

# Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation

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Received 31 January 2003; received in revised form 6 May 2003; accepted 12 May 2003

## Abstract

We investigated roost selection by *Barbastella barbastellus* in a mountainous area of central Italy. Twenty-five bats, mostly lactating females, were radio-tracked to 33 roost trees. Trees in unmanaged woodland were favoured as roost trees; woodland subject to limited logging was used in proportion to availability, and areas where open woodland and pasture occurred were avoided. Selection depended on tree condition (dead beech trees were preferred) and height (roost trees were taller than random ones). Cavity selection was based on cavity type, height and entrance direction: roost cavities were mainly beneath loose bark, at a greater height above ground and facing south more frequently than random cavities. Untouched areas of mature woodland should be preserved to provide roosting conditions for *B. barbastellus*. In logged areas, harvesting protocols should save dead and mature trees; frequent roost switching and small colony size imply that large numbers of roost trees are needed.

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**Keywords:** *Barbastella barbastellus*; Bat; Chiroptera; Italy; Roost selection; Woodland management

## 1. Introduction

Roosts play a crucial role in bat biology (e.g. Kunz, 1982), and their availability affects both the geographic occurrence of bat species and the diversity of bat communities (e.g. Findley, 1993). Many of the nearly 850 microchiropteran species roost in trees (e.g. Kunz, 1982; Brigham et al., 1997; Sedgely and O'Donnell, 1999a; Boonman, 2000; Lacki and Schwierjohann, 2001; Menzel et al., 2002). Deforestation is regarded as a specially serious threat to conservation of these mammals (Hutson et al., 2001). Because old and dead trees are richer in cavities suitable for roosting, they may be particularly important for bats (Hutson et al., 2001; Parsons et al., 2003). The roosting requirements of tree-dwelling bat species represent a major conservation issue, and inves-

tigation of roost selection is needed to set up appropriate guidelines for forest management.

The barbastelle bat (*Barbastella barbastellus* (Schreber, 1774)) is a medium-sized vespertilionid (forearm length = 36.5–43.5 mm, body mass = 6–13.5 g.; Schober and Grimmberger, 1997) occurring in Europe, North Africa and Asia (Hutson et al., 2001; Urbańczyk, 1999). It is recorded over much of Europe, except in the highest latitudes (Iceland, Northern Ireland, Estonia and most of Scandinavia; Urbańczyk, 1999). *B. barbastellus* is classified as 'Vulnerable' at a global scale (Hutson et al., 2001), 'Endangered' in Italy (Bulgarini et al., 1998) and is threatened in many areas of Europe, especially in the west where it may be one of the rarest bat species (Urbańczyk, 1999). The species is protected by European law under Annexes II and IV of the Habitats Directive 92/43/EEC.

*B. barbastellus* shows roosting preferences that should be regarded as a key point in conservation protocols (Hutson et al., 2001). The species has been described as

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roosting mainly in human-made structures in summer, with trees being regarded as of secondary importance (Harrington et al., 1995; Schober and Grimmberger, 1997). However, radio-tracking studies have recently shown that *B. barbastellus* largely selects tree cavities as roosts (Greenaway, 2001; Steinhäuser et al., 2002).

Few studies have dealt with roosting preferences in *B. barbastellus*: Greenaway (2001) examined roosting behaviour and activity of the species in Britain, while observations in continental Europe are limited to Germany (Steinhäuser et al., 2002). Nothing is known about roost selection of *B. barbastellus* in southern Europe.

We examined roost selection in a breeding population of *B. barbastellus* from central Italy at three levels: woodland structure and management type; tree characteristics; and cavity characteristics. Our aim was to contribute to drawing up guidelines for conservation of this sensitive bat species in southern Europe.

## 2. Materials and methods

### 2.1. Study area

The study was carried out at the Abruzzo, Lazio and Molise National Park (Lat 41°48' N, Long 13°46' E; Fig. 1), where Issartel (2001) first documented the occurrence of *B. barbastellus*. To our best knowledge, the area is home to the only breeding population documented for peninsular Italy. For data analysis, the area hereafter named 'study area', of 700 ha, was delimited after locating roosts by choosing limits corresponding to main mountain ridges and other topographic features to encompass all roost and random plots (see below).

The study area is mountainous, with a mean elevation of ca. 1500 m a.s.l. (range 1278–1924 m a.s.l.). The substrate is mainly limestone, and extensively covered with beech (*Fagus sylvatica*) woodland; other habitats occurring in the area are pastures, often associated with woodland. Other tree species, such as scycamore (*Acer pseudoplatanus*), are infrequent. Much of the woodland has not been logged since 1956.

