (8)

The type of habitat and the dominant prey category as estimated through faecal analysis (number of faecal samples in parentheses) are indicated. Question marks denote that the prey may well have been captured outside the food patch, for example in primary feeding habitats.

in the diet of *M. myotis* in July and August, and the proportion of this taxon in the diet increased as the diversity of the main prey categories present in the diet declined. Mole crickets and cockchafers were caught by *M. myotis* only during May and June. There were very few bush crickets in *M. blythii*'s diet early in the season, and an increasing proportion was taken through to September. Cockchafers were the most important prey of *M. blythii* in May and June, but were replaced by bush crickets later in the season.

The diet of individuals captured in some temporary food patches deviated strikingly from the diets of individuals caught at nursery roosts (Table I, Fig. 1). For example, in September, in intensively cultivated orchards, the bats clearly exploited crane flies (Tipulidae); there was also an over-representation of scarabid beetles (Scarabaeidae) in pellets collected in freshly cut meadows between late June and early August.

Phenology of the Main Prey

Forest carabid beetles represented an important and constantly occurring food source in terms both of numbers and biomass (Fig. 2a). In orchards, mole crickets showed strong fluctuations (Fig. 2b). Numbers and biomass of bush crickets increased progressively throughout the

season (Fig. 2c). Cockchafers were present only in spring and early summer, with a population peak around the last 10 days of May (Fig. 2d).

Mean Prey Item Biomass

Table II shows the average item biomass (g dry weight) for the main prey categories. On average, mole crickets and cockchafers were by far the largest prey items (0.34 g and 0.30 g, respectively), followed by carabid beetles in woodland (0.08 g) and bush crickets in steppe (0.07 g).

Feeding Behaviour

Foraging bats were watched primarily in open habitats and in food patches with large aggregations of bats. They were watched for more than 30 nights in freshly cut meadows, hedgerows in pasture and meadows, and intensively cultivated orchards. However, despite intensive radio-tracking, only one *M. myotis* and no *M. blythii* were seen foraging in their basic feeding habitats (forest for *M. myotis* and dense grass cover for *M. blythii*; Audet 1990; Arlettaz 1995).

Gleaning from the soil surface

There was no obvious interspecific difference in the feeding modes of *M. myotis* and *M. blythii*

