Changes in prey abundance unlikely to explain the demography of a critically endangered Central European bat

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Summary

1. Recognizing the factor(s) that caused a demographic crash is a prerequisite to the development of a tailored population restoration plan. While habitat destruction leaves little scope for population persistence, cryptic habitat deterioration (for example through reduction of food resources) may similarly render an area totally inhospitable, while it still appears to have a suitable habitat configuration.

2. Most European bat species have undergone dramatic declines over the past decades. Once among the most widespread and abundant bat species of Central Europe, the lesser horseshoe bat, *Rhinolophus hipposideros* (Bechstein 1800), is today extinct in many regions. Although changes in the agricultural landscape have been suggested as the major cause of decline, recent studies have shown that this bat forages almost exclusively in woodland, a habitat that has increased in area across continental Europe over the past decades. This suggests that habitat eradication *per se* is unlikely to be the main cause of decline. But could cryptic habitat deterioration play a harmful role?

3. We looked at the abundance of insect prey in woodland in the vicinity of colonial roosts with diverging demographic status (extinct, declining or recovering populations), both in the Swiss lowlands (Swiss Plateau) and in the Alps. We predicted that population size correlates positively with prey abundance.

4. Diet composition mirrored local insect prey abundance, confirming an opportunistic foraging strategy. Prey abundance showed marked seasonal variation, but did not differ between sites harbouring extinct, declining or recovering populations. There was also no difference in food abundance between extinct populations in the lowlands and recovering populations in the Alps.

5. *Synthesis and applications.* Cryptic habitat deterioration through a reduction in prey abundance is unlikely to preclude recolonization of abandoned areas by presently recovering populations. However, sufficient areas of natural forest should be preserved or created around potential nursery roosts. Moreover, connectivity between forest patches must be ensured (by creation of hedges and tree lines) to prevent any spatial gap in recolonization within semi-open agricultural landscapes. Other threatened European forest bats may also benefit from these measures.

Key-words: bat conservation, diet, ecological quality, habitat alteration, insect abundance, population decline, prey selection, *Rhinolophus hipposideros*

Introduction

Habitat alteration due to human activities is the major cause of decline or extinction of species today (Wilson 1988; Wilcove

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et al. 1998). Habitat alteration encompasses two distinct processes that pose a threat to species: habitat eradication (total habitat destruction) and cryptic habitat deterioration. The impact of habitat eradication on population dynamics is radical, as it leads to a massive fragmentation of species distribution (Andren 1994). Cryptic habitat deterioration is a more subtle mechanism, which acts through a decrease in the ecological quality of a habitat, although its area and structure

may remain unchanged. Although the physical structure of the habitat is retained, a substantial reduction in local carrying capacity is observed, which may prove dramatic for population dynamics (Vickery *et al.* 2001). This occurs if essential ecological resources such as prey species are eliminated (for example through pesticide use). Under most circumstances, habitat eradication and cryptic habitat deterioration are likely to occur concurrently, although this is not always the case. Careful inspection of both mechanisms is therefore required to identify properly the factors threatening an endangered species and/or population (Caughley 1994).

Most bat species in Central Europe have undergone severe population declines during the second half of the 20th century. Because negative population trends occurred simultaneously with massive habitat transformations, such as large-scale intensification of agriculture and forestry, and rapid urbanization, population declines have often been causally attributed to these changes (Stebbings 1988). The lesser horseshoe bat *Rhinolophus hipposideros* (Bechstein 1800) was once widespread and among the most abundant bat species of Europe. After a tremendous population crash, beginning in the 1940s (Bezem, Sluiter & Heerdt 1960), it became extinct over large areas of Central and Western Europe in the 1950s–1980s (Stutz & Haffner 1984; Ohlendorf 1997; Bontadina *et al.* 2000). The reasons for the massive and widespread decline of the lesser horseshoe bat, which is presently among the most critically endangered bat species of Central Europe (Hutson, Mickleburgh & Racey 2001), remain largely conjectural. This impedes the implementation of tailored conservation actions. In Switzerland, for instance, the lesser horseshoe bat was widespread both on the Swiss Plateau (lowlands) and in the Alps, but populations have declined by over 95% (Bontadina *et al.* 2000). In the 1990s, only 30 breeding colonies remained in four distinct regions of the Swiss Alps, whereas outside the Alps three relict populations became extinct.

Among potential factors thought to have contributed to this large-scale demographic crash, roost availability, general habitat alteration and past use of pesticides were thought to be most important (Biedermann 1997; Ohlendorf 1997; Bontadina *et al.* 2000). Recent radio-tracking studies have revealed that this bat forages principally in forested habitats, and to a lesser extent along hedges and tree lines (Bontadina, Schofield & Naef-Daenzer 1999, 2002; Holzhaider *et al.* 2002; Motte & Libois 2002; Schofield *et al.* 2002; Biedermann *et al.* 2004). It is therefore questionable whether the large-scale decline observed across most of Western and continental Central Europe can be attributed to habitat eradication alone: vast areas covered with forest exist, which no longer harbour lesser horseshoe bats. In many European countries the woodland area has even increased during the period when the decline took place. In Switzerland, forest area progression reached 26% during 1940–90 (Brassel & Brändli 1999; Bontadina, Hotz & Märki 2006). This suggests that habitat eradication *per se* is unlikely to explain the decline. But might cryptic habitat deterioration have played a role in this process, and could it preclude the chances of recolonization of formerly abandoned areas? Changes in forest management could

negatively influence insect prey availability: transformations from deciduous into coniferous woodland may reduce both insect abundance and species richness (Duelli 1994; LAG 1994; Benton *et al.* 2002). We therefore tested whether there was a relationship between recent demographic trajectories of Swiss lesser horseshoe bat populations and current prey abundance in woodland surrounding colonial roosts whose populations show contrasting demographic status (extinct, declining, recovering populations). Although current prey abundance cannot inform about past conditions, it can tell us whether a reduction in prey abundance represents a problem in the present context of population recovery and range recolonization.

