

**Does food scarcity limit the current distribution
of the once widespread
lesser horseshoe bat (*Rhinolophus hipposideros*)?**

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Abstract

The lesser horseshoe bat (*Rhinolophus hipposideros*) is one of the most endangered European bat species. Once it was widespread and common in most countries of Western and Central Europe. A dramatic decline occurred since 1950s, which led to the loss of large areas of its former distribution. This study is part of a nationwide conservation research program (*Rhippos*, see www.Rhinolophus.net) started 2001 with the aim to identify the causes of the regression of *R. hipposideros* in order to propose efficient conservation measures.

We tested if differences in present food availability might explain different conservational status of colonies. Recent radio-tracking studies have shown that woodlands represent key foraging habitats for lesser horseshoe bats. Therefore we compared insect availability and abundance in woodlands near to three types of nursery colonies: roost of increasing, decreasing or extinct populations.

We examined prey selection in term of size and taxa by comparing the diet of *R. hipposideros* with available insect food in the forest. Results suggest that the lesser horseshoe bat appears to be an opportunistic forager, which principally captures prey in relation to its abundance in the environment. Although there were strong seasonal variations in insect abundance, insect availability in the surroundings of extinct, declining and increasing colonies did not differ. In addition, insect availability in woodland was higher on the Swiss plain, where lesser horseshoe bats are extinct today than in the Alps where remnant colonies have survived.

We conclude that food availability *per se* does not limit the present distribution of lesser horseshoe bats, since insect availability was comparable or even higher in areas presently abandoned by the species. A progressive recolonization of abandoned areas could therefore certainly not be impeded by insect availability alone. The results support the view that pesticides are most likely the main reason for the decline of lesser horseshoe bats over the past decades in Europe.

1. Introduction

1.1 Distribution of the lesser horseshoe bat

The lesser horseshoe bat (*Rhinolophus hipposideros*) (Bechstein, 1800) is distributed from Portugal in the west, to the foothills of the Himalayas in Kashmir to the east and as far south as Ethiopia and Sudan. However, its distribution is best documented in Europe, where the lesser horseshoe bat is generally confined to central, western and southern Europe, with records northwards up to Wales, UK and to the south of the Netherlands (Mitchell-Jones, 1999).

In the past the lesser horseshoe bat was known to be widespread and common both on the plain and in the Alps of Switzerland (Furrer, 1957; Aellen, 1961). Since 1950s its overall population has undergone a severe decline (Stutz and Haffner, 1984) as in most countries of Central Europe such as Poland (Kokurewicz, 1990), Germany (Biedermann, 1997; Ohlendorf, 1997), Netherlands (Dann and Glas, 1980), Belgium (Roer, 1983; Fairon, 1997) France (Dubie and Schwaab, 1997) and United Kingdom (Mitchell-Jones, 1995). In Switzerland the few remnant colonies are nowadays all located in the Alps, whereas only one relict colony has survived on the Plateau (Estavayer-le-lac: 3 Individuals, Bontadina et al., 2001).

1.2 Conservational aspects

Many hypotheses have been suggested to explain the dramatic population decline of lesser horseshoe bats: roost destruction, pesticide contamination of both prey and roosts, habitat alteration, climate changes, genetic inbreeding, diseases, predation and competition with other bat species (Schofield, 1996; Arlettaz et al., 2000b; Bontadina et al., 2001). Although, a comprehensive evaluation of the possible causes of population decline has revealed that habitat destruction, food shortage and the effects of pesticides are likely to be the most plausible causes of population decline (Bontadina et al., 2001), there is no conclusive answer to this question yet. As a consequence no focused conservation scheme could be developed up to now; and not surprisingly roost protection has always been given the priority. There is definitely a need for a broader understanding of the problems faced by the species so as to propose effective conservation measures.

1.3 Background knowledge

1.3.1 Habitat selection

In a study in Wales, UK, Bontadina et al. (2002) found that the lesser horseshoe bat forage mainly in a wide range of woodland types and configurations. This result indicates that the whole phenomenon of the decline of lesser horseshoe bats across most of Western Europe could not be explained by habitat loss alone, as many areas do still harbour large forests but no lesser horseshoe bats any more.

Human exploitation of woodland and, especially, farmland, has strongly increased since World War II; simultaneously the use of highly toxic broad-spectrum pesticides as DDT began. The latter were used in great quantities in agriculture, until they were banned in 1972-73. These factors together with habitat transformations (farmland into human settlements), changes in agriculture practices (meadows into crops, pastures into arable land) and sylviculture (deciduous into coniferous woodland) are thought to have reduced both insect species diversity and insect prey abundance in Central Europe (Duelli, 1994; Schweizerischer Bund für Naturschutz (SBN), 1997 and 2000). Although woodlands were affected to a lesser extent by these factors, many characteristic insect species of forests are nowadays endangered in Switzerland (SBN, 2000). Different reasons such as habitat degradation, use of pesticides or changes in the cultivation methods in the surrounding farmland are thought to be responsible for the possible loss of insect availability and diversity.

1.3.2 Foraging behaviour

Only little is known about the feeding techniques used by lesser horseshoe bats, but Jones and Rayner (1989) reported that they use aerial hawking and gleaning from vegetation and the ground to catch their prey. Schofield (1996) recorded prey capture only by aerial hawking, with insects usually caught on the wing and dismembered in flight. He made no observation of prey carried back to perches to be dismembered. Beck and Bontadina (pers. comm.) observed only few bitten-off food remains at night roosts. For this reason it is thought that lesser horseshoe bats eat prey items mainly in flight, dismembering larger items generally on the wing and occasionally within the roost.

Bats are voracious feeders and can consume a sizeable portion of their body mass per night (Gould, 1955; Kunz, 1974; Anthony and Kunz, 1977). Based on studies of insect remains in the faecal pellets of *R. hipposideros*, McAney and Fairley (1989b) in Eire, Beck et al. (1989) and Arlettaz et al. (2000b) in Switzerland reported that this species fed predominantly on Diptera, Lepidoptera and Neuroptera.

Studies of the overnight activity patterns of *R. hipposideros* showed that the time of emergence from and return to roosts is closely determined by ambient light levels (Gaisler, 1963; McAney and Fairley, 1988a). The overnight activity of many bat species is bimodal (Erkert, 1982). McAney and Fairley (1988a) observed that individuals return to the roost during the hours of darkness, but could not find any discernible overnight patterns in activity or any changes related to the reproductive phenology of *R. hipposideros*. Moreover they observed an intensification of foraging activity towards the end of the season (McAney and Fairley, 1988b).

It's unknown whether lesser horseshoe bats conform to predators' optimal foraging models (Begon et al., 1986; Krebs and Davies, 1993) by feeding selectively on more valuable prey if abundant, although (McAney and Fairley, 1988b) suggested that during times of the year when insect prey density is at its highest this species feeds selectively, whilst at other times it may feeds opportunistically. In addition it is not known if individuals of large insect species (e.g. from Lepidoptera or Coleoptera order) are captured, but Arlettaz et al. (2000b) reported that Diptera recovered from faecal pellets had wing length between 4 and 16 mm. It is not known if lesser horseshoe bats forage in specific vertical strata of the trees, e.g. predominantly at low height or within tree canopy, but, since the density of insects decreases with height, they are expected to forage mainly at low height (see section 1.3.3).

1.3.3 Insect availability

Insects are a very rich supply of energy and bats are well adapted to exploit them. It is supposed that both the number of individuals and the number of insect species have strongly decreased in the past century, but detailed information is available only for a few groups. Duelli (1994) reported in the Red list of the endangered species in Switzerland, that 57% of the butterflies (*Papilionioidea* and *Hesperioidea*) and 30% of the *Tipulidae*

are endangered. SBN (1997) pointed out that in regions with intensive agriculture nearly 80% of butterflies species are endangered.

Factors influencing both the momentary and long-term density of flying-insects are light intensity, ambient temperature, wind speed, flight altitude, climate, weather, pollution, natural enemies, food availability, habitat degradation and destruction. These factors are discussed below, with particular reference to the forested habitats:

Abiotic factors

Light intensity (time of day): the greatest number of night-active insects flies during the two hours after sunset. In the course of the night there is a decline in abundance followed by another activity peak just before dawn (Williams, 1939). Bidlingmayer (1964) reported that the flying activity of mosquito increases significantly at full moon, whilst, for other species opposite effects are also shown (e.g. Bidlingmayer, 1964; Kunz, 1988)

Ambient temperature: insects are ectothermic organisms, which means that their body temperature is determined primarily by ambient temperature. The rate of metabolic activity generally increases with temperature. However, some species can regulate their body temperature to a certain degree through physiological or behavioural responses to extreme temperature (Schowalter, 1996). Taylor (1963) pointed out that for flying insect species, temperature acts as a threshold, above which flight is uninhibited and below which it is inhibited. Once temperature has exceed or dropped above or below a given threshold, aerial insect density of a particular species remains constant among individuals with similar phenological conditions. Gaydecky (1984) showed that over 90% of the variance associated with nocturnal light trapping of moths is due to mean night temperature, and is inversely related to the mean night wind speed. Jones (1995) reported that insect abundance increases rapidly above 6-10°C.

