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# Ecological factors affecting the distribution of the sibling species

# Pipistrellus pygmaeus and Pipistrellus pipistrellus in Switzerland

Diplomarbeit der Philosophisch-naturwissenschaftlichen Fakultät der Universität Bern

vorgelegt von

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# **Summary**

In recent years, the newly recognised bat species *Pipistrellus pygmaeus* was discovered in many European countries, including Switzerland. It is the sibling species of the widely distributed P. pipistrellus. While, for example in the UK many records have been made, in Switzerland observations remained very rare. Thus, the aim of this study was to investigate distribution, abundance and habitat preferences of the two sibling species. Recordings of bat calls were made on 20 road transects distributed over the whole of Switzerland. The recorded echolocation calls were represented as sonograms and attributed to species by way of discriminant function analysis. Additional information concerning the distribution of *P. pygmaeus* were gathered from local bat experts. In order to analyse habitat requirements of both species on the basis of presence data only, the spatially explicit "Ecological Niche Factor Analysis" was applied. The overall relation of observations of P. pygmaeus vs P. pipistrellus on transects was 1:33; in Switzerland, P. pygmaeus is much rarer than its sibling species. The fact that P. pipistrellus was recorded on all transects reflects its wide distribution. In contrast, P. pygmaeus was only found on six transects in four regions: in the Rhine valleys (Southeastern Switzerland), in the canton of Geneva (SW-CH), in the Bernese Oberland (N Central Alps) and in the canton of Ticino (S-CH). Thanks to additional observations, reproduction for *P. pygmaeus* could be confirmed in Lucerne (Central CH), Ticino and Lake Constance (NE-CH)). Analysis of habitat requirements shows that *P. pygmaeus* is confined to a small range of habitats. This species only occurs in structured landscapes (hedgerows, woods and open forests) combined with urban areas in the vicinity of wide rivers of the lowlands. It reacts very sensitively to changes in its habitat. While P. pipistrellus prefers habitats very similar to those of P. pymaeus, it - in contrast to its sibling species - is very tolerant of deviations. Both species are more abundant in Southern Switzerland. On the basis of Habitat Suitability maps, we expect *P. pygmaeus* to occur in additional areas (mainly river valleys) in Switzerland where it has been overlooked in the past. Its foraging habitat does not seem to be threatened at the moment, but due to its scarcity, P. pygmaeus is a potentially endangered species in Switzerland. Its presence in high probability areas needs to be confirmed and known roosts need to be monitored carefully.

# Zusammenfassung

In den letzten Jahren wurde die neu beschriebene Fledermausart Pipistrellus pygmaeus in vielen europäischen Ländern beobachtet, auch in der Schweiz. P. pygmaeus ist Zwillingsart zur weit verbreiteten P. pipistrellus. In der Schweiz blieben Beobachtungen sehr selten, ganz im Gegensatz zu bspw. Grossbritannien. Ziel dieser Arbeit war es, mehr über Häufigkeit, Verbreitung und Lebensraumansprüche dieser beiden Arten in der Schweiz zu erfahren. Auf 20 Strassentransekten, verteilt über die Schweiz, wurden Ultraschallrufe von Fledermäusen aufgenommen. Diese wurden als Sonogramme dargestellt und mittels Diskriminanzanalyse den beiden Arten zugeordnet. Zusätzliche Meldungen zu Beobachtungen von P. pygmaeus stammten von regionalen Fledermausfachleuten. Zur Analyse der Habitatsnutzung der beiden Arten wurde die räumlich auflösende "Ecological Niche Factor Analysis" verwendet. Das Verhältnis der Rufsequenzen P. pygmaeus zu P. pipistrellus betrug auf den Transekten 1:33 - P. pygmaeus ist also viel seltener. P. pipistrellus wurde auf allen Transekten registriert, was deren weite Verbreitung herausstreicht. Im Gegensatz dazu wurde P. pygmaeus nur auf 6 der 20 Transekte beobachtet. Die sind zudem beschränkt auf vier Regionen: Rheintal (GR), Kanton GE, Berner Oberland und Kanton TI. Dank den zusätzlichen Beobachtungen konnten Fortpflanzungsnachweise in den drei Regionen Luzern, Locarno, Bodenseegebiet erbracht werden. Untersuchungen der Lebensraumansprüche zeigen, dass P. pygmaeus auf eine kleine Auswahl von Habitaten beschränkt ist. Ihr Auftreten hängt sehr vom Vorkommen breiter Flüsse in der Nähe von strukturierten Landschaften und von menschlichem Siedlungsraum in tiefen Lagen ab. Sie reagiert sehr sensitiv auf Abweichungen ihres optimalen Habitattyps. P. pipistrellus zeigt zwar ähnliche Vorlieben für Optimalhabitate, ist aber im Gegensatz zu ihrer Zwillingsart sehr tolerant gegenüber Abweichungen. Gemäss den Karten potentieller Verbreitung ist zu erwarten, dass P. pygmaeus in zusätzlichen Gebieten innerhalb der Schweiz, insbesondere in Flusstälern, vorkommt, da sie dort von P. pipistrellus bisher nicht unterschieden wurde. Laut vorliegenden Informationen sind ihre Jagdgebiete zur Zeit nicht bedroht, jedoch muss die Art aufgrund ihrer Seltenheit als potentiell gefährdet eingestuft werden. Wir empfehlen, ihr Vorkommen in Gebieten mit hoher Auftretenswahrscheinlichkeit zu bestätigen, bzw. bekannte Kolonien zu überwachen.

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# **1** Introduction

Nowadays, many animal and plant species are declining both in their distribution range as well as population size, mostly due to man's activity (Primack 1998). In order to prevent further decline of threatened species, their status including distribution and population numbers as well as their habitat preferences must be known (Derrickson et al. 1998). It is, therefore, crucial to discern contrasting habitat requirements for different species, especially for morphologically similar ones. Multivariate models analysing ecological variables provide powerful tools to investigate these questions. Integrated into Geographical Information Systems (GIS), they are even able to predict habitat suitability for animal and plant species. Identification of cryptic species, species that look very similar from a morphological point of view, is a long-lasting scientific problem and commonly found in a wide variety of taxonomic groups (Jones 1997). New molecular methods such as Polymerase-Chain Reactions (PCR) for DNA- and Electrophoresis for protein-analysis allowed novel insights in taxonomy and revealed numerous new species, even within well-known groups such as mammals (Yoder et al. 2000, Mayer & von Helversen 2001a).

Occurrence of cryptic diversity is regarded to be very common within the order Chiroptera, class Mammifera (Jones 1997). Even though bats are - at least in Europe - a well studied group, the exact number of species remains unknown, even on this continent (Mayer & von Helversen 2001a). In the last forty years, three new species (Plecotus austriacus, Myotis brandtii, Pipistrellus pygmaeus) were discovered in the family Vespertilionidae (Mayer & von Helversen 1999). More recently, even more species are discussed in the same family: in the genus Myotis, von Helversen et al. (2001) described M. alcathoe. This species was thought to occur on the Balkan peninsula only, until Ruedi et al. (2002) found it in France, too. In the genus *Plecotus* even three new species are argued about. Firstly, the subspecies Plecotus austriacus kolombatovici was upgraded to the true species *Plecotus kolombatovici* (Spitzenberger et al. 2001, Mayer & von Helversen 2001a, Kiefer et al. 2002). Plecotus alpinus (Kiefer & Veith 2002; = *P. microdontus*, Spitzenberger et al. 2002 – see Kock 2002) is described for mainland Europe and Plecotus sardus for Sardinia (Mucedda et al. 2002). There are ongoing investigations whether *Plecotus alpinus* truly is a new species or whether it is identical to a *Plecotus* species known from the Near East (M. Ruedi, pers. comm.). At least two of these four newly described species are also found in Switzerland: *Plecotus alpinus* in canton of Grisons (Kiefer & Veith 2002) and Valais (R. Arlettaz & M. Ruedi, pers. comm.) and *Myotis alcathoe* from a single capture in the Jura Mountains of canton of Vaud (M. Ruedi, pers. comm.) in September 2002.

Worldwide there are nearly 1000 bat species known (Hausser 1996), but it can be supposed that the pattern with cryptic sibling species found in Europe is repeated in many less well-known regions of the world (e.g. Ochoa et al. 2000 for South America). Exact species identification is necessary for understanding species' specific habitat requirements. Knowledge of their habitat preferences in turn is a crucial requirement for conservation measures.

It is problematic to determine niche separation in morphologically nearlyidentical sympatric bat species. Many authors predict only small differences if any at all (Aldridge & Rautenbach 1987, Willig & Moulton 1989, Findley 1993). In practice, however, substantial niche separations between sibling species have been found (Arlettaz & Perrin 1995, Arlettaz et al. 1997, Barlow & Jones 1997a, Mayer & von Helversen 2001a). Predictions of ecological differences derived from echolocation call structure and wing morphology usually are confirmed by studies of resource partitioning with different hunting behaviour and habitat use (Furlonger et al. 1987, Barlow 1997, Vaughan et al. 1997a, Arlettaz 1999).

Integrating the new taxonomical knowledge into an eco-spatial analysis is a prerequisite for envisioning sound conservation measures in order to protect the focal species. We present here a study of the two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*.

# **1.1** The status of the pipistrelle sibling species

#### 1.1.1 Discovering the existence of P. pygmaeus

The common pipistrelle *Pipistrellus pipistrellus* (Schreber 1774) is one of the most abundant (Walsh et al. 1995, Jones et al. 1996) and best-known bat species in Europe (Jones 1999). For a long time it has been considered to consist of one single species.

Although differences in search call frequency were noted early within the species complex (Ahlén 1981, Weid 1987, Zingg 1990), the idea whether *P. pipistrellus* belongs to two phonic types resulting in two cryptic species was concretised only by Jones & van Parijs (1993). They raised the question whether the bimodal distribution of echolocation calls (search calls) in *P. pipistrellus* may reflect the existence of two distinct bat species. For Britain, they were able to show that the species call at two distinct frequency ranges, 46 kHz and 55 kHz, respectively. Yet, the two species remained undistinguishable when analysing wing morphology applying multivariate statistics. From then on, these two groups were referred to as the 45 kHz and 55 kHz phonic types, respectively.

In the following years studies of call structure, behaviour and ecology supported the presence of two distinct, sympatric species: Park et al.'s (1996) analysis of mating groups between August and October showed that none of them ever contained more than one phonic type, even though they were sympatric. The authors conclude that this pattern of assortative roosting leads to reproductive isolation and might have contributed to the evolution of the two species. As one possible factor contributing to the separation is the observation of Barlow & Jones (1997a) who found differences in songflight calls between the two types. If the female uses these calls for operating mate choice, the differences between the species may preserve their reproductive isolation. Barlow & Jones (1997b) noted that social calls emitted when hunting only warn off other bats that belong to the same phonic type. Barlow (1997) also reports dietary differences for the two phonic types. Some prey species, e.g. the dung fly Scatophaga stercoraria, are more commonly found in the 45 kHz phonic type. The latter individuals are supposed to forage more frequently over cattle pasture than the 55 kHz phonic type ones. The latter prefer rivers and lakes (Vaughan et al. 1997a, Oakeley & Jones 1998). Overall, the 45 kHz phonic type was found hunting over a wider range of habitats in Britain (Vaughan et al. 1997a).

Molecular confirmation for two species was given by Barratt et al. (1995 & 1997) through mitochondrial DNA analysis. Between the two phonic types, the mitochondrial genome differed of at least 11% in the cytochrome *b* gene. These

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findings were confirmed for the *ND*1 gene (10-13% difference; Mayer & von Helversen 1999 & 2001a).

Morphological distinction is by far not as clear as discrimination by echolocation call and DNA analysis. Measurable parameters such as skull morphology (Barlow et al. 1997), and wing morphology (forarm length, 3<sup>rd</sup> & 5<sup>th</sup> digit; Barlow & Jones 1999, Häussler et al. 2000) indicate that the 55 kHz phonic type is slightly smaller than its sibling species. But these findings are limited by the fact that there is a big overlap in these characteristics between the two species. Consequently, discrimination of these species with these features is not feasible for single specimens. A few qualitative characteristics for morphological distinction are proposed by Häussler et al. (2000) and von Helversen & Holdried (2003). They are presented and discussed in Appendix 1. Only a combination of different characters and good knowledge of the two species may yield in accurate external determination (Häussler et al. 2000, von Helversen & Holdried 2003, personal observations).

#### 1.1.2 Taxonomical status

The genus *Pipistrellus* consists of about 50 species (Schober & Grimmberger 1998). *Pipistrellus* belongs to the family *Vespertilionidae*, which are the biggest bat family (ca. 317 species, at least 26 in Europe) with a worldwide distribution (Schober & Grimmberger 1998, Mayer & von Helversen 2001a).

All the findings presented above supported the proposition that the 55 kHz phonic type belongs to a so far unrecognised species. Therefore, Jones & Barratt (1999) proposed the name *Pipistrellus pygmaeus* (Leach 1825) for the new species, referring to a previous description of a specimen that later had been mistakenly attributed to *P. pipistrellus*. They suggested to keep the old name *P. pipistrellus* (Schreber 1774) for the 45 kHz type. As it seems uncertain whether the holotype for *P. pygmaeus* indeed belongs to this very species, different authors prefer the name *P. mediterraneus* (Cabrera 1904), referring to a subspecies described from Spain (Häussler et al. 1999, Häussler et al. 2000, von Helversen et al. 2000). As this discussion is still ongoing (Jones 2001, van Cakenberghe 2001) and a decision by the commission of nomenclature is pending (von Helversen & Holdried 2003), it is pointed out that the name applied here is provisionary.