The diet of lesser horseshoe bats has been investigated from remains in faecal pellets in Ireland (McAney & Fairley 1988), Switzerland (Beck, Stutz & Ziswiler 1989; Arlettaz, Godat & Meyer 2000) and Germany (Biedermann *et al.* 2004). Results from all studies showed that their diet consisted predominantly of Diptera, Lepidoptera and Neuroptera. According to Jones & Rayner (1989), the main foraging techniques are aerial-hawking and gleaning of prey from substrate, although the latter hunting technique could not be confirmed from visual observations (W. Schorcht and co-workers, personal communication). It still remains unknown whether lesser horseshoe bats are specialist or generalist predators. This is an important issue, as generalist predators are usually less vulnerable than specialists (Julliard *et al.* 2006). We therefore first compared the diet of lesser horseshoe bats with the abundance of nocturnally flying insects in the forests, in the vicinity of colonial roosts. Then we tested whether forested habitats surrounding nursery colonies with differing demographic status (extinct, declining or recovering populations) harboured a relatively different abundance of suitable prey. Specifically, this enabled us to test whether factors potentially leading to food reduction could still be operating at present. Our prediction was that – if the prey reduction hypothesis holds – abundance of typical prey should be higher in areas with increasing bat populations than in areas with declining populations, whereas areas with extinct populations should show the lowest prey abundance. Finally, we predicted that insect prey abundance is higher in Alpine regions, where remnant colonies have survived – with several colonies even increasing in recent years – than on the Swiss Plateau, where lesser horseshoe bats are extinct today.

Materials and methods

STUDY SITES

The study was carried out from May to September 2002 on the Swiss Plateau (lowlands) and in the Swiss Alps. Nursery colonies of *R. hipposideros*, for which survey data were available between 1990 and 2006 (Bontadina *et al.* 2000; M. Lutz, unpublished data), were our candidate study sites (Table 1). Colonies were placed in three categories according to their demographic status: extinct, declining and recovering populations. Four colonial roosts per demographic status (Fig. 1) were selected randomly from the known roosts in the Alps, providing 12 study sites for the comparison of prey abundance. For

Table 1. Main characteristics of the 15 study sites: location, geographical region, population demographic status, colony size in year 2002 (λ = estimated annual growth rate 1990–2006, or approximate extinction year, respectively), altitude, coordinates, mean hourly temperature in May–September (the course of study), and approximate annual rainfall

Site	Region	Status	Colony size (λ or year of extinction)	Altitude (m)	Coordinates	Temperature (hourly mean, °C)	Annual rainfall (mm
Blumenstein*†	Alps	Increasing	92 (1·11)	785	46°43′N, 7°30′E	11·4	1000–1200
Kleinteil*†	Alps	Increasing	261 (1·04)‡	550	46°50′N, 8°13′E	13·3	1000–1200
Surcasti*†	Alps	Increasing	170 (1·01)	990	46°41′N, 9°10′E	9·8	600–800
Waltensburg*†	Alps	Increasing	136 (1·06)	745	46°46′N, 9°07′E	10·1	800–1000
Broc*	Alps	Decreasing	4 (0·50)	720	46°36′N, 7°05′E	15·5	1000–1200
Meiringen*	Alps	Decreasing	12 (0·90)	605	46°43′N, 8°11′E	14·3	1200–1400
Tomils*	Alps	Decreasing	6 (0·80)	810	46°45′N, 9°26′E	13·1	600–800
Flums*	Alps	Decreasing	8 (0·85)	623	47°05′N, 9°20′E	12·4	1000–1200
Wilderswil*	Alps	Extinct	0 (1988)	585	46°40′N, 7°52′E	15·1	1000–1200
Ried*	Alps	Extinct	0 (1984)	655	47°02′N, 8°39′E	13·3	1400–1600
Surava*	Alps	Extinct	0 (1984)	905	46°40′N, 9°36′E	9·7	600–800
Untervaz*	Alps	Extinct	0 (1999)	585	46°55′N, 9°32′E	12·4	800–1000
Laupen†	Plateau	Extinct	0 (1980)	525	46°54′N, 7°14′E	13·7	800–1000
Liebegg†	Plateau	Extinct	0 (1978)	510	47°20′N, 8°07′E	13·3	800–1000
Montagny†	Plateau	Extinct	0 (1988)	560	46°59′N, 6°59′E	13·6	800–1000

*Sites (*n* = 12) used for comparisons between colonies with different demographic status.
†Sites (*n* = 7) used for comparisons between the Alps and Plateau (lowlands).
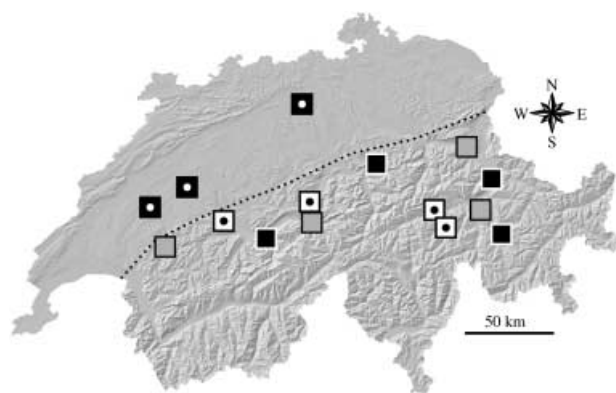‡Colony discovered in 2001, λ estimated for 2001–06.