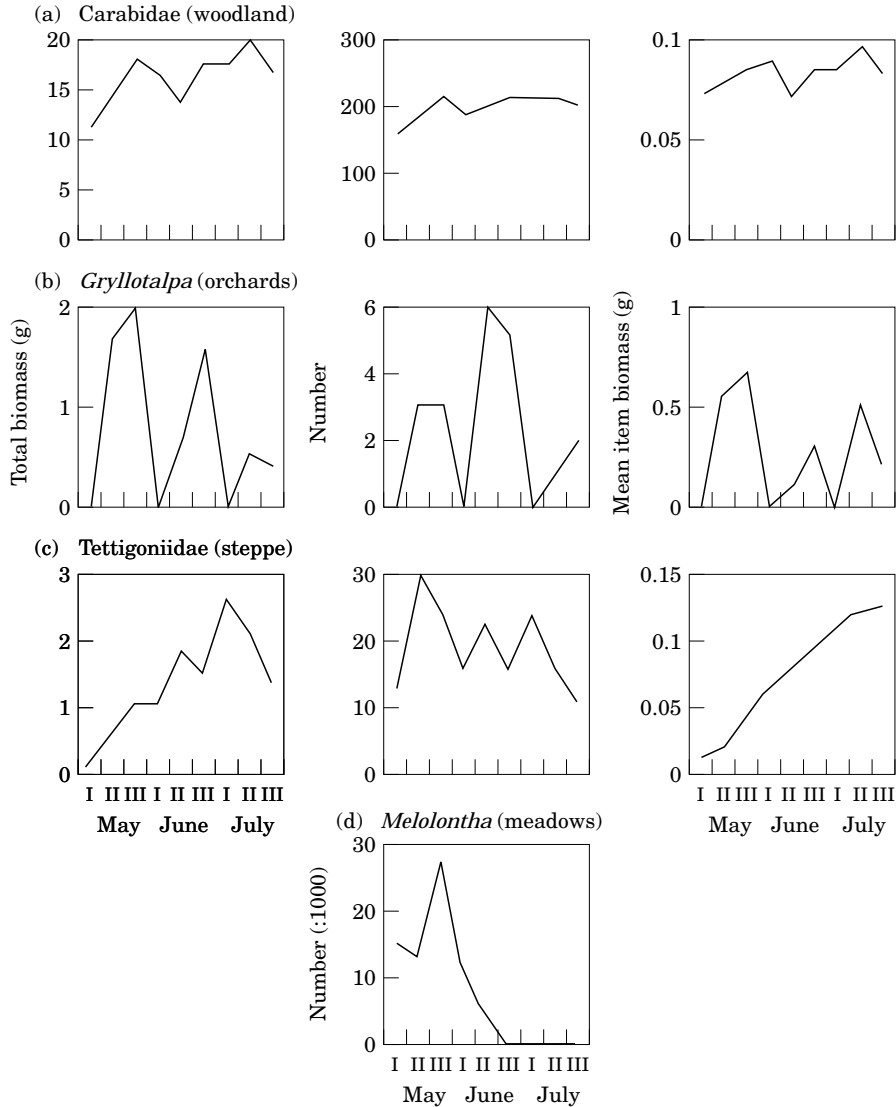


Figure 2. Phenology (total biomass, number of individuals and mean item biomass) of the main prey categories under natural conditions. *M. myotis*: (a) carabid beetles in woodland and (b) mole crickets in orchards. *M. blythii*: (c) bush crickets in steppe and (d) cockchafers in meadows and pastures. (a) and (b) resulted from pitfall trapping; (c) from pitfall trapping and hand-netting; (d) from direct counts of individuals emerging from the soil surface (A. Schmidt, unpublished data). Roman numerals indicate 10-day periods. No quantitative comparison between prey categories should be made from these figures since data did not result from similar sampling designs.

while searching for prey over meadows. However, *M. myotis* systematically avoided the dense grass vegetation of unmowed meadows and concentrated its activity exclusively on freshly cut meadows. By contrast, *M. blythii* preferred dense

grass vegetation, yet it did not fully avoid areas with short, freshly cut grass.

The bats normally foraged close to the ground, usually flying only 30–70 cm above the soil surface. They searched for prey by flying

Table II. Mean item biomass (g dry weight) of the main prey categories trapped or hand-netted in typical foraging habitats of mouse-eared bats: woodland, orchards and meadows (*M. myotis*), and steppe (*M. blythii*)

Prey category	Woodland	Orchards	Meadows	Steppe
<i>Gryllotalpa gryllotalpa</i>	—	0.343	—	—
Tettigoniidae (<i>Platycleis albopunctata</i>)	—	—	—	0.065
Lepidopteran larvae	0.025	0.054	—	0.052
Tipulidae imagos (<i>Tipula paludosa</i>)*	—	0.038	—	—
Carabidae	0.081	0.036	—	0.018
<i>Melolontha melolontha</i>	—	—	0.297	—

*R. Güttinger (unpublished data).

continuously at moderate speed and without obvious systematic prospecting paths. When a prey item was detected on the ground, the bat usually hovered (for about 2–5 s or 2–10 wingbeats) just above the potential target. During a capture attempt, the bat dropped on the prey item, with outstretched wings, and picked it up. Landings lasted about 2–8 s. The bats never searched by walking on the ground. The bat seized the prey in its mouth, briefly struck its mouth at the thorax or possibly at the inter-femoral membrane and took off immediately. Prey was never eaten on the ground, but uneaten parts were discarded on the wing during a slow, widely circling flight at a height of 5–15 m above the ground (10–20 s). Only larger prey (probably *G. gryllotalpa* for *M. myotis*, *Pholidoptera griseoptera* and *Platycleis albopunctata* for *M. blythii*) were apparently carried up to a perch prior to being eaten. Detection of ground-dwelling prey from a perch (fly-catching) was never observed.