A special management protocol is adopted by the Park authorities to preserve a considerable proportion of untouched woodland; limited and highly selective logging is occasionally done in a few forest stands. We classified woodland according to its structure and management procedures as follows (Fig. 1):

1. Pastures + woodland: 54.5% of the study area, at lower altitudes, is characterised by an association of woodland and pastures. In the past, woodland was thinned to favour the presence of pasture. The landscape still maintains this structure but the area has not been logged for over 40 years and grazing by cattle is now moderate. Pastures are interspersed with (or surrounded by) old trees occurring at low densities.
2. Unmanaged woodland: 35.6% of the study area is covered with woodland that has not been logged for at least the past 40 years.
3. Shelterwood-harvested stands: 9.9% of the area is made of stands which had not been disturbed since 1956, but in 1997–2002 were partly and selectively harvested in order to reduce competition among trees. Logging involved only understorey trees, according to the shelterwood harvest system. In no cases were old or dead trees removed.

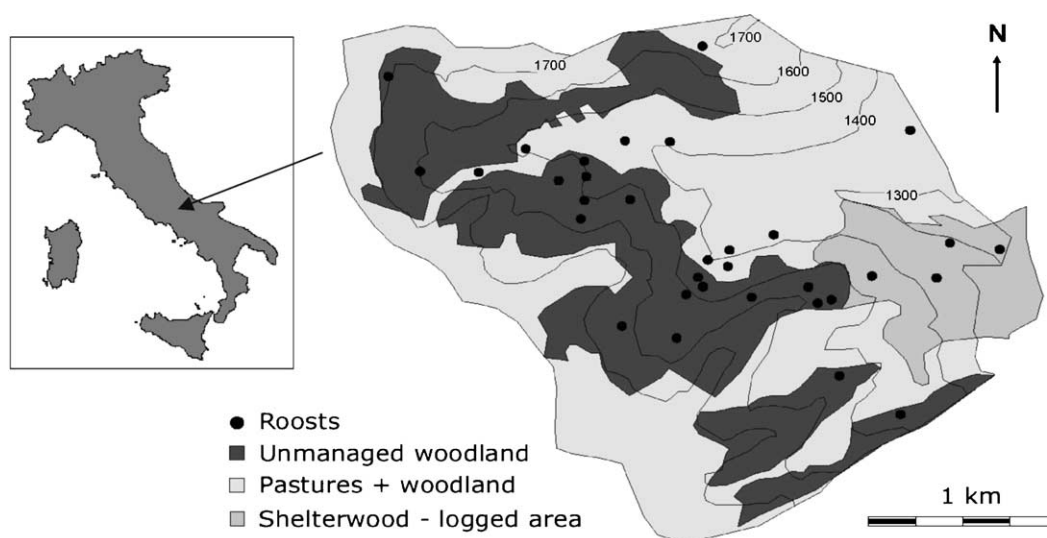


Fig. 1. Left: location of the Abruzzo, Lazio and Molise National Park (box); map of the study area and location of 33 *B. barbastellus* roosts.

## 2.2. Capturing and tagging bats

Field work was conducted in July and August 2001–2002. The bats were captured by placing 2.5×6 m and 2.5×12 m mist-nets (50 denier, mesh size = 38 mm) near cattle troughs frequented by bats for drinking. The nets were erected soon after dusk and kept in place for 2–4 h. The bats captured were promptly removed from the net, and their body mass and forearm length were measured respectively with a digital scale to the nearest 0.1 g and a calliper to the nearest 0.1 mm. Sex was assessed by inspecting genitalia (Racey, 1988), and wings were trans-illuminated to distinguish juveniles from adults, the former showing cartilage epiphyseal plates in finger bones and more tapered finger joints (Anthony, 1988). In females, pregnancy was diagnosed by palpation (Racey, 1988), and lactation was identified by the occurrence of enlarged nipples surrounded by a hairless skin area and by extruding milk with a gentle finger pressure on the nipple base. The bats were fitted with 0.48 g LB-2 Holohil radio-transmitters, attached between the shoulder blades with Skinbond adhesive after clipping the fur, and released ca. 10 minutes after tagging. Captures were conducted under licence from the Park authorities.

## 2.3. Location of roosts and data recorded at roost sites

Radio-tracking was conducted on foot in the day time. To locate the tagged bats while they were roosting, we used an Australis 26 K radio-receiver (Titley Electronics Pty Ltd., Ballina) and a three-element hand-held directional aerial. Once the roost tree was located, when possible we identified the cavity occupied by the bat by assessing radio-signal strength and direction standing near the tree, by visually inspecting cavities with binoculars and sometimes by observing bats on emergence at dusk.