Fig. 1. Location of study sites in Switzerland: extinct populations (black squares), declining populations (grey squares) and recovering populations (white squares). Dotted line, limit between the Plateau (lowlands in the north) and the Alps (south). Sites with a black or white frame were used for comparison of prey abundance in relation to population demographic status; sites with a dot in the centre were used for comparison of prey abundance between the Plateau and the Alps.

the comparison of prey abundance between recovering populations (Alps) and extinct populations (Plateau, i.e. Swiss lowlands), we used the four previous increasing Alpine populations and randomly selected three new sites from the Plateau (due to logistical constraints four sites were not feasible). Study sites were visited monthly (five times during the season), yielding 60 samples for the first analysis and 35 for the second.

SAMPLING DESIGN AND FIELD PROCEDURES

As sampling was possible only at one site at a time, and there were limitations in equipment, study sites were visited in succession, which

also meant avoiding excessive transportation costs. A systematic chronological sampling sequence was applied (Bidlingmayer 1964; Kunz 1988). To avoid the possible influence of moonlight, visits to the study sites were alternated randomly within a stratified design to account for the two major geographical regions (Alps and Plateau). Night-flying insects were sampled using two malaise and two light traps per site per night. The malaise traps were self-constructed, 2 m long and 1 m high, and placed 1 m above the ground. The light traps were built according to Sierro & Arlettaz (1997) and equipped with OSRAM bulbs (HQL MBF-U, 125 W). Petrol generators were used as power supply. Bontadina *et al.* (1999, 2002) found that lesser horseshoe bats forage mainly in woodland, with 50% of hunting time within 600 m radius from the nursery roost. Accordingly, traps were placed (>50 m apart) in forests, within 600 m from occupied roosts. A trap pair, consisting of one malaise and one light trap, was placed in coniferous woodland (≥75% coniferous trees), while the other pair was set in broadleaf woodland (≥75% broadleaf trees). Trap locations were on vantage points to optimize trapping efficacy. In five cases, one of the two habitat types was not available within the 600-m radius; the traps were then placed within 2 km from the roost, which is well within the maximum foraging radius recorded previously (4·2 km, Bontadina *et al.* 2002). Trapping started at dusk and ended at dawn. Nights with full moon, heavy rain, wind and/or ambient temperatures <8 °C (recorded hourly from 22:00 to 05:00 with iButton loggers; Maxim Integrated Products, Sunnyvale, CA, USA) were avoided because these factors influence the flying activity of insects (Taylor 1963).

Trapped insects were preserved in 70% ethanol in double-sealed plastic bags. In the laboratory, the invertebrates were identified to order or family level using reference guides (e.g. McAney *et al.* 1991). Samples of mainly diurnal insects were discarded (Rhophalocera, Homoptera, Sternorrhyncha, Formicidae, Apoidea, Vespoidea). The remaining insects were dried in an oven for 72 h at 60 °C (Southwood 1978), the biomass weighed to the nearest 1 mg, and the number of individuals in each category counted. Arlettaz *et al.*

(2000) showed that, among Diptera, only individuals with a wing length of 4–16 mm are eaten by lesser horseshoe bats, which corresponds to a dry body mass of ≈1–17 mg. In our comparative analysis, only insects within this range were considered as potential prey.

PREY SELECTION

Bat droppings deposited during a single night were collected monthly from May to September underneath two thriving nursery roosts in landscapes with contrasted farming regimes (Surcarsti, Grisons, Alps, rather extensive montane farmland; Blumenstein, Bern, relatively intensive farmland at the northern border of the Alps). Faeces (stored in envelopes) were collected on the same night as insect trapping took place, so as to directly compare diet composition with food abundance. Ten pellets per sample were selected at random for analysis of prey remains. Each pellet was soaked in water, dissected under a binocular microscope with needles and forceps, and searched for taxonomically identifiable fragments. All fragments were spread evenly over a Petri dish so as to visually estimate the biomass by volume (5% accuracy) represented by a given prey category.

For the analysis of prey-size selection, 20 additional faecal pellets per sample were selected from among the remaining droppings. They were checked for wing fragments of Diptera, which enabled reconstituting wing length under a microscope (Leica MZ95) according to Arlettaz *et al.* (2000). Three wing-length categories were distinguished (4–8, >8–12, >12 mm; Arlettaz *et al.* 2000). Diptera trapped at the same sites were also categorized with respect to wing length, enabling comparison between prey size in diet and food supply.

STATISTICS

The relationship between bat population status and both geographical region and prey supply was tested by fitting linear mixed-effects models. Habitat type was nested within site, while month (representing season) was nested within habitat (site) as we were not primarily interested in the trivial seasonal variation. Regarding diet selection, we tested for a significant deviation from a line of non-selection using binomial sign tests (Zar 1999). Most data analyses were performed using the program JMP5 (SAS Institute, Cary, NC, USA). The nested linear mixed-effects models were computed using R (R Development Core Team 2006). Randomized contingency table procedures were performed with ACTUS 2 (Eastbrook & Eastbrook 1989).