Aerial-hawking

In May and June 1992, mouse-eared bats exploited huge concentrations of cockchafers in meadows with hedges and solitary trees. In these circumstances, the foraging pattern was a patrolling flight 1–2 m from the tops of trees. Cockchafers were hunted either on the wing, when they flew from the leaves, or, very occasionally, by gleaning them from the outermost leaves of the canopy foliage.

Temporary Feeding Patches and Switching Behaviour

The area of the temporary feeding patches where mist-netting and visual observations took

place covered, on average, 5.9 ± 4 ha (2–14 ha, $N=12$; see also Table I). Their mean distance to roosts was 8.5 ± 7 km (1–25 km, $N=12$), whereas their average altitude was 899 ± 363 m a.s.l. (458–1560 m, $N=12$).

While exploiting temporary feeding grounds, the bats visited usually between two and five patches on the same night. The closer the patches, the more frequently the bats switched between them. For instance, during 6 h of foraging, one individual switched at least 12 times between four small patches (freshly cut meadows in total ca 10 ha) each about 0.5–1.5 km apart and 2.2–5 km from the nursery roost. By contrast, a female bat that visited two areas of freshly mown meadows of, respectively, ca 6 and ca 8 ha and 9 km apart switched only twice; the second patch was 25 km away from the roost, which is the furthest foraging ground recorded in this study. This bat exploited the first patch just after emergence, and again early in the morning on the way back to the colony.

The flight speed was greatest when the bats were commuting from feeding grounds to their roost at dawn (straight flight at many metres above the ground); for instance, the above-mentioned female travelled twice 25 km within 30 min (50 km/h).

Species Ratio at Temporary Food Patches

Within the 13 temporary food patches where mist-netting was attempted (Table I), there was a considerable bias towards the proportion of *M. myotis*: $89.0 \pm 19\%$ versus $11.0 \pm 19\%$ of *M. blythii* (total number of captures, $N=63$). In one situation *M. blythii* predominated (hedges-within grassland), but sample size was small in this case (three individuals captured).