In cases of doubt about a specific attribution to *P. pipistrellus* or *P. pygmaeus* we followed the following rule: *P. pipistrellus sensu stricto* (*s.str.*) refers to cases where discrimination did take place whereas *P. pipistrellus sensu lato* (*s.l.*) concerns identifications without discrimination (Hanak et al. 2001). The latter case is the more common, especially in older data.

**1.1.3 Geographical distribution of the pipistrelle sibling species in Europe** The range of *P. pipistrellus s.l.* includes the Palaearctic with most of Europe south of about 63°-64° N, some parts of Southwestern Asia and Northern Africa (Jones 1999). If we consider the two species separately, their overall distribution remains similar (Mayer & von Helversen 2001b), with in many countries the two species found in sympatry: Switzerland, Great Britain, Ireland, France, Italy, Germany, Spain, Greece, and Slovenia (Fig. 1, App. 2). The following variations are found: even though *P. pipistrellus s.str.* is considered to be the most common species in central Europe (Mayer & von Helversen 2001b), it is not known from Scandinavia with the exception of very rare observations in the provinces of Gotland and Skane in Southern Sweden as well as Jutland in Denmark (Ahlén 1981, Baagoe 2001). In general, P. pipistrel*lus* is sought to be somewhat rarer near the edge of its distribution range (e.g. in Ireland, Scotland and the Mediterranean countries) than its sibling species (Barratt et al. 1997, Jenkins et al. 1998, Hanak et al. 2001, Mayer & von Helversen 2001b).

### 1.1.4 Knowledge about P. pipistrellus and P. pygmaeus in Switzerland

The present study is the first survey, which is addressing the distinction and distribution of the two species in Switzerland; so far, there is only little information available on the presence and abundance of *P. pygmaeus*. Therefore, all data mentioned for Switzerland in general, have been referred to *P. pipistrellus s.l* upto now.



Fig. 1 : Locations of *P. pygmaeus* (†) and *P. pipistrellus s.str.* (?) in Europe, black and white symbols indicate places where both species are found; modified after Mayer & von Helversen 2001b; published records (Ahlén 1981, Miller & Degn 1981, Weid 1987, Zingg 1990, Jones & van Parijs 1993, Schorr 1996, Russ 1996, Kapeteyn 1997, Barratt et al. 1997, Letard & Tupinier 1997, Vaughan et al. 1997a, Jenkins et al. 1998, Ruedi et al. 1998, Koch & von Helversen 1999, Herzig 1999, Lustrat 1999, Barlow & Jones 1999, Limpens 2000, Häussler et al. 2000, Russo & Jones 2000, Hermanns et al. 2001, Mayer & von Helversen 2001b, Pocha 2001, Hoch 2001, Presetnik et al. 2001, Baagoe 2001, Hanak et al. 2001, Wicht 2001, Zöphel 2001, Zöphel et al. 2002, Centro Protezione Chirotteri Ticino 2002a and 2002b, Dietz 2002; details per country in Appendix 2) and own observations (this thesis).

*P. pipistrellus s.l.* occurs from the plains of the Central Plateau up to the Jura Mountains and in most larger alpine valleys, excluding the Engadin valley in the East. The data analysed in the distribution atlas of Swiss mammals includes 3000 observations stemming from 1200 different km<sup>2</sup>, indicating its wide distribution in Switzerland (Haffner & Stutz 1996). Stutz & Haffner (1985) examined the presence of 112 roosts in Eastern Switzerland. The roosts were found between 406 m and 1274 m. The highest maternity roost is known at

1500 m from the canton of Valais, Southern Switzerland (Arlettaz et al. 1997). *P. pipistrellus* is commonly found in climatic favourable regions of the Prealps and the hilly parts of the Central Plateau avoiding the open plains. Especially the highly structured Prealps, where many stretches of running water occur, seem to fulfil its habitat requirements. In these regions they dominate the local bat fauna (Haffner & Stutz 1996).

Zingg (1990) had assigned Swiss calls of *P. pipistrellus* to two groups, *P. pipistrellus* 1 (echolocating with the frequency constant part above 50 kHz) and *P. pipistrellus* 2 (between 44 and 46 kHz). They can be considered as first evidence that both species do occur sympatrically in Switzerland. But it was only in the year 2000, when M. Moretti and collaborators (pers. comm.) found several roosts in bat boxes in the Bosco Isolino, Locarno (canton Ticino, Southern Switzerland) that the species' presence was assessed. Further investigations revealed more locations of *P. pygmaeus* in Ticino (Wicht 2001, Centro Protezione Chirotteri Ticino 2002a and 2002b).

Further indications were found when analysing the database of *P. pipistrellus s.l.* in Eastern Switzerland (based at the Eastern Centre of the Swiss Bat Conservation, Zürich), assuming that specimen with forarm length (FA) of <30.0 mm belong to *P. pygmaeus*. Results showed that the specimen with FA of <30.0 mm are very rare (79 vs. 2305 records) but found across the whole study area. Yet, when catching and analysing the echolocation calls of about 100 individuals of ten different nursery colonies in the cantons of Argovia and Solothurn in central Northern Switzerland in 1998, the presence of *P. pygmaeus* could not be confirmed. All specimens belonged to *P. pipistrellus s.str.* (F. Bontadina & A. Beck, unpubl. data). In the year 2000, two single specimen of *P. pygmaeus* were found in the small princedom of Liechtenstein which is adjacent to Switzerland (Hoch 2001).

In the Southern part of the Rhine valley in Germany, *P. pygmaeus* has been found in great numbers in late summer/early autumn. The seasonal increase lead to the hypothesis that *P. pygmaeus* may breed in the North and migrate to these latitudes on their way to hibernating roosts only (Häussler et al. 2000, von Helversen & Holdried 2003). This suspicion is contradicted by the fact that *P. pipistrellus s.l.* are rarely caught on the Col de Bretolet (Valais; Arlettaz et al.

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1997), which could indicate that these species do not migrate to the South, over the Alps as do other typically migrating European bats.

Considering the lack of information about the status and distribution of *P. pygmaeus* and its ecological seperation from *P. pipistrellus* in Switzerland, the following questions were addressed in this work: 1) Where and when do the sibling species occur in Switzerland, 2) which ecological factors influence distribution and 3) does *P. pygmaeus* reproduce in CH.

# 2 Materials and Methods

# 2.1 Research design

The study was split into three parts:

**Part I:** The design chosen in this study is called "gradsects" (Austin & Heyligers 1989), which is close to a proportional random-stratified sampling (Hirzel & Guisan 2002). During both reproductive and post-reproductive seasons recording of echolocation calls were performed on 20 transects, which were distributed over all bioregions of Switzerland. Based on an analysis of echolocation calls with sonograms, the bat species were determined using the discriminant functions developed by Zingg (1990). In this way representative samples of observations of the two species were obtained for the entire country. Additional observations of *P. pygmaeus* were collected by the means of an inquiry to bat experts.

**Part II:** The analysis of ecological parameters was performed employing the "Ecological Niche Factor Analysis" (ENFA; Hirzel et al. 2002a). It consists of the following two steps: 1) Based on species presence map, correlations between ecological predictors and independent factors (marginality and specialization) were computed. 2) On the basis of the independent factors habitat suitabilities were calculated.

**Part III:** Reproduction was confirmed for Switzerland through catching individuals at maternity roosts. Additionally, morphological characteristics were recorded.

#### 2.1.1 Study area and biogeographic regions

The study area covers the whole of Switzerland and the princedom of Liechtenstein below 1500 m, which corresponds approximately to the maximum altitude of the distribution of *P. pipistrellus s.l.* (Arlettaz et al. 1997, Holzhaider & Zahn 2001). The total area investigated (25'943 km<sup>2</sup>) includes the main valleys in the Alps, Prealps, Southern Switzerland, the Central Plateau and the Jura range. Switzerland was split into six biogeographic regions, following the criteria proposed by Gonseth et al. (2001). These biogeographic regions covered between 9 and 28 % of Switzerland (for details see Fig. 2).



Fig. 2: Switzerland split into six biogeographic regions (in brackets their percentage of total area of Switzerland): Jura Mountain (10.4%), Plateau (27%), Northern Alps (27.8%), Western Central Alps (Canton of Valais; 11.7%), Eastern Central Alps (parts of the Canton of Grisons; 14.1%) and Southern Switzerland (mostly Canton of Ticino; 8.9%); figure from BFS (2001).

#### 2.1.2 Selection of transects

Twenty transects were attributed to the six biogeographic regions according to a stratified sampling design (criteria: at least two transects per region in order to have a minimum number of replicates, below 1500 m elevation). This procedure resulted in the following transects: six in the Plateau, five in the Northern Alps, three in Southern Switzerland (Ticino), two each in the Western Central Alps (Valais), in the Eastern Central Alps (Grisons), and in the Jura Mountains (Fig. 3). The transects in one region provide a representative sample of available elevation and habitat types below 1500 m a.s.l. Every transect was 40 km long.



Fig. 3: Distribution of the 20 transects over Switzerland; Eastern Alps (EA I-II), Jura Mountain (J I-II), Plain (P I-VI), Northern Alps (NA I-V), Southern Alps (SA I-III), Western Alps (WA I-II).

The single transects were laid according to the following priorities: 1) Choose a transect along an altitudinal gradients. 2) Include all common habitat types of a region. 3) Include typical pipistrelle habitat types such as human settlements and open water. Consider also small river- and lakeside habitats (riparian forest) even though they might be slightly overrepresented. 4) Consider a continuing network of secondary streets, trying to avoid main roads. This criterion was aimed at avoiding dangerous night travelling (low speed due to echolocation call recording) with a car.

#### 2.1.3 Study period

To account for possible migratory behaviour, the investigation was split in two research periods: the 20 transects were run twice (= 2 tours), first in the reproduction period (1/6 - 31/7 2002) and second in the post-reproduction period (1/8 - 30/9 2002). In total we carried out 40 tours (1600 km overall).

#### 2.1.4 Sampling design

Within every biogeographic region all transects were surveyed in a consecutive sequence before moving on to the next region. The visit to regions followed vegetation phenology (Schmid et al. 1998), which influences insect development and thus the reproductive calendar of bats: Southern Switzerland – Western Central Alps – Plateau – Jura Mountain – Northern Alps – Eastern Central Alps.

One transect was surveyed per night. The nights must have been suitable regarding weather conditions (no rainfall, no strong wind, minimum temperature of 10 degrees) and moon visibility (no full moon). Travelling in the car was done at an average speed of 20-30 km/h. The performance of a single transect usually took four hours resulting in an average velocity of approximately 10 km/h (see Table 1 for details).

	Tour start time	Tour end time		Tour duration
Earliest	20:30	23:35	Shortest	3 h
Latest	23:00	04:00	Longest	6:05 h
Average	21:54	02:07	Mean (+/- SD)	4:13 (+/- 0:38) h
			Sum	168:53 h

Table 1: Start time, end time and tour duration (n=40).

The time of survey coincided with the time of highest bat activity. Barlow & Jones (1997b) found that bats reached their peak activity in accordance with highest insect availability, starting 20 minutes after sunset for about three hours. Therefore, start of transect was fixed shortly after sunset (Table 1).

# 2.2 Recording of echolocation calls

According to their echolocation call bats can be classified roughly into one of the following species groups in Europe (Ahlén 1981, Weid 1987, Zingg 1990, Vaughan et al. 1997b, Russ 1999, Parsons & Jones 2000, Russo & Jones 2002): **Category 1:** Genus *Rhinopholus*. Constant frequency (CF) calls beginning with a short upward sweep and ending with a downward sweep, long duration (up to 50 ms) but short-ranged (less than 5 m); at 110 kHz for *R. hipposideros* and at 83 kHz for *R. ferrumequinum*. On transects, no calls belonging to this category were recorded.

**Category 2:** Genus *Pipistrellus, Eptesicus, Nyctalus, Vespertilio, Hypsugo, Miniopterus, Tadarida.* Frequency-modulated (FM) calls terminating with a nearly constant frequency (CF) part (Fig. 4 A & B) with Frequencies of Maximum Energy (FMAXE) varying between 12 kHz (*Tadarida teniotis,* audible by ear) and 55 kHz (*P. pygmaeus;* Fig. 4A). In the Heterodyne modus, a fully sounding, dull noise is indicating the FMAXE of a FM-CF call. According to height of these CF parts, bats could be classified into five different groups (Table 2). For details how to discriminate species of the *Pipistrellus* group see 2.2.2, 2.2.3 and Fig. 4.

Fig. 4: Typical search calls of the sibling pipistrelle species.

A) *Pipistrellus pipistrellus* with end frequencies around 45.9 KHz (Beggingen SH, 6.6.2002, 23:10);

B) *Pipistrellus pygmaeus* with end frequencies around 54.4 KHz (Kreuzlingen, 14.7.2002, 22:50); frequency x 10; time/10. Fig. F. Bontadina.





2)								
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18	6.5 sec 3.	7 0 sec	7.5 sec	8.0 sec	8.5 sec	9.0 sec	9.5 sec	

B)

**Category 3:** Genus *Plecotus, Myotis.* Low amplitude, steep FM calls with FMAXE between 32 kHz (*Plecotus auritus*) and 58 kHz (*Myotis emarginatus*). Very difficult to attribute to single species. In the heterodyne modus, this call produces a "ticking" sound only, indicating that species is using a FM-call only (Ahlén 1981).

**Category 4:** Genus *Barbastella*. Two differently structured calls, one FM sweep followed by a characteristic convex frequency-time progression. In the heterodyne modus, calls of this category sound similar to category 3.

Table 2: Species groups according to FMAXE determined by the heterodyne modus.