Wind speed: the strength of the wind blowing over a forest will vary most notably with altitude and exposure. Within the forest itself, wind movement may be quite complex with vertical as well as horizontal components and wind direction which can even deviate temporarily from that in surrounding open areas (Oliver, 1975). The speed of the wind is generally lower in the forest itself. The wind speed is low close to the ground and also in the canopy, where the wind is slowed by branches and leaves. In the relatively unrestricted trunk zone, however, wind speed is normally higher, and it increases rapidly

with height above the canopy. Speight and Wainhouse (1989) pointed out that flying insects are relatively independent of the wind within the forest but may be displaced for long distances downwind when they fly above the forest canopy.

Flight altitudes: Service (1973) reported that the number of *Tipulidae* species caught in open land rapidly declines with increasing height. Taylor (1960) reported for suction-trap catches in open land that the density of all insects found at 1.5 m was three times higher than that collected at 9 m above ground level. However, in the woodland, especially inside the canopy, insects are in part sheltered from the wind and therefore vertical distribution is consequently less pronounced than in open land.

Climate: the amount and seasonal distribution of precipitation will largely determine its impact on insect populations. Summer rain will have a greater direct effect on insects than winter rain or snow (Speight and Wainhouse, 1986). At the margins of an insect species range (e.g. altitude), climate is likely to be a limiting factor as regards population growth by that means limiting insect density.

Weather: the impact of weather on insects will depend among other things on the extent to which insects are exposed to the effect of wind and rain or are hidden within foliage. But indirect effects on, for example, the amount of food or the time during which it is available, can be equally important. The appearance of large numbers of moths at ground level during rainstorms and thunderstorms associated with cold fronts is historically well documented (Greenbank et al., 1980).

Pollution: atmospheric pollutants can influence forest insects directly (e.g. as toxins), indirectly (e.g. induced changes in the host plant) or by influencing the activities of natural enemies. Like flying insects themselves, pollutants are not uniformly distributed in the air. Concentrations will be highest close to the sources, however, for diffuse sources, concentrations can be affected by temperature inversions and the movement of discrete air masses, whereby pollutants can be deposited hundreds of miles from the sources. There may also be diurnal and seasonal variations in the concentration of pollutants. An early and particularly well-studied example of the effect of pollution on insect populations was that of industrial melanism in the peppered moth, *Biston betularia* (Kettlewell, 1973)

Biotic factors

Natural enemies: many different species of natural enemies are found in the insect community; nevertheless, their number varies considerably among populations. Thus some insect species may be more exposed to strong demographic oscillation because of predators or parasitoids.

Food availability: the nutritional requirements of insects are qualitatively similar to those of other animals. They typically require proteins, carbohydrates, fatty acids, sterols, vitamins, and minerals for growth (Gullan and Cranston, 1994). The availability of this nutriment is generally closely related to abiotic factors. Moreover habitat destruction, degradation and fragmentation is supposed to have destroyed the food source of many species (Duelli, 1994).

Habitat degradation and destruction: the primary cause of the decay is not direct human exploitation or malevolence, but the habitat destruction that inevitably results from the expansion of human population and human activities. The subtlest form of environmental degradation, pollution, has already been discussed. Other factors thought to have caused a decline in insects availability in woodland habitats are: artificial managed forests or tree plantation with monotonous species composition favouring a high yield and economical profit, abandonment of grazing within forest clearings, changes in silvicultural practices and habitat fragmentation (SBN, 2000).

1.4 Aims and hypothesis

This study is part of a nationwide conservation research program (*Rhippos*) initiated in 2001 by the Swiss Bat Conservation with the aim to identify the causes of the regression of *R. hipposideros*, to determine the key factors which may currently be responsible for the survival of the remnant colonies, and, ultimately, to propose efficient conservation strategies for this endangered species. A successful approach would hence include the protection and management of remnant colonies, leading to an increase in population size, and as a result a progressive recolonization of abandoned areas.

Since food is usually the most important factor for species existence and individual's fitness, a decline in insect availability during the past 50 years, which ever its cause (see section 1.3.3), could account for the decline of *Rhinolophus hipposideros*' populations. The main aim of this study was to compare food availability among various forested

habitats in the vicinity of extant, remnant and/or abandoned lesser horseshoe bats nursery roosts.

Before performing this overall comparison, we tested whether lesser horseshoe bats forage selectively by looking at the relationships between the diet of *R. hipposideros* and insect food availability in the forest. As regards the food abundance comparison, we assumed that factors responsible for a depleted food availability (habitat destruction and fragmentation, intensive agriculture, changes in silviculture) are still acting at present, with the prediction that, for the Alps, insect availability is higher in zones with increasing bat populations than in areas with decreasing populations, which in turn are expected to show lower food abundance than areas with extinct populations. We further predicted that insect availability in alpine woodlands where remnant colonies have survived to be higher than on the Swiss Plateau (plain), where lesser horseshoe bats are virtually extinct today.

2. Study areas and methods

2.1 Sampling design and general field procedures

This study was carried out at 15 study sites in Switzerland from the beginning of May to the end of September 2002. Since sampling was only possible at one study site at a time, the different study sites were visited on successive days. At every study site night-flying insect were sampled in the woodland using two malaise traps and two light traps. Generators were used for power supply. Additionally, in May and June, four impaction traps were used, but because only few insects were caught, this trap type and the insects caught by this means were not considered in subsequent analyses. Since Bontadina et al. (1999 and 2002) found the lesser horseshoe bats to forage mainly in woodland and for 50% of the time within 600 m radius from the nursery roost (Bontadina et al., 2002), the traps were placed in woodland at a maximum distance of 600 m from bat-roosts. One malaise and one light trap were placed in coniferous woodland (composed at least of 75% coniferous trees), the other malaise and the other light trap in broadleaf woodland (75% broadleaf trees). In 5 of the 30 cases one habitat type was not available within the fixed radius and the trap was placed within a radius of 2'000 m to the roost. A map with a raster of 20 x 20 m cell units was drawn for each roost surrounding. This raster was stratified

with respect to dominant habitat type, in particular coniferous and broadleaf forests. We selected at random one coniferous and one broadleaf cell for placing our two pairs of traps. Sampling started at dusk and ended at dawn. Nights with full moon, heavy rain or wind, and seasonally unusual cold temperatures were avoided, because these factors are known to have a strong influence on the flying activity of insects (e.g. Taylor, 1963; Bidlingmayer, 1964).

The trapped insects were conserved in 70% ethanol in small labelled plastic bags. In the laboratory, the content of the sample was first identified down to order or family level using reference guides. Collected day-active insects were not considered (Rhophalocera, Homoptera, Sternorrhyncha, *Formicidae*, *Apoidea*, *Vespoidea*). The insects were then dried in an oven for 72 hours at 60°C according to Southwood (1978). Thirdly the biomass to the nearest .001 g and the number of individuals per group were determined.

Arlettaz et al. (2000b) reported that Diptera eaten by lesser horseshoe bats show a minimal wing length of 4 mm and a maximum wing length of 16 mm. Because the insect body mass is probably the decisive factor for prey selection by lesser horseshoe bats, we considered only those items within that range between 4 mm and 16 mm. This corresponded to an insect dry body mass of 1–17 mg.

The temperature was measured and recorded every hour from 22.00 to 05.00 by an ibutton (www.ibutton.com) attached directly on traps. Mean values were calculated for every night and averaged over the season. To estimate colony size we referred to the maximum number of bats emerging from roost from counts carried out during the last 10 years of monitoring.

2.1.1 Prey selection

Droppings from the same nights when insect sampling took place were collected once a month, between May and September, in the colonies of Surcasti (GR) and Blumenstein (BE). In the evening newspapers were spread on the floor of the roost and faecal pellets collected on the following morning. The samples were stored in envelopes. The analysis of faecal pellets was done by Andres Beck, a bat specialist. Ten faecal pellets were selected at random from each sample and each pellet was soaked in water, then dissected using a binocular microscope by means of needles and tweezers and searched for taxonomically ascertainable fragments. The faecal sample was spread evenly over a Petri

dish so that visual estimates of volume could be made. Each prey class identified in a pellet was converted to the nearest 5% into a measure of relative volume (0-100%). “Percentage volume” refers to the volume obtained for each prey type from the total of ten faecal samples from each colony analysed on each date. The volume proportions were used as measures of relative biomass of the different prey categories.

In order to test for selection in terms of prey size, for each date 20 faecal pellets from the colonies of Surcasti and Blumenstein were soaked in water and checked for wing fragments of Diptera. From wing fragments the length of the wings could be reconstructed using a microscope (Leica MZ95). Diptera caught with traps in Blumenstein and Surcasti were divided into 3 groups according to their wing lengths (4-8 mm, 8-12 mm, >12 mm).

2.1.2 Food availability among areas with increasing, decreasing and extinct populations of *R. hipposideros*

Areas located in the Alps from where data about past or present occurrence was available were considered (Fig. 1).

Table 1. Main characteristics of study sites. “Mean temperature during sampling” corresponds to the mean temperature between May and August (see methods). Data about the annual mean rainfall were taken from Kirchhofer et al. (1982).

