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Trophic niche partitioning of cryptic species of long-eared bats in Switzerland: implications for conservation

**Sohrab Ashrafi · Andres Beck · Marianne Rutishauser ·
Raphaël Arlettaz · Fabio Bontadina**

Abstract Dietary niche partitioning is postulated to play a major role for the stable coexistence of species within a community, particularly among cryptic species. Molecular markers have recently revealed the existence of a new cryptic species of long-eared bat, *Plecotus macrobullaris,* in the European Alps. We studied trophic niches as well as seasonal and regional variations of diet in eight colonies of the three *Plecotus* species occurring in Switzerland. Faeces were collected monthly from individuals returning to roost after foraging. Twenty-one arthropod categories were recognized from the faeces. All three species fed predominantly on Lepidoptera, which made up 41%, 87% and 88% (means across colonies) of the diet composition of *P. auritus*, *P. macrobullaris* and *P. austriacus,* respectively. The occurrence of numerous fragments of both diurnal and flightless insects in the diet of *P. auritus* (but rarely in the diet of the other two species) indicates that this species mostly gleans prey from substrates. *P. austriacus* and *P. macrobullaris* are more typical aerial feeders. The latter two species have narrow trophic niches, whilst *P. auritus* has a much broader diet. Comparison of intraspecific and interspecific niche overlaps in *P. auritus* and *P. macrobullaris* in sympatry suggests dietary niche partitioning between these two species. In contrast, the high similarity of the trophic niches of *P. austriacus* and *P. macrobullaris*, associated with a typical parapatric distribution, indicates competitive exclusion. The best conservation measures are preservation and restoration of habitats offering a high abundance of moths, the major prey of the three *Plecotus* species.

Keywords Cryptic species · Niche partitioning · Niche breadth · Niche overlap · *Plecotus* · Switzerland

S. Ashrafi · M. Rutishauser · R. Arlettaz · F. Bontadina
Institute of Ecology and Evolution,
Division of Conservation Biology, University of Bern,
3012, Bern, Switzerland

A. Beck · F. Bontadina
SWILD–Urban Ecology & Wildlife Research,
Wuhrstrasse 12,
CH-8003, Zurich, Switzerland

S. Ashrafi (✉)
Department of Environmental Sciences,
Faculty of Natural Resources, University of Tehran,
P. O. Box 31585-4314, Karaj, Iran
e-mail: Soh_ashrafi@yahoo.com

Introduction

The principle of competitive exclusion (Gause's principle) is one of the most basic rules in ecology. It states that a stable co-existence of species within a community is only possible when the species-specific utilisation of limiting resources is well differentiated (Hutchinson 1957; 1978; Ricklefs 1990; Arlettaz et al. 1997; Wang et al. 2005; but see López-Gómez and Molina-Meyer 2006; Seto and Akag 2007). Similarly, based on the Lotka–Volterra model of competition, a stable co-existence of actual competitors within a community implies that interspecific competition is lower than intraspecific competition (Begon et al. 1986). By corollary, comparing two types of overlap in resource utilization—the intraspecific overlap between all individuals within a single species population and the interspecific overlap between every individual of one species and all

individuals from the other species—allows testing for resource partitioning among co-existing species under conditions of limiting resources (Arlettaz et al. 1997). A narrow niche can result from either a simple, progressive specialisation over evolutionary time, irrespective of any interspecific interaction, or from resource exploitation adjustments under the pressure exerted by sympatric competitors for accessing common resources (Hutchinson 1978).

It has been found that the most important dimensions of the ecological niche are habitat and diet, with most of the ecological differentiation between species occurring along these two axes (Schoener 1986). Consequently, many ecological studies to date have focused on foraging habitats and diet composition of animals (e.g. Arlettaz et al. 1997; Arlettaz 1999; Vitt et al. 2000; Nicholls and Racey 2006). The existence of several taxonomic groups with cryptic species (species which appear morphologically identical but are genetically distinct) provides a unique opportunity to investigate the fine-grained resource partitioning mechanisms at play within animal communities (Arlettaz et al. 1997).