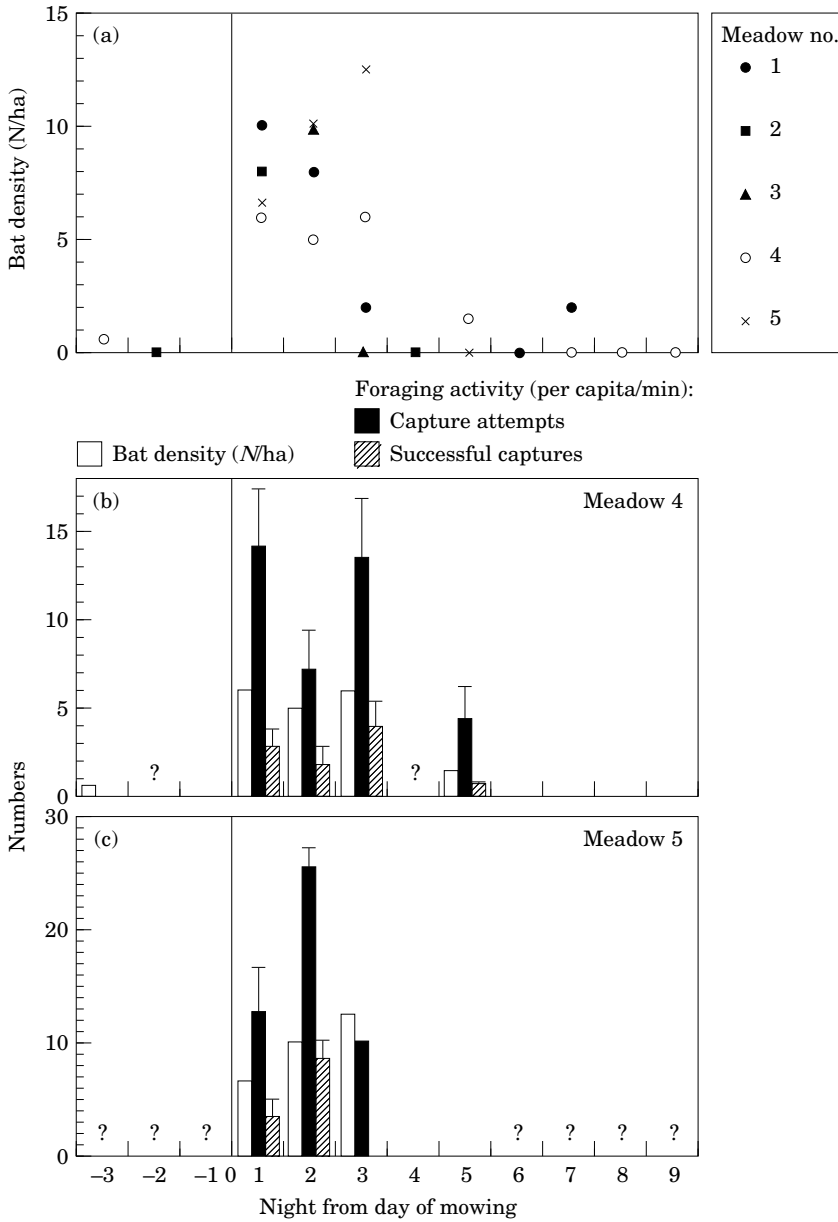


Figure 3. (a) Bat density (N/ha) within five areas of meadows on the nights before and after mowing (indicated by 0). (b) Chronological trends in bat density and feeding rate in meadow number 4; number of capture attempts (i.e. landings on the ground) and successful captures (i.e. up-flights) per bat per min ($\bar{X} \pm SD$; see text for more details). (c) Similar data for meadow number 5. Question marks indicate nights with missing values.

Food Patch Exploitation

Within the five temporary food patches where I could see bats directly (all hay-meadows), bat density was higher during the first 3 nights after

mowing (up to 10 bats/ha) and dropped drastically from the third night onwards (data from 24 nights in five patches: $r_s = -0.739$, $N = 24$, $P < 0.001$; Fig. 3a).

Overall, the mean number of capture attempts per bat was positively correlated with bat density ($r_s=0.667$, $N=12$ nights, $P=0.027$, nights with zero bats were excluded from the analysis) but the mean number of successful captures per bat was not ($r_s=0.373$, $N=8$, $P=0.323$).

Figure 3b, c shows the exploitation of two meadows before and after mowing. The mean feeding rate (number of capture attempts and number of successful captures; see Methods) was higher during the first 2 or 3 nights and decreased afterwards. There were some differences between these two patches: (1) bat feeding activity declined later in the first patch than in the second; (2) the exploitation was bimodal in the first meadow and unimodal in the second; (3) in the second meadow there was still a high bat density on the last night of activity, despite fewer feeding attempts and no evidence for successful captures.

DISCUSSION

Diet Seasonality and Prey Phenology

Although carabid beetles represented a fairly constant, largely predictable food source until early August and, by extrapolation, probably also later in the season (Kolb 1958; Figure 54 in Thiele 1977), *M. myotis* selected other prey in May and September. Obviously, the bats were not forced to switch from their main feeding habitats (forest) as a consequence of shortage or depletion of their basic food source, but did so deliberately. In addition, the main secondary prey categories exhibited stronger population fluctuations than carabid beetles. Mole crickets, for instance, are usually underground, except in May and June when mating takes place, and in midsummer when the larvae disperse (Harz 1957). The peak in late May parallels the period when adults become active on the soil surface (Harz 1957), and therefore are particularly vulnerable to predators (and pitfall traps). Similar patterns occurred in cockchafers.

