

# Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*)

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## Abstract

The bat species *Rhinolophus hipposideros* has undergone a dramatic decline throughout much of western Europe from the 1960s. The mechanisms responsible for this phenomenon have not been conclusively identified. At the same time, some populations of *Pipistrellus pipistrellus* have increased substantially, possibly as a consequence of foraging upon insects attracted by street lamps. To evaluate whether there might be some ecological link between the opposite demographic trends observed in the two species, we compared the diets of two sympatric populations of *R. hipposideros* and *P. pipistrellus* in south-west Switzerland. The two bat species fed upon the same categories of prey, mainly moths and Diptera, and we were not able to recognize interspecific differences in diet composition in spring when resources were most likely to be limiting. Although using different foraging strategies, both species may visit the same or adjacent feeding grounds, therefore potentially competing for the same populations of prey. Although conclusive evidence is still needed, bat conservation policy should pay more attention to this possibility. © 2000 Elsevier Science Ltd. All rights reserved.

**Keywords:** Bat conservation; Interspecific competition; *Pipistrellus pipistrellus*; *Rhinolophus hipposideros*; Trophic niche

## 1. Introduction

The lesser horseshoe bat (*Rhinolophus hipposideros*) is probably the bat species that has faced the most dramatic decline in western Europe over the past decades (Roer, 1972, 1983–1984; Schober and Wilhelm, 1983–1984; Stutz and Haffner, 1984; Rudolph, 1990; Kokurawicz, 1990; Kulzer, 1995; Mitchell-Jones, 1995). Many hypotheses have been proposed to explain its decline, which occurred over only two decades in the 1960s and 1970s, but there has been no conclusive answer to this question as yet. Factors implicated are, among others, contamination by pesticides, habitat destruction and climatic changes (see the review by Kulzer, 1995). In Switzerland, for instance, the extinction of *R. hipposideros* in the lowlands (Stutz and Haffner, 1984) can be attributed to general environmental degradation,

including systematic eradication of hedges in the countryside (Schofield, 1996) and extensive use of pesticides in modern agriculture. Yet, even in the better preserved Swiss highlands, most valleys which were still harbouring large populations of *R. hipposideros* until the 1960s are nowadays virtually abandoned although landscape, roosts and insect fauna have certainly not suffered such dramatic alterations (Stutz and Haffner, 1984; Zingg and Maurizio, 1991; Arlettaz et al., 1999). This suggests that other causes could be involved.

In contrast, the common pipistrelle (*Pipistrellus pipistrellus*) is currently considered to be the most widespread and abundant bat species in continental Europe and Britain (Stebbins and Griffiths, 1986). Some studies have inferred recent population increases (Stutz and Haffner, 1985; Speakman et al., 1991). Arlettaz et al. (1999) have further documented massive population expansions in Switzerland; they speculated that this might result from a propensity of pipistrelle bats to prey upon insects attracted by street lamps, an extraordinarily profitable food source (Rydell, 1989).

*R. hipposideros* and *P. pipistrellus* are species of similar body size that differ in several life history traits.

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According to Gaisler (1989), *R. hipposideros* is a typical 'K-strategist' that exhibits long average lifespan, delayed sexual maturity and reduced reproductive rate (no production of twins). In comparison, *P. pipistrellus* appears at the opposite end of the so called 'r-K selection continuum', with shorter longevity, females giving birth at one year old, regular production of twins in many areas. This points to a potentially greater vulnerability of *R. hipposideros*, as compared to *P. pipistrellus*, to any sudden environmental changes. The systematic use of lit roads by pipistrelle bats is also characteristic of the species today, at least in central western Europe where white lamps are available (Rydell and Racey, 1995). On the contrary, *R. hipposideros* has not been reported foraging extensively around street lamps.

As the actual causes of decline of *R. hipposideros* have not been clearly identified, it has not been possible to develop adequate conservation schemes, although roost conservation has been given the priority. This paper compares the trophic niches of two sympatric colonies of *R. hipposideros* and *P. pipistrellus* in the Swiss Alps, testing the hypothesis that the two bats exhibit similar diets, with respect to prey taxon and/or size, which would theoretically create conditions potentially leading to interspecific competition.