Study site	Population status	Colony size (n)	Altitudes (m asl)	Coordinates	Mean temperature during sampling (°C)	Mean annual rainfall (mm)
Blumenstein	Increasing	94	785	46°43'N, 7°30'E	11.4	1'000 - 1'200
Kleinteil	Increasing	262	550	46°50'N, 8°13'E	13.3	1'000 - 1'200
Surcasti	Increasing	142	990	46°41'N, 9°10'E	9.8	600 - 800
Waltensburg	Increasing	121	745	46°46'N, 9°07'E	10.1	800 - 1'000
Broc	Decreasing	4	720	46°36'N, 7°05'E	15.5	1'000 - 1'200
Meiringen	Decreasing	12	605	46°43'N, 8°11'E	14.3	1'200 - 1'400
Tomils	Decreasing	8	810	46°45'N, 9°26'E	13.1	600 - 800
Flums	Decreasing	8	460	47°05'N, 9°20'E	12.4	1'000 - 1'200
Wilderswil	extinct	0	585	46°40'N, 7°52'E	15.1	1'000 - 1'200
Ried	extinct	0	655	47°02'N, 8°39'E	13.3	1'400 - 1'600
Surava	extinct	0	905	46°40'N, 9°36'E	9.7	600 - 800
Untervaz	extinct	0	585	46°55'N, 9°32'E	12.4	800 - 1'000

Four roosts with large and increasing populations, four roosts with decreasing populations and four roosts formerly inhabited but today extinct were chosen at random. The study sites were visited once a month, which means that until the end of the summer each study site was visited five times. To avoid moon lighting (Bidlingmayer, 1964; Kunz, 1988) on a systematic chronological sampling sequence, the study sites were subdivided into two zones and the succession of the zones was randomized. Yet, succession of the study sites within one zone was not random due to logistical constraints (transportation).

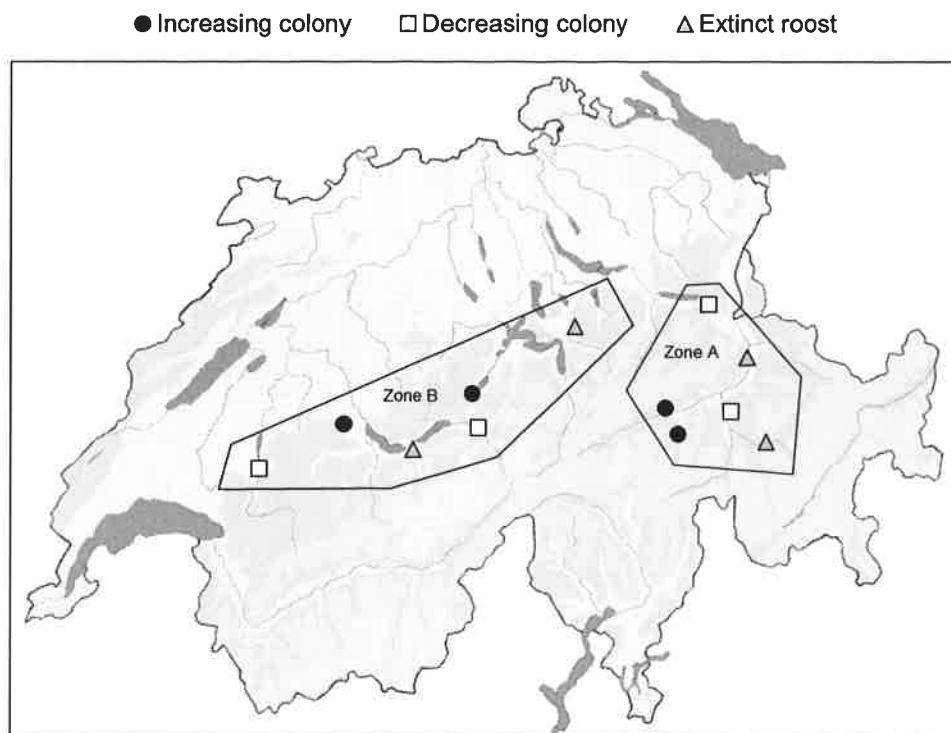


Fig. 1. Map of Switzerland showing our 12 study sites in the Alps, grouped in two sampling zones.

2.1.3 Comparison of prey availability in the Swiss Alps vs Swiss lowlands

Three extinct roosts on the Swiss plain and three of the large, increasing colonies described in section 2.1.2 were chosen randomly. The procedures of sampling and the analysis are identical to section 2.1.2.

The larger colonies in the Alps were visited as described in section 2.1.2. Liebegg was always visited on the way between the two zones (see Fig. 1 and 2). To avoid that

Montagny and Laupen were sampled one after another, Blumenstein was always visited in between the two study sites (see Fig. 2).

Table 2. Main characteristics of study sites. “Mean temperature during sampling” corresponds to the mean temperature between May and August (see methods). Data about the annual mean rainfall were taken from Kirchhofer et al. (1982).

Study site	Region	Population status	Altitudes (m asl)	Coordinates	Mean temperature during sampling (°C)	Annual mean rainfall (mm)
Blumenstein	Alps	Increasing	785	46°43'N, 7°30'E	11.4	1'000 - 1'200
Kleinteil	Alps	Increasing	550	46°50'N, 8°13'E	13.2	1'000 - 1'200
Waltensburg	Alps	Increasing	745	46°46'N, 9°07'E	10.1	800 - 1'000
Laupen	Swiss plain	extinct	525	46°54'N, 7°14'E	13.7	800 - 1'000
Liebegg	Swiss plain	extinct	510	47°20'N, 8°07'E	13.3	800 - 1'000
Montagny	Swiss plain	extinct	560	46°59'N, 6°59'E	13.6	800 - 1'000

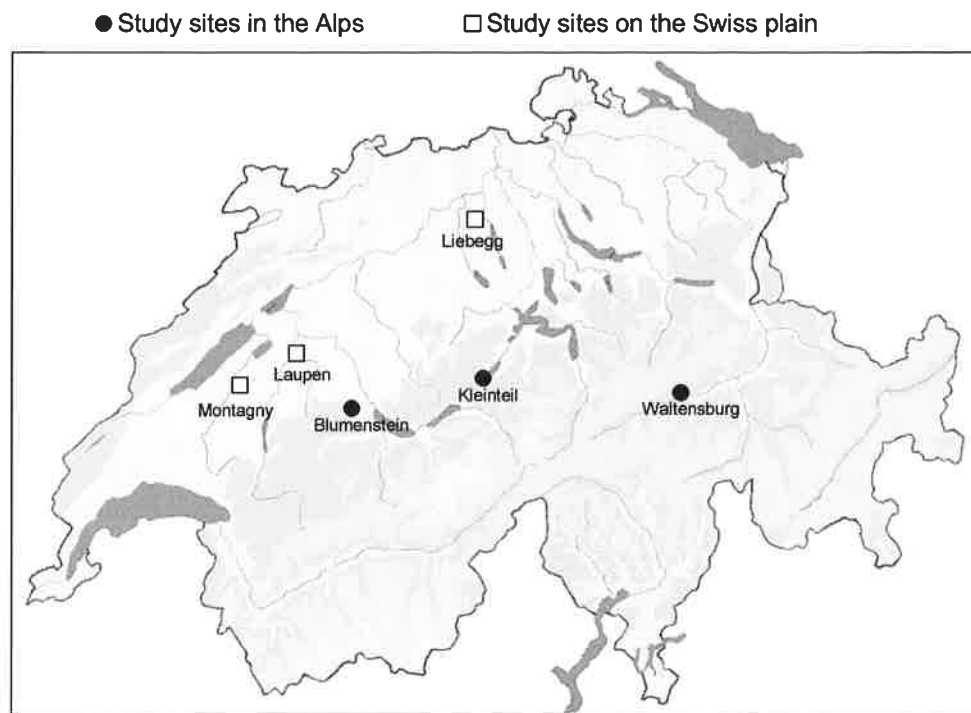


Fig. 2. Map of Switzerland showing the six study sites used for the comparison of insect abundance between the Alps and the Plateau.

2.2 *Statistical analysis*

All variables were tested for homogeneity and normality before running ANOVAs. The variables that were not normally distributed were transformed into normality using a $\sqrt{\log(x+1)}$ transformation (Zar, 1999).

First we tested by means of a matched pairs t-test if the insect dry biomass available to the lesser horseshoe bat differed significantly between coniferous and broadleaf woodland, the pairs comprising data from coniferous and broadleaf woodland of each study site, respectively. In case of no statistically significant difference the samples from the two woodland types will be pooled. Otherwise, analyses should be carried out for the two forest types separately. Then we tested the influence of the factors month and population status (respectively: region) on the insect availability by means of a two-way analysis of variance (ANOVA). As regards, food selection, the significance of deviation from the line of no selection was assessed using sign-tests (Zar, 1999).

The largest part of the data analyses were performed using the program JMP4 (SAS Institute Inc. 2001, Cary, NC, USA), only the randomised contingency table procedures were done with Actus 2 (Eastbrook and Eastbrook, 1989).