One such group of cryptic species has been the subject of many recent discoveries and requires further investigation, namely the bat species. Bats are one of the most diverse mammalian taxa, with more than 1,100 species described globally. Bats also belong to the most endangered vertebrates in the world, with 22% of the species classified as threatened or near threatened (IUCN Red list 2009). In the Western world, bats have undergone massive population declines since the mid 20th century. Widespread habitat loss and transformation, large-scale agricultural intensification, including pesticide application, are considered as the primary factors of bat population declines (Stebbings 1988; Ransome 1990; Walsh and Harris 1996a, b; Wickramasinghe et al. 2004; Bontadina et al. 2008).

Recently, several cryptic species of bats have been discovered (e.g. Kiefer and Veith 2001; Benda et al. 2004a, b). The taxonomic status of European long-eared bats (genus *Plecotus*), which are widespread in the whole Palearctic zone, was scrutinized by Kiefer et al. (2002), Benda et al. (2004b) and Spitzenberger et al. (2006). Beside the two formerly recognized species (*Plecotus auritus* and *P. austriacus*), molecular markers could evidence the existence in the European Alps of a third cryptic species, *P. macrobullaris* (Kiefer and Veith 2001; Spitzenberger et al. 2002, 2003). In Switzerland, this species was mainly known in the Alpine massif, above 600 m altitude, where it can be found in sympatry with *P. auritus* and in the vicinity of *P. austriacus* (Rutishauser et al. unpublished data; Ashrafi et al. 2010).

The three long-eared bats of Europe are not only morphologically extremely similar but also genetically closely related (Kiefer et al. 2002; Spitzenberger et al.

2006): actually, there is no single external morphological character that enables full species distinction (Ashrafi et al. 2010). The apparently stable co-existence of sympatric populations of *P. macrobullaris* and *P. auritus* in the Swiss Alps has to have been achieved through a process of ecological niche differentiation (Arlettaz et al. 1997). In contrast, there is so far no evidence for sympatric populations of *P. austriacus* and *P. macrobullaris*. Although potential distributions predicted via spatial modelling overlap (Rutishauser et al. unpublished data), all areas checked so far harbour only one of the two species. This situation may reveal interspecific spatial exclusion (outcompetition) caused by too similar ecological niches, i.e. a too wide niche overlap.

Previous faecal analysis led to characterize *P. auritus* as a generalist forager (e.g. Beck 1995). Although sympatric co-existence of *P. auritus* and *P. macrobullaris* could be achieved through a simple partitioning of foraging habitat (Arlettaz 1999) or foraging activity time (e.g. Rydell et al. 1996) without obligatory diet segregation, we predict for *P. macrobullaris* a narrower trophic niche, i.e. a higher prey specialization. This may be a way to decrease interspecific pressure in resource utilization, i.e. to achieve an acceptable balance in interspecific food resource sharing, although such a mechanism would bear costs (lower survival rates, reproductive performance and/or population density) for the species whose niche is included in that of the other (asymmetric species-specific competition coefficients; Lotka–Volterra model, Begon et al. 1986). In contrast, given the apparent parapatric distribution of *P. austriacus* and *P. macrobullaris*, a large dietary niche overlap between these two species would be expected. Finally, as we worked in several areas of Switzerland with varying land-use intensity, we expected narrower dietary niches in regions characterized by high-intensity agriculture, because industrial farming reduces species richness and invertebrate abundance (Britschgi et al. 2006) in comparison with traditional, low-intensity agriculture.

To summarize, this study evaluates the extent to which ecological niche specialization and differentiation occur between the three species of long-eared bats in Switzerland along one major niche dimension, the trophic axis. It further aims at identifying the ecological requirements of the three *Plecotus* species with the idea to draw recommendations for better targeted conservation management.

Materials and methods

Field sampling and data collection

In May–September 2007 and 2008, we collected a total of 899 faecal samples from 251 long-eared bats ($n=137$

P. auritus, 41 *P. austriacus* and 73 *P. macrobullaris*) captured at eight colonies in southern, northern and south-western Switzerland (Appendix S1). All sites were already known as relatively large maternal colonies (20–40 females) from a previous study (Ashrafi et al. 2010). Faecal samples were obtained from bats mist-netted at the entrance of their attic roost—to minimise disturbance of the colony —when returning from their nocturnal forag-ing. For each roost, the species' identity had been previously assessed (in 2006) by DNA analysis of several individuals in each roost (Ashrafi et al. 2010). During the present study, we further identified individuals based on eight external characters, as suggested by Ashrafi et al. (2010). The bats were kept in linen bags until defecation, which took place within 30–120 min after capture. Individual faecal samples were dry-stored in paper envelopes. In the laboratory, the faecal pellets were soaked in water for at least 10 min and teased apart with dissecting needles on a Petri dish under a binocular microscope (Leica MZ9.5, Leica Microsystems, Switzer-land; 10–60x magnitude). Identification of arthropod remains to order or family was achieved using several identification keys (e.g. Shiel et al. 1997; Whitaker 1988) and referring to our own collection of identifiable arthropod remains in bat faeces (Arlettaz et al. 2000). The proportion (% volume) of each prey category was estimated for each faecal pellet to the nearest 5%, and then estimated for the whole individual sample.