The roost tree position was determined with an Eagle Expedition Global Positioning System receiver (Eagle Electronics, Catoosa) and mapped on a 1:25,000 map (Istituto Geografico Militare, Florence). Elevation was recorded with an altimeter, terrain main aspect and percent slope were measured with a compass and a clinometer respectively. Distances from the nearest woodland edge, potential drinking site and source of disturbance (i.e. main paths frequented by tourists, forest roads) were taken from 1: 10,000 orthophotos. All roost trees were classified as belonging to the following classes: class 1 *Fagus sylvatica*, i.e. live beech trees showing < 50% of dead limbs and loss of foliage; class 2 *Fagus sylvatica*, live beech trees with 50–90% of dead limbs and loss of foliage; class 3 *Fagus sylvatica*, dead beech trees (> 90% of dead limbs and loss of foliage); and *Acer pseudoplatanus* trees (all live individuals).

From each roost tree we recorded: height with a clinometer, mean DBH (stem diameter at breast height),

percent canopy closure (the degree of canopy closure around the roost tree assessed visually from the base of the tree), and total number of cavities visible from the ground on trunk and main limbs. When the roost cavity was located, we recorded its type (loose bark, rot cavity, mechanical break such as vertical splits, woodpecker hole) and measured its height above ground (with a clinometer) and entrance direction (with a compass). In a few cases it was not possible to pinpoint the roost exactly. However, by carefully scanning the tree for cavities and loose bark, we could be confident of the type of roost used as there were no cases where different roost types on the same tree could be confused.

Following Sedgeley and O'Donnell (1999a), we marked four quadrants around each roost tree and located the nearest tree potentially suitable for roosting in each quadrant (point-centred quarter method; Causton, 1988). Each roost tree and its four neighbours constituted a roost plot (Sedgeley and O'Donnell, 1999a). Previous observations carried out in the area showed that cavities were mostly absent in trees with a height above ground < 3 m and a DBH < 30 cm; when a cavity was present, this was too small (entrance diameter < 5 cm ca.) and superficial to be used by bats, and in no case was flaking bark present (D. Russo, pers. obs.). Radio-tracking data confirmed this assumption (see Results). Hence, only trees of a larger size were included in the roost plot. The distance between the roost tree and each of the four neighbours was measured with a Sonin Combo Pro ultrasonic distance measurer (Sonin Inc., Brewster), and density of potential roost trees was calculated (in hectares) as  $10000/(\text{mean of the four distances to nearest trees in metres})^2$ . From each neighbouring tree we also recorded tree type according to the same classification used for roost trees, height, DBH, number of cavities and percent canopy closure.

## 2.4. Data recorded from random trees and cavities

To investigate whether *B. barbastellus* selected particular roost trees, 100 trees in the study area were chosen at random and regarded as potentially available to roosting bats; their features were compared with those of roost trees. To locate random trees, we modified the procedure adopted by Sedgeley and O'Donnell (1999a), adapting it to the study area topography: in this way, we selected at random 25 locations (point-centres; Causton, 1988) around which the four nearest available trees (one in each quadrant) with a height  $\geq 3$  m and DBH  $\geq 30$  cm were located. The set of four trees around each point-centre was defined a random plot. From each random tree, we recorded the distance from the point-centre to calculate density and measured site and tree features in the same way as for roost plots.

To investigate roost cavity selection, we located cavities potentially suitable to bats in all trees along a 2000×60 m strip transect crossing the area where most *B. barbastellus* roosts occurred. Because this survey was carried out after locating *B. barbastellus* roosts, we assessed suitability of random cavities subjectively on the basis of the cavity size observed in roosts. All cavities were classified according to type, and their height and entrance direction were measured with a clinometer and a compass respectively. One cavity per tree was then chosen: when more than one cavity occurred on a specific tree, only one was selected at random.

### 2.5. Statistical analysis

Woodland was classified according to its structure and to the management protocol adopted as follows: pastures + woodland, unmanaged woodland and shelterwood-harvested woodland (see 'study area' for definitions). Autocad release 14.0 was used to map the woodland accordingly and measure the area occupied by each category. A chi-square analysis was applied to see whether the observed proportion of use (number of roosts occurring in a woodland category/total number of roosts located in the study area) departed from the expected proportion (calculated as the area of the corresponding woodland category/ overall size of the study area). Selection was then established by calculating Bonferroni's confidence intervals for use of each woodland category (Neu et al., 1974) using the standard normal deviate or Z statistic.

The following univariate comparisons were carried out:

- roost plots were compared with random plots to see whether there was any difference in elevation, terrain exposure, percent terrain slope, distances from the nearest woodland edge, potential drinking site and source of disturbance;
- Both roost trees and roost plot trees were compared with random trees to test for the occurrence of differences in tree type frequency, height, mean DBH, percent canopy closure, and total number of cavities;
- roost cavities were compared with random cavities to see whether their type frequency, height above ground and entrance direction differed significantly.