In contrast to forest-living carabid beetles, bush crickets did not represent a stable food resource throughout the season. Owing to their successive instars, bush crickets showed very low biomasses in spring, increased steadily until June, and largely predominated afterwards. Cockchafers accounted for a high proportion of the diet of *M. blythii* in

May (compared with *M. myotis*), presumably because there was no alternative prey available for this species at that time of the year.

Foraging Behaviour

Very few studies carried out under natural conditions have described in detail the foraging behaviour of insectivorous bats gleaning prey from the soil in a low continuous flight. This is probably because of either the secretive habits of gleaning bat species or the complex structure of their habitat. Of the studies that have been carried out, those on the Nearctic *Antrozous pallidus* and the Palaearctic *Otonycteris hemprichi* (Bell 1982; Horacek 1991; Krull 1992; Arlettaz et al. 1995), show a similar ground-gleaning behaviour in these species as in *M. myotis*.

In the present study I did not observe *M. blythii* gleaning its prey in its main habitat (dense grass). Nevertheless, one may speculate that *M. blythii* does not 'land' while searching for prey in dense grass, for practical reasons, but gleans prey, for example by hovering.

Temporary Food Patches and Habitat Selection

The prevalence of *M. myotis* (89%) among the captures in temporary food patches reflects the species-specific patterns of habitat selection by these two species (Arlettaz 1995; Arlettaz & Perrin 1995). Since *M. myotis* usually gleans its prey from bare ground, whereas *M. blythii* catches its prey from dense grass, there is a higher probability of encountering the former species over freshly cut meadows which comprise most of the temporary feeding patches localized during this study.

However, although the two species of mouse-eared bats usually show strong habitat partitioning (Arlettaz 1995), their segregation within temporary feeding grounds appeared much weaker (e.g. exploitation of dense versus cut grass in meadows) or even disappeared completely (hunting cockchafers). As only aerial hunting is involved in the latter case, one may argue that the two species no longer benefit from the species-specific adaptations (design constraints: Stephens & Krebs 1986) they have probably evolved for gleaning prey from different types of substrates (Arlettaz 1995). Accordingly, neither species should be more favoured in aerial hunting, and

one species should not out-compete the other under such circumstances. In addition, cockchafers occur at such high densities that they hardly constitute a limiting resource, which is a prerequisite of competition.

Temporary versus Traditional Feeding Grounds

Previous radio-tracking studies have established that mouse-eared bats usually exploit feeding grounds covering several dozen of hectares each (50 ha: Audet 1990; 36–38 ha: Arlettaz 1995). The mean area usually visited by foraging mouse-eared bats thus appears much larger than when temporary feeding patches are exploited since they then concentrate their activity on much smaller zones (this study).

These temporary patches were not closer to the nursery roosts than traditional feeding grounds: 8.5 km versus 6.3 ± 5 km (1.8–21 km, $N=20$); they were also at similar altitudes: 899 m versus 945 ± 321 m a.s.l. (460–1600 m, $N=20$; unpublished data). Moreover, some patches were at the outermost boundaries of the whole geographical area used by the radio-tracked bat population (Arlettaz 1995).

Optimal Foraging

Although I did not try to test predictions of foraging theory, some quantitative data are worth discussing a posteriori in the context of diet optimization (Stephens & Krebs 1986).

Prey versus habitat selection

One prediction of the prey model (Stephens & Krebs 1986) of optimal foraging is that predators should specialize when profitable food types are common and/or difference in profitability between prey items is great (Begon et al. 1986). Compared with their main prey types (carabid beetles for *M. myotis* and bush crickets for *M. blythii*; Arlettaz et al. 1993; Arlettaz & Perrin 1995), the alternative categories of prey captured by mouse-eared bats either occur at huge densities at certain times of the year (e.g. *M. melolontha*, Scarabaeidae, Tipulidae: personal observations), or have much higher body masses or nutritional values (e.g. *M. melolontha*, *G. gryllotalpa*; Juillard 1984; this study), if not both (e.g. *M. melolontha*).