Trophic niche breadth and niche overlap

Trophic niche breadths were estimated using Levin's index (Krebs 1999; Arlettaz et al. 1997), from the proportion p_i of all prey categories in the diet:

$$B = \frac{1}{\sum p_i^2}$$

The index B ranges from 0 to *n*, with *n* corresponding to the number of prey categories. Niche breadth was calculated at the individual level in monthly intervals in order to account for possible species-specific seasonal effects (Appendix S1). Moreover, individual niche breadth for colonies in the low-intensity (Upper Valais, Alps) vs. high-intensity (Lower Valais, Rhone valley) cultivated areas were compared statistically. Assumptions of nor-mality and homogeneity were tested using Shapiro's test and Leven's test. Due to significant deviation from normality we had to rely on non-parametric tests for estimating niche breadths in either geographic (Mann–Whitney *U* test) or seasonal (monthly; Kruskal–Wallis test, using the *pgirmess* package) comparisons (R pro-gram; R Development Core Team 2009).

Individual niche overlaps were calculated using Freeman and Tukeys' index according to Matusita (1955).

$$FT_{ij} = \sum_{r=1}^{k} \left(p_{ir} \cdot p_{jr} \right)^{\frac{1}{2}}$$

FT_{ij} measures the niche overlap between the individuals *i* and *j*, where *k* is the total number of used resources (prey categories) and p_{ir} and p_{jr} are the proportions of the resource, *r*, utilized by individual *i* and *j*, respectively. The index ranges from 0 (no overlap) to 1 (complete overlap). Overlaps were measured monthly for the sole situation of sympatry (mixed colony harbouring both *P. auritus* and *P. macrobullaris*), both intraspecifically and interspecifically (through a matrix of individual samples with all possible monthly pairwise comparisons), as out-lined in Arlettaz et al. (1997). To test for differences between the two types of overlap, we used a randomization procedure, which generated random series of matrices of similar size and compared their outcomes with the observed matrix (J. Goudet, unpublished, available upon request from the first author). However, sample sizes that were too small prevented calculations of inter- and intraspecific niche overlaps for the mixed colony at the beginning and at the end of the season.

Results

Diet composition

Overall, 21 prey categories were identified in the faecal samples of *P. auritus*, 15 categories in *P. macrobullaris* and 12 in *P. austriacus* (Table 1). The major prey categories in *P. auritus'* diet were Lepidoptera adults (between colonies mean 41.0% [of prey fragments' volume]; range 13.0–68.0%; calculated from individual faecal samples), Cole-optera (mean 7.0%, range 0.6 11.3%), Diptera (16.6%, 9.6–20.7%), Dermaptera (14%, 0.6–30.0%), Arachnida (8.0%, 0.5–17.2%) and Chilopoda (4.2%, 0.0–10.0). The diet of *P. macrobullaris* comprised Lepidoptera (mean 88.0%, range 82.0–93.0%), Coleoptera (3.5%, 1.2–7.9%) and Diptera (6.7%, 3.8–9.0%), that of *P. austriacus* comprised Lepi-doptera (87.0%, 86.0–89.0%), Coleoptera (1.3%, 0.0–2.6%), Diptera (4.8%, 3.1–6.4%) and Hymenoptera (0.8%, 0.0–1.6%). These main categories made up 90.8%, 98.2% and 93.9% of the diet composition of *P. auritus*, *P. macrobullaris* and *P. austriacus*, respectively. Prey catego-ries typically revealing a ground-foraging behaviour made up, on average, 27.8%, 0.9% and 2.7% of the diet of *P. auritus*, *P. macrobullaris* and *P. austriacus*, respectively. There was no significant seasonal variation in the main prey category Lepidoptera adults for any of the three species

