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Prey selection by *Myotis myotis* (Vespertilionidae) in a Mediterranean region

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Seasonal variations in the diet composition and prey selection by *Myotis myotis* were studied in a Mediterranean region dominated by open stone oak woodlands, olive groves, and cereal steppes. The diet and food abundance were determined by faecal analysis and pitfall trapping, respectively. Overall, the diet (expressed as % frequency) was dominated by carabid beetles (Carabidae, 52%), crickets (Gryllidae, 43%), and spiders (Arachnida, 34%). Food was far more abundant in the spring than in the summer and autumn. The dietary composition varied significantly throughout the year. In the spring, it was dominated by carabids and crickets, and in the summer by spiders. These were then replaced by carabids, which became the most frequently eaten prey in autumn. The spring-summer switch to spiders coincided with a marked drop in food abundance. Some of the temporal variations in bats' diet can be explained by parallel changes in prey abundance. In comparison to central European populations, our Mediterranean colony of *M. myotis* consumed much more crickets and spiders, which was balanced with a lower use of carabid beetles. Prey selection was tested using logistic regression models. The results suggest that, although carabids are the most consumed, crickets are preferred. Spiders seem to represent mostly a complement preyed upon at times of lower food abundance. It is not clear if the preference for crickets is simply due to their great conspicuousness, or to the choice based on energetic rewards or taste. Overall, our results are consistent with the predictions of the optimal foraging theory.

Key words: *Myotis myotis*, diet, prey selection, Mediterranean, Chiroptera

Introduction

The greater mouse-eared bat, *Myotis myotis* (Chiroptera, Vespertilionidae), is a globally near threatened species (Hutson *et al*., 2001). It preys almost exclusively on ground insects, especially large non-flying carabid beetles (Bauerová, 1978; Graf *et al*., 1992; Arlettaz, 1995, 1996; Arlettaz and Perrin, 1995). Arlettaz (1995) suggests that the large consumption of carabid beetles

is probably due to the comparatively high availability of these insects (either due to higher detectability or accessibility), and the particular types of habitats used by foraging *M. myotis*.

Most of the aforementioned studies have been conducted in Central Europe. Arlettaz (1995) collected data on the diet of *M. myotis* in some Mediterranean regions, but did not study either seasonal variations in the diet or prey selectivity. Consequently,

the trophic ecology of *M. myotis* in the Mediterranean remains poorly known. Extrapolation of results from Central Europe to the Mediterranean region could be incorrect, particularly due to markedly different climatic conditions: in Central Europe the summers are in general wet and the winters cold, whereas in the Mediterranean summers are very hot and dry and the winters mild. Such differences are likely to have an effect on the type and abundance of potential prey, and on the seasonal patterns of their availability.

The objectives of this study are: (a) to characterize the seasonal variation of the diet of *M. myotis* in a Mediterranean region; (b) to describe the seasonal variation in abundance of potential prey; and (c) to compare variation in diet with that of prey abundance in order to understand how *M. myotis* responds to seasonal variations in trophic resources, and whether it shows active prey selection. We analyzed our results in light of foraging theory.

MATERIALS AND METHODS

This study was conducted in Eastern Alentejo (S Portugal, 38°10'N, 7°30'W) between March and November 1999. The area around the colony is dominated by plains, mostly covered with open stone oak woodlands, olive groves and cereal steppes. Summers are hot and dry, with temperatures often exceeding 40°C. Most of the precipitation occurs during the winter (average rainfall: 520 mm/year; average annual temperature: 17°C).

The diet of *M. myotis* was investigated through the analysis of 212 faecal samples collected in a nursing colony that harbours ca. 1,000 individuals. Most of the adults in the colony were females, although males were also present. Despite some limitations, faecal analysis is considered to be a reliable methodology to determine the diet of insectivorous mammals (Kunz and Whitaker, 1983; Dickman and Huang, 1988) and has been widely used with bats (e.g., Swift *et al.*, 1985; Whitaker and Lawhead, 1992; Shiel *et al.*, 1998; Arlettaz *et al.*, 2000; Brack and Whitaker, 2001). Bat droppings were collected inside the roost in five sampling periods: March/April, May/June, July/August, September, and November. A cloth

sheet was placed beneath the colony for a period of seven days, and over 20 pellets were randomly chosen from the sheet at the end of each period. The droppings were teased apart and inspected for prey remains using a binocular microscope. Identification of fragments, in general to the family level, was done using a reference collection of arthropods from the study area and published identification guides (Whitaker, 1988; McAney *et al.*, 1991). The importance of various prey in each month was calculated as the frequency of occurrence of prey in the droppings.