In most cases, variables did not follow a normal distribution according to a Ryan–Joiner test, so we used a Mann–Whitney test to analyse differences between datasets; when data were normally distributed, a *t*-test was applied; frequency data were analysed with a chi-square analysis. In chi-square tests, to avoid >20% expected frequencies being <5 (Dytham, 1999), data

from several categories were lumped together when necessary.

Logistic regression models were developed to explore which of the variables differing significantly between (a) roost and random trees, and (b) roost and random cavities actually influenced selection. To assess the effect of each variable on the significance of the model, we generated several models by removing one variable in turn, and measured the corresponding reduction in deviance (e.g. Sedgeley and O'Donnell, 1999a). Because logistic regression models presence and absence data, we assumed that random trees and cavities were not being used for roosting (Sedgeley and O'Donnell, 1999a). Univariate tests were made with Minitab release 9.0, and logistic regression was performed with SPSS release 11.0. In all tests, significance was set at  $P < 0.05$ .

## 3. Results

### 3.1. The bats and their roosting behaviour

We tagged 31 adult *B. barbastellus*, 10 lactating females in 2001 and 21 (19 lactating females, one pregnant female and one male) in 2002. No juvenile was observed, probably because most of them were not volant at the time captures were made. The male we captured was the only one ever recorded in the study area (Issartel, 2001; D. Russo, unpublished data). Fore-arm length was  $39.8 \pm 1.0$  mm, and body mass was  $8.2 \pm 1.1$  g; on average, the tag weighed  $6.0 \pm 0.7\%$  of the bat's body mass (range 4.0–7.2%). The bats were tracked for  $4.5 \pm 3.7$  days (range: 0–12 days). We located 33 roosts (Fig. 1) used by 25 subjects ( $1.8 \pm 1.2$  roosts/bat, range 1–5); four bats were never detected after release, and we received radio-signals from two further bats only on one day, but their roost was not identified. Some of the bats tracked in 2002 used four of the roost trees located in the previous study year. In four cases, two tagged bats shared the same roost; three tagged bats roosted together in one tree.

The bats switched roosts frequently: 13 bats used more than one tree over the study period, and for a given bat a new roost was located on average every  $2.6 \pm 1.6$  days (range: 1–6 days,  $n = 13$  bats). These data may underestimate roost switch frequency since not all bats could be located every day due to limited search effort. Eight bats checked every day occupied the same roosts over the entire tracking period ( $9.4 \pm 1.8$  days, range 6–12 days). For four bats only one roost could be found before contact was lost. Two bats moved together from one roost to another. The number of bats in a colony was counted in seven cases, and equalled  $16.7 \pm 4.2$  (range 12–23) bats.

On three occasions roosting bats reacted to the presence of an approaching observer by flying away in the



day-time. One of these bats was tagged, so we were able to follow it to a nearby roost tree, located in the previous year.

### 3.2. Selection of woodland and roost trees

Chi-square analysis showed that the roosts were not distributed at random across woodland categories; unmanaged woodland was positively selected, whereas shelterwood-harvested woodland was used in proportion to its availability, and the 'pastures + woodland' category was avoided (Table 1).

Most roost trees (20 out of 33) were class 3 (=dead) *F. sylvatica* trees; eight roost trees belonged to class 1 and five to class 2; *Acer* trees were not used (Fig. 2). Conversely, Class 1 *F. sylvatica* dominated (89 out of 100 trees) in the random sample; five trees belonged to class 3 *F. sylvatica*, one to class 2 *F. sylvatica* and five were *Acer* trees (Fig. 2). To meet chi-square analysis assumptions, we lumped together class 1 + 2 *F. sylvatica* trees and removed *Acer* from the dataset; class 3 *F. sylvatica* was used more than expected ( $\chi^2$  with Yates' correction = 46.71; d.f. = 1;  $P < 0.001$ ).

Overall, roost trees were significantly taller and had a larger DBH and more cavities than random ones (Fig. 2). Identical results were obtained for class 1 *F. sylvatica* trees, but the two samples in class 3 *F. sylvatica* did not differ significantly. When the total data set was analysed, roost trees had a lower percent canopy closure than random trees.