Mouse-eared bats are able to prey on the largest members amongst the European arthropod fauna (e.g. *Tettigonia viridissima*, *G. gryllotalpa*, *Gryllus campestris*, *M. melolontha*; Arlettaz et al. 1993; Arlettaz 1995). These bat species are furthermore very efficient at subduing and consuming such large prey (personal observations with captive individuals). Consequently, as differences in the costs of handling prey items of different sizes may be assumed to be relatively slight in mouse-eared bats (Arlettaz & Perrin 1995), the consumption of larger prey is energetically much more beneficial. As most of these alternative prey furthermore occur at high densities (i.e. represent a higher capture rate per unit time), mouse-eared bats should take advantage of them.

Food selection was apparently not achieved by active prey selection within a given microhabitat (as assumed in the prey model), but mostly by switching to habitats offering more abundant and/or profitable prey. Arlettaz & Perrin (1995) suggested that both *M. myotis* and *M. blythii* do not actively select prey, with respect to both taxa and size, at least while feeding in their normal habitats. In conclusion, mouse-eared bats can be regarded as opportunistic, generalist predators that are capable of maximizing their average rate of energy intake by balancing habitat selection.

Patch exploitation: stay-time and switching

The marginal value theorem (Charnov 1976) predicts that stay-times within a patch should be longer when travelling distances between patches are greater. Despite their powerful flight (up to 50 km/h: Arlettaz 1995), mouse-eared bats apparently conformed to this rule since switches between closer patches were much more frequent than between more distant patches.

Patch use: are mouse-eared bats ideal-free?

According to Fretwell & Lucas (1970), Recer et al. (1987) and Tregenza (1994), the ideal free distribution model predicts that the density of predators matches the density of prey so that the average per capita feeding rate in patches of different prey density equalizes rapidly.

In the present study, I assumed that bat density reflects the quantity of food available within patches, both at a spatial and temporal scale. The average feeding rate (circular up-flights following

landings) apparently did not depend on bat density. In other words, the per capita food intake would not appear significantly greater in patches yielding more prey, other things being equal. This would indicate that mouse-eared bats distribute themselves among patches, temporally and spatially, so that the instantaneous profitability of each patch becomes similar.

Prey and patch profitability: touch and taste?

The mean number of capture attempts (landings on the ground) was higher at higher bat density but there was still an intense, but unsuccessful foraging activity within the second meadow on the third night. Obviously, the bats could not evaluate the nature of prey items before attempting to catch them, that is patch profitability could not be readily estimated. This may be related to the detection systems used by mouse-eared bats which seem to rely exclusively on passive listening to locate and catch prey (Deutschmann 1991).

The high bat density in the second patch on the third night may be explained similarly by the proximity of the nursery roost (ca 2 km); many bats may have stopped by on their way to or from other feeding zones, as they probably did during the 2 previous nights when the patch was still profitable. They apparently learned on that third night that the patch was depleted since they did not visit it again on the following nights.

Prey Availability within Meadows

The small differences in the chronology of exploitation of the two meadow patches (Fig. 3) may be simply explained by differences in farmers' timetables. In the first patch, the hay lay on the ground for 2 nights, and was removed on the third day. In the second patch, the grass was removed on the second day. The two peaks of bat activity thus probably coincided with peaks in prey availability: first, on the night following mowing, when disturbed prey were moving in the grass; and, second, on the night following hay removal, when arthropods hidden in the hay were disturbed for the second time. In addition, as there were clearly more bats and more landings and captures per capita at the second than at the first event, foraging was obviously more efficient then.

Recent Habitat Change

Previous investigations on the feeding habits of *M. myotis* (Bauerova 1978; Gebhard & Hirschi 1985; Liegl & Helversen 1987; Rudolph 1989; Audet 1990) have suggested that this species is principally a forest bat which specializes to a large extent on carabid beetles. However, Kolb (1958) suggested that this species also forages frequently outside wooded habitats. Since most of the alternative prey of *M. myotis* largely depend on traditionally cultivated landscape (Kolb 1958; this study), this shift in habitat use probably reflects the loss of meadows and pastures over the past 40 years in central Europe.

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