Abundance of potential food resources was sampled at the same time as the pellets using pitfall traps placed in stone oak woodlands, olive groves, cereal steppes, margins of reservoirs, and riparian galleries. Only habitats with low ground cover were sampled, given that this is a general characteristic of the foraging habitats of *M. myotis* (Arlettaz, 1996). The 10 sampling stations were located within 6 km of the roost. In each of these, three separate groups of five pitfall traps (diameter = 10 cm) were set up, comprising 150 pitfalls in the entire area. The trapped arthropods were stored in 70% ethanol. Bauerová (1978), Pont and Moulin (1985), and Arlettaz (1995) concluded that the minimal length of the prey consumed by *M. myotis* in Central Europe is about 12 mm. However, as Iberian *M. myotis* are somewhat smaller than those of Central Europe (Palmeirim, 1990), we included all arthropods above 10 mm, i.e., the threshold used by Graf *et al.* (1992). Arthropods were usually identified to family level, using Chinery (1986), Baez (1988), Barrientos (1988), Garcia *et al.* (1988), Gayubo (1988), Salgado *et al.* (1988), Roberts (1995) and Quartau and Luna de Carvalho (1998).

Seasonal variation in the relative consumption of the three main prey groups was tested using χ^2-contingency table analyses (Sokal and Rohlf, 1995). The same method was applied to test seasonal differences in the pitfall captures. A monthly index of species diversity was obtained using the Shannon-Wiener function (Krebs, 1989).

Prey selection was investigated via logistic regression models (Hosmer and Lemeshow, 2000). The dependent variable, presence/absence of a prey type in the n examined pellets, is a binomial random variable – X ~ Bi (n, π) –, with π being the probability of presence. The predictor variables used were the absolute and relative abundance of each prey type in the pitfalls. The model we propose states that if there is no selection, the most abundant prey in the diet will be the one with biggest relative abundance:

$$\pi_T = \frac{\exp(a + bR_T)}{1 + \exp(a + bR_T)}$$

where π_T is the probability of finding prey T in

a pellet, R_T is the relative abundance of prey T, and a and b are the regression coefficients to be estimated.

In contrast, if prey is preferred, the probability of presence in the diet will depend not on its relative abundance but on its absolute abundance. In this case, the abundance of other preyed taxa does not influence this probability:

$$\pi_P = \frac{\exp(a + bA_P)}{1 + \exp(a + bA_P)}$$

where π_P is the probability of finding the preferred prey P in a pellet and A_P is its absolute abundance. In this case, the probability of presence of the other preyed taxa will be negatively influenced by the absolute abundance of the preferred taxon, because the former will be used as complements to the latter:

$$\pi_{NP} = \frac{\exp(c + dR_{NP} - eA_P)}{1 + \exp(c + dR_{NP} - eA_P)}$$

where π_{NP} is the probability of finding non-preferred prey (NP) in a pellet, R_{NP} its relative abundance and A_P the absolute abundance of the preferred prey, and c, d and e are the regression coefficients to be estimated.

In order to test the goodness-of-fit of each model it was compared with the saturated model, i.e., a model that has as many parameters (p) as there are data points (n), by means of the statistic: $D = -2 \log_e[likelihood\ of\ the\ fitted\ model]$ which, under the assumption that the null hypothesis is true, i.e., the model fits to the data, has a χ^2-distribution with $n–p$ degrees of freedom. In this context, a model that fits well to data is one where the associated P-value is not significant, i.e., $P > \alpha$ ($\alpha = 0.05$). The statistical packages used were Statistica for Windows 5.1 (StatSoft Inc., 2000) and R-package (Ihaka and Gentleman, 1996).

RESULTS

Diet and Food Availability

Eight prey categories were identified in pellets (Fig. 1). Carabids (Carabidae, Coleoptera) were found in 52% of the pellets, crickets (Gryllidae, Orthoptera) in 43%, and spiders (Arachnida) in 34%. Mole crickets, *Gryllotalpa* sp. (Gryllotalpidae, Orthoptera) were present in 5% of the pellets. Four families of Coleoptera — rove beetles (Staphylinidae), chafers (Scarabaeidae), burying beetles (Silphidae), and darkling beetles (Tenebrionidae) were found in

the pellets in a proportion superior to 2% each.