The variables considered were significantly inter-correlated (Table 2): to highlight which of them were actually associated with selection, we devised a logistic regression model based on tree type, height, DBH, number of cavities and percent canopy closure. The full model was significant ( $\chi^2 = 102.72$ , df = 8,  $P < 0.001$ ) and a goodness-of-fit test did not reject the null hypothesis of an adequate fit (Pearson  $\chi^2 = 117.06$ , df = 125,  $p = 0.681$ ). The model classified correctly 95.0% of available trees and 75.8% of roost trees (overall correct classification = 88.9%,  $n = 133$ ). Removal of tree type and tree height affected the model significantly, but the other variables did not produce detectable effects (Table 3).

### 3.3. Comparison between roost and random plots

In all, we took measurements of tree features and density from 29 roost plots (= 116 trees). The number of roost plots is less than the overall number of roosts (33) because four roost trees had no roost plot trees in their surroundings. Roost plots consisted of 105 trees from class 1 *F. sylvatica*, six from class 3, four from class 2 and one *Acer* tree (Fig. 2). Descriptive statistics for features of roost sites are shown in Table 4. Roost and random plots showed similar altitude, slope, main direction faced and density of potential roost trees; no significant differences were found in distances from woodland edge, potential sources of disturbance and nearest water sites (Mann–Whitney and *t*-tests, n.s.). In both plot samples, dead trees were equally rare (5%;  $\chi^2$  with Yates' correction = 0.096; d.f. = 1; n.s.) to meet chi-square analysis assumptions, trees from classes 1 and 2 *F. sylvatica* were lumped together and *Acer* trees were removed from the dataset). Overall, trees in roost plots were taller and had a larger DBH than those in random plots; in class 1 *F. sylvatica*, roost plot trees were also significantly taller than random trees (Fig. 2). All other differences were either not significant or not analysed statistically because of the small sample sizes (Fig. 2).

### 3.4. Comparison between roost and random cavities

The roost cavity type was determined for 27 out of 33 trees, height above ground and entrance direction for 22. The bats roosted under loose bark in 20 of 27 trees; four roosts were rot cavities, and three were vertical splits. Sixty cavities potentially suitable to bats were recorded from 30 of the transect trees, and one cavity/tree was used for analyses: the available sample included 14 cavities behind loose bark, 14 rot cavities, one woodpecker hole and one vertical split. After grouping all cavities as 'defoliating bark' and 'others', it was found that the bats roosted under loose bark more frequently than expected and avoided all other types ( $\chi^2$  with Yates' correction = 4.51, d.f. = 1,  $P < 0.05$ ).

*B. barbastellus* preferred cavities at a greater height (median roost height = 10.1 m; range = 1.8–16.7 m,  $n = 22$ ;

Table 1

Results of chi-square and selection analyses (Bonferroni's confidence intervals) for woodland categories according to structure/management protocol. Proportion of use expected = area of woodland managed as in 'Management type' column/overall size of the study area (700 ha); Proportion of use observed = number of roosts occurring in the corresponding woodland category/number of roosts in the study area

Management type	Area (ha)	Number of roosts	Proportion of use expected	Proportion of use observed	Chi-square value	Selection
Pastures + woodland	381.3	10	0.545	0.303	3.539	Negative
Unmanaged	249.6	19	0.356	0.576	4.446	Positive
Shelterwood-harvested	69.1	4	0.099	0.121	0.169	Absent
Total	700.0	33	1.000	1.000	8.154*	

\*  $P < 0.05$ .