3. Results

3.1 *Availability of night-flying insects*

Overall, from May to September we collected 135'170 insects during 75 nights, which corresponds to a mean number of 1804 ± 2023 insects captured per night (range: 255 – 11'153 per night). The major part of the insects were collected by light traps, with only 0.8% (range: 0.2% - 2.9%) of insects collected with malaise traps; results of both trap types were therefore pooled.

From the total number of items, 27'080 (23.7% of frequency, 32.6% of total dry biomass) insects can be considered as available to *R. hipposideros* (body mass 1-17 mg, see methods). Among the remaining potential prey items, 96'000 insects had a dry body mass lighter than 1 mg, whereas 7'090 insects had a dry body mass greater than 17 mg. Diptera (84% of total insects number) were by far the most common insects in the class of less than 1 mg dry weight. In the «available» class 1-17 mg body mass, Lepidoptera (56.3%)

were the most abundant, followed by Diptera (16%) and «Others» (27%). Neuroptera (0.7%) were rare throughout and consisted predominantly of individuals from the *Chrysopidae* family. In the class of insects heavier than 17 mg, Lepidoptera (90.5%) were by far the predominant insects, with Diptera representing as little as 3% and «Others» (may-bugs not included) 6.5%. «Others» consisted of: 1) 48.6% Trichoptera, with largest catches between July and September 2) 32.9% Coleoptera, with more individuals caught at the beginning of the season 3) 17.9% Hymenoptera, with the largest catches in June, 4) 0.4% Plecoptera and, 5) 0.2% Ephemeroptera.

Both insect number and biomass captured during one sample night correlated significantly with each other (Fig. 3); as a result, only the dry biomass was used for subsequent analyses.

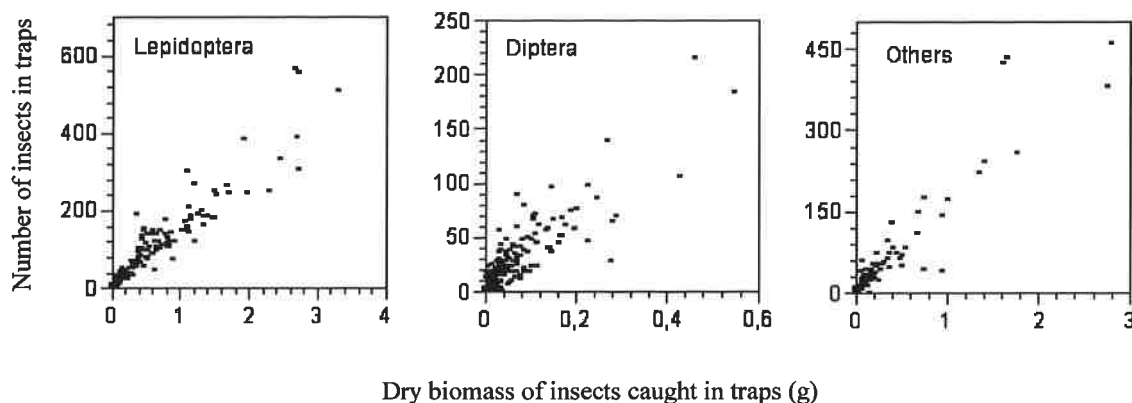


Fig. 3. Correlation between number of insects and dry biomass of insects caught during one night. Diptera ($r = 0.79$, $n = 150$, $P < 0.0001$) Lepidoptera ($r = 0.95$, $n = 150$, $P < 0.0001$) «Others» ($r = 0.60$, $n = 150$, $P < 0.0001$). Only prey available to *R. hipposideros* (dry body mass 1–17 mg) was considered.

Table 3 shows for every study site ($n = 15$) the average dry biomass of different insect categories and body mass classes. Note that the greatest biomass per night (huge quantity of Lepidoptera) was collected in July in a broadleaf woodland close to an abandoned nursery (Wilderswil, 7.477 g). This value represents an exceptional outlier, being much greater than the average dry biomass collected in July (1.967 g). In contrast, the lowest dry biomass was achieved in a coniferous woodland in May at a study site harbouring a

Table 3. Mean (\pm SD) dry biomass (mg) of the various insect categories and size classes trapped at 15 study sites with respect to population status and habitat type; n refers to the number of sampling nights per site.

Study site	Pop. Status	Woodland type	n	Diptera		Lepidoptera		Neuroptera		Diptera		Others		Lepidoptera		Diptera		Others		Total biomass	
				< 1 mg	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean		SD
Blumenstein	increasing	conifer	5	57	34	500	518	0	0	108	91	130	103	3'095	1'746	4	8	181	198	4'074	
		broadleaf	5	31	43	367	439	0	0	67	39	350	700	2'408	2'715	0	0	4	9	3'228	
Kleinteil	increasing	conifer	5	37	29	414	455	1	2	45	27	358	270	1'123	691	5	12	112	181	2'095	
		broadleaf	5	115	59	639	583	1	2	59	34	267	259	1'728	983	30	54	110	161	2'949	
Surcasti	increasing	conifer	5	29	24	500	285	0	0	158	198	739	1'263	2'290	480	0	0	431	863	4'148	
		broadleaf	5	87	45	360	189	0	1	239	327	17	24	1'651	846	11	15	5	11	2'370	
Waltensburg	increasing	conifer	5	39	49	355	327	0	0	55	38	59	35	1'133	775	0	0	133	284	1'775	
		broadleaf	5	84	54	845	921	3	5	49	55	161	114	2'070	1'375	12	27	155	292	3'378	
Broc	decreasing	conifer	5	192	342	988	1'400	15	32	89	50	336	305	2'457	3'174	25	44	76	110	4'176	
		broadleaf	5	66	65	546	454	0	1	99	45	480	383	1'600	1'167	45	69	91	86	2'927	
Flums	decreasing	conifer	5	43	33	683	602	2	3	31	29	242	112	1'278	839	28	26	65	108	2'372	
		broadleaf	5	29	17	568	643	0	1	153	251	116	77	2'910	4'243	9	13	48	25	3'834	
Meiringen	decreasing	conifer	5	89	70	442	377	3	5	54	36	209	134	1'412	445	0	0	58	82	2'267	
		broadleaf	5	47	55	393	528	4	5	45	33	258	289	1'921	1'171	38	71	101	143	2'806	
Tomils	decreasing	conifer	5	321	455	483	247	39	51	194	248	907	1'328	1'690	728	696	1'374	21	43	4'350	
		broadleaf	5	160	183	741	365	27	44	341	631	368	488	2'238	209	207	375	243	429	4'325	
Ried	extinct	conifer	5	109	57	747	743	0	0	108	97	340	363	2'153	1'316	37	41	158	161	3'650	
		broadleaf	5	100	57	1'091	978	4	4	111	88	284	213	3'477	2'471	34	62	81	88	5'181	
Surava	extinct	conifer	5	74	116	589	777	0	0	66	83	432	604	851	357	0	0	53	88	2'064	
		broadleaf	5	78	97	886	1'372	59	108	71	102	81	87	832	494	8	19	5	11	2'019	
Untervaz	extinct	conifer	5	68	53	615	646	0	0	162	182	111	72	1'031	473	4	9	50	90	2'042	
		broadleaf	5	36	52	854	674	19	18	144	164	135	134	3'124	2'112	20	36	0	0	4'331	
Wilderswil	extinct	conifer	5	66	46	926	1'094	0	0	78	94	290	284	3'378	2'606	87	176	93	123	4'917	
		broadleaf	5	66	39	1'871	2'883	13	19	43	34	417	492	4'616	5'161	17	12	222	156	7'265	
Laupen	extinct (plain)	conifer	5	185	141	329	143	1	2	90	51	210	109	2'213	1'516	39	62	79	91	3'147	
		broadleaf	5	188	145	939	1'054	5	6	68	63	354	424	1'887	1'563	19	25	171	278	3'630	
Liebegg	extinct (plain)	conifer	5	121	106	798	641	19	31	182	210	585	714	2'011	1'592	127	127	409	887	4'251	
		broadleaf	5	121	117	865	942	5	11	66	52	525	699	1'684	686	15	24	970	1'994	4'251	
Montagny	extinct (plain)	conifer	5	118	139	1'160	1'045	2	2	110	86	274	247	2'917	1'773	10	23	162	161	4'754	
		broadleaf	5	312	377	636	656	0	0	156	220	547	753	1'937	918	31	48	94	113	3'712	
Total biomass				150	3'065	21'129		222	3'240		9'581		63'113		1'557		4'380		106'288		

large population of *R. hipposideros* (Blumenstein, 0.050 g); the latter value was much smaller than the average dry biomass collected in May (0.320 g).