Results

ABUNDANCE OF NOCTURNAL INSECTS

Overall, 135 170 insects were collected from May to September, with on average 1804 (± 2023 SD) insects captured per site per night (range: 255–11 153 items). The majority of insects were collected by light traps, with only 0·8% (range 0·2–2·9%) obtained with malaise traps; for further analyses the results of both trap types were pooled.

From the total number of items, 27 080 insects (23·7% of frequency, 32·6% of total dry biomass) were considered as potential prey of *R. hipposideros* as they were within the body mass range of 1–17 mg (Arlettaz *et al.* 2000). Among the remaining prey items caught, 96 000 insects had a dry item body mass lighter than 1 mg, whereas 7090 insects had a dry item body mass heavier than 17 mg. Diptera (84% of total number of items) were by far the most common insects in the smallest class. For insects heavier than 17 mg, Lepidoptera (90·5%) predominated. Within the suitable size class (1–17 mg body mass), Lepidoptera (56·3%) were the most numerous, followed by Diptera (16%) and 'others' (27%). Neuroptera (0·7%) were rare throughout and consisted predominantly of Chrysopidae. Among prey of suitable size, insect number correlated positively with biomass in the dominant groups (Diptera and Lepidoptera, $r_s > 0·8$, $n = 150$, $P < 0·001$). Only dry biomass was used in subsequent analyses.

The average dry biomass of different insect categories and body mass classes with respect to study site and habitat type (coniferous and broadleaf forest) is presented in Table 2. The highest biomass was caught in July, and the lowest in May. Lepidoptera were by far the most abundant group in June (54% of total biomass), July (73·5%) and August (73%). There was no clear seasonal trend in the biomass of Diptera, although the largest catches were achieved in September. The heaviest biomass collected during a single night was in July, in broadleaf forest close to an extinct lesser horseshoe bat population, when a massive flight of Lepidoptera occurred (Wilderswil, 7·5 g). This value represents an exceptional outlier compared with the average dry biomass collected per site in July (2 g). In contrast, the lowest dry biomass ever was obtained in a coniferous forest in May at a study site harbouring a large breeding colony (Blumenstein, 0·050 g), a value much smaller than the average biomass collected in the same month (0·320 g).

DIET COMPOSITION AND PREY SELECTION

Seven prey categories (orders) were determined from the faeces collected underneath the two nursery roosts. Diptera (50% by volume) and Lepidoptera (32%) dominated the diet. They were also the most abundant taxa in the traps (37 and 48%, respectively). Lepidoptera were the most common category in traps in June (60%), July (59%) and August (59%); they also predominated in faeces in July (59%). Diptera were most abundant in traps in September (55%); in faeces they peaked in May (63%) and September (66%). Although Neuroptera were rarely found in the traps (0·01%), they represented as much as 12% of the diet. Trichoptera represented, on average, 7% of the insects caught in the traps, but only 0·1% of the fragments in faeces. There was no clear evidence for seasonal changes in dietary diversity, but in September, when food supply, especially moths, was less abundant, seven prey groups were present in the faeces compared with five from May to July and four in August.

Given that only Diptera, Lepidoptera and Hymenoptera were regularly present in both traps and faeces, analysis of prey selection was performed with these taxa (Fig. 2). The occurrence of Lepidoptera and Diptera in the diet was directly comparable with their abundance in the nearby forest ($r_s = 0·644$, $n = 10$, $P < 0·05$; $r_s = 0·697$, $n = 10$, $P < 0·05$, respectively), but there was no clearly significant relationship for Hymenoptera ($r_s = –0·596$, $n = 10$, $P = 0·069$).

Table 2. Mean (SD) dry biomass (mg) per session* of major insect groups trapped at 15 study sites, with respect to three body mass classes

		Body mass class															
		<1 mg		1–17 mg								>17 mg					
		Diptera		Lepidoptera		Neuroptera		Diptera		Others†		Lepidoptera		Diptera		Others†	
Site	Habitat	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Blumenstein	Conifer	57	34	500	518	0	0	108	91	130	103	3095	1746	4	8	181	198
	Broadleaf	31	43	367	439	0	0	67	39	350	700	2408	2715	0	0	4	9
Kleinteil	Conifer	37	29	414	455	1	2	45	27	358	270	1123	691	5	12	112	181
	Broadleaf	115	59	639	583	1	2	59	34	267	259	1728	983	30	54	110	161
Surcasti	Conifer	29	24	500	285	0	0	158	198	739	1263	2290	480	0	0	431	863
	Broadleaf	87	45	360	189	0	1	239	327	17	24	1651	846	11	15	5	11
Waltensburg	Conifer	39	49	355	327	0	0	55	38	59	35	1133	775	0	0	133	284
	Broadleaf	84	54	845	921	3	5	49	55	161	114	2070	1375	12	27	155	292
Broc	Conifer	192	342	988	1400	15	32	89	50	336	305	2457	3174	25	44	76	110
	Broadleaf	66	65	546	454	0	1	99	45	480	383	1600	1167	45	69	91	86
Flums	Conifer	43	33	683	602	2	3	31	29	242	112	1278	839	28	26	65	108
	Broadleaf	29	17	568	643	0	1	153	251	116	77	2910	4243	9	13	48	25
Meiringen	Conifer	89	70	442	377	3	5	54	36	209	134	1412	445	0	0	58	82
	Broadleaf	47	55	393	528	4	5	45	33	258	289	1921	1171	38	71	101	143
Tomils	Conifer	321	455	483	247	39	51	194	248	907	1328	1690	728	696	1374	21	43
	Broadleaf	160	183	741	365	27	44	341	631	368	488	2238	209	207	375	243	429
Ried	Conifer	109	57	747	743	0	0	108	97	340	363	2153	1316	37	41	158	161
	Broadleaf	100	57	1091	978	4	4	111	88	284	213	3477	2471	34	62	81	88
Surava	Conifer	74	116	589	777	0	0	66	83	432	604	851	357	0	0	53	88
	Broadleaf	78	97	886	1372	59	108	71	102	81	87	832	494	8	19	5	11
Untervaz	Conifer	68	53	615	646	0	0	162	182	111	72	1031	473	4	9	50	90
	Broadleaf	36	52	854	674	19	18	144	164	135	134	3124	2112	20	36	0	0
Wilderswil	Conifer	66	46	926	1094	0	0	78	94	290	284	3378	2606	87	176	93	123
	Broadleaf	66	39	1871	2883	13	19	43	34	417	492	4616	5161	17	12	222	156
Laupen	Conifer	185	141	329	143	1	2	90	51	210	109	2213	516	39	62	79	91
	Broadleaf	188	145	939	1054	5	6	68	63	354	424	1887	1363	19	25	171	278
Liebegg	Conifer	121	106	798	641	19	31	182	210	585	714	2011	1592	127	127	409	887
	Broadleaf	121	117	865	942	5	11	66	52	525	699	1684	686	15	24	970	1994
Montagny	Conifer	118	139	1160	1045	2	2	110	86	274	247	2917	1773	10	23	162	161
	Broadleaf	312	377	636	656	0	0	156	220	547	753	1937	918	31	48	94	113
Total		3065		21 129		222		3240		9581		63 113		1557		4380	