## 2. Methods

From April to September 1991, we studied the seasonal variation in the composition of the diets of two neighbouring colonies of *R. hipposideros* and *P. pipistrellus* inhabiting the Val de Bagnes (Valais Alps, southwestern Switzerland; 46°05'N, 7°20'E). Val de Bagnes is a very deep and narrow valley, oriented north-south, which is bordered by two high mountain ridges culminating at 4314 m altitude (Grand Combin). There is no plain at the bottom of the valley. The two bat roosts (1450 m apart) are situated in the immediate proximity (<200 m) of the river Dranse, at 830–840 m a.s.l. We therefore considered the two populations as sympatric. The *R. hipposideros* nursery is in a church loft. The nursery colony of *P. pipistrellus* was settled in the insulation gap between the external and internal walls of a wooden chalet.

Bat droppings were collected every month from underneath the main roosting place (*R. hipposideros*), or on the floor below the crevice entrance to the roost (*P. pipistrellus*). For each species, 20 faecal pellets were selected randomly from the monthly samples ( $n$  total = 240 droppings analysed), teased apart and inspected for identifiable prey remains under a binocular microscope. Determination of fragments was achieved using various identification guides (e.g. McAney et al., 1991), the collection of microscope slides established by Beck et al. (1989), and a slide reference collection obtained

from insects captured with a suction trap on the banks of the river Dranse on 2 nights in May and June 1991.

Diet composition was estimated by the frequency of occurrence of each prey category within each monthly sample. Values were expressed as percentages (5% = taxon present in one single pellet only; 100% = taxon present in all 20 pellets). Prey were usually determined to order, but family level was possible for Nematocera (Diptera). Moth scales can remain in the digestive tract for long periods after digestion (Robinson and Stebbings, 1993). In the absence of other moth fragments, we considered that Lepidoptera were part of the composition of one pellet only if their occurrence amounted to at least 5% (approximate visual estimation) of the total volume of debris, or an absolute number of ca. 200 scales.

Niche breadth was estimated for every month using Levin's index, whereas overlap in dietary niches was determined using the 'minimum percent overlap index' (Krebs, 1989). Prey size was determined from two types of fragments: wings and halteres of Diptera.

Statistical analyses consisted of randomized contingency table procedures ( $\chi^2$ , programme MacActus; see Estabrook and Estabrook, 1989, for details about the method) and Mann–Whitney  $U$ -tests (Systat package; Wilkinson et al., 1992).

## 3. Results

The diets of both bat species comprised nine orders of insects, with Lepidoptera, Diptera and Neuroptera slightly predominating during April to September. Coleoptera were present primarily early in the season (Fig. 1). Amongst Nematocera (Diptera), 12 families were recognized, but none was really prevalent (Fig. 2).

Randomized contingency tables ( $\chi^2$ ) yielded monthly significant differences ( $p < 0.05$ ) in overall diet composition (prey orders) in June, July, August and September, but non-significant values for April and May. Significant deviations (observed vs. expected frequencies) for individual orders were obtained only for Neuroptera in August and Trichoptera in September, both of which were consumed almost exclusively by *R. hipposideros*. Among families of Nematocera (Fig. 2), non-significant values were obtained in April, May and June, whilst the overall consumption differed between species in July, August and September, with significant deviations for Tipulidae in May and July, Anisopodidae in August and Mycetophilidae in September (again, all more frequently eaten by *R. hipposideros*).

There was no apparent difference in the size of Diptera captured by the two bat species (Fig. 3). Neither the length of wings (mean  $\pm$  SD: 9.36  $\pm$  3.1 vs. 8.30  $\pm$  4.1 mm,  $U_{16,39} = 226.5$ , NS), nor the diameter of the head of the halteres (0.96  $\pm$  0.04 vs. 0.96  $\pm$  0.08 mm;  $U_{21,11} = 111$ ,