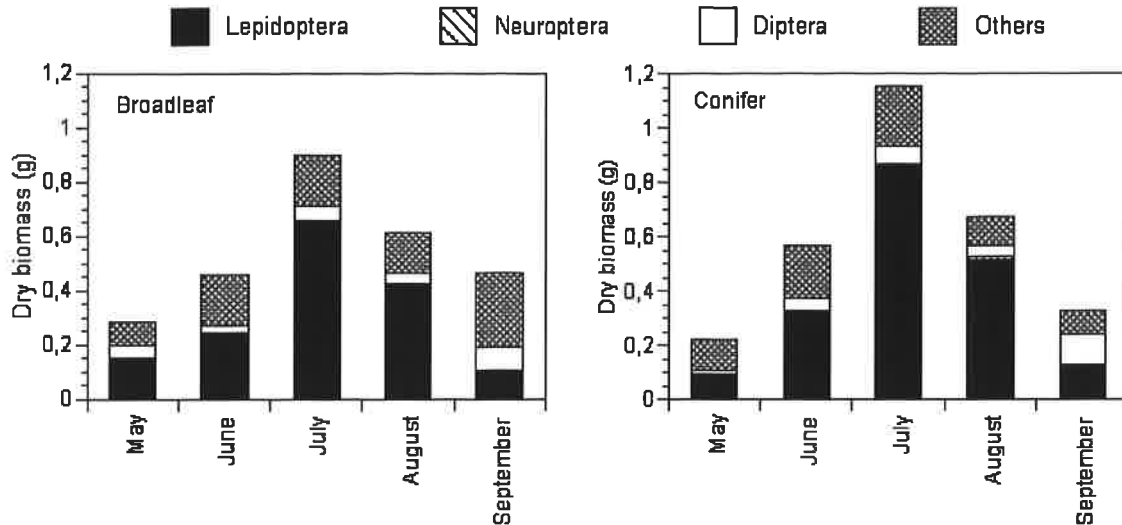


Fig. 4. Among sites ($n = 12$, only the study sites in the Alps considered) average seasonal trends in dry biomass of «available» (1-17 mg) insect categories caught in broadleaf woodlands and in coniferous forests.

Changes in collected dry insect biomass (Fig. 4) showed the following seasonal patterns: most items were caught in July, with the smallest numbers in May. Lepidoptera were by far the most frequent group in June (54%), July (73.5%) and August (73%), while «Others» were predominant in September (46.5%). There was no clear seasonal trend in the abundance of Diptera, although the largest catches took place in September.

3.2 Prey selection

3.2.1 Prey group selection

The frequency of the prey categories found in traps and in faeces are shown in Figure 5. Overall, 7 prey categories were determined in the analysis of the faeces collected at the two nursery roosts in Surcasti and Blumenstein. This analysis revealed that in *R. hipposideros* diets Diptera and Lepidoptera were throughout the season by far the most abundant insect groups (Diptera 49.9%; Lepidoptera 32.1%). Both prey groups were also found to be most frequent in the traps (Diptera 36.6%; Lepidoptera 48.1%). Lepidoptera

was the most common group in traps in June (59.9%), July (58.9%) and August (58.9%) and predominant in faeces in July (58.5%), while Diptera was most frequent in traps in September (55%) and in faeces in May (63%) and September (65.5%). Neuroptera were rarely found in traps (0.01%), but represented as many as 12.3% of diet. Trichoptera represented on average 6.7% of the insects caught in traps, but only 0.1% of the fragments in the faeces. There was no clear evidence for seasonal changes in dietary diversity, but in September when food, especially moths, was less abundant, seven prey groups were present in the faeces compared to 5 from May to July and 4 in August.

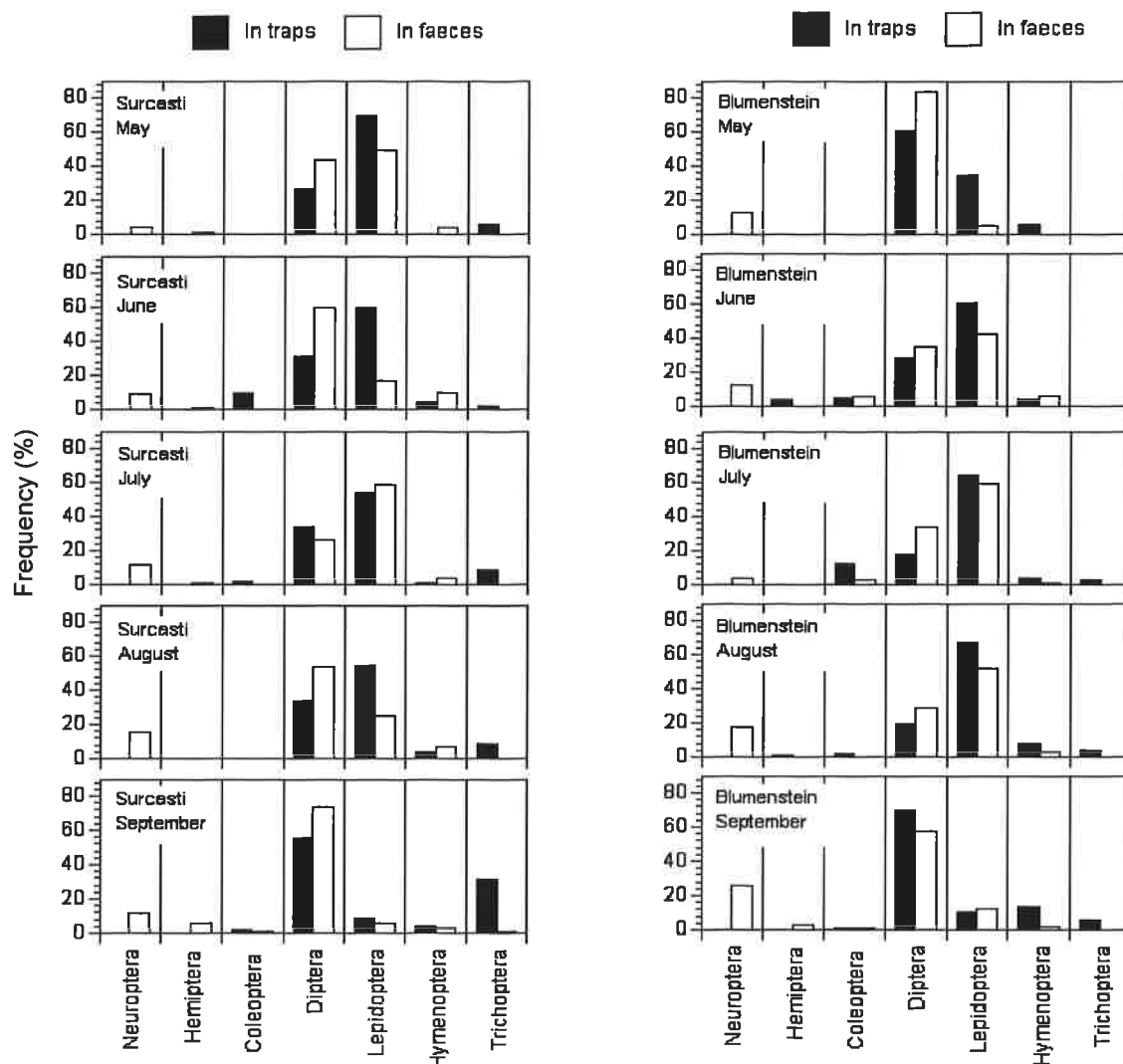


Fig. 5. Comparison of mean percent frequency of insect taxa in the diet of *R. hipposideros* in relation to the percent frequency of insect availabilities measured in woodlands between May and September.

Since only Diptera, Lepidoptera and Hymenoptera were regularly present in both traps and faeces, analysis of prey selection was performed only with these taxa. Scatter plots of the incorporation of Lepidoptera, Hymenoptera and Diptera in the diet in relation to the abundance of these taxa in woodlands are presented in Fig. 6. Lepidoptera and Diptera were incorporated into the diet in direct relation to their abundance, but there was no correlation between dietary incorporation and abundance for Hymenoptera. The presence of points consistently below or above the dotted line of no selection indicated whether a prey category was consistently under- or over-represented in the diet, respectively.

Spearman rank correlation coefficients indicate a positive significant relationship between the percentage of Diptera and Lepidoptera in diet vs in the traps ($r_s = 0.644$, $n = 10$, $p < 0.05$; $r_s = 0.697$, $n = 10$, $p < 0.05$, respectively; Fig. 6). Although Diptera seem to be slightly over-represented and Lepidoptera somehow under-represented in faeces with respect to availability, sign-tests did not yield significant values ($p > 0.05$, ns).

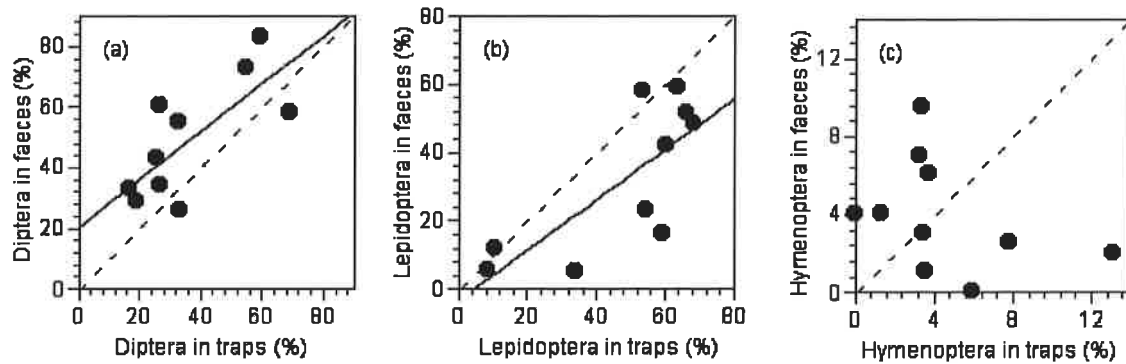


Fig. 6. Proportion of insect biomass percentage in the diet of *R. hipposideros* in relation to insect availability in traps. The line of no selection is the dotted line. (a) Percent Diptera in faeces in relation to Diptera abundance ($r_s = 0.644$, $n = 10$, $p < 0.05$); (b) Percent Lepidoptera in faeces in relation to moth abundance ($r_s = 0.697$, $n = 10$, $p < 0.05$); (c) Percent Hymenoptera in faeces in relation to Hymenoptera abundance ($r_s = -0.596$, $n = 10$, $p = 0.069$). Where the relations are significant lines of best fit are drawn.