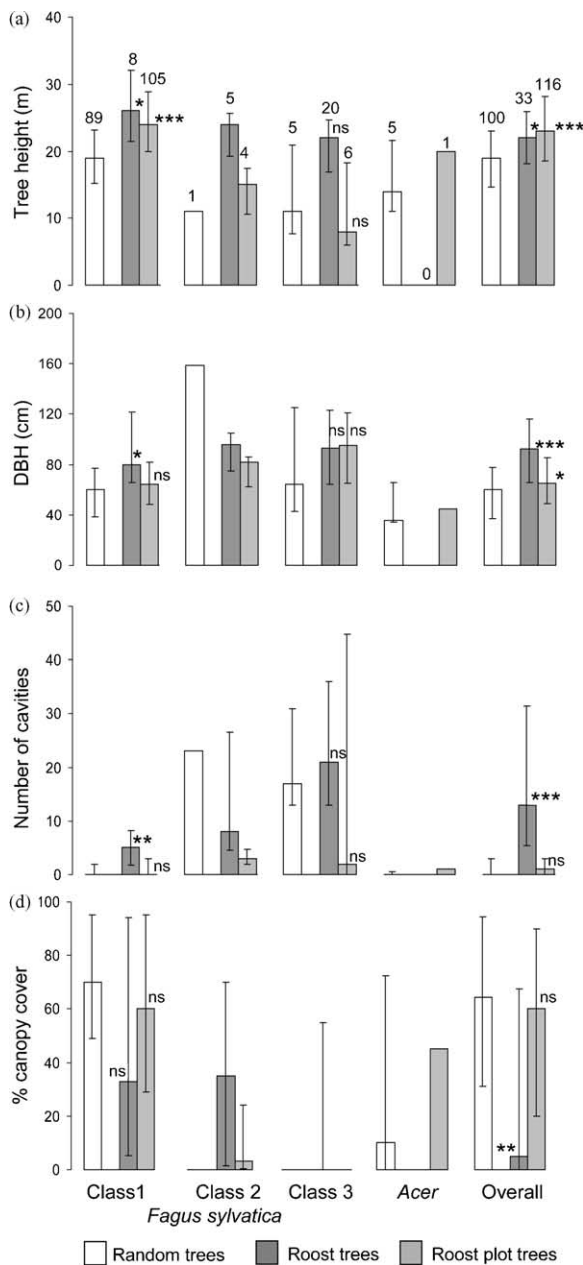


Fig. 2. Median and interquartile range of a) tree height, b) DBH (diameter at breast height), c) number of cavities and d) percent canopy closure for random trees, roost trees and roost plot trees, and results of Mann–Whitney test (features of roost and roost plot trees were compared with those of random trees both within each tree class and in the overall sample). Class 1 *Fagus sylvatica*=live beech trees showing <50% of dead limbs and loss of foliage; class 2 *Fagus sylvatica*=live beech trees with 50–90% of dead limbs and loss of foliage; class 3 *Fagus sylvatica*=dead beech trees (> 90% of dead limbs and loss of foliage); *Acer*=maple trees. No analysis was performed for class 2 *F. sylvatica* and *Acer* trees since the random sample of the former comprised only one tree and no roost and only one roost plot tree were *Acer* ones; statistical analysis of percent canopy closure for class 3 *F. sylvatica* could not be made because values from all random sample units were zero. Numbers labelling bars in graph a) indicate sample sizes. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns = difference not significant.

median random cavity height = 4.5 m; range = 1.5–13.7 m,  $n = 30$ ; Mann–Whitney  $W = 634$ ,  $P < 0.01$ ). There was also a tendency for roosts to face south (63.6% south facing: 91–270 degrees; 36.4% north facing: 271–90 degrees,  $n = 22$ ). The distribution of directions of roost cavities differed significantly from that of random cavities (70% north facing, 30% south facing,  $n = 30$ ;  $\chi^2 = 5.88$ ,  $P < 0.05$ , Yates' correction applied). Identical results were obtained when all 60 cavities from transect trees were used as the 'available' sample in the analysis.

Logistic regression was applied to identify factors determining selection of cavities. Cavities were classified as follows: loose bark, rot cavity, vertical split, woodpecker hole. The model included cavity type, height above ground and direction faced (Table 3). The full model was significant ( $\chi^2 = 22.07$ ,  $df = 6$ ,  $P < 0.01$ ) and a goodness-of-fit test did not reject the null hypothesis of an adequate fit (Pearson  $\chi^2 = 51.96$ ,  $df = 46$ ,  $P = 0.253$ ). The model classified correctly 86.7% of random cavities and 72.7% of roost ones (overall correct classification = 80.0%,  $n = 52$ ). All variables contributed significantly to the model (Table 3).

## 4. Discussion

### 4.1. *B. barbastellus* roosting preferences

In this study, *B. barbastellus* made a great use of dead trees for roosting as observed in northern Europe (Greenaway, 2001; Steinhauser et al., 2002), as also found for other tree-dwelling bat species (Brigham et al., 1997; Sedgely and O'Donnell, 1999a; Law and Anderson, 2000; Weller and Zabel, 2001; Lumsden et al., 2002; Kurta et al., 2002). In the study area, dead trees occurred most frequently in unmanaged woodland, where the number of roosts we located was higher than expected from the availability of this woodland type. When live trees were used for roosting, their size was larger than that of random trees, as large trees are more likely to bear suitable cavities than small (= young) ones.

In England, Greenaway (2001) found that the understorey covering the roosting area protected roosts from temperature and humidity variation. In our study area, the absence of undergrowth in most of the pastures + woodland area, together with a lower availability of dead trees, may help explain why this habitat was avoided for roosting. Unmanaged woodland, the preferred roosting habitat, showed a dense understorey.

The few differences between roost and random plots mainly concerned the occurrence of relatively larger trees around the roosts. This was expected since most roost plots were located within the unmanaged woodland area, where large trees are frequent.

Some of the differences between roost and available trees probably depended on the higher percentage of dead trees in the roost sample. Dead trees normally have more cavities and a larger diameter than live ones; furthermore, because dead trees have no foliage and a lower number of branches, they often have less contact with the crowns of surrounding trees. These considerations explain why percent canopy closure correlates negatively with DBH and number of cavities (Table 2).