Table 1 Mean percentage volume of prey categories found in individual faecal samples

Species	Place	Lepidoptera adults	Lepidoptera larvae *	Scarabidae	Curculionoidae *	Other Coleoptera	Tipulidae	Syrphidae *	Chironomidae	Brachycera	Other Diptera	Chyrsopidae
P. auritus	Obergesteln (Upper VS)	**32.0**	0.0	0.1	0.0	**0.5**	1.0	3.5	0.1	0.1	**16.0**	0.7
	Blitzingen (Upper VS)	**13.0**	0.7	1.2	0.1	**10.0**	4.7	0.0	0.0	0.0	**13.0**	0.5
	Salins (Lower VS)	**68.0**	0.0	0.3	10.0	**3.0**	2.3	0.0	0.0	1.2	**6.1**	2.0
	Kirchrued (AG)	**52.0**	8.5	0.0	0.0	**2.6**	5.1	0.3	0.0	0.0	**14.0**	0.4
	Average	**41.0**	2.3	0.4	2.5	**4.1**	3.3	1.0	0.0	0.3	**12.0**	0.9
P. macrobullaris	Obergesteln (Upper VS)	**82.0**	0.0	0.4	0.0	**7.5**	**3.7**	0.0	0.0	0.0	**5.3**	0.0
	Lax (Upper VS)	**89.0**	0.0	0.1	0.0	**1.2**	**4.7**	0.0	0.0	0.4	**2.6**	0.0
	Basse Nendaz (Lower VS)	**93.0**	0.0	0.0	0.0	**1.2**	**1.0**	0.0	0.1	0.0	**2.7**	0.0
	Average	**88.0**	0.0	0.2	0.0	**3.3**	**3.1**	0.0	0.0	0.1	**3.5**	0.0
P. austriacus	Mandach (AG)	**89.0**	0.1	0.0	0.0	**2.6**	**1.7**	0.0	0.0	0.2	**4.5**	0.2
	Mönthal (AG)	**86.0**	0.0	0.0	0.0	**0.0**	**0.8**	0.0	0.0	0.0	**2.3**	0.0
	Average	**87.0**	0.1	0.0	0.0	**1.3**	**1.3**	0.0	0.0	0.1	**3.4**	0.1

Species	Place	Hemerobiidae	Hymenoptera	Trichoptera	Dermaptera *	Hemiptera	Orthoptera	Blattodea *	Opiliones *	Other Arachnida *	Chilopoda
P. auritus	Obergesteln (Upper VS)	2.7	0.2	2.7	**19.0**	3.5	5.8	0.0	2.0	**8.4**	**2.6**
	Blitzingen (Upper VS)	0.0	0.7	0.0	**30.0**	0.2	4.4	0.0	0.2	**17.0**	**3.6**
	Salins (Lower VS)	0.2	0.0	0.0	**5.4**	0.9	0.3	0.1	0.1	**0.4**	**0.0**
	Kirchrued (AG)	0.5	0.6	0.0	**0.6**	0.1	2.0	0.0	0.0	**3.7**	**10.0**
	Average	0.9	0.4	0.7	**14.0**	1.2	3.1	0.0	0.6	**7.4**	**4.2**
P. macrobullaris	Obergesteln (Upper VS)	0.0	0.0	0.0	0.0	0.8	0.0	0.1	0.0	0.2	0.1
	Lax (Upper VS)	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.1
	Basse Nendaz (Lower VS)	0.0	0.1	0.0	1.8	0.0	0.0	0.0	0.0	0.1	0.2
	Average	0.0	0.3	0.0	0.6	0.3	0.0	0.0	0.0	0.3	0.1
P. austriacus	Mandach (AG)	0.0	**1.6**	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.1
	Mönthal (AG)	0.0	**0.0**	0.0	0.0	5.8	0.0	0.0	0.0	5.0	0.0
	Average	0.0	**0.8**	0.0	0.0	3.0	0.0	0.0	0.0	2.6	0.1

n=251, totalling 899 pellets of six sympatric and two parapatric populations of the three *Plecotus* species from different regions in northern (*AG* Argovia), southern and southwestern Switzerland (*VS* Valais). Major prey taxa in a given species diet are marked in *bold*, whereas non-flying or diurnal prey taxa are marked with an *asterisk*

during the season (Kruskal–Wallis test, $\chi^2=3.7$, 5.19 and 3.35, $p=0.085$, 0.18 and 0.50 in *P. auritus*, *P. macrobullaris* and *P. austriacus,* respectively).