3.2.2 Prey size selection

From 32 wing fragments found in faeces wing length could be reconstructed. No Diptera had wing lengths smaller than 4 mm or larger than 16 mm, confirming former findings by Arlettaz et al. (2000b). Figure 7 shows the frequency distribution of Diptera wing length

classes in traps and in faeces. There was no difference in the frequency of the wing length classes in Blumenstein ($\chi^2 = 4.0$, df 2, $p = 0.130$), but a significant difference occurred in Surcasti, with wing lengths from the class 8-12 mm occurring significantly more frequently than expected from availability ($p < 0.05$, randomized contingency tables).

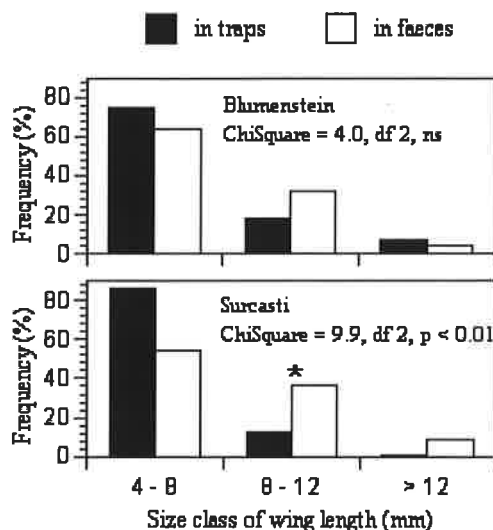


Fig. 7. Relative frequency distribution (%) of the different wing length classes of Diptera in traps and in faeces. Blumenstein (in traps $n = 329$ items, in faeces $n = 21$). Surcasti (in traps $n = 1090$, in faeces $n = 11$). Overall results of randomisation tests are indicated, whereas significant deviations ($p < 0.05$) between observed and expected frequencies for a given size class are depicted by one star.

3.3 Differences in food availability between areas with increasing, decreasing and extinct populations of *R. hipposideros*

Since the study about prey selection showed that Lepidoptera and Diptera were the two main prey categories for *R. hipposideros* making up 83% of its diet, we focused on those two insect taxa in further comparisons. A total of 18'157 insect items with a dry body mass 1–17 mg were considered for this analysis. First we tested by means of a matched-pairs t-test if the insect biomass collected in coniferous and broadleaf woodland differed significantly from each other (Appendix I). Since differences were significant neither for Lepidoptera nor for Diptera, we pooled the data collected from the two woodland types in further statistical analyses.

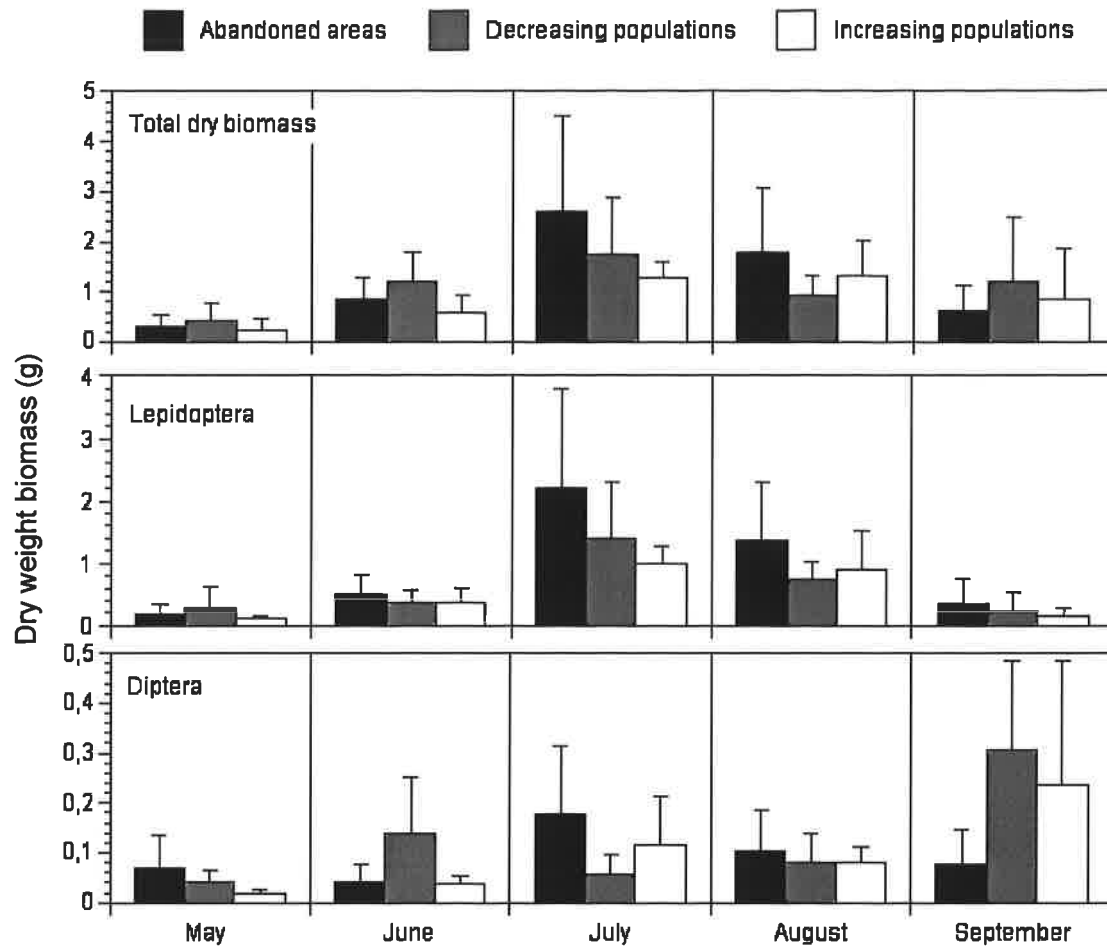


Fig. 8. Comparison of available dry biomass (g) (mean \pm SD) from May to September in abandoned areas, areas with decreasing and areas with increasing populations. Note that colony status was a non significant factor (ANOVA, see Table 4)

A two-way analysis of variance was used to test whether the factors population status (extant, relict and extinct) and month (seasonality) had an effect on the availability of insects (Table 4). The factor month appeared highly significant as regards total biomass as well as for Lepidoptera. Concerning Diptera the difference was still significant but less so pronounced. In contrast, population status was not significant. The interactions between month and population status were all not significant.

Table 4. Effects of the two factors population status and month on the availability of total insect biomass, and on the abundance of Lepidoptera and Diptera biomass, respectively. A two-way analysis of variance (ANOVA) was performed. df = degrees of freedom; F = F statistics; P = rejection probability.

Source of variation	Sum of squares	df	Variance	F ratio	P
Total biomass					
Status	0.0322	2	0.016	1.011	0.372
Month	0.0322	4	0.008	11.777	< 0.001
Status x month	0.0791	8	0.010	0.621	0.755
Error	0.0716	45	0.002		
Lepidoptera					
Status	0.0609	2	0.030	2.889	0.066
Month	1.1651	4	0.291	27.620	< 0.001
Status x month	0.0233	8	0.003	0.277	0.970
Error	0.4745	45	0.011		
Diptera					
Status	0.0010	2	0.000	2.848	0.935
Month	0.0831	4	0.021	0.067	< 0.05
Status x month	0.0683	8	0.009	1.169	0.338
Error	0.3284	45	0.007		

3.4 Comparison of prey availability in the Swiss Alps vs the Swiss lowlands

A total of 8'923 insects with a dry biomass between 1-17 mg were counted on the Swiss Plateau, while 5'495 items belonging to that same body mass class were counted in the surroundings of the increasing alpine populations. We first tested by means of a matched-pair t-test whether, at the six selected study sites, insect biomass differed significantly between coniferous and broadleaf woodlands (Appendix II). In July, Lepidoptera were significantly more abundant in broadleaf woodland (df 5, t-value = 5.50, $p < 0.01$) and Diptera were significantly more abundant in coniferous woodland in September (df 5, t-value = 2.287, $p < 0.05$). Because of these differences the following analysis were performed for the two woodland types separately.

