Do traditionally managed chestnut orchards represent optimal foraging and roosting habitats for the rare Leisler's bat (*Nyctalus leisleri*)?

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Leiter der Arbeit: Dr. Fabio Bontadina und Prof. Dr. Raphaël Arlettaz, Conservation Biology, Zoologisches Institut der Universität Bern

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Abstract

 During the last fifty years deciduous woodland management has undergone major changes in Europe, with traditional management being more and more abandoned. Intensively managed, closed coniferous plantations have replaced traditionally managed park like stands to a large extent.

2. In the Alto Malcantone Valley (Switzerland), a hilly woodland area with traditionally managed, open chestnut orchards, biodiversity was assessed in order to identify the ecological value of historic management practice. Results from a previous bat box study have highlighted the importance of this area as a stop-over site for the migratory bat species *Nyctalus leisleri*. This rare species was common in bat boxes, with 9 times more individuals in managed chestnut orchards compared to unmanaged stands.

3. The goal of this study was to explain this biased roosting pattern towards managed sites. The following two hypotheses were tested: 1) managed orchards represent optimal foraging sites (foraging hypothesis); 2) bat boxes in managed orchards offer more favorable microclimatic conditions (roost microclimate hypothesis)

4. By means of radio-tracking (n = 12 bats) and roost temperature loggers (n = 53) we investigated foraging habitat selection and roost use.

5. Leisler's bat positively selected deciduous woodland types as foraging area compared to coniferous woodlands, pastures and settlements. Managed chestnut orchards were used frequently for foraging (35 times more as expected from availability) but not significantly selected over other woodland habitat types. Leisler's bat did not select foraging areas in regard to distances to water courses or artificial streetlights.

6. In managed orchards bats used mainly cooler bat boxes. But boxes used in managed chestnut orchards did not differ in terms of microclimate from boxes in unmanaged stands. A dense canopy cover had a negative influence on temperatures in bat boxes.

7. None of our three hypotheses seem to explain the pattern of abundance of *Nyctalus leisleri*. As an alternative hypothesis, not tested here, we suggest that managed orchards may be optimal lekking arenas for Leisler's bats due to their open structure and abundance of roosts. These conditions should be ensured by resuming an appropriate traditional management of chestnut orchards, whereas closed stands should be progressively restored.

Key words: habitat selection, radio-tracking, roosts, open stands and park forests, management, conservation

INTRODUCTION

1 Introduction

Woodland habitats have undergone major structural changes over the last hundred years on the whole European continent (Steele, 1975). After the progressive abandonment of historic woodland management systems, an increase in deforestation, forestry intensification and scrub encroachment took place. Large areas of natural and semi-natural woodland have therefore disappeared and were replaced with tree plantations, improved grassland or arable fields. Management of woodland nowadays mainly concentrates on artificial plantations of predominantly coniferous character.

Open stands and park forests are characterized by their open structure with mature trees that are usually spread in a geometric arrangement, i.e. allowing regular distances between trunks for improving growth. This vegetation structure can be used by several animal species as commuting or even foraging habitat. The percentage of understory in open stands and park forests is limited, but there are usually large patches of unimproved grassland and, often, natural watercourses present. Such typical parkland habitats, which combine pasture- and woodland features, result from traditional, historical land-management. Over hundreds of years these groves were a predominant feature in the European's landscape, fulfilling a key role in the maintenance of biodiversity. Open stands and park forests do not only have a high recreational and cultural value but also provide suitable habitat for a wide range of bird, mammalian and arthropod species. Management of such open stands and park forests includes mowing of the understory and the frequent use as pasture. With the ongoing decrease of open stands and park forests, their ecological role in an environment of increasingly intensively managed landscape gained importance over the last decades (Glendell, 2002). From the 20th century onwards, open stands and park forests got more and more abandoned and are now seriously threatened by intensive agriculture and forestry. The abandonment of traditional agro-forestal activity in the last fifty years has led to a fast invasion of the existing park

landscapes by other tree species. As a consequence, the originally open structured stands became denser and old trees died out quickly (Conedera *et.al.*, 2001, Vale, 1987), factors which reduce the initially high ecological value of that habitat and directly threatened its persistence.