Species group	FMAXE around	
Tadarida teniotis	12 kHz	
Nyctalus noctula	18-21 kHz	
N. leisleri, Vespertilio murinus, Eptesicus	24-30 kHz	
serotinus		
E. nilsonii, Hypsugo savii	31-36 kHz	
Species of genus Pipistrellus	> 37 khz	

On transects, all bat calls were recorded using a Pettersson S980 bat detector (Pettersson Electronic AB, Uppsala, Sweden). With the one ear it was listened to all frequencies, applying the broadband mechanism "Frequency Division" (FD) in order to hear any approaching bat. Simultaneously, with the other ear was paid attention to the sound of the heterodyne mode while manually adjusting its frequency. As soon as an echolocation call was noted, the Time Expansion (TE) mechanism was triggered manually. Subsequently a sequence of 3 s was recorded and time-expanded (10x) with a sampling frequency of 350 kHz (resolution: 8 bits) onto metal dioxide tapes using a Sony WM-D6C Stereo Cassette-Recorder (Sony, Tokyo, Japan). To obtain the exact location for the record, x- and ycoordinates of the Swiss grid system were noted with a GPS (Garmin etrex, Olathe KA, USA). As the car was stopped for recording the call sequences onto tapes, distinction of individual bats and, thus, estimation of the number of bats present at a given location is practically impossible (Russ 2003). Neither has it been possible to know whether bats heard near previous records represent the same individuals. Therefore, it was decided to ignore bat calls of the same FMAXE within the next 500 m of a previous record. This enabled to achieve data independency and to avoid spatial correlation for the subsequent ENFA.

#### 2.2.1 Sound analysis with Canary

All bat calls were analysed later in the lab with the program Canary 1.2.4 (Charif et al. 1995). Sampling frequency was set to 440 kHz, with 8 bits/ sample, and a 512 points Fast-Fourier-Transformation with a Blackman window analysis. For spectrograms a resolution of 861.3 Hz was applied.

#### 2.2.2 Species identification: discriminating the sibling species

The main difference between the sibling species lays in the difference in the CF part of the call, which comprises EF and FMAXE. In fact, these two frequencies are highly correlated and often distinguish only in few kHz (0.1-3.2 kHz for *P. pygmaeus* and 0.4-2.7 kHz for *P. pipistrellus*; Vaughan et al. 1997b, Parsons & Jones 2000, Russo & Jones 2002). Many authors use only one of these two characteristics to discriminate between species (Jones & van Parjis 1993, Park et al. 1996, Barlow & Jones 1999, Hanak et al. 2001, Mayer & von Helversen 2001b, Braun et al. in prep.).

Crassian	Country	FMAXE	SD		Assthar
Species		(kHz)	(kHz)	n	Author
		53.2	+/-1.76	220	Barlow & Jones 1999
	U.K.	53.8	+/- 1.7	59	Vaughan et al. 1997b
		55.1	+/-2.62	398	Jones & van Parijs 1993
	Germany	57.0	+/-2.2	88	Mayer & von Helversen
Р.	Germany	0110	17 2.2	00	2001b
pygmaeus	Greece	55.9	+/-1.7	168	Mayer & von Helversen
					2001b
	Spain	55.2	+/-1.3	25	Mayer & von Helversen
	opum	00.2			2001b
	Italy	57.7	+/-2.35	27	Russo & Jones 2002
		45.1	+/-1.77	181	Barlow & Jones 1999
	U.K.	46.0	+/-1.77	60	Vaughan et al. 1997b
		46.3	+/-1.97	174	Jones & van Parijs 1993
	Cermany	45.2	+/-17	231	Mayer & von Helversen
Р.	Germany	10.~	1/ 1.7	~01	2001b
pipistrellus	Greece	46.2	+/-19	351	Mayer & von Helversen
	Greece	10.~	17 1.0	001	2001b
	Spain	46.2	+/-0.8	114	Mayer & von Helversen
	Span				2001b
	Italy	46.9	+/-1.81	61	Russo & Jones 2002

Table 3: Values for FMAXE of *P. pygmaeus* according to various sources.

For the purpose of this study, for species identification the linear discriminant analysis of Zingg (1990), based mainly on bat calls from Switzerland, was applied. Thus, the following five parameters were determined for every echolocation call (frequency dimensions measured in the centre of call width): Start frequency (SF), End frequency (EF), Central frequency (ZF; frequency at T/2), Frequency of Maximum Energy (FMAXE), Duration (D).

These parameters were calculated using the classification functions by Zingg (1990). He developed an equation for all 12 species belonging to category 2. Scores indicate the most probable species (higher value). For the two sibling species, the equations are the following (for abbreviations see above):

#### P. pygmaeus

=(173.94)\*(LN(D))-124.234\*(LN(SF))-0.502\*(LN(ZF))+324.692\*(LN(FMAXE))+1489.316\*(LN(EF))-3543.53)+1489.316\*(LN(EF))+1489\*(LN(EF))+148\*(LN(EF))+

#### P. pipistrellus

 $= (171.277)^*(LN(D)) - 116.986^*(LN(SF)) + 0.386^*(LN(ZF)) + 314.498^*(LN(FMAXE)) + 1412.653^*(LN(EF)) - 3231.204^*(LN(EF)) + 1412.653^*(LN(EF)) - 3231.204^*(LN(EF)) + 314.498^*(LN(EF)) + 314.498^*(LN(EF)$ 

Between one and eleven echolocation calls from a single sequence were analysed before deciding upon species. If no clear attribution was achieved, the call sequence was considered as unidentified and consequently discarded.

Due to clear interspecific differences all studies have found only little overlap between the sibling species (Table 3), e.g. concerning approximately 2% of bat calls in UK (G. Jones, pers. comm.). Thus, to increase precision of species discrimination different authors proposed to exclude search calls within a certain range. For the purpose of this study calls with FMAXE between 50 and 51 kHz were excluded. In this case reliability of correct identification is expected to be between 95% (Jones & van Parijs 1993, Russo & Jones 2000) and 100% (Barlow & Jones 1997a).

Additional information for species identification could be obtained from social calls (Barlow & Jones 1997a and 1997b, Russ et al. 1998, Russo & Jones 1999). The social call is a sweep that undulates between 35 and 18 kHz approximately two to four times in 35 ms, and is generally used in an agonistic context (Russ et al. 1998). Frequency and number of components were used to differentiate between species. Social calls have a mean frequency of 22 kHz (Russ 1999) and a maximum energy at about 20 kHz (Russ et al. 1998). If they are composed of two or three components they are assigned to P. pygmaeus, while those consisting of four to five components are assigned to *P. pipistrellus*. In this way 90% of the observations are correctly classified, reaching a value that does not represent enough reliability for species discrimination on its own (Barlow & Jones 1997b). Barlow & Jones (1997a) showed that songflight calls (also labelled mating calls; Russ et al. 1998) recorded between August and September are very similar to social calls with the difference that only males around mating roosts emit them. Therefore, it was assumed that their function is female attraction. 100% of individuals were classified into the correct species by a discriminant analysis based on songflight calls (Barlow & Jones 1997a).

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#### 2.2.3 Differentiating P. pipistrellus and P. pygmaeus from other species

Beside calls of the sibling species, search phase calls of additional species, which show the typical FM-CF pattern in this frequency range, may lead to identification problems (Zingg 1990, Russo & Jones 2002). Russo & Jones (2002) point out that EF was the call characteristic that overlapped least between *Miniopterus schreibersii, Hypsugo savii* and the three pipistrelle species investigated (*P. kuhlii, P. pygmaeus* and *P. pipistrellus*, excluding *P. nathusii* which is rare in Italy). When discriminating echolocation calls of the genus *Pipistrellus*, the main problem does not occur between the sibling species but between *P. nathusii* and *P. kuhlii* (Zingg 1990, Russo & Jones 2002). The analysis of social calls may help to distinguish between them (Russo & Jones 1999). For the purpose of this study these two species were grouped together. There is a small overlap in call frequency between *P. pipistrellus* and *P. nathusii/kuhlii* (Zingg 1990, Russo & Jones 2002). If the discriminant function analysis of five or more calls of one sequence of these three pipistrelle species left any doubts about species belonging, the observation was discarded.

A clear distinction between *P. pygmaeus* and *M. schreibersii* is not always easy (Zingg 1990, Russo & Jones 2002). Absence of similar social calls in the latter helps identification. Additionally, *M. schreibersii* is very rare in Switzerland, regularly known at only two caves in the Jura Mountain (Moeschler 1996). Zingg (1990), in his extensive research in Switzerland, had recorded them in the Jura only. Therefore, in one case when species attribution between *P. pygmaeus* and *M. schreibersii* was not clear, the observation was attributed to *P. pygmaeus*. The observation originated from a region with known occurrence of the latter species (Bernese Oberland). Recently, *M. schreibersii* has not been noted in the canton of Berne (T. Fankhauser pers. comm.).

# 2.3 Sighting Probability & Descriptive Statistics

The unit for the estimation of the sighting probabilities were the surveyed square kilometres (= patch). On each of the two visits it was noted whether the species was detected or not, resulting in three possible "capture histories" for a single patch (1/1 = species detected on both visits; 1/0 = species detected only on the first visit; 0/1 = species detected only on the second visit. No patch dynamics was assumed (i.e. no occupied patch gets unoccupied from the first to the second visit and no unoccupied patch gets occupied from the first to the second visit). Consequently, the occurrence of these three capture histories is only due to the sighting probability. They were then analysed with a closed population capture-recapture model (Williams et al. 2002) that allow the estimation of the sighting probability, i.e. the probability that the species is sighted on a visit given that it occurs in the patch. Accordingly, sighting probability must be smaller than 1. These estimations were computed with the software MARK (White and Burnham 1999). Descriptive statistics followed the principles of Sokal & Rohlf (1994).

#### 2.4 Ecological Niche Factor Analysis (ENFA)

ENFA was performed applying the GIS-software Biomapper 2.1 (Hirzel et al. 2002b), which performs well when only presence data is available. ENFA compares the ecogeographical predictor distribution for presence data with the predictor distribution for the whole study area. Doing so, ENFA aims at summarising a large number of variously correlated ecogeographical variables (EGVs) into a small number of independent factors, which contain the major part of the habitat information (Hirzel et al. 2002a). The set of all cells of the study area defines a cloud of points in the environmental space, whilst the cells where the species has been observed are some subset of this cloud. ENFA is based on the concept of the ecological niche (Hutchinson 1957). This concept is based on the assumption that the occurrence of a species is limited to a certain range within the multidimensional space of ecological variables.

#### 2.4.1 Study Area and Ecogeographical Variables (EGV)

Switzerland below 1500 m was modelled as a raster map (cell size of 1 ha) based on the Swiss Coordinate System (plane projection), including 2'470'145 squares. The basic data for the ecogeographical maps was obtained from gov-ernmental databases (Table 4).

Source	Official database	Торіс
Federal Office of Statistics	AS85R (GEOSTAT	Cover use
	database)	
Federal Office of Statistics	DHM	Topography
Federal Office of Statistics	GWN	Hydrography
Federal Office of Topography	Vector 200	Land map
Federal Office of Meteorology	BIOCLIMM	Climatic maps
and Climatology		

Table 4: Sources of databases used for ecogeographical variables.

All variables must be quantitative. As provided, the topographic variables (Elevation, Slope, Exposition and Latitude) were already continuous. Ecological data such as land cover, hydrographical and anthropogenic data (forests, agriculture, rivers, villages etc.) were boolean (indicating presence/absence) and had to be quantified using the module "Distance" of the Program IDRISI 32.01 (Eastman 2002) and the module "CircAn" of Biomapper. Radius for frequency of occurrence calculations had to be calculated according to the species' home range. As such data was not available for the species seperately, it had to be reverted to information for home ranges of P. pipistrellus s.l. In northeast Scotland marked bats have been found foraging within an average radius of 1 km from the roost (Racey 1985). In 2002, F. Bontadina (unpubl. data) conducted a preliminary radio-tracking study of *P. pipistrellus s.str.* in the Eastern Alps of Switzerland. He found maximum distances of up to 4 km but a mean foraging distance of about 1 km for this species. Thus, a radius of 1 km was chosen for frequency analysis. Frequency describes proportion of cells within a circle of 1 km radius around the focal cell. An overview of all ecogeographical variables included in the analysis can be found in Table 5. The distributions of the EGV were normalised by the Box-Cox algorithm (Sokal & Rohlf 1994).

Table 5: List of ecogeographical predictors and their respective map quality used for Ecological Niche Factor Analysis

# EGV

### Map quality

## Topographical and Biogeographical EGV

Altitude	Quantitative
Slopes	Quantitative
Eastness	Quantitative (Sin [aspect])
Northness	Quantitative (Cos [aspect])
Latitude	Quantitative

#### **Ecological EGV**

_	
Meadow	Frequency
Alpine meadow	Frequency
Pasture	Frequency
Grass	Frequency
Forest edge	Proximity
Dense forest	Frequency
Open forest	Frequency
Bushy forest	Frequency
Hedgerow	Frequency
Bushy landscape	Frequency
Riparian forest	Frequency
Riparian vegetation	Frequency
Wetland	Frequency
Lake-border	Frequency
Wide rivers (> 12m)	Proximity
Small stream	Frequency

# Human related EGV

Town	Frequency
Village	Frequency
Single building	Frequency
Highway	Frequency

#### 2.4.2 Species data

Species data came from two sources: all data for *P. pipistrellus* and a portion of the observations of *P. pygmaeus* were obtained trough bioaccustic transects as described in 2.1. With a careful sampling design, covering all possible habitats, the number of presence points needed for ENFA can be minimized to as little as 20 or 30 points (A. Hirzel, pers. comm.). The number of EGVs is not to exceed the number of records included in the analysis.

In addition, supplementary observations for *P. pygmaeus* were collected by contacting the regional professionals involved in bat research and bat protection. If species recognition was not secure, further echolocation studies on sites were undertaken following the principles described in 2.2 in order to clarify species belonging. Species maps were computed applying the "Convertor" tool of Biomapper.