Trophic niche breadth and niche overlap

The trophic niche breadths of *P. austriacus* and *P. macrobullaris* were smaller (Levin's index of 1.22 and 1.26, respectively, Fig. 1) than that of *P. auritus* (1.90, multiple Kruskal–Wallis test, $p<0.05$). There was no indication for a significant seasonal variation in niche breadth for any of the three species (Kruskal–Wallis test, $\chi^2=6.31$, 10.53 and 6.98; $p=0.052$, 0.17, 0.13 for *P. auritus*, *P. macrobullaris* and *P. austriacus*, respectively).

A comparison of monthly interspecific vs. intraspecific (individual) niche overlaps in the sole available sympatric population (*P. auritus* and *P. macrobullaris,* Upper Valais) yielded a significant difference between intraspecific and interspecific overlaps in July and August for *P. auritus* ($p<0.05$, randomization tests) and in August for *P. macrobullaris* ($p<0.05$;Fig. 2). No tests could be performed in June and September due to too small sample sizes.

Comparisons of niche breadths between colonies in Upper Valais (low-intensity agriculture) and Lower Valais (high-intensity agriculture) revealed a much narrower prey spectrum for *P. auritus* in the intensively cultivated area (1.7 vs 2.2 for low-intensity farming; Mann–Whitney U test, $W=288.5$, $p<0.01$), whilst no such difference existed for *P. macrobullaris* (1.2 vs 1.3, respectively, $W=161.5$, $p=0.81$).

Discussion

This study establishes an overall trophic specialisation on moths in all three species of long-eared bats occurring in Switzerland. Yet, *P. auritus*, the least specialized (broader niche) among the three *Plecotus* species, incorporates many more Dermaptera, Diptera, Arachnida, Coleoptera and
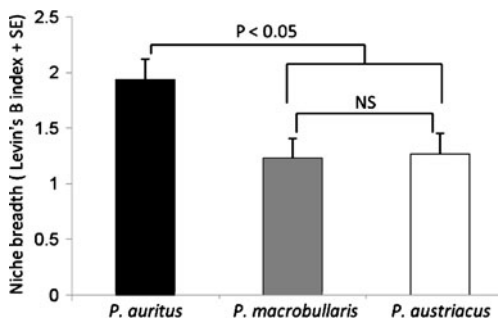
Fig. 1 Mean (+SE) trophic niche breadth (Levin's index) computed for the three long-eared bat species from May to September 2007 and 2008. The significance of pairwise comparisons is indicated (multiple Kruskal–Wallis test, $p<0.05$; *NS* not significant)
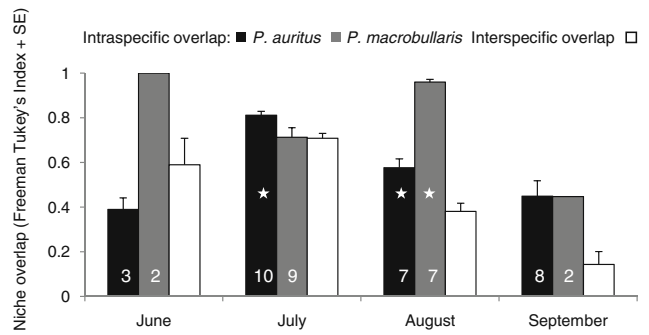
Fig. 2 Monthly niche overlaps (Freeman–Turkey's index+SE, sample size given in *columns*) in a sympatric population of *P. auritus* and *P. macrobullaris*. *Stars* show significant intraspecific–interspecific pairwise comparisons (randomization tests, $p<0.05$)

Chilopoda in its diet, which reveals a greater reliance on substrate gleaning as regards to foraging tactics. In the sole sympatric population found, there was evidence for a mechanism of trophic niche partitioning between *P. auritus* and *P. macrobullaris*.