In the southern part of Switzerland and in Northern Italy a particular form of open stands and park forests can be found: the traditionally managed chestnut orchards which were of great economic interest until the first part of the 20th century. They consist of sweet chestnut trees, *Castanea sativa*, which prosper mainly in a mild climate. Although chestnut orchards often follow a less linear pattern and offer less open space than other open stands and park forests usually do, their vertical structure reminds of Britain's landscape parks (Prince, 1959, Slater, 1977). However, chestnut orchards do have a specific particularity: mature chestnut trees exhibit a lot of dead wood and offer a wide range of cavities for numerous animal species.

During the second part of last century no new chestnut orchards have been created and traditionally managed orchards have even been progressively abandoned since other, faster growing tree species became easier to use commercially (Conedera *et al.*, 2001). Open chestnut orchards have thus undergone major structural changes implying a loss of biodiversity. In order to assess the influence of abandonment on the orchards' biodiversity, the status of species which make particular use of this kind of habitat was examined in an ongoing study conducted by the *Swiss Federal Institute for Forest, Snow and Landscape research* (WSL). Besides arthropods and specific bird species, bats (*Chiroptera*), as representatives of the mammalian taxon and indicator species, were investigated in that programme. As the second most species rich order among mammals, bats play an important ecological role as predators of nocturnal flying insects. Many bat species use tree holes as roosts, forage within or close to woodland patches or edges and use linear vegetation structures not only for commuting between suitable foraging habitats but also as proper

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foraging sites (Walsh and Harris, 1996). The situation of bats in Switzerland reflects the global trends in decline which have been shown for most species since the 1950ties (Mickleburgh *et al.*, 2002). Tree-dwelling bat species are threatened by changes in forest management and logging, due to their high degree of specialization (Safi & Kerth, 2004). This makes them good potential indicators for studying the impact of changes in forest management on open stands and park forests in general, and chestnut orchards in particular.

In the above mentioned long-term study conducted by the forest authorities of the Ticino and the Swiss Federal Institute for Forest, Snow and Landscape research (WSL), which intends to assess the current biodiversity of chestnut orchards, a bat box study has shown clear differences in the presence of bats between managed and unmanaged (e.g. abandoned) orchards. Between 1999 and 2004, 150 bat boxes were placed in five managed chestnut orchards and 50 bat boxes were put into two unmanaged orchards (Alto Malcantone, Ticino, Zambelli, 2002). The boxes were inspected four times a year for the presence of bats. The results revealed two surprising facts. First, Leisler's bat, Nyctalus leisleri, a rare species in Europe and Switzerland (Stebbings, & Griffith, 1986; Zingg, 1988), was the dominant bat species, totalling 97% out of 990 bat observations. Second, more Leisler's bats occurred in the managed chestnut orchards than in the unmanaged ones, although bat boxes were equally distributed in both woodland types. Out of 959 individuals, 880 (91.76%) have been found in bat boxes located in managed orchards (Appendix 1). The managed chestnut orchards seemed thus to be of an outstanding importance for this rare bat species. In the present study we attempt to understand the reasons of the occurrence pattern. More specifically, we tested the following hypotheses:

 managed orchards offer more optimal foraging sites than unmanaged ones (foraging hypothesis);
bat boxes in managed orchards offer more favorable microclimatic conditions (roost microclimate hypothesis). We thus investigated habitat selection by radio-tracking, and microclimate of roosts with data loggers. This study is part of a research program assessing

the importance of different management practices in historic chestnut orchards for

biodiversity.