In this way, two sets of species data of presence maps for *P. pygmaeus* could be obtained, varying both in quantity and quality. One map, called species map A, originates from observations along transects only, which represent a rigid regime for data collection. In opposite to map A, species map B was accomplished through adding to transect data records stemming from findings by regional collaborators. In this way some regions are rather well investigated (e.g. Bernese Oberland, Geneva, Ticino) while in other regions topicspecific studies are lacking. So, map B is quantitatively better than map A but subject to potential biases due to non systematic data collection.

#### **2.4.3 Factor Calculation**

Species are expected to be non-randomly distributed regarding ecogeographical variables. In ENFA, variables of the cells with presence data are compared to the values of all reference grid cells. In this way factors are calculated in a multivariate way until all information is extracted. The first factor to be extracted is termed the "marginality factor". The second factor is the first "specialisation factor"; the next factor is the second specialisation factor, etc. This procedure is repeated until all information is extracted. For mathematical details see Hirzel et al. (2002a). At the end, the number of factors is the same as the number of ecogeographical variables but 1) they are uncorrelated and 2) the major part of the information is contained within the first factors. A species is expected to show some marginality (due to the fact that the species' mean differs from the global mean) and some specialization (the species' variance is lower than the global variance). A marginality factor close to one means that the species lives in a very particular habitat relative to the reference set. The first-ranked specialisation factors provide information upon the species' dependence on a specific variable. A randomly chosen set of cells is expected to have a specialization of one. Thus, any value exceeding this value indicates some form of specialization. The reciprocal of specialization is tolerance, with a value close to one indicating high tolerance to deviations of optimal habitat.

For *P. pygmaeus* two species mapscalled map A and B, were drawn (see above). Consequently, two ENFAs were calculated. Analysis of both maps with the same EGVs allows comparing them. For *P. pipistrellus* only one ENFA based on transect data was computed.

# 2.5. Habitat Suitability (HS) analysis

#### 2.5.1 Calculation

Habitat Suitability maps are calculated based on the independent factors obtained by the ENFA (2.4.3). The suitability defines the probability that a given cell is inhabited by the species. On one factor axis, calculation is based on a count of all cells from the species distribution that lay at least as far apart from the median than the focal cell. This procedure is repeated a number of times corresponding to the number of factors included in the HS calculation. This number of independent factors to be included is decided upon Mac Arthur's Broken-stick distribution (Hirzel et al. 2002a). As 25 EGVs were included in the analysis, factors explaining a fraction of 4% (= 100% : 25) or more were incorporated in HS calculation. Thus, 2 factors were included for computation of the HS for species map A of *P. pygmaeus*, 8 for the HS of map B and 13 factors for the HS of *P. pipistrellus*.

#### 2.5.2 Validation

The Jack-knife cross-validation (Fielding & Bell 1997) computes a confidence interval on the predictive accuracy of the HS model. The species locations are randomly partitioned into 100 mutually exclusive but identically-sized subsets. 99 partitions will be used to calibrate a HS model and the left-out partition will be used to evaluate it. This process is repeated 10 times, each time by leaving out a different partition. In this way a confidence interval on the prediction accuracy indices can be computed. Two indices demonstrating the accuracy of the distribution model are calculated. The Absolute Validation Index (AVI) is the proportion of validation points occurring in the predicted core habitat. This indicates the fraction of validation cells (in the left-out partition) that have a HS value greater than 50. This statistics gives an absolute assessment of the model quality. The Contrast Validation Index (CVI; equals the AVI minus the AVI that would have been obtained with a model predicting ubiquitous core habitat) gives an indication of how well the model discriminates poor from good habitat. It is indicating the fraction of these cells that are greater than 50 with deduction of those cells that achieve this result by chance. This statistics gives an indication of how well the model discriminates high suitable from low suitable areas.

# 2.6 Catching individuals of P. pygmaeus

Where *P. pygmaeus* was recorded, it was tried to confirm reproduction. At maternity roosts of *P. pipistrellus s.l.* located close to observation sites of *P. pygmaeus*, specimens were caught by hand netting (n=9). Roosts were controlled in Ticino (3), Lucerne (3), Grisons (2) and Thurgovia (1). Species identification was achieved with ultrasound recording and with morphological characteristics (von Helversen 1989). Reproduction was confirmed by checking the mammary glands of females; juveniles were identified by their cartilaginous joint of the 5<sup>th</sup> digit. Additionally, measurements of forearm length, 5<sup>th</sup> finger and weight were obtained.

# **3** Results

#### 3.1 Observations on transects

Overall, 1811 sequences of bat calls were recorded on transects. Of those, 236 (13%) were either of bad quality or could not be identified reliably; they were therefore excluded. Altogether, observations reached an overall density of 1.13 observations per road km (0.98 km<sup>-1</sup> for identified call sequences). The 1575 identified call sequences (697 in the reproductive and 878 in the post-reproductive season) were grouped into the six classes presented in Table 2 (results shown in Table 6). With the discriminant function (Zingg 1990), the *Pipistrellus* group was split further into species. In this way 250 observations were attributed to the *P. kuhlii/nathusii* call complex, data which was not considered further.

Species group	Number of observations	Fraction (%)
Myotis ssp., B. barbastella	57	3.62
Tadarida teniotis	7	0.44
Nyctalus noctula	69	4.38
N. leisleri, V. murinus, E. serotinus	125	7.94
E. nilsonii, H. savii	87	5.52
Pipistrellus ssp.	1230	78.10
Total	1575 observations	100 %

Table 6: Total record number attributed to species groups.

#### 3.1.1 Observations of P. pygmaeus

On 10 tours a total of 29 observations of *P. pygmaeus* were made. These records originated from 27 locations on 6 different transects (Table 7, Fig. 5). The distribution of locations can be appreciated in Fig. 3. The only biogeographic region with observations of *P. pygmaeus* on all tours are the Eastern Alps (canton Grisons). On these 4 tours 16 observations could be noted, which represents 55% of all records on transects. Only in the Eastern Alps records in the same ha-grid on both tours (reproduction and post-reproduction phases) could be obtained on two occasions.

Transect name	N of observations reproductive season	N of observations post-reproductive season	Total (Number of locations)
Plain I	4	4	8 (8)
Northern Alps I	1	-	1 (1)
Northern Alps II	1	2	3 (3)
Eastern Alps I	3	3	6 (5)
Eastern Alps II	5	5	10 (9)
Southern Alps III	1	-	1 (1)
Total	15	14	29 (27)

Table 7: Observations of *P. pygmaeus* on transects. For locality of transects see Fig. 3.



Fig. 5: Point map of locations of *P. pygmaeus* on transects (= species map A).

In addition, 83 observations of *P. pygmaeus* from 59 locations (ha-cells) were obtained from regional bat experts (Table 8). Summing up all records, there are in total 112 observations from 86 locations (ha-cells) available for the purpose of this study (Fig. 6). 60 observations were made in the years 2001

and earlier (37 before 1993 by P. Zingg), 51 in 2002 and one observation in 2003 (for more details see Appendix 3).

Observer	Year(s)	Observations	Locations		
P. Zingg	1979-1992	37	24		
M. Ruedi	1999-2002	15	13		
T. Sattler <sup>1</sup>	2002	10	8		
M. Roesli, M.	2000-2002	10	6		
Moretti					
F. Bontadina	1997-1998	4	4		
S. Hoch	2000	2	2		
R.Pierallini	2002	2	1		
H. Schnitzler	2001	1	1		
WD. Burkhard, F.	2002	1	1		
Bontadina					
R. Ehrenbold	2003	1	1		
Total		83	<b>59</b> <sup>2</sup>		

Table 8: Additional records of *P. pygmaeus*, including observers.

<sup>1</sup>off transects, in collaboration with regional bat experts. <sup>2</sup> Total number of locations arithmetically = 61, but three locations are the same.



Fig. 6: Point map of all locations (n=86) of *P. pygmaeus* (= species map B).

# 3.1.2 Observations of P. pipistrellus

*P. pipistrellus* was recorded 951 times on all 40 tours originating from 873 locations (Table 9, Fig. 7). The calculation of the species map was based on these transect observations only. Observations per tour varied greatly between 3 and 62, with an average of 23.8 records per tour.

Table 9: Observations of *P. pipistrellus* on transects, observations km<sup>-1</sup> of tour 1 in the reproductive season and tour 2 in the post-reproductive season; fraction of a specific transect on total number of records.

Transect	Abbre- viation Transect	Reproductive season		Post- reproductive season		Sum of both seasons		
		Obs.	Obs. km <sup>-1</sup>	Obs.	Obs. km <sup>-1</sup>	Obs.	Obs. km <sup>-1</sup>	% sum (total)
Jura Mountain I	JI	6	0.15	36	0.90	42	0.53	4.42
Jura Mountain II	J II	12	0.30	36	0.90	48	0.60	5.05
Central Plains I	ΡI	20	0.50	19	0.48	39	0.49	4.10
Central Plains II	P II	15	0.38	19	0.48	34	0.43	3.58
Central Plains III	P III	15	0.38	29	0.73	44	0.55	4.63
Central Plains IV	P IV	29	0.73	15	0.38	44	0.55	4.63
Central Plains V	ΡV	11	0.28	3	0.08	14	0.18	1.47
Central Plains VI	P VI	14	0.35	13	0.33	27	0.34	2.84
Northern Alps I	NA I	36	0.90	31	0.78	67	0.84	7.05
Northern Alps II	NA II	41	1.03	49	1.23	90	1.13	9.46
Northern Alps III	NA III	8	0.20	21	0.53	29	0.36	3.05
Northern Alps IV	NA IV	39	0.98	9	0.23	48	0.60	5.05
Northern Alps V	NA V	33	0.83	10	0.25	43	0.54	4.52
Eastern Alps I	EA I	25	0.63	23	0.58	48	0.60	5.05
Eastern Alps II	EA II	22	0.55	25	0.63	47	0.59	4.94
Southern Alps I	SA I	27	0.68	48	1.20	75	0.94	7.89
Southern Alps II	SA II	11	0.28	11	0.28	22	0.28	2.31
Southern Alps III	SA III	21	0.53	62	1.55	83	1.04	8.73
Western Alps I	WA I	26	0.65	37	0.93	63	0.79	6.62
Western Alps II	WA II	13	0.33	31	0.78	44	0.55	4.63
Total		424	0.53	527	0.66	951	0.59	100



Fig. 7: Observations of *P. pipistrellus* on the 40 tours (20 in the reproductive season and 20 in the post-reproductive season). Codes on the x-axis refer to Table 9.
### 3.1.3 Sighting probabilities

Calculations of sighting probabilities were based on the species' presence in single square kilometres. *P. pygmaeus* was observed in 9 km<sup>2</sup> in the reproductive season only, in 5 km<sup>2</sup> in the post-reproductive season only and in 3 km<sup>2</sup> on both tours. *P. pipistrellus* occurred in 145 km<sup>2</sup> in the reproductive season only, in 202 km<sup>2</sup> in the post-reproductive season only and in 167 km<sup>2</sup> on both tours. The applied road transect method resulted in mean sighting probabilities of 41.1% for the reproductive season and 27.4% for the post-reproductive season for *P. pygmaeus*. The values for *P. pipistrellus* reached 45.4% for the reproductive season and 53.6% for the post-reproductive season (Table 10).

Table 10: Sighting probabilities (mean and	95% Confidence	Interval) per	square	kilo-
meter for <i>P. pygmaeus and P. pipistrellus</i> .				

Species	Tour	Mean	95% Confidence Interval
P. pvømaeus	Reproductive season	41.1%	14-75%
r. pygmacus	Post-reproductive season	27.4%	9.3-58.2%
P. pipistrellus	Reproductive season	45.4%	40.3-50.5%
<i>P. pipistrenus</i>	Post-reproductive season	53.6%	48.1-59.1%

## 3.2 Ecological Niche Factor Analysis

### 3.2.1 ENFA of P. pygmaeus

The five most important EGVs, explaining most of the marginality of *P. pyg-maeus* with transect data (species map A) are Proximity to wide rivers, Hedgerow frequency, Latitude, Bushy landscape frequency and Single building frequency (Table 11). For all data (species map B) the five most important

EGVs are Latitude, Pasture frequency, Proximity to wide rivers, Town frequency and Bushy landscape frequency (Table 12).

Table 11: ENFA for *P. pygmaeus* based on species map A (transect data only). Variance explained by the 25 EGVs (marginality), and coefficient values for the first specialisation factor (the only two factors used for HS calculation). EGVs are sorted by decreasing absolute value of coefficients on the marginality factor. Positive values for marginality mean that the bat species prefer locations with higher values on the corresponding EGV than the mean location in Switzerland. Negative values mean the opposite. Signs of coefficient have no meaning on the specialization factors. The amount of specialization accounted for is given in parentheses in each column heading.