*Sampling sessions ($n = 5$) for each site and habitat type (forest) took place in May, June, July, August and September.
†Others: other categories found in traps.

PREY SIZE SELECTION

Based on wing-shape reconstruction from 32 fragments found in faeces, all Diptera samples had wing lengths between 4 and 16 mm, confirming the results of Arlettaz *et al.* (2000). There was no difference in the frequency distribution of the three wing-length classes in traps and in faeces at Blumenstein ($n = 329$ and 21, respectively; $\chi^2 = 4 \cdot 0$, df $= 2$, $P = 0 \cdot 130$, randomized contingency table), but a significant difference occurred at Surcasti, with wing lengths from 8 to 12 mm occurring significantly more frequently than expected from supply ($n = 1090$ and 11, respectively; $\chi^2 = 9 \cdot 9$, df $= 2$, $P < 0 \cdot 01$).

COMPARISON OF PREY ABUNDANCE BETWEEN COLONIES WITH DIFFERENT DEMOGRAPHIC STATUS

Given that our analysis of prey selection showed that Lepidoptera and Diptera made up the bulk of the diet (83%), the present comparison focuses on these two taxa. A total of 18 157 items within the dry body mass range of 1–17 mg were considered. Linear mixed-effects models showed that neither population status (extinct, declining, recovering) nor habitat type (coniferous vs. broadleaf woodland) affected the abundance of insects (all $P \geq 0 \cdot 16$; Table 3; Fig. 3a).

COMPARISON OF PREY ABUNDANCE IN THE ALPS VS. THE PLATEAU (LOWLANDS)

In total, 8923 items belonging to potential prey (1–17 mg) were found on the Swiss Plateau vs. 5495 in the Alps. Linear mixed-effects models showed that neither geographical region (Swiss Plateau vs. Alps) nor habitat type (coniferous vs. broadleaf woodland) influenced the abundance of insects (all $P \geq 0 \cdot 13$; Table 3; Fig. 3b).
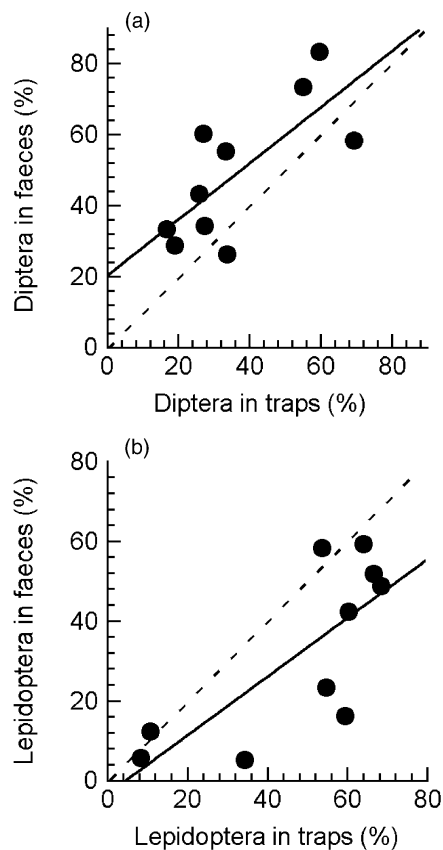
Fig. 2. Prey type selection: relationship between insect prey volume (%) in diet vs. biomass (%) in traps. Dotted line shows non-selection; solid line, linear fit to the data. (a) Diptera ($r_s = 0.644$, $n = 10$, $P < 0.05$); (b) Lepidoptera ($r_s = 0.697$, $n = 10$, $P < 0.05$).
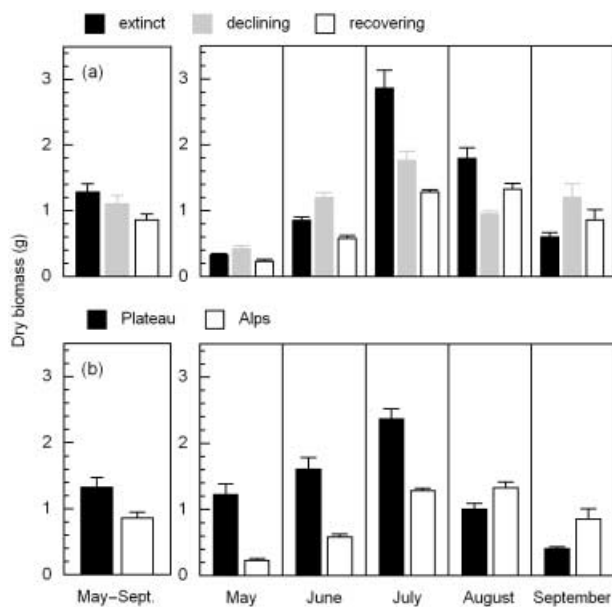