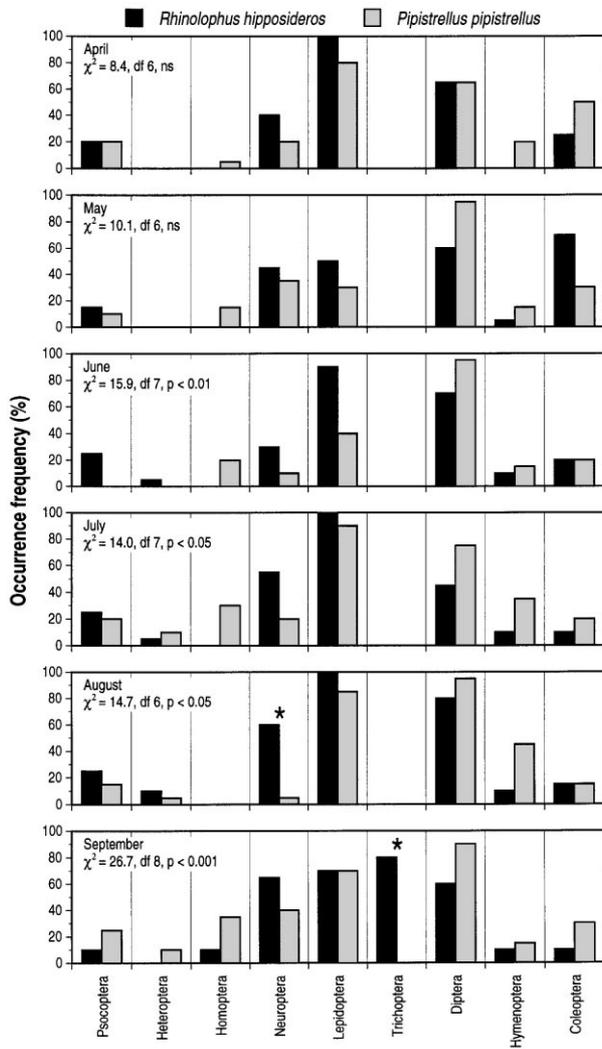


Fig. 1. Seasonal variation in diet composition (insect orders) of sympatric populations of *R. hipposideros* and *P. pipistrellus* in Val de Bagnes (Valais, Swiss Alps). Overall results of randomization tests are indicated in the grey frame, whereas significant deviations ( $p < 0.05$ ) between observed and expected frequencies for a given prey category are represented by one star.

NS), for *R. hipposideros* and *P. pipistrellus*, respectively, was statistically different.

Levin's niche diversity indices, calculated on the basis of the monthly samples, did not differ between the two species ( $4.3 \pm 0.5$  vs.  $4.5 \pm 0.9$ ,  $U_{6,6} = 15$ , NS; Fig. 4a). The average monthly niche overlap amounted to  $72.2 \pm 6\%$  (range: 65–81%; Fig. 4b), with the highest interspecific overlap in April.

#### 4. Discussion

##### 4.1. Convergence of trophic niches

In the sympatric bat populations of Val de Bagnes, the diets of the two species differed from June to September,