A trophic specialisation of *Plecotus* on moths confirms previous European studies. The proportion recorded here for *P. auritus* (41%) is similar to the values reported by Swift and Racey (1983, 40.5%), Rydell (1989, 27.2%) and Beck (1995, 61%). A very high proportion of moths in *P. austriacus'* diet in Beck 1995, 90%; (see also Swift and Racey 1983 and Rydell 1989) is also corroborated by our findings (87.4%). To our knowledge, the present study represents the first analysis of the diet of *P. macrobullaris* in Central Europe: 88.0% of moths in diet composition corroborates the findings (90%) made by Whitaker and Karatas (2009) in Turkey. Thus, this species appears to be as specialised on moths as *P. austriacus*. With a diet composed of 27.8% diurnal and non-flying prey taxa, *P. auritus* is expected to glean much of its prey from substrates. This contrasts with the foraging behaviour of *P. austriacus* and *P. macrobullaris,* as inferred from their diet composition, which would be much more adapted to prey capture by aerial hawking. The similarities in morphology (Ashrafi et al. 2010) and echolocation calls (Dietrich et al. 2006) of *P. auritus* and *P. macrobullaris* had led to the idea of similar gleaning foraging strategies in the two species, which is invalidated by our findings, as *P. macrobullaris* only had 0.9% typical non-flying and diurnal arthropods in its diet. Hence, although it is still able to pick up insects from surfaces, *P. macrobullaris* mostly captures aerial prey. The same holds for *P. austriacus,* with only 2.7% of flightless and diurnal taxa in its diet. Yet, the exact amount of prey consumed by gleaning is most probably underestimated as other prey not classified among diurnal and flightless categories can also be obtained from gleaning. The seasonal variation in the occurrence of moths observed in the diet of the bats was only slight, which is

likely to indicate a rather constant occurrence of this food source in the environment.

These noticeable divergences in prey spectra and niche breadths of Swiss long-eared bats are reflected in our unique niche overlap estimation for the sole situation where two out of the three species occurred in sympatry, and even in syntopy (sharing the same colonial roost). Competition avoidance between *P. auritus* and *P. macrobullaris* was clearly achieved through a mechanism of food resource partitioning, with the intraspecific overlap being larger than the interspecific overlap, a situation which was sufficient to allow a stable coexistence. Interestingly, this pattern was apparent even in the middle of the summer, when food abundance peaks, i.e. when the basic assumption of limiting resources was less likely to be true. This apparent niche structure maintenance leaves open the question whether the underlying ecological segregation mechanism is competitive exclusion or rather niche specialisation independent from interspecific competition. The convergent diets and niche breadths of *P. austriacus* and *P. macrobullaris* may be a sign that these two species actually compete for the same food resources. The fact that *P. austriacus* inhabits exclusively lowland areas of Switzerland north of the Alps, while *P. macrobullaris* occurs mostly above 600 m altitude north of the Alps but also at low elevation in the southern Alps (Ashrafi et al. 2010; Mattei-Roesli 2010) evokes a parapatric distribution. Predictive habitat suitability models have recently confirmed this view (Rutishauser et al. unpublished data). There is thus growing evidence that the two species actually occupy the same niche and could not coexist in sympatry in the long term.

Bats are a specious group of mammals playing an important role as bioindicators (Jones et al. 2009). The recent discovery of new cryptic species of bats poses new conservation challenges, as species status and ecological requirements are to be re-evaluated. In the extreme cases, the discovery of new species within a cryptic species complex may lead to the recognition that some species, previously considered as threatened, are indeed critically endangered, if not on the brink of extinction, thus requiring immediate action (e.g. Sattler et al. 2007).

Like many other European Microchiroptera (Stebbings 1988; Mitchell-Jones 1995; Hutson et al. 2001; Bontadina et al. 2008), long-eared bats have faced strong declines in the last decades. This is not surprising, given that niche specialists are more vulnerable than generalists (Safi and Kerth 2004). Because *P. austriacus* and *P. macrobullaris* have smaller niche breadths than *P. auritus*, we expect the former two species to be more sensitive to changes in their immediate environment; therefore, a higher conservation concern status for these two species is justified. Our finding that diet diversity of *P. auritus* is lower in high-intensity than in low-intensity farmland suggests that even this more generalist species is under environmental pressure in high-intensity farmland, which is in line with the general view that agricultural intensification has caused a dramatic impoverishment of foraging conditions for insectivorous vertebrates across temperate Europe (e.g. Wickramasinghe et al. 2004; Britschgi et al. 2006; Buckingham et al. 2006). Our results suggest that less intensive agricultural management and any kind of habitat management, which favours the abundance of moths, would be profitable to long-eared bats.

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