Fig. 3. Mean (+SE) dry biomass of insects (body mass 1–17 mg) trapped in woodland in the vicinity of lesser horseshoe bat colonies. (a) Comparison between sites with different demographic status (extinct, declining, recovering populations). (b) Comparison between the Plateau (Swiss lowlands) and the Alps. Both comparisons yielded non-significant results (Table 3).

Table 3. Results of linear mixed-effects models performed on biomass of Lepidoptera, Diptera and total biomass with respect to demographic population status (extinct, declining, recovering populations; $n = 12$ sites) and habitat type (broadleaf vs. coniferous forest); and region (Plateau vs. Alps, $n = 7$ sites) and habitat; the factors: site, habitat (site) and month [habitat (site)] were entered as random effects

Fixed effects	Numerator df	Denominator df	*F*	*P*
Status				
Lepidoptera				
Status	2	9	2·30	0·156
Habitat	1	11	0·97	0·346
Diptera				
Status	2	9	0·11	0·897
Habitat	1	11	0·29	0·600
Total biomass				
Status	2	9	1·19	0·347
Habitat	1	11	0·19	0·671
Region				
Lepidoptera				
Region	1	5	3·21	0·133
Habitat	1	6	0·20	0·671
Diptera				
Region	1	5	0·18	0·687
Habitat	1	6	0·11	0·752
Total biomass				
Region	1	5	3·19	0·134
Habitat	1	6	0·02	0·886

Discussion

PREY ABUNDANCE WITH RESPECT TO COLONY DEMOGRAPHIC STATUS

There was a strong seasonal effect concerning insect abundance, but prey supply did not show any statistically significant difference between populations with differing demographic status. The food reduction hypothesis (cryptic habitat deterioration; see Introduction) is therefore not supported. Although the evidence remains purely correlative, it is very unlikely that current conditions of prey abundance may represent an obstacle to population recovery (Warren & Witter 2002; Bontadina *et al.* 2006).

We were surprised to discover that insect abundance in coniferous woodland was comparable with abundance in broadleaf woodland. This apparently contradicts observations from Wales (Schofield 1996; Bontadina *et al.* 2002), where deciduous woodland is the main foraging habitat of lesser horseshoe bats, presumably supporting a higher diversity of insect species (no data on food supply are available for the Welsh studies). It must be noted, however, that the coniferous forests in the present study were mostly natural and seminatural stands, with site-adapted native species of trees and a rich understorey with dead wood, whereas the Welsh coniferous stands were predominantly artificial plantations. Our findings suggest that lesser horseshoe bats should forage evenly in deciduous and coniferous forests in Central Europe, at least where natural and seminatural forests predominate.

COMPARISON OF PREY ABUNDANCE IN THE ALPS VS. PLATEAU

We found no difference in insect abundance between woodlands on the Plateau (extinct populations in the Swiss lowlands; Stutz & Haffner 1984; Bontadina *et al.* 2000) compared with the Alps, where remaining lesser horseshoe bat populations now thrive. This again suggests that present-day insect abundance could not restrict the occurrence of lesser horseshoe bats on the Swiss Plateau.

PREY SELECTION

A positive correlation between the occurrence of Diptera and Lepidoptera in diet and prey supply confirms a non-selective, opportunistic foraging behaviour (Arlettaz *et al.* 2000). Also in accordance with Arlettaz *et al.* (2000), all Diptera samples detected in our dietary analysis had wing lengths between 4 and 17 mm. We found no evidence for prey size selection in lesser horseshoe bats (Arlettaz *et al.* 2000). Distribution of prey size classes differed slightly from those reported by Arlettaz *et al.* (2000), with a relatively larger amount of smaller items (<8 mm: 60% compared with 32%) eaten at one of our study sites, yet this difference may be biased by our comparatively smaller sample size.

Prey size selection in echo-locating bats may be more complex than in visually hunting predators. For instance, the peculiar characteristics of bat sonar may impose constraints on prey choice (Arlettaz, Jones & Racey 2001; Siemers & Güttinger 2006). Small prey items may be difficult to locate in front of the vegetation clutter (Barclay 1985), even though *R. hipposideros* emits constant high frequency calls (112 kHz; Jones & Rayner 1989), a short wavelength theoretically enabling fine-grained target discrimination of fluttering insects through the reflected acoustic glints produced by wing beats (Schnitzler 1968).

PREY ABUNDANCE

Estimates of insect abundance depend largely on the capture method. In this study, light traps collected a much greater number of insects than malaise traps. Jones (1990) pointed out that with light traps, certain categories of prey, such as Coleoptera, are not caught in proportion to availability. According to Muirhead-Thomson (1991), this bias does not apply to Lepidoptera and Diptera, two major prey categories of lesser horseshoe bats (McAney & Fairley 1988; Arlettaz *et al.* 2000; this study).