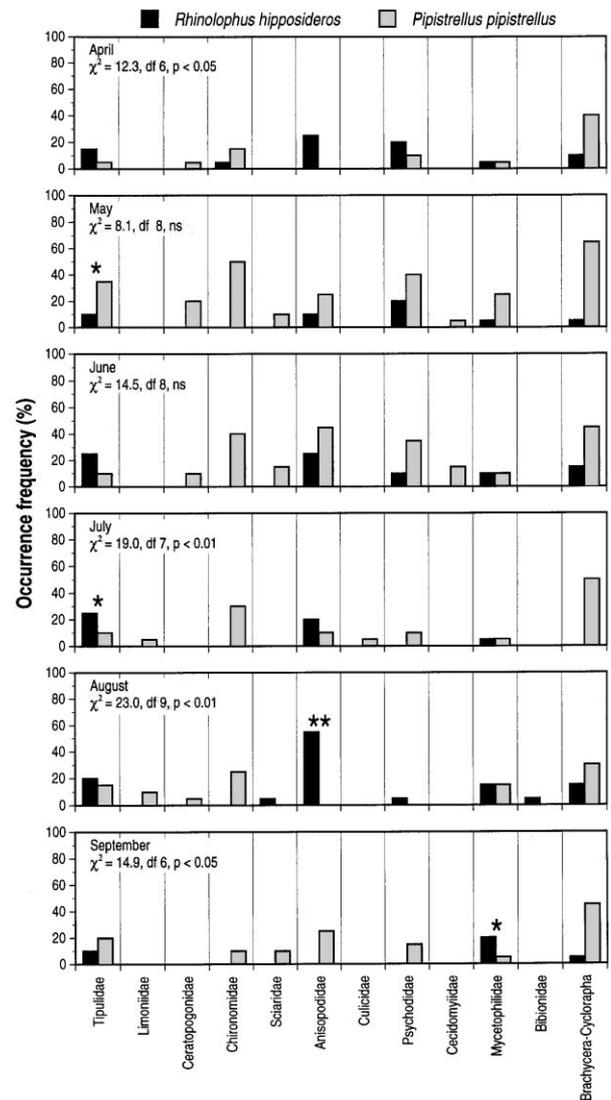


Fig. 2. Seasonal variation in the consumption of Diptera (families) by sympatric populations of *R. hipposideros* and *P. pipistrellus* in Val de Bagnes (Valais, Swiss Alps). Overall results of randomization tests are indicated in the grey frame, whereas significant deviations between observed and expected frequencies for a given prey category are represented by one ( $p < 0.05$ ) or two ( $p < 0.01$ ) stars.

but not earlier in the season (April and May), at least at the level of resolution achieved with the semi-quantitative method used. Significant deviations between observed and expected frequencies of a given insect order occurred only for Neuroptera in August and Trichoptera in September, pointing to only two months with distinct dietary specializations. It is perhaps noteworthy that the dietary overlap was greatest in April (81%) and May (72%), when food resources were most likely to be limiting and the potential risk of competition therefore greatest. There was also no noticeable difference in the size of Diptera making up the diets.

Although the biases inherent to the various methods used for faecal analysis render comparisons between

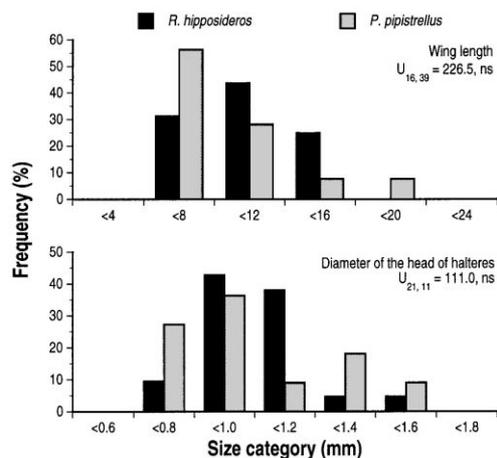


Fig. 3. Comparison of the size of Diptera captured by sympatric populations of *R. hipposideros* and *P. pipistrellus* in Val de Bagnes, (Swiss Alps). Upper part: wing length; lower part: diameter of the head of halteres. Results of statistical tests are also given.

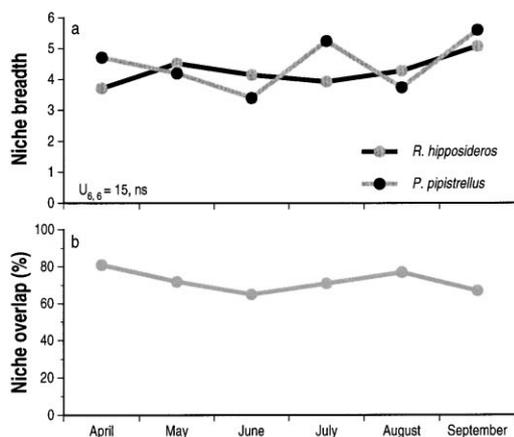


Fig. 4. (a) Niche breadth (Levin's index) and (b) niche overlap (minimum percentage overlap) drawn from the composition of the diets (insect orders) of sympatric populations of *R. hipposideros* and *P. pipistrellus* in Val de Bagnes (Valais, Swiss Alps).

studies difficult, the interspecific dietary overlap between *R. hipposideros* and *P. pipistrellus* seems to be higher than among any pair of European bat species investigated so far. The two sibling species *Myotis myotis* and *M. blythii*, for instance, exploit very distinct trophic niches albeit they are hard to distinguish from their external appearance (Arlettaz et al., 1997). Even the two *P. pipistrellus* phonic types, which are actually two cryptic bat species (Jones and van Parijs, 1993; Barlow and Jones, pers. comm.) have apparently more divergent diets (Barlow, 1997) than the phylogenetically unrelated *R. hipposideros* and *P. pipistrellus*.