	Marginality	Specialisation 1
	(86%)	(7%)
Proximity to wide rivers	0.527	0.314
Hedgerow frequency	0.364	0.224
Latitude	0.329	0.113
Bushy landscape frequency	0.308	0.127
Single building frequency	0.288	-0.105
Highway frequency	0.209	0.088
Pasture frequency	-0.196	0.244
Open forest frequency	0.175	-0.109
Bushy forest frequency	0.164	-0.053
Altitude	-0.156	0.061
Small stream frequency	-0.146	-0.178
Riparian forest frequency	0.144	0.175
Riparian vegetation frequency	0.135	0.11
Village frequency	0.129	0.03
Alpine meadow frequency	-0.098	-0.07
Grass frequency	-0.094	-0.071
Dense forest frequency	-0.092	0.473
Town frequency	0.083	0.439
Slopes	-0.081	0.147
Lake-border frequency	0.079	0.098
Proximity to forest edge	0.075	-0.076
Eastness	-0.071	-0.141
Wetland frequency	-0.059	-0.118
Northness	0.036	0.102
Meadow frequency	0.017	0.378

	Marginality (10%)	Spec. 1 (22%)	Spec. 2 (13%)	Spec. 3 (8%)	Spec. 4 (6%)	Spec. 5 (6%)	<b>Spec.</b> 6 (5%)	Spec. 7 (4%)
Latitude	0.387	0.235	0.381	0.169	-0.187	0.031	0.201	-0.066
Pasture frequency	-0.352	0.208	0.122	0.12	0.308	-0.01	0.252	0.062
Proximity to wide rivers	0.351	-0.089	-0.059	0.116	0.157	-0.077	0.228	-0.174
Town frequency	0.316	0.13	0.006	-0.147	-0.079	0.158	0.425	0.071
Bushy landscape frequency	0.288	-0.139	0.015	0.146	0.067	-0.203	0.008	-0.215
Altitude	-0.27	0.392	0.393	-0.249	-0.302	0.226	-0.179	-0.223
Single building frequency	0.261	-0.021	-0.207	-0.181	0.152	-0.262	-0.222	0.057
Hedgerow frequency	0.259	0.267	-0.343	0.063	-0.076	-0.008	0.035	-0.039
Proximity to forest edge	0.214	0.259	-0.333	0.054	-0.129	-0.175	0.431	0.055
Meadow frequency	-0.157	-0.483	0.272	0.248	-0.293	0.005	0.214	0.268
Lake-border frequency	0.153	0.099	0.086	-0.014	-0.282	0.14	0.079	-0.04
Dense forest frequency	-0.147	0.197	-0.302	-0.204	-0.374	0.275	-0.283	-0.127
Open forest frequency	0.144	0.078	0.057	0.45	0.256	0.123	-0.076	0.235
Riparian vegetation								
frequency	0.133	0.019	0.131	0.011	0.017	-0.043	0.036	-0.028
Bushy forest frequency	0.128	-0.154	0.071	-0.108	-0.106	0.044	-0.091	0.033
Slopes	-0.11	-0.174	0.12	0.035	-0.122	-0.336	0.226	0.202
Riparian forest frequency	0.091	-0.407	0.319	-0.582	0.441	0.272	0.189	0.024
Village frequency	0.081	-0.047	0.032	-0.028	-0.13	0.165	0.236	-0.318
Northness	0.074	-0.001	-0.134	0.029	-0.08	-0.191	0.215	0.147
Highway frequency	0.069	0.106	-0.056	0.106	-0.153	-0.035	0.089	0.178
Grass frequency	-0.043	-0.023	0.266	-0.286	-0.113	-0.339	-0.027	-0.094
Alpine meadow frequency	-0.033	-0.07	-0.043	0.146	-0.054	0.221	-0.151	0.662
Eastness	-0.026	-0.009	-0.031	0.009	0.082	-0.212	-0.136	-0.16
Wetland frequency	-0.021	-0.06	-0.016	0.119	0.014	0.447	-0.097	-0.149
Small stream frequency	0.01	0.184	0.022	0.111	-0.193	0.053	0.022	0.13

Table 12: ENFA for *P. pygmaeus* based on species map B (transect and additional data). Variance explained by the 25 EGVs, and coefficient values for the first seven variables (equals number of factors used for HS calculation). For additional remarks see Table 11.

Table 13: ENFA for *P. pipistrellus*. Variance explained by the 25 EGVs, and coefficient values for the first 12 variables (equals number of factors used for HS calculation). For additional remarks see Table 11.

	Marg.	Spec. 1	Spec. 2	Spec. 3	Spec. 4	Spec. 5	Spec. 6	Spec. 7	Spec. 8	Spec. 9	Spec.	Spec.	Spec.
	(4%)	(10%)	(9%)	(7%)	(7%)	(6%)	(5%)	(4%)	(4%)	(4%)	10 (4%)	11 (4%)	12 (4%)
Latitude	0.377	0.302	0.215	-0.431	0.281	-0.075	0.099	-0.108	0.266	0.189	0.03	-0.105	-0.225
Village frequency	0.331	0.053	0.07	0.078	0.1	-0.05	0.11	0.158	-0.219	-0.073	0.147	0.173	0.324
Hedgerow frequency	0.307	0.103	-0.045	-0.348	-0.274	-0.44	-0.048	-0.046	0.017	-0.008	0.088	-0.105	0.167
Riparian vegetation													
frequency	0.298	-0.016	0.012	0.06	-0.003	0.004	-0.043	-0.104	-0.079	0.136	0.09	0.101	-0.049
Proximity to wide rivers	0.27	0.082	0.04	-0.111	0.269	-0.275	-0.03	0.174	-0.192	0	-0.146	0.111	0.007
Bushy landscape frequency	0.252	-0.128	0.061	0.091	-0.049	0.01	0.296	0.329	-0.177	-0.082	-0.429	0.254	-0.403
Single building frequency	0.244	-0.254	-0.044	0.238	-0.182	0.06	-0.188	0.442	-0.254	0.28	0.11	0.214	-0.223
Pasture frequency	-0.24	0.115	-0.25	-0.027	0.131	-0.315	-0.282	0.135	-0.099	-0.049	-0.082	0.066	-0.097
Open forest frequency	0.212	0.12	-0.139	-0.013	0.154	0.214	-0.148	0.037	0.038	-0.032	-0.036	0.23	0.022
Grass frequency	0.211	-0.142	0.059	0.007	0.079	0.051	-0.103	0.037	-0.035	-0.047	0.061	-0.244	0.348
Altitude	-0.206	0.222	0.18	0.097	-0.2	0.533	0.144	0.081	-0.032	0.157	0.205	0.21	0.011
Lake-border frequency	0.205	0.006	-0.04	0.089	-0.098	0.101	-0.029	-0.159	-0.027	0.062	0.051	-0.111	-0.013
Riparian forest frequency	0.171	0.195	0.006	0.515	0.479	-0.004	-0.412	-0.091	-0.208	-0.014	0.152	0.286	0.31
Bushy forest frequency	0.141	0.015	-0.059	-0.12	0.002	0.124	-0.023	0.112	0.09	-0.079	-0.059	-0.152	0.212
Highway frequency	0.136	-0.001	0.001	0.003	-0.019	0.029	0.051	0.15	-0.088	-0.23	-0.066	-0.25	-0.148
Alpine meadow frequency	0.135	-0.093	-0.057	-0.027	-0.138	-0.059	-0.212	-0.248	0.499	0.141	0.143	-0.097	-0.081
Slopes	-0.128	0.028	-0.162	-0.079	0.18	0.072	0.043	0.15	-0.12	0.464	0.149	-0.39	0.123
Small stream frequency	0.127	0.114	-0.033	0.158	-0.142	0.02	0.276	-0.093	0.02	-0.079	-0.076	-0.485	-0.388
Dense forest frequency	-0.106	0.352	0.701	0.098	-0.416	-0.373	-0.098	0.093	-0.02	0.135	0.242	-0.101	-0.006
Meadow frequency	-0.066	-0.368	0.372	-0.354	0.327	-0.011	-0.149	-0.064	0.231	0.318	0.187	-0.168	-0.011
Eastness	0.032	-0.027	0.009	0.018	-0.053	-0.021	-0.023	-0.367	-0.183	0.315	-0.649	0.002	0.05
Wetland frequency	-0.03	0.069	-0.086	0.278	0.08	-0.159	0.253	0.034	0.503	0.098	-0.009	0.154	0.041
Proximity to forest edge	0.026	-0.617	-0.384	-0.24	0.164	0.09	0.534	-0.405	-0.204	-0.025	0.289	0.006	-0.219
Northness	0.025	0.035	-0.035	0.068	0.023	0.012	0.172	0.157	-0.112	0.504	0.099	-0.07	0.25
Town frequency	0.013	0.042	-0.007	0.03	0.113	-0.281	0.099	0.301	0.101	0.192	0.012	-0.103	0.144

### 3.2.2 ENFA of P. pipistrellus

The five most important EGVs, explaining most of the distribution of *P. pipis-trellus* are Latitude, Village frequency, Hedgerow frequency, Riparian vegetation frequency and Proximity to wide rivers. Details are given in Table 13.

### **3.2.3 Comparison of sibling species**

The overall "*P. pipistrellus* vs *P. pygmaeus* observation ratio" on transects is 32.8 : 1. The lowest value for a single tour was reached with 4.4:1 in the reproductive period on transect Eastern Alps II (Grisons). While *P. pipistrellus* could be recorded on all 40 tours, *P. pygmaeus* could only be observed on 10 tours.

Table 14: Comparison between *P. pipistrellus* and *P. pygmaeus*.

A) Number of observations and locations, marginality, specialisation and tolerance factors.

B) Marginality according to the 25 EGV predictors. The symbol + means that the species was found in locations with a higher value than the average of all hectare cells (the reverse for -). The greater the number of symbols, the higher the correlation. 0 indicates a very weak correlation.

A)	P. pygmaeus	P. pygmaeus	P. pipistrellus
	(transect data)	(transect &	(transect data)
		add. data)	
Number of observations	29	112	951
Number of locations	27	86	873
Number of tours with records	10	-	40
Number of transects with records	6	-	20

Marginality	0.868	0.78	0.607
% of specialisation explained by marginality factor	86%	10%	4%
Specialisation (S)	17.206	1.469	1.05
Tolerance (1/S)	0.058	0.681	0.952

Eastness	-	0	0
Slopes	-	-	-
Northness	0	+	0
Altitude			
Latitude	+++	++++	++++
Alpine meadow frequency	-	0	+
Bush frequency	+++	+++	+++
Proximity to forest edge	+	++	0
Bushy forest frequency	++	+	+
Dense forest frequency	-	-	-
Open forest frequency	++	+	++
Hedgerow frequency	++++	+++	+++
Grass frequency	-	0	++
Small stream frequency	-	0	+
Proximity to wide rivers	++++	++++	+++
Lake-border frequency	+	++	++
Meadow frequency	0		-
Pasture frequency			
Riparian forest frequency	+	+	++
Riparian vegetation			
frequency	+	+	+++
Wetland frequency	-	0	0
Town frequency	+	+++	0
Village frequency	+	+	+++
Single building frequency	+++	+++	++
Highway frequency	++	+	+

## 3.3 Habitat Suitability map

### 3.3.1 Habitat Suitability map of P. pygmaeus

The Broken stick-advice was used in order to decide on the number of independent factors to include in HS computation. 25 EGVs had been included for all analyses. Consequently, the factors explaining 4% or more were incorporated. The calculation of the HS maps for *P. pygmaeus* with species map A was

B)

based on marginality and the first specialisation factor only, whereas for the computation with species map B marginality and the first eight specialisation factors were used. They explain 96.4% and 86.5%, respectively of the global information. This value is composed of the total marginality and of 92.9% and 73% of the specialisation, respectively. The resulting maps for Switzerland are given in Fig. 8 & 9.

### 3.3.2 Habitat Suitability map of P. pipistrellus

The calculation of the Habitat Suitability map for *P. pipistrellus* was based on marginality and the first 12 specialisation factors. They explain 86% of the total information. This value is composed of total marginality and of 72.1% of the specialisation. The resulting map is given in Fig. 10.

## 3.4 Validation

The values for the Absolute Validation Index (AVI) and the Contrast Validation Index (CVI) for the three Habitat Suitability analyses are found in Table 15. Standard deviations and confidence intervals are based on a 10x jack-knife cross-validation.

Table 15: Absolute Validation Index (AVI) and Contrast Validation Index (CVI) for *P. pygmaeus* (map A and B) as well as for *P. pipistrellus*. The high numbers for SD and the large conficence interval indicate that both values provide a far better validation index for *P. pipistrellus* than for *P. pygmaeus*. This is mainly caused by the relatively small sample size. Negative signs are a mathematical artefact because the same reason.

Statistics	Mean	SD	90% confidence interval
AVI for <i>P. pipistrellus</i>	0.716	0.0367	0.654 - 0.762
AVI for <i>P. pygmaeus</i> (A)	0.7	0.306	0.225 - 1
AVI for <i>P. pygmaeus</i> (B)	0.732	0.166	0.436 - 0.883
CVI for <i>P. pipistrellus</i>	0.192	0.0334	0.137 - 0.236
CVI for <i>P. pygmaeus</i> (A)	0.00769	0.306	-0.467 - 0.308
CVI for <i>P. pygmaeus</i> (B)	-0.0152	0.154	-0.294 - 0.117



Fig. 8: Habitat Suitability map for *P. pygmaeus* based on species map A (transect data only).



Fig. 9: Habitat Suitability map for *P. pygmaeus* based on species map B (all observations).



Fig. 10: Habitat Suitability map for *P. pipistrellus*.

## 3.5 Numbers of roosts and individuals of *P. pygmaeus*

At 4 maternity roosts lactating females and subadults of *P. pygmaeus* were caught. Overall 16 subadults (Table 16) and 29 lactating females (Table 17) were measured. In Lucerne 35 individuals left the roost (R. Ehrenbold, 13.7.2002), in Meggen (LU) at least 30 specimens were counted (10.7.2002), in Locarno (TI) there were at least 15 individuals observed (15.7.2002). By far the largest roost was found in Kreuzlingen (TG) with 229 individuals leaving the roost (W.-D. Burkhard & F. Bontadina, 14.7.2002). Exact locations and dates can be found in Appendix 3. The remaining roosts investigated consisted of the following species: *P. kuhlii* (Arcegno, TI), *P. pipistrellus* (Tavanasa, GR) and a male *N. leisleri* (Locarno, TI). On two occasions (Illanz, GR and Meggen (LU; Jugistr.) no bats were captured.