There were 3,175 arthropods longer than 10 mm captured in pitfalls and they belonged to 46 taxonomic groups. The most abundant were ants (Formicidae), carabids, crickets, and spiders (mainly Gnaphosidae and Lycosidae). Mole crickets comprised 2% of the captures. Scarabaeidae, Silphidae, Staphylinidae and Tenebrionidae added to 4%. Other also fairly abundant taxa in the study area, but not found in pellets of *M. myotis*, included grasshoppers (Acrididae, Orthoptera, 4%), isopods (Isopoda, 4%), millipedes (Diplopoda, 2%) and centipedes (Chilopoda, 0.6%) (Fig. 1).

Carabid beetles were more common in forested areas, cereal crops and riparian galleries. Crickets were particularly common in cereal crops and olive groves. Spiders, the third most abundant taxon in the diet, were numerous mainly in olive groves, cereal crops and margins of reservoir.

Seasonal Variations

The diet showed a clear seasonal variation ($\chi^2 = 154.2$, *d.f.* = 8, $P < 0.001$) (Table 1). *Myotis myotis* fed predominantly on carabid beetles during the March/April and November periods, on crickets during the May/June period, and on spiders during July/August (Fig. 2a). The abundance of the three main prey items, Carabidae, Gryllidae and Arachnida, showed a clear seasonality ($\chi^2 = 247.5$, *d.f.* = 8, $P < 0.001$) (Table 1). They were far more abundant during the March/April and May/June sampling periods than in the summer and autumn, when their number was quite low (Table 1; Fig. 2b).

The Shannon-Wiener diversity index (Table 1) indicated that in months of prey abundance – March/April and May/June – the diet of *M. myotis* was more

homogeneous than in July/August and September, i.e., periods of prey scarcity. This diversity declined again in November.

Prey Selection

If there is no selectivity prey items should be consumed proportionally to their relative abundance. The results based on the no-selectivity model (Table 2) suggested that the consumption of Carabidae followed, to a certain extent, this no-selection scheme. Nevertheless, this model did not explain the probability of presence of Gryllidae and Arachnida in the diet of *M. myotis*. Additional analyses were therefore required to understand their patterns of occurrence.
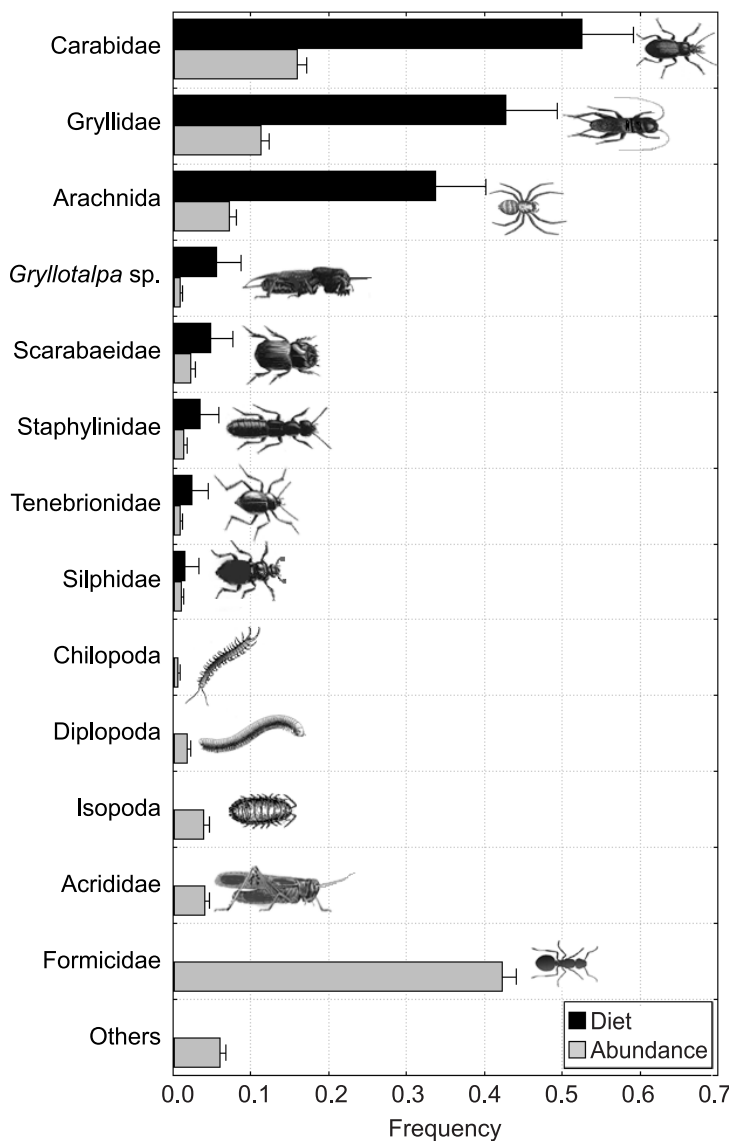