2 Methods

2.1 Study area

The study was conducted in Alto Malcantone (Ticino, Switzerland 46°02'52.76"N / 8°54'01.23"E). The region is characterized by vast wooded areas consisting mainly of sweet chestnut, Castanea sativa, interspersed with pastures and settlements. The study area encompasses the minimum convex polygon of all radio-tracked individuals (12137 ha); it is very hilly with elevation between 613 m and 930 m. Besides the main river Magliasina that meanders through the valley, a remarkable number of small streams, a pond and a fire fighting pond can be found at the study site. A total of 5 transects in managed and 2 transects in unmanaged chestnut orchards have been equipped with 200 bat boxes in 1999 and 2001 (Zambelli, 2002, Appendix 2). The seven orchards are situated on the two flanks of the valley. The bat boxes were initially distributed in equal parts among managed and unmanaged chestnut orchards, after 2001 they were spread among the managed (150) and unmanaged (50) sites according to size. The managed and unmanaged chestnut orchards differ fundamentally in their structure. While managed orchards represent a rather typical park landscape with open space between neighbouring trees and no understory, the unmanaged orchards are dense woodland blocks with a high percentage of understory and a large amount of dead wood.

2.2 Radio-tracking

Female and male Leisler's bats exhibit a similar phenology in our bat boxes (Appendix 3). They are quite abundant from March until the end of May, and from August until the end of October. In June and July only very few and mainly male individuals were observed. For the months November and December very little presence data are available since only one

inspection has been made. Due to this phenology, the field work was carried out in two parts, the first taking place between 14th March and 26th May 2005 and the second between 16th August and 26th October 2005. We tried to radio-tag an equal number of individuals originating from the two habitat management modes, and to have a balanced sex ratio. The bats were caught in bat boxes under licence from the office of nature conservation of the Canton of Ticino (24.02.2005). They were tagged with Holohil BD-2 0.45 and Holohil BD-2 0.62 transmitters. The hair between the scapulae was trimmed and the radiotag bonded to the skin with SkinBond® surgical cement (SkinBond, Smith & Nephew United Inc., Largo, Florida, U.S.A.). The tags used did not exceed 6% of body weight and should therefore not have affected the bat's manoeuvrability (Neubaum et al., 2005). Maximum operating time of the tags was 21, respectively 40 days, but bats were observed over 9 nights at maximum. Data stem from eight animals in spring and four in fall. The bats were tracked by car as well as on foot using an omnidirectional aerial mounted on car roof, 3-element yagi aerials and two Australis 2k scanning receivers (Titley Electronics, Australia). The individuals were followed during their entire foraging bouts using cross-triangulations performed at 5-min intervals, in order to determine their location. The 'homing-in on the animal' (White & Garrott, 1990) method was also used. An evaluation of the error polygon size in ArcView GIS 3.3 revealed an average diameter of the error polygon of 200 m. Therefore we added a buffer zone of 200 m to the original locations for the calculation of the individual minimum convex polygons. Only locations of an accuracy of up to 200 m have been used for further analysis. All tagged individuals were consequently followed to their roosts in order to determine which roost type they choose, this during the whole working time of the tags.

2.3 Roost microclimate

We tested for possible temperature differences between four different types of potential roosting sites: 1) used bat boxes in managed orchards; 2) unused bat boxes in managed

orchards; 3) bat boxes in unmanaged orchards and 4) potential natural roosts. A total of 56 data loggers of two different brands, TinyTalks (TK-0014, Gemini, UK) and ibuttons (DS1921G-F5 with DS9093F Flanged Fob, Maxim Integrated Products Inc., U.S.A.) were equally distributed among the four roost types. Hourly temperature measurements were collected in spring and autumn. Bat boxes were defined as used on the basis of data obtained in the previous six years. The entrances of boxes classified as unused were blocked to prevent bats or any other animals from using the boxes and thereby influencing box temperature. Potential natural roost sites were chosen randomly among the seven orchards based on the knowledge obtained by observing natural roosts which were currently used by radio-tracked bats. Additionally, the geographical exposure of the roosts was taken and the degree of canopy cover around them was defined as one of the following three classes: (1) uncovered, (2) half covered (25-75%) and (3) highly covered (> 75%).