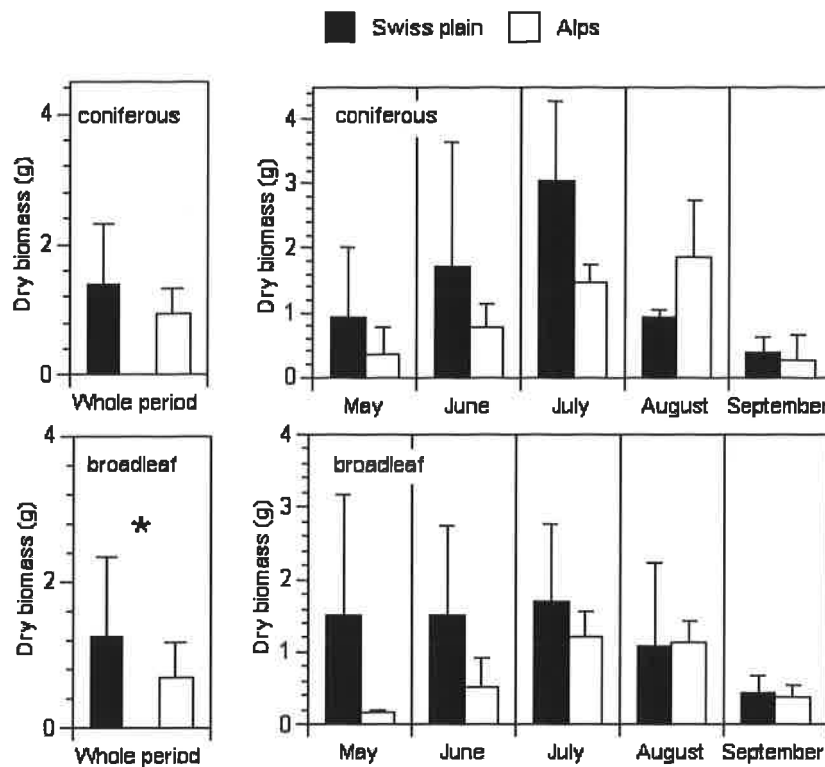


Fig. 9. Comparison of available dry biomass (mean \pm SD) in coniferous and broadleaf woodlands in areas with extinct populations on the Swiss Plateau with areas with increasing populations in the Alps . The only significant difference ($p < 0.05$, ANOVA, * see also Tables 5 and 6) is depicted by one star.

A two-way analysis of variance was used to test whether the factor geographic region (Swiss Plateau vs Alps) and month had an effect on the availability of insect biomass in the coniferous and in the broadleaf woodlands, respectively. For the broadleaf woodland (Table 6) the effects of the factor month were significant only for Lepidoptera. The factor region had a significant effect on the availability of both total and Lepidoptera biomass, in both cases the abundance was significantly higher on the Swiss Plateau. Furthermore, the interaction term region*month was significant as regards the total biomass. In coniferous woodlands (Table 5) the factors had no significant effect on prey availability, however Figure 9 shows that the available biomass was higher on the Swiss Plateau from May to July, whereas in August, the biomass was higher in the Alps.

Table 5. Effects of factors geographic region and month on the availability of total biomass, of Lepidoptera and Diptera in coniferous woodlands. A two-way analysis of variance (ANOVA) was performed. df = degrees of freedom; $F = F$ statistics; P = rejection probability.

Source of variation	Sum of squares	df	Variance	F ratio	P
Total biomass					
Region	0.0091	1	0.009	1.816	0.193
Month	0.0965	4	0.024	4,7892	< 0.01
Region x month	0.0201	4	0.005	0.996	0.433
Error	0.1007	20	0.005		
Lepidoptera					
Region	0.0207	1	0.021	1.38	0.254
Month	0.7093	4	0.177	11.76	< 0.001
Region x month	0.0159	4	0.004	0.26	0.898
Error	0.3015	20	0.015		
Diptera					
Region	0.0058	1	0.006	0.996	0.330
Month	0.0268	4	0.007	1.156	0.359
Region x month	0.0124	4	0.003	0.533	0.713
Error	0.1159	20	0.006		

Table 6. Effects of factors geographic region and month on the availability of total biomass, Lepidoptera and Diptera biomass in broadleaf woodland. A two-way analysis of variance (ANOVA) was performed. df = degrees of freedom; $F = F$ statistics; P = rejection probability.

Source of variation	Sum of squares	df	Variance	F ratio	P
Total biomass					
Region	0.0173	1	0.017	5.474	< 0.05
Month	0.0343	4	0.009	2.723	0.059
Region x month	0.0264	4	0.007	2.096	< 0.05
Error	0.0629	20	0.003		
Lepidoptera					
Region	0.0681	1	0.068	5.011	< 0.05
Month	0.4282	4	0.107	7.879	< 0.001
Region x month	0.1169	4	0.029	2.151	0.112
Error	0.2718	20	0.014		
Diptera					
Region	0.0143	1	0.014	1.866	0.187
Month	0.0354	4	0.009	1.157	0.359
Region x month	0.0070	4	0.002	0.229	0.919
Error	0.1531	20	0.008		

4. Discussion

4.1 *Availability of night-flying insects*

Estimation of insect availability is influenced by the capture method. Our light traps collected a greater number of insects than malaise traps. Jones (1990) pointed out that with light traps, for instance, Coleoptera are not caught in proportion to their availability. We noticed the same for Neuroptera, where almost exclusively individuals from the *Chrysopidae* family were caught, whereas we don't know if other representatives of the order were present in the field. However, in accordance with Muirhead-Thomson (1991), we believe that at least the two main prey groups relevant to lesser horseshoe bats, namely Lepidoptera and Diptera, were caught in proportion to their availability in the environment. In any case, since number of traps and sampling design were the same throughout the season, a putative systematic error in assessing insect availability would not falsify the results concerning the comparison of insect availability among different areas.

We found a strong seasonal variation of insect abundance with a peak of abundance in July. This was probably amplified by a very warm weather at the end of June and at the beginning of July 2002. While the availability of medium-sized Diptera (1-17 mg) did not vary much throughout the season, medium-sized moths (1-17 mg) were scarce in May, reaching peak numbers in July before becoming scarce again in the course of September. We know no other study, which systematically assessed the night-flying insect availability in woodlands. At a first glance it was surprising to find that insect abundance in coniferous woodland was comparable to the abundance in broadleaf woodland. Whereby it is noteworthy that the insect collection at the majority of sites took place in relatively natural-looking coniferous woodland stands with often plenty of deadwood, scrubs and undergrowth, but not in coniferous plantations.

4.2 *Prey selection*

Opportunistic foraging predicts that a positive correlation should occur between the incidence of a particular prey in the diet and its abundance in the environment. For selective foraging a similar comparison would yield no significant relationship (Anthony & Kunz, 1997). Since correlation was significantly positive for the two main prey groups,

Diptera and Lepidoptera, our results do not falsify the parsimonious hypothesis that lesser horseshoe bats exert no active prey selection.

Although differences were not significant, Diptera were apparently somehow over-represented whilst Lepidoptera under-represented in faeces, suggesting that, other things being equal, lesser horseshoe bats would prefer to prey on Diptera. However, this apparent difference might be considered with caution, as several factors might interact. For instance trapping with light traps may reflect the true abundance of nocturnal Lepidoptera, whereas it may attract only certain types of Diptera (Jones, 1990). There may also be a constraint on Lepidoptera availability to the lesser horseshoe bat, firstly, because some species are known to take evasive actions (Rydell et al., 1995), secondly, because fast-flying moths might be more difficult to pursue than slow-flying Diptera.

There was no clear evidence for seasonal changes in dietary diversity as shown by Jones (1990) in *Rhinolophus ferrumequinum*. Only in September when food, especially moths, was scarce, more prey groups were integrated in the diet.

In Accordance to the findings by Arlettaz et al. (2000b) no Diptera with wing length smaller than 4 mm or larger than 16 mm were detected in faeces. Although Beck (pers. comm.) found in roosts a small number of bitten off wings larger than 16 mm, based on our results we predict that prey with wing length larger than 16 mm (i.e. heavier than 17 mg) are only very occasionally taken. Our size class frequencies differed from those found by Arlettaz et al. (2000b), as we found more smaller items. This difference could partly be caused by our reduced sample size. Although the correlation between the wing length of Diptera from faeces and those collected in the environment was pretty good, the bats incorporated more larger items in their diet than expected if prey were eaten in relation to availability. However, the difference was only significant at one study site (Surcasti) for wing lengths between 8–12 mm (randomisation tests). Note that these discrepancies may also stem from violations of two assumptions: first, large wing fragments could be found more frequently in faeces than smaller ones because they are easier to spot with the binocular microscope, and, second, the frequencies of the wing size classes collected with traps may differ from real frequency in the environment.

Finally it has to be taken into account that selection of prey size in bats may be more complex than in visually hunting predators, which may perform a more accurate prey size choice. The peculiar characteristics of bat sonar might impose drastic constraints upon

prey choice; in particular small prey items might be difficult to locate (e.g. Barclay, 1985), even though *R. hipposideros* calls with a high frequency of 112 kHz (Jones & Rainer, 1989), a short wavelength that would theoretically enable fine-scaled target detection.