~ .		Forarm length	
Specimen	Weight (g)	(mm)	5th digit (mm)
L1	4.2	30.1	35.5
L7	4.5	29.9	35.4
L8	3.5	28.4	33.0
Lo4	3.5	30.1	34.9
Lo5	3.3	28.5	32.2
Lo7	3.5	29.2	33.8
M3	3.6	29.9	31.0
M5	3.6	29.3	33.9
K2	Not measured	30.1	35.0
КЗ	Not measured	31.5	39.0
K4	Not measured	27.1	32.4
K5	Not measured	31.2	37.3
K8	Not measured	30.5	38.9
K10	Not measured	31.8	38.5
K11	Not measured	28.4	32.3
K (dead)	Not measured	32.0	39.7
Minimum	3.3	27.1	31.0
Maximum	4.5	32.0	39.7
Average	3.7	29.9	35.2
SD	0.4	1.4	2.8

Table 16: Morphological details of subadults (N=16, 10 males and 6 females) caught in Luzern (L; n = 3), Meggen (M; n = 2), Kreuzlingen (K; n = 8), Locarno (Lo; n = 3). Data obtained in collaboration with R. Ehrenbold, M. Roesli and W.-D. Burkhard.

Specimen	Weight (g)	Forarm length (mm)	5th digit (mm)
M1	5.7	31	40
M2	5	29.1	38.7
M4	4.9	29.3	37.6
M6	5	30.9	37.3
M7	4.9	29.9	39.3
M8	5.6	30.9	40
M9	5.1	30	38.2
M10	5.3	31.1	40
M11	4.4	29.9	38
M12	5.4	31	39.4
M13	4.7	31	39.2
M14	5	30.5	40
M15	5.2	30	38.1
M16	5.3	30.1	40.1
L2	4.7	31.8	40.9
L3	4.9	31.4	40.3
L4	5.4	32.9	42
L5	5.2	31.4	39.7
L6	5.4	30.9	40
L9	4.6	29.1	38
L10	4.9	30.3	38.9
L11	4.9	31.2	38.9
Lo1	4.5	30.1	36.9
Lo2	4.8	30.7	38.2
Lo3	4.5	28.9	37
Lo6	5.9	30.8	37.9
K6	Not measured	30.4	40
K7	Not measured	32	41.4
K9	Not measured	32.8	39.3
Minimum	4.4	28.9	36.9
Maximum	5.9	32.9	42.0
Average	5.0	30.7	39.1
SD	0.4	1.0	1.3

Table 17: Morphological details of lactating females (n = 29) caught in Luzern (L; n = 8), Meggen (M; n = 14), Kreuzlingen (K; n = 3), Locarno (Lo; n = 4). Data obtained in collaboration with R. Ehrenbold, M. Roesli and W.-D. Burkhard.

## **4** Discussion

#### 4.1 Data sampling

The sampling strategy affects the quality of a subsequently derived habitat suitability model (Hirzel & Guisan 2002). The design "gradsects" (Austin & Heyligers 1989) is close to a proportional random-stratified sampling (Hirzel & Guisan 2002). This cost-effective approach concentrates points into geographical transects distributed over the main landscape gradients. It was shown that "gradsects" produce just as good results as complete random-stratified samples (Wessels et al. 1998). This representative transect data, hence, is in opposite to the additionally collected data set of *P. pygmaeus* (species map B), which is based on heterogeneous species records. These data points are obviously biased towards regions with high activities of bat experts. As Hirzel & Guisan (2002) found out, sample size is the most important factor, which determines sampling efficiency and consequently accuracy of the model. Additionally, ENFA is more robust to poor data quality compared to e.g. General Linear Models (GLM; Hirzel et al. 2001).

### 4.2 Call analysis

Bat calls show a large within-species plasticity (Obrist 1995; c.f. Table 4). The source of this variation is not fully understood, but most probably is influenced by the following factors: 1) Bat individuals call at different frequencies (Murray et al. 2001). 2) In *Pipistrellus*, Park et al. (1996) found that males, being smaller, emit calls at a slightly higher frequency than females in both species. Juveniles also call differently, usually at higher frequencies than adults (Jones et al. 1992, Murray et al. 2001). 3) Bats shift call frequencies depending on presence of other bats, probably to avoid confusing echoes of their own calls with those of conspecifics (Miller & Degn 1981). 4) Bats adjust calls to the environment (habitat structure) and flight height: in open space calls the FM component is reduced or even omitted while in cluttered areas calls may lose their CF tail when emitted (Ahlén 1981, Zingg 1990, Kalko & Schnitzler 1993, Park et al. 1996). 5) Geographic variation in echolocation call frequency corresponds to variation in size with individuals getting smaller to the South (Russo &

Jones 2002). 6) While flying the bat changes its position relative to the microphone. This phenomenon, called Doppler shift causes a certain intra-individual variation in frequency measurements (Jones & van Parijs 1993).

It is assumed that differences between various sound recording instruments, computer programs and different observers interpreting sonograms are equally likely to cause some variances (P. Zingg, pers. comm.). Additionally, for hand-released bats it is known that they usually emit more FM calls with FMAXE a few kHz higher than normal and with a shorter duration (Ahlén 1981, Russo & Jones 2000). These factors increase the variance of the echolocation call parameters, which makes it more difficult to discriminate between species. In this study this variability lead to the exclusion of 236 call sequences that could not be classified to species prior to analysis. But in general, it can be assumed that these factors did not affect species discrimination in a general way. This is especially true for the discrimination of the sibling species.

### 4.3 GIS models

Multivariate models analysing ecological variables of animal and plant species are widely used. Integrated into Geographical Information Systems (GIS), they provide powerful tools to predict the respective habitat suitability. Based on these models distribution maps can be derived (Guisan & Zimmermann 2000). Different models such as the Generalised Linear Model (GLM; e.g. Austin et al. 1984, Augustin et al. 1996) or the Canonical Correspondence Analysis (CCA; e.g. Guisan et al. 1999, Jaberg & Guisan 2001) were developed in order to analyse a species' distribution. All these investigations rely on presence (locations where the species of interest has been recorded) and absence data (locations where species was not found). Reliable data, especially absence data for animals, is difficult to obtain (Kéry 2000, 2001). ENFA has the great advantage that it relies on presence data only (Hirzel et al. 2002a). This analysis is generally very robust to quality and quantity of presence data (Hirzel et al. 2001) and therefore was appropriate for the purpose of this study.

### 4.4 Observation on transects

Including records of bad quality and unidentified ones we made, on average, 1.13 observations per kilometer (obs.  $km^{-1}$ ). Identified calls (= 0.98 obs.  $km^{-1}$ ) split into the two seasons reveal 0.87 obs.  $km^{-1}$  in the reproductive and 1.10 obs.  $km^{-1}$  in the post-reproductive season.

Density comparison of all bats encountered on transects with similar studies are difficult, as different factors affecting this value (such as car speed, type of light bulbs used for streetlights, definition of a single observation event, species composition, season) varied between them. The average of 1.13 obs. km<sup>-1</sup> for all calls (identified ones = 0.98 obs. km<sup>-1</sup>) of this study is similar to the result of 1.07 obs. km<sup>-1</sup> in Southern Sweden (Rydell 1992). Amount and type of street lamps do strongly affect abundance of bat species along roads (Haffner & Stutz 1985/86, Blake et al. 1994). In Southern England the latter authors found a varying mean density from 0.7 obs. km<sup>-1</sup> for unlit roads, to 1.2 obs. km<sup>-1</sup> for orange street lamps up to 3.2 obs. km<sup>-1</sup> for white lamps.

Our results from road transects reveal the outstanding position of *P*. pipistrellus s.str. in the Swiss bat community along roads. We selected transects in order to represent all habitat types, however as road transects, they inevitably always included roads. This may be a habitat factor, which favours P. pipistrellus s.str. Together with the methodological factors discussed above, the recorded density of P. pipistrellus may be biased towards species which are more easily detected and identified by their ultrasound calls, and use roads and illuminated areas for foraging. Nevertheless, because this is true for many of the non-Myotis species group, the high amount of P. pipistrellus in the Swiss bat community remains striking. The fact that 60.3% of all acoustic observations refer to *P. pipistrellus* is a clear indication of its abundance. This rough estimate corresponds to the findings of different bat surveys on the British Isles. The Swiss fraction may be compared with these results even though different methods were used: applying a very extensive method based on echolocation surveys including volunteers, 71% of all bats were attributed to P. pipistrellus s.l. (Walsh et al. 1995, Walsh & Harris 1996a & 1996b). Harris et al. (1995) estimated the British bat population to consist of 76% P. pipistrellus s.l.

In another study including all species but differentiating the sibling species, Vaughan et al. (1997a) found 30% *P. pipistrellus* and 34% *P. pygmaeus*. In Ireland, Russ & Montgomery (2002) found different species compositions in different habitat types: with 43.1% for *P. pipistrellus* and 28.0% for *P. pygmaeus*, they take up a higher fraction of global bat population in habitats with linear structures than in two-dimensional habitats where they reach fractions of 23.7% and 18.4%, respectively. So it can be concluded that on the British Isles, and especially in the UK, where the presence of the sibling species was discovered, *P. pygmaeus* seems to be very abundant. These results contrast very much with the findings for *P. pygmaeus* in this study: *P. pygmaeus* made only 1.84% of our global record number.

Different studies in the UK looked at the fraction of the sibling species at maternity roosts. The percentage of *P. pygmaeus* colonies was 75% in Scotland (Jenkins et al. 1998) vs. 55% and 58%, respectively in England (Jones & van Parijs 1993, Barlow & Jones 1999). In Switzerland, the fraction of *P. pygmaeus* among all observations of both species on all transects was only 2.9%, the maximum value of a single transect reached 18.5% in Eastern Switzerland. On 14 of the 20 transects, no *P. pygmaeus* was recorded on neither tour. We can conclude that *P. pygmaeus* is a rare bat species in Switzerland.

Due to the low number of records for *P. pygmaeus*, the mean sighting probabilities of 41.1% for the reproductive season and 27.4% for the post-reproductive season have large confidence intervals (Table 10). Thanks to a higher number of records, the sensitivity of these estimations for *P. pipistrellus* are by far greater: the probabilities of 45.4% for the reproductive season and 53.6% for the post-reproductive season have a comparatively smaller confidence interval of roughly 10% (Table 10). For *P. pipistrellus* the sighting probabilities are in a similar range of about 50%. This means, that, by a single tour, *P. pipistrellus* was recorded roughly in every second square km that indeed is inhabited by the species.

The inclusion of additional observations of *P. pygmaeus* into the data set (species map B) produced several results. First, it lead to more observations in regions where the species had been observed on transects already (canton of Geneva, Bernese Oberland, Sopra Ceneri in Ticino, Rhine valleys in Grisons);

second, new regions with a number of records (> 2) were found around the city of Lucerne, in the Sotto Ceneri in Ticino and the Val Bregaglia in Grisons; third, a few regions (northern shore of Lake Neuchatel, city of Zürich, southern border of Lake Constance, princedom of Liechtenstein) were identified with one or two observations of *P. pygmaeus* only. Braun et al. (in prep.) found nine locations with *P. pygmaeus* in the greater region of Basel, Northern Switzerland. These observations complete the current knowledge about the species' distribution in Switzerland.

Interestingly, in this study *P. pipistrellus* shows signs of regional differences in abundance (Table 9, Fig. 7) that were noted before by different bat experts in Switzerland: for a long period of time this species was considered absent or rare in the northern parts of the cantons of Argovia and Zürich as well as in the adjacent canton of Schaffhausen (H. Alder, A. Beck, F. Bontadina, H.-P. Stutz pers. comm.). Stutz & Haffner (1985) judged *P. pipistrellus s.l.* to be especially common in the Prealps and the hilly areas of the Central Plateau partially avoiding the cleared countryside of the flat regions. These findings are corroborated by this study: the typical transects of the Swiss Plains showed comparatively low numbers of records (Table 9, Fig. 7).

*P. kuhlii* is suspected to exhibit a severe inter-specific competition pressure onto *P. pipistrellus* in the southern parts of Switzerland (Haffner & Stutz 1985/86). The findings of this study (assuming that most calls attributed to the *P. nathusii/kuhlii* complex actually concern *P. kuhlii*; Stutz & Haffner 1996, Gebhard 1996, Vernier & Bogdanowicz 1999) support this hypothesis: in Southern Switzerland, call sequences of *P. nathusii/kuhlii* reach or even outnumber call sequences of *P. pipistrellus*. There are some indications that *P. pygmaeus* could be profiting of the resulting decrease of *P. pipistrellus* populations. Further investigations are needed to show these interspecific relations.

### 4.5 Ecological parameters affecting distribution

The marginality factor for *P. pygmaeus* calculated by the ENFA represents 0.868 for the transect data (species map A) and 0.78 for all data (species map B), respectively (thereafter called analysis A and analysis B). This means that deviation from an average Swiss habitat by the squares inhabited in map A is a

greater than in map B. This suits the expectations, as for map A sample size n is only 31% of that of map B. Consequently, there is also a substantial difference in tolerance between the two analyses (0.058 vs. 0.681). At this point a critical remark concerning confiability of the results for *P. pygmaeus* needs to be made. Both, analysis A and B, have their limitations in the fine-grained approach of a GIS analysis based on ha-cells: data for analysis A were obtained performing a systematic scheme but are restricted by the small sample size (n = 27). Sample size for analysis B is more than three times higher than data for analysis A but underlays a significant bias due to non-systematic data collection. It is difficult to anticipate consequences of these limitations. Thus, the conclusions as stated in this work indicate the state of knowledge; they might be subject of adjustments when more information (especially more presence points) of this species is available.

The values for marginality indicate that the distribution of *P. pygmaeus* in Switzerland is limited to a very narrow range of habitats. Additionally, the species is not tolerant to departures from its optimal habitat. These findings for *P. pygmaeus* are contrasted very much by the results for *P. pipistrellus*: the marginality of 0.607 indicates that the sibling species' habitat needs are better matched by the average Swiss ha-cell. Supplementary, the tolerance coefficient of 0.952 shows that deviation from optimum habitat does not necessarily imply absence of species.