FIG. 1. Frequency of occurrence of prey in the droppings of *Myotis myotis*, and arthropod abundance according to the results of pitfall trapping. Whiskers represent 95% confidence intervals

When selectivity is present, favored prey should be consumed proportionally to their absolute abundance. The relationship between the seasonal variation in the importance of the three main prey types and their absolute abundances, suggests that crickets were the only prey preferentially selected (Fig. 2). A regression model assuming selectivity supported this outcome (Table 2), further suggesting that crickets were preferred prey.

Assuming this preference, we tested models that would explain the consumption of the other two prey types as complements to crickets, i.e., models that explain the occurrence of carabids and spiders in the diet using as predictor variables the absolute abundance of crickets and their own relative abundance. In both cases, the fitted models were not significantly worse than the saturated models (Fig. 3). These results indicate that *M. myotis* preys preferentially on Gryllidae, and consumes Carabidae and Arachnida complementarily. The patterns portrayed by the fitted models (Fig. 3) suggest the close relationship between the absolute abundance of crickets and their consumption. The consumption of carabids closely followed its own relative abundance, but also declined with the increasing abundance of crickets. The exploitation of spiders was not only dependent on their relative abundance, but also had a strong negative association with the abundance of crickets.

DISCUSSION

Diet composition

In all dietary studies of *M. myotis* in Central Europe (e.g., Bauerová, 1978; Graf *et al.*, 1992; Arlettaz, 1995, 1996; Arlettaz and Perrin, 1995), Carabidae formed the dominant group. In our Mediterranean site carabids were also the most important prey (52%), although somewhat less so than in Central Europe. Arlettaz (1995) partly attributed the smaller fraction of carabids that he observed at one of his study sites in Switzerland (Upper Valais), to the relatively xeric nature of the region, less suitable for carabids. This is in line with the results we obtained, where the woodlands were quite xeric, and carabids not abundant.

The lower consumption of carabids also may be a consequence of the apparent preference for crickets. In fact, the abundance of crickets (34%) in the diet of the studied colony was much higher than in any

TABLE 1. Seasonal variation in diet and prey abundance, and values of the Shannon-Wiener diversity index. Diet is the frequency of occurrence of each prey type in droppings. Abundance of each prey is relative to total number of arthropods belonging to taxa consumed. The numbers of droppings analysed and the total number of prey captured in the pitfalls are shown in parentheses

Taxa	March/April Diet (24)	March/April Abund. (215)	May/June Diet (55)	May/June Abund. (363)	July/August Diet (51)	July/August Abund. (98)	September Diet (21)	September Abund. (105)	November Diet (61)	November Abund. (101)
Carabidae	0.79	0.59	0.46	0.47	0.25	0.30	0.53	0.41	0.70	0.45
Gryllidae	0.50	0.21	0.83	0.27	0.35	0.33	0.24	0.30	0.16	0.32
Arachnida	0.25	0.17	0.07	0.21	0.75	0.32	0.47	0.25	0.23	0.17
Gryllotalpa sp.	0.00	0.01	0.10	0.02	0.07	0.01	0.06	0.02	0.00	0.02
Scarabaeidae	0.00	0.01	0.07	0.02	0.00	0.00	0.06	0.01	0.11	0.02
Silphidae	0.00	0.00	0.00	0.01	0.07	0.03	0.00	0.01	0.00	0.00
Staphylinidae	0.17	0.01	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.01
Tenebrionidae	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.01	0.07	0.01
Shannon-Wiener Index	1.77		1.66		2.00		2.06		1.83	

a)

b)