As shown by logistic regression analysis, roost tree selection by *B. barbastellus* was based only on tree type and height. Because tall trees project above the canopy, they may be easy to locate for a bat returning to the roost or looking for a new one (Vonhof and Barclay, 1996; Brigham et al., 1997), particularly for a species such as *B. barbastellus* which often flies above the canopy (Sierro and Arlettaz, 1997). Furthermore, tall trees may be preferred because they are more exposed to solar radiation (Brigham et al., 1997; Ormsbee and McComb, 1988; Sedgeley and O'Donnell, 1999a; Law and Anderson, 2000; Greenaway, 2001), and may offer a warm roost microclimate, especially if cavities are located at greater heights above ground, like the

*B. barbastellus* roosts in this study. Reproductive females need to remain homoeothermic to allow foetal development to occur and for lactation (e.g. Racey, 1973; Grinevitch et al., 1995; Altringham, 1996), and selecting a warmer roost may conveniently limit the costs of homoeothermy. The fact that the entrance of roost cavities faced south more frequently than random ones is in agreement with the hypothesis that thermal preferences play an important role in roost selection by lactating *B. barbastellus*. In this respect, roosting in dead trees may be advantageous because the absence of living wood tissue may determine warmer roosting conditions (Law and Anderson, 2000). Males were almost absent in the study area, possibly because, unlike females, they do not need to maintain homoeothermy in summer and may save fat reserves more efficiently by becoming torpid during the day in cooler roosts (e.g. Grinevitch et al., 1995; Altringham, 1996)—such as caves—found elsewhere. Roost temperature may be the key factor on which roost selection is based, as found in *Myotis bechsteinii* (Kerth et al., 2001) which prefers colder roosts before parturition, whereas warmer ones are selected by lactating females.

As observed in Germany and Britain (Greenaway, 2001; Steinhäuser et al., 2002), *B. barbastellus* frequently roosted under loose bark in this study. In Abruzzo, as in Germany (Steinhäuser et al., 2002), lactating bats commonly used this roost type; in Britain, however, Greenaway (2001) found that flaking bark was most frequently chosen in spring and autumn, while lactating bats mostly roosted in vertical splits and rarely behind bark. Such differences might be due to climatic differences between the areas investigated.

Most tree-dwelling bat species in different genera studied to date select roost types other than defoliating bark (Wilkinson, 1985; Brigham, 1989; Swift, 1998; Sedgeley and O'Donnell, 1999b; Boonman, 2000; Law and Anderson, 2000; Sedgeley, 2001; Lumsden et al., 2002). A number of bat species besides *B. barbastellus* frequently roost beneath bark, including *Myotis californicus* (Brigham et al., 1997), *M. sodalis* (Kurta et al., 2002), *M. septentrionalis* (Lacki and Schwierjohann,

Table 2

Correlation matrix (Spearman's rank correlation coefficient) for variables measured from roost and random trees ( $n=133$ ). DBH=diameter at breast height

	<i>n</i> cavities	DBH	Tree height
DBH	0.70*** <sup>b</sup>	–	–
Tree height	0.13 (ns) <sup>a</sup>	0.37***	–
Percent canopy closure	–0.48***	–0.45***	0.14 (ns)

<sup>a</sup> ns = not significant.

<sup>b</sup> \*\*\* $P < 0.001$ .

Table 3

Reduction in deviance expressed as a  $\chi^2$  value in the logistic regression models for selection of a) tree-roosts and b) roost cavities caused by the removal of one factor in turn ('Effect' column). *p* values illustrate that tree selection (a) was based only on tree class and height; cavity selection model (b) was affected significantly by all factors. Tree class abbreviations as in Fig. 2. DBH = diameter at breast height

Effect	Reduction in deviance	
	$\chi^2$ <sup>a</sup>	df
<i>Tree selection</i>		
Class (1, 2, 3 <i>F. sylvatica</i> , <i>Acer</i> )	32.64***	4
Tree height	6.67*	1
Percent canopy closure	0.05 (ns)	1
Number of cavities	0.27 (ns)	1
DBH	0.97 (ns)	1
<i>Cavity selection</i>		
Type (flaking bark, rot, vertical split, woodpecker hole)	21.45***	4
Height above ground	10.30**	1
Direction faced	4.09*	1

<sup>a</sup> ns = not significant; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

Table 4

Descriptive statistics for features of roost sites ( $n=33$ )

Variable	Mean $\pm$ S.D.	Range
Altitude (m a.s.l.)	1487 $\pm$ 103	1280–1710
Slope (%)	44 $\pm$ 19	7–76
Direction faced (degrees)	94 $\pm$ 91	0–340
Distance from woodland edge (m)	84 $\pm$ 105	0–500
Distance from nearest source of disturbance (m)	1031 $\pm$ 514	20–2000
Distance from nearest water (m)	1790 $\pm$ 745	300–3500
Density of potential roost trees in ha (*) <sup>a</sup>	125 $\pm$ 86	11–308

<sup>a</sup> (\*) = density of potential roost trees could be measured in only 29 out of 33 roost sites (roost plots).