2.4 Statistical analyses

2.4.1 Foraging habitat selection analysis

For land mapping we distinguished the following eight habitat types: 1) deciduous woodland with less than 20% chestnut trees; 2) deciduous woodland with more than 20% chestnut trees; 3) managed chestnut orchards; 4) unmanaged chestnut orchards; 5) riparian woodland; 6) coniferous woodland; 7) pasture and 8) settlements. Basic information was available as ArcView shape files (Sezione Forestale, canton Ticino, Stanga, 1994 & 1999). In a first step, the five deciduous woodland types were grouped together into the general habitat class deciduous forest. Additionally, two continuous distance variables "distance to next watercourse" and "distance to next artificial streetlight" were recorded for an analysis of the distances. By comparing foraging locations with randomly generated points we tested for differences in mean distances to water courses and artificial streetlights applying an ANOVA. The variables were tested for variance homogeneity and normality prior to running ANOVAs.

Variables which were not homogenous or normal were transformed by square root transformation in order to conduct ANOVAs.

In order to determine home ranges the 100% - minimum convex polygon (MCP) of all locations of an individual was calculated using GIS, adding the above 200 m buffer around all locations. Core foraging areas were calculated using the 50% - Kernel Density Estimator (Worton 1989, Harris *et al.*, 1990). Thereby the smoothing factor h in all calculations was set to 200 m according to the mean location error (Bontadina & Naef-Daenzer, 1996, Hemson et al., 2005, Naef-Daenzer & Gruebler, unpubl. data).

We investigated habitat selection using compositional analyses (Aebischer & Robertson, 1992, Aebischer *et al.*, 1993). For computation we used an Excel macro (Smith, 2003) applying randomization as recommended by Aebischer *et al.* (1993). First, the four main habitat categories deciduous forest, coniferous woodlands, pasture and settlements were tested by comparing the available habitats within each individual's MCP to the selected habitats present in the 50% - core foraging area of each individual. Second, we split the class deciduous forest into its five logical types (see above) and, for a clear presentation of the intensity of selection of the single habitat types, we calculated the Jacobs' (1974) preference index J (Revilla, Palomares and Delibes 2000) according to the following formula:

J = (u-a)/[(u+a) - 2ua]

where u is the proportion of used and a the proportion of available habitat types. This index ranges from (-1) for maximum avoidance up to (+1) for maximum preference. Statistical significance of deviations from zero was calculated by applying t-tests where the null hypothesis corresponds with a Jacobs' index equal to zero.

2.4.2 Roost microclimate

The two dependent parameters "mean day temperature" and "mean delta temperature" (maximum day temperature minus minimum day temperature) were calculated for each roost. We only used temperature data gained during the day from 06:00 until 18:00 because bats roost in the boxes during the day and Kerth *et al.* (2001) found no significant differences in night temperatures of bat boxes. Since a strong positive correlation existed between those two parameters (spring: r = 0.68, n = 53, p < .0001, autumn: r = 0.72, n = 53, p < .0001), only mean day temperature was used in further analyses.

Combining the temperature data of spring and autumn season to one data set, ANOVAs were performed in JMP Version 4 (SAS Institute Inc., Cary, NC, USA, 2000) testing for significant differences between the four roost categories: used boxes in managed orchards (m+), unused boxes in managed orchards (m-), unused boxes in unmanaged orchards (um-) and natural roosts (nat). The mean daily temperature served as response variable, the geographical exposure in deviations from north (0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°), the degree of canopy cover divided into three classes (see above), the study plot and season (spring and autumn) as independent variables. Tukey – Kramer post-hoc tests were conducted to identify significant differences within pairs of variables. Again, all variables were tested for variance homogeneity and normality prior to running ANOVAs. Variables which were not homogenous or normal were transformed using square transformation in order to conduct ANOVAs.