Comparison of marginality values of the EGVs for *P. pygmaeus* reveals great similarities between analysis A and B: in both calculations, the seven factors that influence distribution most are also found within the first ten ranks of the individual analyses (Table 13B). There is not a single case where influence of an EGV is contradictory, meaning positive in one and negative in the other analysis. Two EGVs exhibit greatest influence on *P. pygmaeus*' occurrence: Latitude has a positive influence, meaning that *P. pygmaeus* occurs preferably in the South of Switzerland. Of the same importance is Proximity to wide rivers; *P. pygmaeus* likes to be close to streams. Whereas landscapes with bushes and hedgerows are attractive, pastures appear to be avoided. The orientation system of bats can help to explain this result: hedgerows are often used by bats, leading them to or from feeding grounds where open air space above pastures do not provide any assistance for orientation. An other reason

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for this preference could be improved food availability because of rich edge effects (Limpens & Kapteyn 1991). Single building frequency is more important than towns, while villages seem to play only a minor although positive role. The average location with *P. pygmaeus* are found at 610 m for the transect data and 565 m for all data, which is substantially below the average altitude of the study area (739m).

Occurrence of forest (4 EGVs) has a positive effect on *P. pygmaeus* unless it is dense forest, the latter exerting a small but negative effect. Open forest frequency and Bushy forest frequency express the highest influence, over again reinforcing the importance of loosely growing and structured woods. They are more valuable when they extend along rivers (riparian forests). Highway frequency can be interpreted as an indicator for the influence of human activities, especially roads. Along with the built-up areas, this EGV expresses a positive influence of man, pointing at the fact that human buildings are used for roosts and lighted roads for hunting grounds. Lake-border frequency strikes out the importance of open water areas. In both analyses it remains less important than wide rivers, possibly because riparian forest is an important factor, Swiss lakes rarely being bordered by forest. Meadow frequency has a negative influence, possibly due to absence of orientation aids as seen previously for pastures.

Specialisation factors indicate the tolerance of *P. pygmaeus* towards departures from optimum habitat. In this regard, a big difference between the two analyses appears: in the analysis with the transect data marginality alone accounts already for 86% of the specialisation, with the first specialisation factor accounting for only another 7%. In the analysis with all data, marginality accounts for only 10% while the 7 specialisation factors explain 64%. Marginality explaining a high fraction of the specialisation indicates that the species is very exigent on the habitat characteristics it is most marginalized. This difference in explained specialisation emerges because the species data for analysis A (transects) originate of a smaller area range than for analysis B (all data). Thus, the factors of analysis A indicate a more extreme distribution for *P. pygmaeus* than analysis B. Nevertheless, the tolerance of 0.681 for analysis B does not change the principal conclusion: this value shows that, also with this calculation, its habitats differ significantly from the average Swiss ha-cells below 1500 m.

Sensitivity of *P. pygmaeus* seems to depend especially from deviations from two landscape characteristics: availability of trees and bushes, especially along rivers and the structure richness of the countryside. If woody plants (Riparian forest, Hedgerows, Bushy forest) augment and distances to forest borders are small, *P. pygmaeus* reacts positively. On the opposite, if areas with open air space (Meadows, Pasture, Grass) increase, this species' abundance declines. An increasing amount of dense forest cover has also a negative effect. Additionally, altitude plays an important role, with the species preferring low altitudes.

In general, *P. pipistrellus* occurs in similar habitats as *P. pygmaeus*. The 7 most important EGVs of *P. pygmaeus* are also found in the 10 most important variables for *P. pipistrellus* (Table 14B). Though, there are some interesting differences: whereas *P. pygmaeus* lives in areas with a higher frequency of Towns than average, *P. pipistrellus* exists in areas with an average town frequency. The opposite is the case for villages: in *P. pipistrellus* it is the second most important factor, while in *P. pygmaeus* this EGV exhibits hardly any influence. Riparian vegetation, namely bushes along rivers, has a greater positive effect for *P. pipistrellus* than for *P. pygmaeus*, whereas the former species is less dependent on small distances to forest edges.

As previously noted, *P. pipistrellus* shows a very high tolerance to deviations from its optimum habitat. The bat species shows – again similar to *P. pyg-maeus* – some sensitivity to increasing frequency of meadows, pastures and dense forests. *P. pipistrellus* also prefers to live in southern and low altitude areas.

In summary, it can be concluded that both species prefer similar habitat types with more southern latitudes, occurrence of wide rivers, hedgerows, woods, open forests and single buildings in lower areas, all being positive predictors of their distribution. Increasing pasture and meadows frequency has a negative impact. The only big difference in habitat selection was found in the use of built-up areas: *P. pygmaeus* rather sticks to towns whereas *P. pipistrellus* prefers villages. The greatest difference between the sibling species influencing their actual distribution in Switzerland is their dependence on the EGVs mentioned: whereas *P. pipistrellus* is very tolerant to deviations from the optimum habitat, *P. pygmaeus* is highly specialised regarding its favourite environment.

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### 4.6 Habitat Suitability maps

Comparing the two maps of *P. pygmaeus* (Fig. 8, 9) some quite substantial differences in suitability of the Plains can be noted: whereas in map B ample areas near wide rivers and lakes are depicted as high suitability areas, this area is restricted to punctual spots in the urban area near wide rivers in map A. Interestingly, in both maps the main alpine valleys (Rhone valley VS, Reuss valley UR, Maggia and Ticino valley TI, Rhine valley GR/SG) are represented as high suitability areas. Of those, the Reuss valley has not been studied. While there are partly numerous observations in the Rhine, Maggia and Ticino valleys, records from the Rhône valley in canton of Valais are completely missing (Fig. 4). Only further and more detailed studies can reveal the reason for this failure: did this happen due to overlooking the species with this coarse method applied in the field or because the model does not include all important variables? Or is it the vast and intensive agriculture on the bottom of the valley that is limiting the occurrence of *P. pygmaeus*? Production of fruits and vegetables has very much altered potential habitats along the Rhône River.

As expected, the map for *P. pipistrellus* (Fig. 10) shows high habitat suitability on the plains and in the alpine valleys. Only the Jura Mountain range and the canton of Schaffhausen partially show lower suitability.

### 4.7 Comparison of habitat selection with Swiss studies

In Switzerland, the single other study differentiating between the two sibling species is a study in the greater area of Basel (Braun et al. in prep.). The authors point out the importance of water bodies for hunting areas of both species. Additionally, they mention urban areas, forest edges and hedgerows as important habitats supporting the findings of this study.

The remaining studies had been conducted without the knowledge of the existence of *P. pygmaeus* and are therefore referring to *P. pipistrellus s.l.* But as comparison of abundance in the present work shows, it can be assumed that they usually are referring to *P. pipistrellus*. Stutz & Haffner (1996) note the importance of waterbodies with extensive riparian vegetation. Bushes, trees, water edges, roads and urban areas are important feeding grounds. Stutz &

Haffner (1985) summarize the occurrence of *P. pipistrellus s.l.* as commonly found in climatic favorable regions of the Prealps and the hilly parts of the Central Plateau, avoiding open, tree- and bush-less plains. In the Jura Mountain, Moeschler & Blant (1990) studied the species in a more fine-scaled approach than the present investigation. Nevertheless, they found similar results with watercourses in the company of bushes and trees to be the most important habitat type, followed by urban areas and hedgerows.

#### 4.8 Comparison of habitat selection with European studies

For the UK Vaughan et al. (1997a) found the following differences for the two species: *P. pipistrellus* is active and widespread in all land use types, but shows a significantly higher activity over rivers and lakes, in unimproved grasslands, improved cattle pastures, and in conifer and mixed plantations. In comparison with P. pipistrellus, P. pygmaeus hunts mainly over lakes and rivers. These results are supported by diet analysis where Barlow (1997) found differences between the sibling species. The main prey groups for *P. pipistrellus* were the insect families Psychodidae, Anisopodidae, Muscidae whereas the main prey groups for *P. pygmaeus* were the smaller Chironomidae and Ceratopogonidae. The latter insect groups are known to have aquatic larval stages pointing out to differences in bats' foraging grounds. Oakeley & Jones (1998) did an analysis of habitats around maternity sites of *P. pygmaeus*. They found a preference for open water with either woodlands or hedgerows on the bank. Hedgerows are important in general, probably as they are used as flight corridors, as shelters against wind and predation, and because they support high insect densities (Limpens & Kapteyn 1991). For Ireland, Russ & Montgomery (2002) found similar results for habitat selection: both species selected rivers and canals with P. pipistrellus also selecting treelines and P. pygmaeus also selecting deciduous woodland habitats and lake margins. Although P. pipistrellus selected fewer habitat types, it also avoided fewer and was found, consequently, in a wider range of habitats. This study is in agreement with these findings elsewhere.

Different authors (Häussler et al. 1999, 2000, von Helversen & Holdried 2003, Braun et al. in prep.) suggest a migration behaviour for *P. pygmaeus*. They

noted a higher seasonal occurrence of *P.pygmaeus* in Southern Germany and in the region of Basel, Northwestern Switzerland. The present study did not find any support for this phenomenon on a national level in Switzerland (Table 8).

### 4.9 Comparison with other Habitat Suitability maps

Habitat Suitability maps are static or empirical models that assume that the distribution of a species is in equilibrium with the EGVs used (Guisan & Theurillat 2000). They fail to include history of colonisation, past incidents that influenced population size and population dynamics in general.

In the Swiss mammal distribution atlas Hausser and collaborators (1996) calculated Habitat Suitability maps for all mammal species based on km<sup>2</sup> grid cells. Comparison of overall distribution of the two maps for *P. pipistrellus s.l.* of the atlas with the one for *P. pipistrellus s.str.* of this study reveals similar trends. Some differences are found, when comparing predicted suitability. The atlas map shows higher percentages for the Central Plateau than for many regions in the Prealps and the Alpine valleys. This is due to the fact that the calculation of this map was based mainly on data of known roosts and on findings of injured individuals (Haffner & Stutz 1996). As chances for these sightings are much higher in densily human-populated areas the data is biased to these regions. In opposite our data is biased towards road networks.

### 4.10 Roosts & Morphology

The morphological measurements on captured *P. pygmaeus* obtained are comparable with previous studies (Jones & van Parijs 1993, Barlow & Jones 1999, Häussler et al. 2000). Interestingly, maternity roosts are less numerous in Switzerland than in the U.K. where colony size ranged from 30-650 individuals with a median of 203 (Barlow & Jones 1999).

### 4.11 Conservation status of the species

Results of this study show that *P. pygmaeus* is reproducing in Switzerland but has a patchy distribution confined to a small range of habitats. This species is highly dependent on the occurrence of wide rivers closed to structured land-

scapes (hedgerows, woods and open forest) near urban areas in the lowlands. *P. pipistrellus* is using similar habitats but – in contrast to its sibling species - is not affected significantly by deviations from optimum habitats. Results show that population size of *P. pipistrellus* is topping the abundance of *P. pygmaeus* by a magnitude of 30.

Different authors point out that foraging sites for bats are badly protected (Moeschler & Blant 1990, Vaughan et al. 1997a, Russ & Montgomery 2002). For many centuries, watercourses were canalised and consequently riparian forests, an important habitat type of *P. pygmaeus*, were destroyed. Since World War II, the cultivated landscape has been changed tremendously in Switzerland (Ewald 1978, Schmid et al. 1998). Especially clearence of hedgerows is assumed to affect bats. On the opposite, the increase of insect-attracting street lights, which provide optimal feeding grounds for bats, are sought to exhibit positive impacts on those species that are capable of using this resource (Rydell 1992, Blake et al. 1994). As both species are seemingly using this resource (Haffner & Stutz 1985/86, own observations) one could expect an increase in population size. Increase in populations of *P. pipistrellus* is even suspected to have negatively affected other bat species such as Rhinopholus hipposideros (Arlettaz et al. 2000). Retrospectively, it cannot be judged which of these arguments had been more important for population developments of the two sibling species.

Looking at the results of this coarse survey in the year 2002 and the results of the Habitat Suitability map, we expect *P. pygmaeus* to occur in more areas in Switzerland where it had been overlooked in the past. Its foraging habitats do not seem to be further threatened at the moment but due to its scarcity in Switzerland, *P. pygmaeus* is a potentially endangered species.

#### 4.12 Recommendations for conservation

In order to be able to protect *P. pygmaeus* accurately, different measures have to be envisaged: this investigation has to be looked at as a starting point for a regular survey (monitoring) of this species in order to be capable to recognise changes in population sizes at an early stage. Its presence in from us depicted high probability areas should be confirmed and known roosts need to be monitored carefully. This means that results of this study need to be communicated effectively to local people involved in bat research and protection.

On the administrative side, this species has to enter the Swiss Red List of endangered species (Duelli 1994). We conclude that *P. pygmaeus* deserves a higher conservation status and thus more attention than its sibling species which does not figure in the list. Thanks to absence of acute threat but due to its small population size it is proposed to incorporate *P. pygmaeus* into category 4a (Potentially threatened; species with a small population size but no appearent threat) of the Red List of Switzerland.

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## 6 Appendix

Appendix 1: Comparison of morphological characters as dicussed by Häussler et al. (2000), Zöphel et al. (2002), Sendor et al. (2002), von Helversen & Holdried (2003), Braun et al. (in prep.); see also picture at the end of the Appendix.