2001) and *M. thysanoides* (Weller and Zabel, 2001). Although *M. septentrionalis* uses cavity roosts more often than flaking bark, roosts under bark contain a larger number of bats (Lacki and Schwierjohann, 2001). *Nyctophilus geoffroyi* uses several roost types, including loose bark which is occasionally used by breeding females (Taylor and Savva, 1988). In *C. tuberculatus*, solitary bats sometimes roost beneath bark (Sedgely and O'Donnell, 1999b).

Loose bark provides a less stable microclimate than do deep tree holes (Greenaway, 2001); moreover, strong wind, heavy rain or snow can easily remove pieces of bark from the trunk so this roost type is likely to be unsafe under poor weather conditions. *B. barbastellus* and other species roosting beneath bark may do so to avoid competition from birds and other mammals which prefer more stable roosts (Greenaway, 2001). Dead trees may be preferred because they often have loose bark.

As several other tree-dwelling bat species (e.g. Brigham et al., 1997; O'Donnell and Sedgely, 1999; Law and Anderson, 2000; Weller and Zabel, 2001; Kurta et al., 2002; Menzel et al., 2002), *B. barbastellus* switches roost frequently; this behaviour may reduce predation risk, parasite load and roost fouling (Fenton, 1983; Lewis, 1995).

Our observations on colony size, although from a limited roost sample, are in agreement with other studies (Schober and Grimmberger, 1997; Greenaway, 2001; Steinhäuser et al., 2002) and confirm that maternity colonies in this species are relatively small.

We failed to document any effect of topographic features on the choice of roosting sites, probably because both random and roost plots occurred within an area which was relatively homogeneous.

#### 4.2. Management implications

In our study, several bats travelled for over 2 km from their roosts to reach drinking sites and quite large numbers of *B. barbastellus* congregated at cattle troughs together with several other bat species. Hence, in roosting areas where water sites are rare or absent, the presence of cattle troughs and small ponds should be encouraged (Russo and Jones, 2003).

The occurrence of a significant breeding population of *B. barbastellus* at our study site was certainly made possible by the preservation of large areas of ancient woodland: protection of such areas is probably the most important conservation measure to ensure optimal roosting conditions. In our study area, dead trees were a rare resource even where mature woodland was widespread. The scarcity of dead trees is undoubtedly a crucial limiting factor for *B. barbastellus*. Moreover, this species' other stringent roosting habits (small maternity colonies, frequent roost switching) imply that even a

small breeding population requires the availability of quite a large number of roost trees. *B. barbastellus* is probably unable to find suitable roosting sites where intensive and non-selective logging is conducted. In roosting areas, felling operations should be avoided as far as possible: when they are necessary, tree cavities—especially those of mature or dead trees—should be carefully inspected beforehand for the presence of bats. In logged areas, selective timber harvesting protocols preserving dead trees and a significant fraction of mature trees should be adopted. Besides *B. barbastellus*, several other woodland species of bat would benefit from these management procedures (Mayle, 1990; Hutson et al., 2001).

Our observations of bats leaving the roost in daylight when approached by people suggest that disturbance to roosting areas should be avoided. The tendency to leave the roost in the daytime may allow the bats to shelter at a new site in order to avoid predators, and may be a consequence of bats being vulnerable under flaking bark. Forest roads and trails should avoid likely *Barbastella* roosting areas; in nature reserves accessible to visitors, tourist paths should pass around potential roost sites whenever possible.

#### Acknowledgements

We gratefully acknowledge the Nando Peretti Foundation and the Abruzzo, Lazio and Molise National Park for funding the study. Francesco Garofano and Giovanni Mastrobuni helped in capture operations and radio-tracking. Cinzia Sulli and Carmelo Gentile provided information on woodland management at the Abruzzo, Lazio and Molise National Park. Colin O'Donnell and Jane Sedgely gave precious advice on data collection and analysis, Mark Weir kindly made some linguistic improvements to the ms. and Antonello Migliozi and Sandro Strumia helped in preparing illustrations. Brian N.K. Davis, Anthony M. Hutson and an anonymous referee made valuable comments which greatly improved a previous version of the ms.

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