Although it must be kept in mind that our small sample size makes the above discussion fairly speculative, we conservatively conclude that lesser horseshoe bats, throughout the summer, appear to feed unselectively, which corroborates previous findings with other bat species (e.g. Arlettaz & Perrin, 1995; Arlettaz, 1996; Belwood & Fenton, 1976; Swift, Racey & Avery, 1985; Rydell, 1986). It remains therefore to demonstrate that *R. hipposideros* can behave as an active selective predator as suggested for *Rhinolophus ferrumequinum* (Jones, 1990) and other bats (e.g. Anthony & Kunz, 1977; Belwood & Fullard, 1984; Brack & LaVal, 1985)

4.3 Differences in food availability between areas with increasing, decreasing and extinct populations of R. hipposideros

Our results show that although there were strong seasonal variations in insect abundance, insect availability in the surroundings of extant, declining and extinct colonies was comparable. Also, insect availability was similar in coniferous and broadleaf woodlands. As a result, we predict that lesser horseshoe bat should forage equivalently in both woodland types. This contradicts the view by Schofield (1996) and Bontadina et al. (2002) who reported deciduous woodland to be the main foraging habitat of lesser horseshoe bats, assuming a higher insect abundance, among forests, in that habitat. However, these studies were conducted in Wales, UK, where coniferous woodland often are artificial plantations (Bontadina, pers. comm.).

4.4 Comparison of prey availability in the Swiss Alps vs the Swiss lowlands

Our results suggest that today insect availability in woodlands is certainly not a limiting factor to lesser horseshoe bat occurrence on the Swiss Plateau. However, the actual amount of wooded areas in the direct surroundings of a potential roost is perhaps a decisive factor for among-roost dispersion and thus the recolonization of abandoned nursery roosts. Fragmentation of woodlands on the Swiss Plateau might therefore appear

as a constraint on future recolonization potential by the species. Recent studies (Schofield, 1996; Reiter, in press) have shown a positive correlation between the location of maternity roosts and the availability of woodland. It has even been suggested that for a successful colonisation of a roost, woodland cover within a radius of 2500 m from the roost must not be less than 50% (Reiter, in press). This could be a severe limitation for a future successful recolonization of lowland areas where a dramatic urbanisation has taken place over the past 50 years. Under Swiss conditions, *R. hipposideros* roosts in large attics in summer, such as old historical buildings and churches; today, those are often located in the centre of villages, i.e. far away from forests, in a modern habitat more and more dominated by mineral and artificial urban structures.

It seems probable that colonies of lesser horseshoe bats have been affected by small-scaled reduction of wooded zones in their vicinity. Yet, it appears fairly implausible that the large-scaled abandonment of the entire Swiss Plateau was caused by forest extirpation only, particularly as the coverage of woodland since 1950s has not been altered in Switzerland, including the lowlands (Brassel et al. 1999). This would support the view that a catastrophic event, such as the generalized use of pesticides from World War II, might be the ultimate reason for species population decline.

4.5 Implications for conservation

The main loss of large areas of the former distribution of *R. hipposideros* occurred between 1950 and 1970. Nowadays we cannot fully and conclusively establish which factors caused the dramatic decline of *R. hipposideros* populations in western Europe, as every study is performed *a posteriori*. It remains possible, however, to see if presumed factors having affected the population still exist and could further influence colony status, thereby affecting recolonization potential. Our results reveal that present-day food availability *per se* cannot explain the current isolation of population remains of *R. hipposideros*. A progressive recolonization of former areas would therefore certainly not be impeded by a drastic limitation in prey availability.

A ranked evaluation of possible factors of decline obtained from an enquiry addressed to Swiss bat experts showed that the main factors thought to be responsible for lesser horseshoe bats decline are, in decreasing order of relevance: habitat destruction, pesticide contamination and food shortage (Bontadina et al., 2001). As the woodland cover as well as the silvicultural practices have not changed radically since the 1950s (Brassel et al.,

1999), we can now predict, from the data collected in the present study, that habitat alteration and food shortage, the first and third hypotheses, were certainly not the major factors causing the decline of lesser horseshoe bats which began about 50 years ago.

Concerning habitat, recent radio-tracking studies in the UK (Bontadina et al., 1999 and 2002), in Germany (Holzhaidner et al., 2002) and in Belgium (Motte & Libois, 2002) showed that lesser horseshoe bats forage mainly in woodland. If woodland is the key habitat of this species, then large-scaled forest destruction or drastic degradations of forest ecological conditions should have taken place during the past decades. However, neither the total woodland area did decrease since 1950s in Switzerland (Brassel et al., 1999), nor did forestry practices changed to such an extent that could explain the dramatic drop observed in lesser horseshoe bat range and density. Indeed, most loss of woodland in Switzerland occurred before 1900. As a consequence, we can safely reject the hypothesis that the drastic decline of *R. hipposideros* in our country was merely due to an impoverishment of forest ecosystems.

As a consequence, it seems that the hypothesis of a contamination by pesticides remains the most probable factor having caused the collapse of lesser horseshoe bats populations in Switzerland. The extensive use of pesticides began during the period of World War II, particularly in agriculture. Many animal species began to decrease soon after, as exemplified by raptors (e.g. *Falco peregrinus*, *Accipiter nisus*) (e.g. Newton and Bogan, 1974) that were heavily contaminated by organochlorinated pesticides (e.g. DDT). As upper food chain consumers, lesser horseshoe bats may have faced similar intoxication problems as raptors. Indeed, a comprehensive ecotoxicological analysis by Arlettaz et al. (2000a), carried out in the framework of the *Rhippos* conservation programme, provides sound support to this view. The hypothesis that pesticides may be responsible for the decline of lesser horseshoe bat is especially appealing, as it fits well with a global catastrophic phenomenon. As most raptors that were formerly severely contaminated have nowadays largely recovered in Europe, including Switzerland, we can expect that a bat species, which has a much longer generation turnover and a lower dispersal power than raptors, will inevitably follow a similar population trend, with, however, a greater time lapse.

Additional reasons why lesser horseshoe bats have not yet recolonized former areas are, firstly, that lesser horseshoe bats are highly susceptible to human disturbance in their

roost (Stebbing & Griffith, 1986), and show a high degree of roost fidelity (Schofield, 1996). And, secondly, that hedgerows and woodlands, presumed to be important for *R. hipposideros*' metapopulation connectivity (Schofield, 1996) have been systematically eradicated in vast regions. In the case of Switzerland, the impact of the first factor is difficult to evaluate, but we conservatively assume it must be negligible in respect to the global population collapse observed over the past decades. In contrast, habitat connectivity could be a problem within the modern Swiss Plateau landscape; here, however, the landscape has fortunately not reached the high level of fragmentation and desertification seen in other intensively used central European countries.

Within the *Rhippos* research programme, this study has provided crucial information so as to elaborate a sound conservation strategy for the endangered Swiss lesser horseshoe bat. For the future, conservation research should now focus on 1) gathering additional data about present-day contamination of roosts, 2) launching investigations on population dynamics, in order to support population recovery and 3) enhancing the limited dispersal potential in order to promote progressive recolonization of former areas.

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Appendices

Appendix I Differences (matched-pair t-test) in available biomass (g) in coniferous vs broadleaf woodlands in the Alps, with respect to overall biomass and the two dominant prey categories.

Group	Whole period n = 60			May n = 12			June n = 12		
	df	t-Ratio	Prob > t	df	t-Ratio	Prob > t	df	t-Ratio	Prob > t
Total biomass	59	0.520	0.605	11	1.324	0.212	11	1.417	0.184
Lepidoptera	59	1.966	0.054	11	1.546	0.151	11	2.043	0.051
Diptera	59	1.045	0.300	11	1.424	0.182	11	1.243	0.240

Group	July n = 12			August n = 12			September n = 12		
	df	t-Ratio	Prob > t	df	t-Ratio	Prob > t	df	t-Ratio	Prob > t
Total biomass	11	0.979	0.349	11	0.247	0.809	11	0.949	0.363
Lepidoptera	11	1.170	0.267	11	0.270	0.792	11	0.342	0.739
Diptera	11	0.087	0.933	11	0.148	0.885	11	1.197	0.256

Appendix II Differences (matched-pair t-test) in available biomass (g) in coniferous vs broadleaf woodlands in the six study site used for the comparison between Swiss lowland vs Swiss Alps, with respect to overall biomass and the two dominant prey categories.

Group	Whole period n = 30			May n = 6			June n = 6		
	df	t-Ratio	Prob > t	df	t-Ratio	Prob > t	df	t-Ratio	Prob > t
Total biomass	29	0.184	0.855	5	1.024	0.353	5	0.115	0.913
Lepidoptera	29	0.820	0.419	5	2.449	0.058	5	0.493	0.643
Diptera	29	1.306	0.202	5	0.834	0.442	5	0.595	0.578

Group	July n = 6			August n = 6			September n = 6		
	df	t-Ratio	Prob > t	df	t-Ratio	Prob > t	df	t-Ratio	Prob > t
Total biomass	5	1.181	0.291	5	0.769	0.477	5	1.863	0.122
Lepidoptera	5	5.500	0.003	5	0.356	0.736	5	1.930	0.111
Diptera	5	0.030	0.977	5	0.560	0.600	5	2.587	0.049