c)
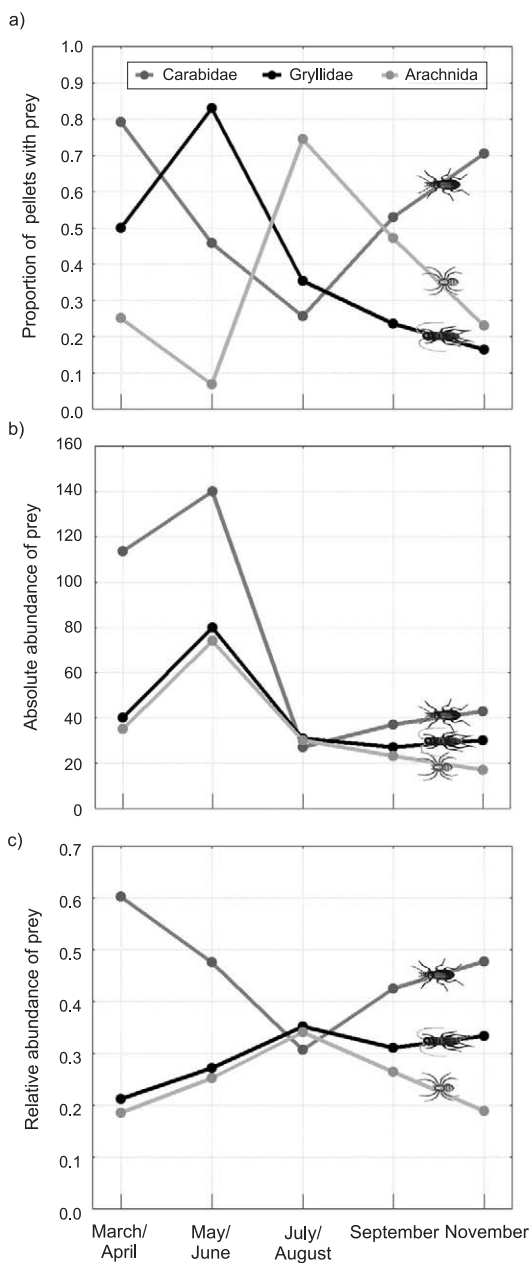

FIG. 2. Seasonal variation in (a) consumption, (b) absolute abundance, and (c) relative abundance of the three main prey types

frequently eaten at our site than in any other studied European location. No Tettigonidae were found at our site, although Arlettaz *et al.* (1997) discovered some in droppings collected in summer in another place in southern Portugal. This absence may be due to the scarcity of these insects at our study area.

Seasonal Variation and Diversity

The most striking seasonal pattern emerging from our data was the switch from a spring diet dominated by crickets and carabids, to one that incorporated a high proportion of spiders in the summer (Fig. 2a). This agreed well with the strong decline in overall food abundance, which remained very low until the November sampling season. This coincidence suggests that *M. myotis* was forced to switch to consuming spiders at times of food scarcity. In fact, spiders were even more abundant in the spring, when they were consumed less. The use of spiders tapered off towards November, when their abundance was a fraction of that observed in the summer, and they represented a very small proportion of the potential prey (Fig. 2b). At this time carabids, although still scarce, were by far the most abundant animals hunted. It is quite clear that the seasonal variation in the diet of *M. myotis* is related to changes in the abundance of prey (see also Bauerová, 1978; Arlettaz, 1996). Like in Central Europe, where the diet of *M. myotis* is generally dominated by just 2–3 prey groups (Bauerová, 1978; Graf *et al.*, 1992; Arlettaz, 1995, 1996), the diet of our colony was also dominated by three prey types (carabid beetles, crickets and spiders), supplemented by small contributions of other prey.

The seasonal variation of the Shannon-Wiener diversity index values was consistent with the theory that states that

other Central European site. A considerable proportion of crickets also was observed in other Mediterranean locations (Arlettaz, 1995). The third most important prey, spiders (20%), were also more