3 Results

3.1 Foraging habitat selection analysis

From 18 tagged individuals we collected successfully 261 locations (n = 8 in spring, 4 in autumn) from 7 males and 5 females during a total of 109 tracking nights (Table 1). Six individuals either left the area or the transmitter failed before sufficient data was collected. Tracking sessions lasted from three to nine nights per individual.

Individual home ranges (MCP areas) had a mean size of 1501 ha (SD = 1869 ha, range: 133 - 6668 ha). Thus, our radio-tracked bats used very large home ranges as it has also been shown in other studies (Shiel *et al.*, 1999, Waters *et al.*, 1999). The area of single MCPs still increased in relation to the number of locations taken which means the MCP areas are not saturated and present minimal activity areas during the study periods. Maximum distance flown by a bat in one night was 13'614 m, mean flown distance was 1969 m (SD = 1754 m, Table 2). The main habitats present in the study area were deciduous woodlands with chestnut trees (36%), pastures (23.1%), deciduous woodlands (22%), settlements (15.4%), unmanaged orchards (1.6%), coniferous woodlands (1.4%), managed orchards (0.3%), riparian woodland (0.25%) (Table 4). Core foraging areas, depicted by 50%-kernels, were used in habitat selection analysis to identify the mostly used areas within an individual home range. Mean core foraging area was 43.7 ha (SD = 41.34 ha, 16.8 - 131 ha). There are quite large discrepancies between animals in regard to the relative use of the habitats (Appendix 4).

A first habitat selection analysis with the five main habitat classes revealed a significant habitat selection ($x^2 = 21.06$, d.f. = 3, randomized P = 0.006; Fig. 1). Deciduous forest was significantly selected over pasture, coniferous woodlands and settlements. In the second analysis Jacobs' index for habitat preferences confirmed the pattern found in the first analysis, with the two types of chestnut orchards and deciduous woodlands tending to be preferred. The subsequent t-test showed a significant avoidance of settlements but no significant positive

selection of any other habitat type (Fig. 2). Finally, Leisler's bats did select their foraging areas neither with respect to the distance to watercourses nor to the distance to artificial streetlights (ANOVA, $F_{521,1} = 0.0015$, p = 0.15 and $F_{521,1} = 0.0012$, p = 0.97, respectively).

3.2 Roost microclimate

Microclimatic differences with respect to roost type, canopy cover, study plot and season were tested by ANOVA (Table 3). The factor season accounted for the highest part of variation, autumn temperatures were significantly higher than spring temperatures (Tukey-Kramer HSD, n = 2, p < 0.05). Following were the factors roost type, canopy cover and study plot. Post-hoc tests indicate that natural roosts have significantly lower temperatures than all other roost types (Tukey-Kramer HSD, n = 4, p < 0.05). There was no significant difference between the temperatures measured in used boxes in unmanaged orchards and used boxes in managed orchards (Fig. 3), which means that our hypothesis was rejected. There was a significant negative influence of canopy cover on roost temperatures (Tukey-Kramer HSD, n = 3, p < 0.05): The higher the amount of canopy cover around a roost, the lower temperatures within roosts (Fig. 4).

DISCUSSION

4 Discussion

In this study we could show that Leisler's bats positively select deciduous woodlands compared to coniferous woodlands, pastures and settlements. However, they did not show any significant preference, during foraging, for managed vs unmanaged chestnut orchards. Also, the bats did not forage preferentially close to streams and street lamps. Although trends are not significant it must be pointed out that managed and unmanaged chestnut orchards made up only 0.3 and 1.6%, respectively, of the study area but harboured each 9% of foraging activity and 47 out of 261 locations. This indicates that managed chestnut orchards, as a particular form of open stands and park forests, seem to be of special importance to Leisler's bat as shown previously for landscape parks in the UK (Glendell and Vaughan (2002). The most remarkable difference, however, is that foraging habitats of Leisler's bat in Great Britain are mainly pastoral and arable land, whereas colonies are located in building roofs but not primarily in tree cavities (Waters et. al., 1999). In contrast, Swiss Leisler's bat forage and roost mainly in woodland as evidenced in Germany (Schorcht, 2002). As there was no evidence for a lower availability of natural cavities in managed vs unmanaged chestnut orchards, the high occupancy of bat boxes in open, managed stands is due to a higher bat concentration in that habitat. What may then explain this preference of roosting in managed chestnut orchards? We showed that microclimatic conditions in bat boxes do not differ between managed and unmanaged plots, with the only perceptible difference being that used bat boxes in managed chestnut orchards have cooler temperatures than unused bat boxes. A preference for cooler roosts may be explained by physiological constraints. In spring and autumn, bats still engage regularly into daily torpor so as to save a maximum of energy. In contrast, reproducing bats would probably have selected warm roosts (Kerth et al., 2001), but Leisler's bats do not reproduce in our study area which represents only a transitory seasonal habitat. We showed that it is the density of canopy which adversely influences the