Qualitative external	Second opinion (criticised	Assessment of reliability
characteristic for P.	or supported trough	based on literature and
pygmaeus	further studies)	own observations
2 <sup>nd</sup> phalange app. same	Critisised by Braun et al.	Not reliable
size as $3^{rd}$ of the $3^{rd}$ finger	(in prep.), Sendor et al.	
	2002)	
Shorter muzzle	Supported trough	To be applied with good
	personal observation	knowledge of species
Internarial ridge (hump	Supported by Sendor et	To be applied with good
between nostrils)	al. (2002)	knowledge of species
Uropotagium densely	Questioned by Braun et	Unclear
covered with hair	al. (in prep.)	
Plagiotopagium with a	Critisised by Braun et al.	Not reliable
white border	(in prep.)	
Orange brown furr (adults		Difficult as exceptions
only!)		occur regularly
Paler skin pigmentation		To be applied with good
		knowledge of species, age
		of individual must be
		known
Orange coloured penis	Supported by Ziegler et al.	To be applied with good
without paler medial	(2001), including	knowledge of species
stripe	differences in baculum	
Continuous wing cells	Questioned by Braun et	Unclear
	al. (in prep.)	
Odour similar to Nyctalus	Supported by R.	To be applied with good
noctula	Ehrenbold (pers. comm.)	knowledge of species

Appendix 2: Distribution of *P. pipistrellus s.str.* and its sibling species *P. pygmaeus* according to various sources (countries in alphabetical order).

<b>Country/Region</b>	Status of P.	Status of P.	Author
	pygmaeus	pipistrellus	
		s.str.	
Bulgaria	Present	Present	Dietz 2002
Croatia	Not recorded	Present	Mayer & von Helversen 2001b
Cyprus	Present	Present	Hanak et al. 2001
Denmark: North	Present	Not recorded	Miller & Degn 1981, Jones &
			van Parijs 1993, Barratt et al.
			1997
Denmark: South	Present	Present	Baagoe 2001
France: Bretagne	Not recorded	Present	Jones & van Parijs 1993,
and Normandie			Barratt et al. 1997
France	Present	Present	Barratt et al. 1997, Letard &
			Tupinier 1997, Lustrat 1999,
			Mayer & von Helversen 2001b
Greece	Present	Present	Weid 1987, Hanak et al. 2001,
			Mayer & von Helversen 2001b
Germany: Baden-	Present	Present	Braun, M. & Häussler 1999,
Wuerttemberg			Nagel 1999
Germany: Bayern	Present	Present	Koch & von Helversen 1999
Germany: Hessen	Present	Present	Herzig 1999, Häussler et al.
			2000
Germany:	Present	Present	Hermanns et al. 2001
Mecklenburg-			
Vorpommern			
Germany:	Present	Present	Schorr 1996
Rheinland-Pfalz			
Germany:	Present	Present	Pocha 2001, Zöphel 2001,
Saxonia			Zöphel et al. 2002
Hungary	Present	Present	Mayer & von Helversen 2001b
Ireland	Present	Present	Russ 1996, Barratt et al. 1997
Israel	Not recorded	Present	Mayer & von Helversen 2001b
Italy: Peninsula	Present	Present	Russo & Jones 2000
Italy Sardinia	Present	Present	Russo & Jones 2000
Liechtenstein	Present	Present	Hoch 2001
Moldova	Not recorded	Present	Limpens 2000
Netherlands	Not recorded	Present	Jones & van Parijs 1993,
			Barratt et al. 1997, Kapeteyn
			1997
Portugal	Present	Not recorded	Barratt et al. 1997
Russia	Present	Not recorded	Mayer & von Helversen 2001b
Slovenia	Present	Present	Presetnik et al. 2001
Spain: Central	Present	Present	Ruedi et al. 1998, Mayer & von
			Helversen 2001b
Spain: South	Present	Present	Weid 1987, Barratt et al. 1997,
			Mayer & von Helversen 2001b
Sweden	Present	Rare presence	Ahlén 1981, Jones & van Parijs
		in South only	1993, Barratt et al. 1997

Switzerland	Present	Present	Zingg 1990, Barratt et al. 1997, Wicht 2001, Centro Protezione Chirotteri Ticino 2002 & 2002b
Turkey	Not recorded	Present	Mayer & von Helversen 2001b
United Kingdom:	Present	Present	Vaughan et al. 1997a
England			
United Kingdom: England & Wales	Present	Present	Jones & van Parijs 1993, Barratt et al. 1997, Barlow & Jones 1999
United Kingdom: Scotland	Present	Present	Jones & van Parijs 1993, Barratt et al. 1997, Jenkins et al. 1998, Barlow & Jones 1999
Ukraine	Present	Not recorded	Mayer & von Helversen 2001b

Appendix 3: Details of all 112 observations from 86 locations (transect and additional observations) of *P. pygmaeus* included in this study. In italics the four maternity roosts found in 2002.

Date	X-Coord.	Y-Coord.	Canton	Observer	Location or Call-Nr.
Observations 2003					
14.01.2003	665100	210900	LU	R. Ehrenbold	Bruchmattstr. 21, Luzern
19 09 2002	720600	178000	GR	T Sattler	
19.09.2002	724000	179300	GR	T Sattler	$\begin{array}{c} OAII_2_{41} \\ OAII_2_{36} \end{array}$
19.09.2002	724000	179400	GR	T Sattler	$\begin{array}{c} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 $
19.09.2002	723200	179400	GR	T. Sattler	OAII 2 40
19.09.2002	733700	181500	GR	T Sattler	$\begin{array}{c} OAII_2 \\ OAII_2 \\ 25 \end{array}$
18.09.2002	753700	175600	GR	T Sattler	OAL 2.8
18.09.2002	753600	176200	GR	T Sattler	OAI 2 9
18.09.2002	753400	177400	GR	T Sattler	OAL 2 13
08.09.2002	632800	171200	BF	T Sattler	NAIL 2 39
08.09.2002	641100	177300	BE	T Sattler	NAIL 2 53
21 08 2002	502300	115400	GE	M Ruedi MHNG	Conches Genf
17 08 2002	489900	114400	GF	T Sattler	MLI 2 11
17.08.2002	495100	115400	GE	T Sattler	MII 2 24
17.08.2002	494900	115700	GE	T. Sattler	MLI 2 21
17.08.2002	495400	115900	GE	T. Sattler	MLI 2 25
23.07.2002	753600	176200	GR	T. Sattler	OAL 1
23.07.2002	749900	187500	GR	T. Sattler	OAL 1
23.07.2002	754900	190200	GR	T. Sattler	OAL 1
18.07.2002	727200	180400	GR	T. Sattler	OAII 1
18.07.2002	730800	181300	GR	T. Sattler	OAII 1
18.07.2002	733200	181300	GR	T. Sattler	OAII 1
18.07.2002	733700	181500	GR	T. Sattler	OAII 1
18.07.2002	731700	181600	GR	T. Sattler	OAII 1
18.07.2002	704500	113800	TI	M. Roesli	 Via San Jorio, Locarno
17.07.2002	705100	113900	ΤI	T. Sattler, M. Roesli	Via Luini, Locarno
14.07.2002	705300	113500	TI	T. Sattler	Bosco Isolino, Locarno
14.07.2002	731500	278800	TG	WD. Burkhard, F. Bontadina	Kreuzlingen
13.07.2002	705300	113500	TI	T. Sattler	Bosco Isolino, Locarno
12.07.2002	724200	179400	GR	T. Sattler	Tavanasa Dorf
12.07.2002	723400	179400	GR	T. Sattler	Danis
12.07.2002	724600	179700	GR	T. Sattler	Tavanasa
12.07.2002	722500	83200	TI	R.Pierallini	Fiume Breggia, Muggio
10.07.2002	670000	210200	LU	R. Ehrenbold, T. Sattler	Naumattrasse, Meggen
05.07.2002	669300	210600	LU	T. Sattler	Rebstockhalde, Meggen
05.07.2002	665500	212700	LU	R. Ehrenbold, T. Sattler	Jugistrasse, Luzern
04.07.2002	722500	83200	TI	R.Pierallini	Mte Generoso, Castel S.Pietro
02.07.2002	632500	170900	BE	T. Sattler	NAII_1_39
01.07.2002	578600	146800	BE	T. Sattler	NAI_1_39
15.06.2002	491100	114800	GE	T. Sattler	MLI_1_5
15.06.2002	499500	120200	GE	T. Sattler	MLI_1_20
15.06.2002	499700	120500	GE	T. Sattler	MLI_1_21
15.06.2002	500100	124100	GE	T. Sattler	MLI_1_26
11.06.2002	700500	120200	TI	T. Sattler	SAIII_30
07.06.2002	705300	113500	TI	T. Sattler	Bosco Isolino, Locarno
01.06.2002	722500	83200	TI	M.Moretti	Mte Generoso, Castel

					S.Pietro
30.05.2002	498300	120000	GE	M. Ruedi, MHNG	Parc des Mayens, Genf
21.05.2002			GE	M. Ruedi, MHNG	Genf
21.05.2002	705300	113500	TI	M. Roesli, M. Moretti	Bosco Isolino, Locarno
13.03.2002	499200	120000	GE	M. Ruedi, MHNG	Rte de Ferney, Genf
28.02.2002	502000	117500	GE	M. Ruedi, MHNG	College de Gradelle
29.01.2002	499900	114900	GE	M. Ruedi, MHNG	Ch. De Pinchat, Carouge

## **Observations before 2002**

24.05.2001	705300	113500	TI	M. Roesli, M. Moretti	Bosco Isolino, Locarno
Jun.01	735100	181900	GR	H. Schnitzler	Bahnhof Illanz
02.06.2001	705300	113500	TI	M. Roesli, M. Moretti	Bosco Isolino, Locarno
19.06.2001	700200	120000	TI	M. Roesli, M. Moretti	Gordevio
17.07.2001	700600	114500	TI	M. Roesli, M. Moretti	Losone, Piano di Arbigo
15.08.2001	505000	118500	GE	M. Ruedi, MHNG	Seymaz
16.08.2001	500000	111000	GE	M. Ruedi, MHNG	Collonge s Saleve
22.08.2001	505000	118500	GE	M. Ruedi, MHNG	Seymaz
12.09.2001	504400	118200	GE	M. Ruedi, MHNG	Ch. De la Blonde
14.10.2001	721200	116900	TI	M. Roesli, M. Moretti	Giubiasco
19.10.2001	705300	113500	TI	M. Roesli, M. Moretti	Bosco Isolino, Locarno
05.06.2000	501100	117200	GE	M. Ruedi, MHNG	Musee de Geneve, Genf
07.06.2000	511600	120500	GE	M. Ruedi, MHNG	Maison de la foret, Jussy
25.08.2000	504100	117300	GE	M. Ruedi, MHNG	Seymaz
27.09.2000	705300	113500	TI	M. Roesli, M. Moretti	Bosco Isolino, Locarno
06.10.2000	497500	114900	GE	M. Ruedi, MHNG	Gr. Lancy
11.03.2000	758700	220200	LI	S. Hoch	Triesen
24.04.2000	757500	222700	LI	S. Hoch	Vaduz
21.10.1999	507900	128700	GE	M. Ruedi, MHNG	Hermance, Genf
07.09.1998	681900	247000	ZH	F. Bontadina	Zurlindenstrasse, Zürich
21.09.1998	683600	249200	ZH	F. Bontadina	unter Rietlisiedlung, Zürich
28.08.1997	734900	179800	GR	F. Bontadina	bei Stall um Luven
10.09.1997	736000	179900	GR	F. Bontadina	bei Stall Sevgein
08.08.1992	656000	174000	BE	P. Zingg	Meiringen
30.06.1992	632000	170000	BE	P. Zingg	Interlaken
30.05.1989	628080	170300	BE	P. Zingg	Beatenberg
07.08.1988	656860	174640	BE	P. Zingg	Schattenhalb
07.08.1988	651700	176700	BE	P. Zingg	Meiringen
05.08.1988	656860	174640	BE	P. Zingg	Schattenhalb
29.06.1988	632000	171000	BE	P. Zingg	Interlaken
01.05.1983	705000	114000	TI	P. Zingg	Locarno
14.09.1982	551200	201460	NE	P. Zingg	Gorges de l'Areuse
28.08.1982	759950	133670	GR	P. Zingg	Castasegna
13.08.1982	764000	134200	GR	P. Zingg	Stampa
25.05.1982	655760	176620	BE	P. Zingg	Meiringen
08.05.1982	659500	173640	BE	P. Zingg	Innertkirchen
05.05.1982	660800	173100	BE	P. Zingg	Innertkirchen
29.10.1981	655760	176620	BE	P. Zingg	Meiringen
29.10.1981	655760	176620	BE	P. Zingg	Meiringen
29.10.1981	655760	176620	BE	P. Zingg	Meiringen
16.09.1981	658580	177860	BE	P. Zingg	Meiringen
07.09.1981	659500	173640	BE	P. Zingg	Innertkirchen
06.09.1981	660940	173320	BE	P. Zingg	Innertkirchen
06.09.1981	664980	174640	BE	P. Zingg	Gadmen
06.09.1981	656900	175540	BE	P. Zingg	Meiringen
19.10.1980	664980	174640	BE	P. Zingg	Gadmen

13.10.1980	660940	173320	BE	P. Zingg	Innertkirchen
11.10.1980	660940	173320	BE	P. Zingg	Innertkirchen
09.10.1980	660460	173040	BE	P. Zingg	Innertkirchen
09.10.1980	660940	173320	BE	P. Zingg	Innertkirchen
09.10.1980	660940	173320	BE	P. Zingg	Innertkirchen
08.10.1980	665500	174720	BE	P. Zingg	Gadmen
27.09.1980	657360	175600	BE	P. Zingg	Meiringen
27.09.1980	657000	175400	BE	P. Zingg	Meiringen
26.08.1979	761660	134340	GR	P. Zingg	Soglio
26.08.1979	761660	134340	GR	P. Zingg	Soglio
23.08.1979	761660	134340	GR	P. Zingg	Soglio
21.08.1979	763140	133800	GR	P. Zingg	Bondo
20.06.1979	768000	135630	GR	P. Zingg	Vicosoprano
18.06.1979	761660	134340	GR	P. Zingg	Soglio



*P. pygmaeus* (left) and *P. pipistrellus*; picture S. & R. Ehrenbold.