TABLE 2. Results of the fitted models regarding no-selectivity and selectivity. π_G, π_C and π_A are the probabilities of finding correspondingly Gryllidae, Carabidae and Arachnida in the diet. R_G, R_C and R_A are the relative abundances of Gryllidae, Carabidae and Arachnida, respectively. A_G is the absolute abundance of Gryllidae

| Taxon	No-selectivity model			Selectivity model		
	equation	P-value	d.f.	equation	P-value	d.f.
Gryllidae	$\pi_G = \dfrac{\exp(4.615 + 15.956 \times R_G)}{1 + \exp(4.615 + 15.956 \times R_G)}$	<0.001	3	$\pi_G = \dfrac{\exp(-2.635 + 0.054 \times A_G)}{1 + \exp(-2.635 + 0.054 \times A_G)}$	0.928	3
Carabidae	$\pi_C = \dfrac{\exp(-3.553 - 8.182 \times R_G)}{1 + \exp(-3.553 - 8.182 \times R_G)}$	0.055	3	$\pi_C = \dfrac{\exp(-3.429 + 9.695 \times R_C - 0.017 \times A_G)}{1 + \exp(-3.429 + 9.695 \times R_C - 0.017 \times A_G)}$	0.573	2
Arachnida	$\pi_A = \dfrac{\exp(-4.657 + 15.408 \times R_A)}{1 + \exp(-4.657 + 15.408 \times R_A)}$	<0.001	3	$\pi_A = \dfrac{\exp(-2.387 + 14.106 \times R_A - 0.046 \times A_G)}{1 + \exp(-2.387 + 14.106 \times R_A - 0.046 \times A_G)}$	0.473	2

increasing food abundance should lead to greater food specialization (see Pyke *et al.*, 1977 for a review); in months of high prey abundance (March/April and May/June) the dietary composition was more homogeneous than in periods of prey scarcity (July/August and September). In November, however, despite the low overall abundance of prey, the magnitude of the diversity index decreased again, probably due to a slight increase in the abundance of the two most preferred prey groups — crickets and carabids.

Prey Selection

Although pitfall trapping certainly results in somewhat biased estimates of numbers of the ground-dwelling arthropods, it does provide a useful index of their abundance (Kunz, 1988). In addition to these biases, the fact that a prey is more abundant does not necessarily mean that it is more available to bats. In fact, availability is likely to be influenced not only by abundance of prey but also by their detectability and accessibility (Arlettaz, 1995). Although in this study the monthly values of abundance are probably not an accurate estimate of prey availability to *M. myotis*, they likely portray the temporal patterns of variation in availability. We based our analyses on temporal variations of abundance and consumption, instead of simply comparing total abundance to total consumption.

A high consumption of one type of prey is likely to affect the use of alternative prey, as observed in the present study. Such interactions are not detectable in χ^2-analyses, traditionally used to test for selectivity, but are taken into consideration in logistic regression approach. The colony of *M. myotis* we studied based its diet on the most abundant large ground arthropods, and as referred above the seasonal variations in diet
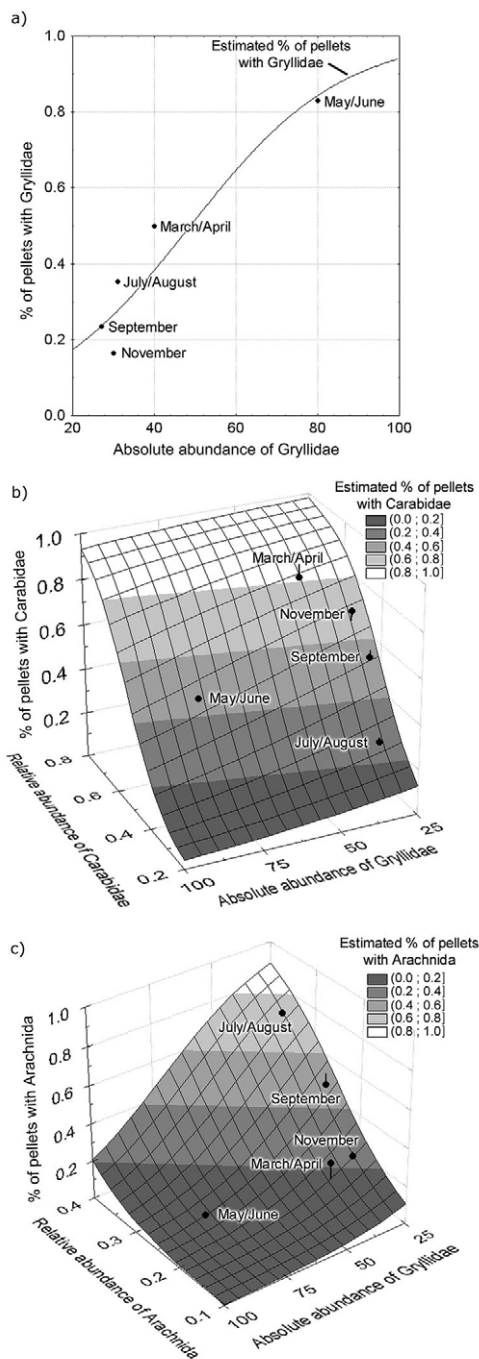
FIG. 3. Graphical representation of the results of the logistic models: (a) regression curve between consumption of crickets and its absolute abundance, showing the close positive relationship between the two variables; (b) and (c) regression surfaces describing the relationship between the consumption of spiders and carabids (independent variables in the models) with the their own relative abundance and the absolute abundance of crickets (predictor variables). The consumption of spiders only rises substantially if they are relatively abundant and crickets are scarce. In contrast, the consumption of carabids is almost solely dependent on its relative abundance, and only rises slightly with cricket scarcity