temperature within bat boxes: denser the canopy, lower and more constant the temperature. Forestry should therefore maintain a dense canopy around hollowed trees and bat boxes. Neither roost availability, nor microclimate seems to explain bat aggregations in managed orchards.

We believe that this pattern of roost occupancy is mostly due to flight constraints. With their high aspect ratio and high wing loading (Norberg & Rayner, 1987), Leisler's bats belong to fast flying species requiring enough room for proper flight manoeuvrability. This would be especially crucial during the courtship season when bats engage in display flights to attract mates to their roosts. These display flights are performed close to mating roosts where males tend to attract females in order to form their periodic harems. Males are also known to call for females from roost entrance (Helversen, & Helversen, 1994); in the latter case, the roosts play the role of leks (Bradbury, 1977; Hammer, & Helversen, 1994). Males therefore choose roosts of high accessibility (Ohlendorf, 1998), such as our bat boxes in managed orchards, whilst boxes hung up in clustered conditions (e.g. unmanaged stands) are avoided. We thus believe that managed orchards offer thanks to their semi-open structure a very optimal situation for forming leks during the mating season. This is reflected in the fact that bat boxes in managed orchards were used by Leisler's bat immediately after installation. Managed chestnut orchards, as one particular form of park like landscape, are of prime importance for the persistence of Leisler's bat populations.

Our results reveal, first, that deciduous woodlands are of great importance to *Nyctalus leisleri* as foraging habitat and, second, that managed chestnut orchards – as one particular form of deciduous woodland - are frequently used habitats. The present study also indicates that suitable stop-over habitats are crucial for this migratory bat which flies long distances from nursery roosts in North-Eastern Europe to mating and wintering grounds in South-Western Europe. Due to flight constraints, a dependence on specific roosting habitat makes Leisler's bat vulnerable to alterations in woodland structure. In this context, the progressive

abandonment of traditional park like forests in general and traditional chestnut orchards in particular, has probably affected Leisler's bat status in Europe. Thus management of abandoned chestnut orchards should be resumed in order to enhance the chances of survival of this potentially vulnerable tree-dwelling species of the European fauna.

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Individual	sex	site	managed	Ν	High	Medium	Ν
				bearings	accuracy	accuracy	nights
1	f	Breno	-	7	2	5	5
2	f	Mugena	+	5	2	3	3
3	m	Cassina	-	9	0	9	3
5	f	Vezio	+	47	2	45	6
6	m	Fescoggia	+	13	2	11	5
7	m	Vezio	+	19	4	15	4
8	f	Vezio	+	29	10	19	6
9	f	Vezio	+	28	18	10	5
10	m	Vezio	+	33	11	22	3
12	m	Breno	-	18	17	1	6
16	m	Ascigna	+	29	16	13	9
17	m	Cassina	-	24	24	0	5
12 bats	5females / 7males			261	108	153	109

Table 1. List of successfully radio-tracked individuals of *Nyctalus leisleri* indicating sex, capture site, management form of the orchard (+ = managed, - = unmanaged), number of radio bearings with accuracy level and total number of radio-tracking nights.