IMPLICATIONS FOR CONSERVATION

Although we cannot establish irrefutably which factors caused the dramatic crash that began 50 years ago in lesser horseshoe bat populations in Western and Central Europe, the present study suggests that cryptic habitat deterioration, through a reduction of food supply in otherwise largely preserved forest habitat matrices, is unlikely to have caused that decline. Modifications of forestry practices have had an impact on Central European woodland (e.g. Brassel & Brändli 1999), but not to an extent capable of provoking such a massive reduction of habitat carrying capacity and total demographic collapse.

If it is improbable that cryptic habitat deterioration impedes progressive range recolonization from currently recovering populations, which conservation recommendations can be drawn? Enhancing forest ecological quality would contribute only marginally to conservation of the lesser horseshoe bat. Forest type appears to be a secondary factor, at least as long as forests remain as natural stands and not purely artificial plantations. Preserving large areas of forest within 4 km from nursery roosts, the main activity radius around large colonies (Reiter 2004; Bontadina *et al.* 2006) would probably provide the most effective conservation benefits. In this respect, lesser horseshoe bats differ from other bats, which often rely on very complex species-specific habitat features (Jones, Duvergé & Ransome 1995; Sattler *et al.* 2007). Second, although there is presently no problem of discontinuity between forest patches in the Swiss Alps, as blocks of woodland are mostly naturally interconnected, lack of habitat connectivity may be an obstacle to area recolonization in the voided, intensive agricultural matrices in the lowlands. Recreating woodland habitat networks by reconnecting patches of forests through hedges and tree lines would therefore be essential.

As lesser horseshoe bats are generalist forest bats, which can potentially occupy a broad palette of woodland types (Bontadina *et al.* 2006), their dramatic, generalized population decline across Central and Western Europe after World War II still points to a single major factor of demographic collapse. It has been shown that habitat eradication (Schofield 1996; Bontadina *et al.* 2002; Reiter 2004), cryptic habitat deterioration through food reduction (this study) and loss of roosts (Bontadina *et al.* 2000) cannot explain this wide-scale phenomenon. In our opinion, a factor compatible with such a large-scale, massive incident is mortality through bioaccumulation from the past use of pesticides for agriculture, forestry or timber treatment in attics (Newton & Wyllie 1992). This hypothesis has not received sufficient attention from bat conservationists. The extent to which other forest bats may have suffered from similar symptoms remains to be investigated, with most species being presently red-listed in Central and Western Europe (Hutson *et al.* 2001).

References

Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.

Arlettaz, R., Godat, S. & Meyer, H. (2000) Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). *Biological Conservation*, **93**, 55–60.

Arlettaz, R., Jones, G. & Racey, P.A. (2001) Effect of acoustic clutter on prey detection by bats. *Nature*, **414**, 742–745.

Barclay, R.M.R. (1985) Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. *Canadian Journal of Zoology*, **63**, 2507–2515.

Beck, A., Stutz, H.P.B. & Ziswiler, V. (1989) Das Beutespektrum der Kleinen Hufeisennase *Rhinolophus hipposideros* (Bechstein, 1800) (Mammalia, Chiroptera). *Revue Suisse de Zoologie*, **96**, 643–650.

Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, **39**, 673–687.

Bezem, J.J., Sluiter, J.W. & van Heerdt, P.F. (1960) Population statistics of five species of the bat genus *Rhinolophus* hibernating in the caves of S. Limburg. *Archives Néerlandaises de Zoologie*, **13**, 511–539.

Bidlingmayer, W.L. (1964) The effect of moonlight on the flight activity of mosquitos. *Ecology*, **45**, 87–94.

Biedermann, M. (1997) Zur Situation der Kleinen Hufeisennase (*Rhinolophus hipposideros* Bechstein, 1800) in Thüringen. *Zur Situation der Hufeisennasen in Europa* (ed. B. Ohlendorf), pp. 19–23. IFA, Berlin.

Biedermann, M., Meyer, I., Schorcht, W. & Bontadina, F. (2004) *Sonderuntersuchung zur Wochenstube der Kleinen Hufeisennase in Friedrichswalde-Ottendorf/Sachsen*. Report by BMS GbR, Erfurt & SWILD, Zürich. DEGES, Berlin.

Bontadina, F., Schofield, H.W. & Naef-Daenzer, B. (1999) Habitat preferences in lesser horseshoe bats as revealed by radio-tracking. *Bat Research News*, **40**, 110–111.

Bontadina, F., Arlettaz, R., Fankhauser, T., Lutz, M., Mühlethaler, E., Theiler, A. & Zingg, P.E. (2000) The lesser horseshoe bat *Rhinolophus hipposideros* Switzerland: present status and research recommendations. *Le Rhinolophe*, **14**, 69–83.

Bontadina, F., Schofield, H.W. & Naef-Daenzer, B. (2002) Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *Journal of Zoology, London*, **258**, 281–290.

Bontadina, F., Hotz, T. & Märki, K. (2006) Die Kleine Hufeisennase im Aufwind. *Ursachen der Bedrohung, Lebensraumansprüche und Förderung einer Fledermausart*. Haupt, Berne.

Brassel, P. & Brändli, U.-B. (1999) *Schweizerisches Landesforstinventar. Ergebnisse der Zweitaufnahme 1993–1995*. Haupt, Berne.

Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215–244.

Duelli, P. (1994) *Rote Liste der Gefährdeten Tierarten der Schweiz*. BUWAL, Berne.