The high proportion of Lepidoptera in the diet of *P. pipistrellus* at the study site differs from the findings in other studies, both on pipistrelle bats (Swift et al., 1985; Barlow, 1997) and other bat species feeding in the air (see the review by Rydell et al., 1995), and this cannot

be attributed solely to methodological differences. The use of high frequency calls in *R. hipposideros* has been described as a strategy evolved to bypass the detection ability of moths, whereas the lower frequencies used by *P. pipistrellus* appear not especially suited for hunting tympanate prey (Jones, 1992). However, moths attracted by lamps are rendered particularly vulnerable to bat predation because intense light inhibits their ability to take evasive actions (Svensson and Rydell, 1998). Pipistrelles and other bat species thus often concentrate their foraging activity around lit areas (Rydell, 1989). Could the exploitation of insects attracted by artificial lights be the reason for an apparent switch of *P. pipistrellus* towards moths at the study site where white lights are numerous along road sides?

#### 4.2. Foraging space

Interspecific exploitative competition is possible only if species exploit the same populations of prey. This may first happen when species visit the same feeding grounds. Both species regularly hunt side by side within (*R. hipposideros*), or close to (*P. pipistrellus*) the clutter of deciduous vegetation, mostly along hedges or stretches of riparian forests (Swift et al., 1985; Schofield, 1996; Oakeley and Jones, 1998; authors' own unpublished data).

Second, street lamps cannot sustain insect populations per se, but attract insects from the surrounding natural environment (Rydell, 1991, 1992; Rydell and Racey, 1995). In consequence, attraction of the prey available within the basic habitats of *R. hipposideros* towards the artificial lights where pipistrelles hunt — but not lesser horseshoe bats due to different echolocation constraints — could contribute to deplete food in the former zones and, eventually, create situations for diffuse exploitative competition.

Both conditions are definitely met at the study site where foraging habitats, villages, roads, and therefore street lamps, are situated along the valley axis. Similar conditions doubtless exist over most of the historical range of *R. hipposideros* in central Europe.

#### 4.3. Interspecific competition within bat communities

A case of competitive exclusion would not be unique among European bat species. Baagøe (1986) has suggested that *Vespertilio murinus* is excluded by *Eptesicus serotinus* on some Danish islands, presumably as a consequence of competition. Haffner and Stutz (1985–1986) have shown that *P. pipistrellus* and *P. kuhlii* in southern Switzerland exhibit complementary geographic distributions, which indicates parapatric competition; the former species is apparently confined to the uplands as a result of the competitive pressure exerted by the latter, slightly larger and more aggressive, species. Rydell

(1992) also suggests that the rarity of *P. pipistrellus* along rows of street lamps in Sweden could result from the competitive pressure exerted by the larger *Eptesicus nilssonii*, which is the most common species exploiting lamp patches in Scandinavia. This suggests that European bat communities are somehow saturated; if so, the expansion of one particular species (*P. pipistrellus*) would imply some negative impact on other representatives of the same community (*R. hipposideros*). If population increase of one potential competitor is substantial, as demonstrated for populations of pipistrelle bats close to our study area (Arlettaz et al., 1999), then competitive exclusion could act even if a small proportion of the spreading species somehow exploit part of the food resources of the other species part of the time (see the Lotka–Volterra model of competition; Begon et al., 1986).

## 5. Conclusion

This study suggests that the hypothesis of a decrease of *R. hipposideros* resulting from an increase of *P. pipistrellus* represents an ecologically plausible scenario. Of course, the validity of the model of competitive exclusion still needs to be demonstrated. A comparison of the status, density and population dynamics of the two species in various areas could provide some answer to the question. Interestingly, the last valley in Switzerland which still shelters a dense population of *R. hipposideros* (Lutz et al., 1986) has very few street lamps (pers. obs.) — and presumably few pipistrelles — because natural geological instability has impeded urbanization.

For the time being, we simply urge bat conservationists to remain aware of this possibility when developing conservation schemes for *R. hipposideros*. The effect of artificial lighting on bat population dynamics would benefit from being evaluated in a wider perspective: within saturated communities, what provides immediate advantages for some species could well prove detrimental in the long term to others.

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