Table 2. List of successfully radio-tracked individuals indicating home ranges (MCP), mean distance (m) of foraging locations to roost with standard error (SE) and maximum distance (m) to roost.

Individual	Foraging area (MCP ha)	Mean distance	SE	Maximum distance (m)
1	222	472	301	1080
2	337	582	1758	3553
3	133	748	408	1338
5	2697	5693	1284	8109
6	199	728	352	1514
7	2131	2020	1693	5165
8	1108	2107	965	4743
9	1814	3405	1988	6538
10	2054	4266	2393	7107
12	432	591	450	1730
16	6668	2754	4635	13614
17	216	258	363	1647
Total	12137 (SA)	1969	1754	4678 (+ 3747)

Table 3. ANOVA on mean daily bat box temperature (n = 106 roosts) showing the effects of roost type, exposure, canopy cover, site and season (df = degree of freedom, p = probability).

Variable	Sum of squares	df	Variance	F Ratio	р
Roost type	100.95	3	33.65	15.37	< .0001
Exposure	41.24	7	5.89	2.04	0.0575
Canopy cover	43.10	2	21.55	7.89	0.0006
Site	82.45	2	13.74	5.62	< .0001
Season	73.77	1	73.77	30.62	<.0001

Table 4. Availability of habitat types in the whole study area depicted by the minimum convex polygon (MCP) obtained from all individuals' locations pooled together.

Habitat	Availability	Availability
	in ha	in %
Deciduous woodland	2671	22
Deciduous with chestnut trees	168	36
Coniferous woodland	4361	1.4
Managed chestnut orchards	31	0.3
Unmanaged chestnut orchards	193	1.6
Riparian woodland	30	0.25
Pasture	2810	23.1
Settlements	1873	15.4

Figure captions

Fig. 1. Habitat selection by 7 male and 5 female *Nyctalus leisleri* (mean \pm SD): comparison of habitat available in the individual home ranges with habitat used within the 50% core foraging areas (mean percentage area + SD). Classes to the left are selected over those to the right in decreasing order of preference. >>>, indicates a significant difference with sequence (p < 0.01, compositional analysis). All deciduous woodland types are grouped together to deciduous forest.

Fig. 2. Jacobs' index of selection (for details see methods) for each individual (n = sample size) habitat. Positive and negative values indicate preference and avoidance, respectively. * = significantly different from zero (t-test, p < 0.05).

Fig. 3. Mean day temperature (+SE) with respect to roost type: Significant differences between pairs are shown (*: p < 0.05, Tukey-Kramer comparison of means).

Fig. 4. Mean day temperature and (+SE) with respect to canopy cover: Significant differences between pairs are shown (*: p < 0.05, Tukey-Kramer comparison of means).





Fig. 1



Habitat type

Fig. 2



Fig. 3



Fig. 4



Appendix 1. Number of bats (mean + SE) per box and year in managed and unmanaged orchards (data from Zambelli, 2004).



Appendix 2. Core study area with the five managed and two unmanaged orchards. "A"– Mugena, managed orchard with 20 bat-boxes, "B"–Vezio, managed orchard with 30 batboxes, "C"–Fescoggia, managed orchard with 50 bat boxes, "D"-Breno, unmanaged orchard with 26 bat boxes, "E"-Ascigna, managed orchard with 26 bat boxes, "F"-Cassina, unmanaged orchard with 23 bat boxes, "G"-Coren, managed orchard with 25 bat boxes.



Appendix 3. Number of female and male *Nyctalus leisleri* (mean + SE) observed per box and inspection. Twenty-seven inspections were carried out in managed areas between 1999 and 2004 and 22 inspections were carried out in unmanaged areas between 2001 and 2004 (no inspections in November and December - black dots) at 200 bat boxes (data from Zambelli, 2004).



Appendix 4. Foraging areas delimited by minimum convex polygon (MCP) of 12 radio-tracked *Nyctalus leisleri*. The study area is given as the MCP of all individual foraging areas