Eastbrook, C.B. & Eastbrook, G.F. (1989) ACTUS: a solution to the problem of small samples in the analysis of two way contingency tables. *Historical Methods*, **82**, 5–8.

Holzhaider, J., Kriner, E., Rudolph, B.U. & Zahn, A. (2002) Radio-tracking a Lesser horseshoe bat (*Rhinolophus hipposideros*) in Bavaria: an experiment to locate roosts and foraging sites. *Myotis*, **40**, 47–54.

Hutson, A.M., Mickleburgh, S.P. & Racey, P.A. (2001) *Microchiropteran Bats: Global Status Survey and Conservation Action Plan*. IUCN – The World Conservation Union, Cambridge, UK.

Jones, G. (1990) Prey selection by the Greater Horseshoe Bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *Journal of Animal Ecology*, **59**, 587–602.

Jones, G. & Rayner, J.M.V. (1989) Optimal flight speed in pipistrelle bats, *Pipistrellus pipistrellus. European Bat Research 1987* (eds V. Hanak, I. Horacek & J. Gaisler), pp. 247–253. Charles University Press, Prague.

Jones, G., Duvergé, P.L. & Ransome, R.D. (1995) Conservation biology of an endangered species field studies of greater horseshoe bats. *Symposia of the Zoological Society, London*, **67**, 309–324.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D. (2006) Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, **9**, 1237–1244.

Kunz, T.H. (1988) *Ecological and Behavioural Methods for the Study of Bats*. Smithsonian Institution Press, London.

LAG (Lepidopterologen-ArbeitsGruppe) (1994) *Schmetterlinge und ihre Lebensräume*. Schweizerischer Bund für Naturschutz – Pro Natura, Fotorotar AG, Egg, Zürich.

McAney, C.M. & Fairley, J.S. (1988) Habitat preference and overnight and seasonal variation in the foraging activity of lesser horseshoe bats. *Acta Theriologica*, **33**, 393–402.

McAney, C., Shiel, C., Sullivan, C. & Fairley, J. (1991) *The Analysis of Bat Droppings*. The Mammal Society, London.

Motte, G. & Libois, R. (2002) Conservation of the lesser horseshoe bat (*Rhinolophus hipposideros* Bechstein, 1800) (Mammalia: Chiroptera) in Belgium. A case study of feeding habitat requirement. *Belgian Journal of Zoology*, **132**, 49–65.

Muirhead-Thomson, R.C. (1991) *Trap Response of Flying Insects. The Influence of Trap Design on Capture Efficiency*. Academic Press, London.

Newton, I. & Wyllie, I. (1992) Recovery of a sparrowhawk population in relation to declining pesticide contamination. *Journal of Applied Ecology*, **29**, 476–.

Ohlendorf, B. (1997) *Zur Situation der Hufeisennasen in Europa*. IFA, Berlin.

R Development Core Team (2006) *ʀ A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Reiter, G. (2004) The importance of woodland for *Rhinolophus hipposideros* (Chiroptera, Rhinolophidae) in Austria. *Mammalia*, **68**, 403–410.

Sattler, T., Bontadina, F., Hirzel, A. & Arlettaz, R. (2007) Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. *Journal of Applied Ecology*, **44**, 1188–1199.

Schnitzler, H.-U. (1968) Die Ultraschall-Ortungslaute der Hufeisen-Fledermäuse (*Chiroptera: Rhinolophidae*) in verschiedenen Orientierungssituationen. *Zeitschrift für Vergleichende Physiologie*, **57**, 376–408.

Schofield, H.W. (1996) *The ecology and conservation biology of Rhinolophus hipposideros, the lesser horseshoe bat.* PhD thesis, University of Aberdeen, Aberdeen, UK.

Schofield, H., Messenger, J., Birks, J. & Jermyn, D. (2002) *Foraging and Roosting Behaviour of Lesser Horseshoe Bats at the Ciliau, Radnor (Wales, UK)*. Vincent Wildlife Trust, Ledbury, UK.

Siemers, B.M. & Güttinger, R. (2006) Prey conspicuousness can explain apparent prey selectivity. *Current Biology*, **16**, R157–R159.

Sierro, A. & Arlettaz, R. (1997) Barbastelle bats (*Barbastella* spp.) specialize in the predation of moths: implications for foraging tactics and conservation. *Acta Oecologica*, **18**, 91–106.

Southwood, T.R.E. (1978) *Ecological Methods*. Chapman & Hall, London.

Stebbings, R.E. (1988) *Conservation of European Bats*. Christopher Helm, London.

Stutz, H.P. & Haffner, M. (1984) Arealverlust und Bestandesrückgang der Kleinen Hufeisennase *Rhinolophus hipposideros* (Bechstein, 1800) (Mammalia: Chiroptera) in der Schweiz. *Jahresbericht der Naturforschenden Gesellschaft Graubünden*, **101**, 169–178.

Taylor, L.R. (1963) Analysis of the effects of temperature on insects in flight. *Journal of Animal Ecology*, **32**, 99–117.

Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. & Brown, V.K. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, **38**, 647–664.

Warren, R.D. & Witter, M.S. (2002) Monitoring trends in bat populations through roost surveys: methods and data from *Rhinolophus hipposideros*. *Biological Conservation*, **105**, 255–261.

Wilcove, D., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *Bioscience*, **48**, 607–615.

Wilson, E.O. (1988) *Biodiversity*. National Academy Press, Washington, DC, USA.

Zar, J.H. (1999) *Biostatistical Analysis*. Pearson Education, Upper Saddle River, NJ, USA.