prey selectivity — some relatively abundant arthropods were not consumed (Formicidae, Acrididae, and Isopoda), and even among the eaten groups Gryllidae were preferred.

The reasons why some arthropod groups are not consumed by *M. myotis* are several. Even the largest ants present in our study area have low biomass, and consequently their energetic return may not compensate the cost of capture. This, and/or the unpleasant taste due to formic acid, may justify the fact that although large ants were very abundant they were not consumed. Nevertheless, Bauerová (1978) found a few ants in the diet of a Czech population of *M. myotis* so it seems that at least some ant species are edible. Acridids have been consumed in other examined populations (Graf *et al.*, 1992) but not found consumed in our study. This is not surprising as acridids were not very abundant, and their diurnal habits make them relatively inconspicuous to bats. Isopods were also not consumed, and this is most likely due to chemical substances used as a defense from predators (Meglitsch and Schram, 1991). Such defenses are probably efficient with bats, given that this group is rarely consumed by these predators (see compilations of diets of insectivorous bats by Freeman, 1981 and Vaughan, 1997).

followed, to a great extent, the patterns of prey abundance. These results support conclusions from other studies presenting *M. myotis* as an opportunistic species (e.g., Bauerová, 1978; Arlettaz, 1995). However, our results also suggest a certain degree of

The regression analyses indicate that crickets were preferred over the other two main prey types — carabids and spiders. This preference was particularly clear in the case of spiders, where consumption was strongly affected by that of crickets. This analysis corroborates the idea stated above that spiders acted as a complement to the other two main prey. Previous studies on this species had not detected prey selection.

Optimal foraging theory predicts that animals should not simply consume prey in accordance to their frequency, but also take into consideration their profitability (e.g., Schoener, 1971, 1987; Pyke *et al*., 1977), i.e., the ratio between the net energy gain and the handling time, which includes both the effort to subdue prey and the search time. Our results with *M. myotis* are consistent with the predictions of this theory. In fact, according to Arlettaz and Perrin (1995) *M. myotis* is very efficient in subduing and consuming large prey, and differences in the costs of handling prey items of distinct sizes by this species may be assumed to be relatively low. Consequently, the theory would predict that a few large prey items would be more profitable than a large number of small prey (Barclay, 1985). Indeed, the most frequently consumed items, Carabidae, Gryllidae and Arachnida include some of the largest ground arthropods in the study area.

In the case of *M. myotis* the expense to take prey includes that for search, the second component of the 'handling time', so theory predicts that conspicuousness, which reduces search time, is an important factor in the choice of prey (Schoener, 1971). Prey movement plays an important role in detection by bats (Anderson and Racey, 1993) and facilitates the distinction between edible and non-edible arthropods (Barclay and Brigham, 1994). In fact, the main taxa, including carabids and some families of spiders (e.g., Lycosidae — Lang *et al*., 1999) that constituted the diet of *M. myotis* have intense nocturnal activity. Several authors suggested that sounds might increase the probability of prey detection by gleaning bats (Neuweiler, 1989; Faure and Barclay, 1992; Arlettaz *et al*., 2001), and prey calls are used by bats to locate potential victims (Belwood and Morris, 1987). The great conspicuousness of calling crickets may partly justify the selection pattern we have observed.

In summary, *M. myotis* does not seem to actively prefer carabids, which were consumed according to their relative abundance. Spiders seemed to act as an alternative to other prey, and crickets seemed to be preferred. It is not clear, however, if this preference for crickets, particularly over the spiders, was simply due to their great conspicuousness, or to the choice based on energetic rewards or taste.

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