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ORIGINAL PAPER

Reconsidering the importance of harvested forests for the conservation of tree-dwelling bats

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Abstract Intensively managed forests are often seen as of low priority to preserve forest bats. The main conservation strategy recommended, i.e. saving unmanaged "habitat islands" from logging to preserve some suitable habitat, detracts conservationists' attention from ameliorating conditions for bats in harvested sites. We studied the threatened bat *Barbastella barbastellus*, mostly roosting in snags, in two beech forests: an unmanaged forest—the main maternity site—and a nearby, periodically logged area. We compared roost availability, roost use, capture rates, food availability and movement between these areas. The managed forest had a greater canopy closure, fewer dead trees, a smaller tree diameter and trees bearing fewer cavities than the unmanaged one. These differences helped explain the larger number of bats recorded in the unmanaged forest, where the sex ratio was skewed towards females. Prey availability was similar in both areas. We radiotracked bats to 49 day roosts. Five individuals caught in the managed area roosted in the unmanaged one at 6.7–8.2 km from the capture site. Few bats roosted in the managed forest, but those doing so proved flexible, using live trees and even rock crevices. Therefore, bats utilise areas in the matrix surrounding optimal roosting sites and sometimes roost there, highlighting the conservation potential of harvested forests. Besides leaving unmanaged patches, at least small numbers of dead trees should be retained in logged areas to favour population expansion and landscape connectivity. Our findings also question the validity of adopting presence records as indicators of forest quality on a site scale.

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Introduction

In many regions, the removal of dead or defective trees is still a common silvicultural practice, justified in terms of concerns over forest safety, fire risk, productivity and parasite spread. Its adverse effects on forest biodiversity are significant, causing a marked decline in many animal species whose life cycle depends on dead wood, including insects, birds, and mammals (e.g. Morrison and Raphael 1993; Martin et al. 2004; Jonsell et al. 1998; Bütler et al. 2004; Jonsell et al. 2004; Hilszczajski et al. 2005; Djupström et al. 2008).

In recent years, the impact of forest harvesting on bat populations has received considerable attention (Barclay and Kurta 2007). Key activities of forest bats, such as foraging and roosting, are strictly dependent on forest structure, which is in turn greatly influenced by traditional silvicultural practices geared to commodity production (Graves et al. 2000). Because many forest bats are threatened (Hutson et al. 2001), understanding the consequences of different forestry options for their conservation is paramount in implementing sustainable management.

Although forest management may affect bat populations directly (e.g. by mortality determined by logging; Hayes and Loeb 2007), most impacts on demographics and behaviour are indirect and involve changes in the availability of roosting and foraging habitats. A wealth of information is available for indirect influences on bat foraging, especially from studies carried out in North America (e.g. Grindal and Brigham 1998; 1999; Patriquin and Barclay 2003; Tibbels and Kurta 2003).

For the many bats that roost in forest (Carter and Menzel 2007), preferred roost trees constitute a main spatial resource. Although no study has directly assessed changes in the abundance and viability of bat populations following the decline in the numbers of potential roost trees (Hayes and Loeb 2007), the most logical consequence of this habitat alteration is a decrease in the carrying capacity of populations of tree-dwelling species. Roosting requirements of forest bats are species-specific and depend on several spatial scales, from cavity to landscape level (Russo et al. 2004; Barclay and Kurta 2007; Carter and Menzel 2007; Duchamp et al. 2007). Generally speaking, roost cavities are found in defective, large-diameter, or standing dead trees—the latter hereafter termed “snags” (Graves et al. 2000; Smith et al. 2008).

Snags—a tree roost type naturally rare even in unmanaged forest—are preferred by several bat species (Russo et al. 2004; Barclay and Kurta 2007). Decreased snag availability is a typical long-term consequence of intensive forest management (e.g. McComb et al. 1986). Besides direct snag logging, short harvest rotations, improvement thinnings and clearcuts typical of intensive forest management also decrease tree mortality by reducing competition and removing senescent or defective trees that might replace dead ones naturally eliminated over time by mechanical and biological agents. For example, in an Appalachian hardwood stand, snag stem density and volume decreased as much as threefold when comparing uncut controls to heavily thinned treatments (Graves et al. 2000). Due to low snag density, intensively managed forests are seen as of little importance for endangered bat species that depend on such trees. This may lead conservationists to discourage habitat improvement actions there, perhaps limiting their attention to unmanaged forest. This site-focused view may overlook all potential interactions between managed and unmanaged sites encompassed within colony home ranges and may therefore miss conservation benefits originating from an integrated, landscape-scale management approach.

In some regions, retaining “habitat islands”, i.e. unmanaged patches in logged forest landscapes, is recommended to conserve populations of roosting bats (Anonymous 2005). Because forest bats often switch roosts (Lewis 1995; Kerth and König 1999; Willis and Brigham 2004; Russo et al. 2005; Popa-Lisseanu et al. 2008), the effectiveness of this mitigation to sustain even small populations depends on retaining a sufficiently large area, that is one that includes enough suitable trees (Russo et al. 2005). Unanswered questions remain concerning the role of nearby “sub-optimal” forest to promote landscape connectivity for bats and its influence on the long-term survival of bat populations in untouched habitat fragments.

Bats are highly mobile mammals: they often use a variety of foraging habitats and travel long distances to preferred feeding sites (e.g. Rabe et al. 1998). Some species are migratory (Hutterer et al. 2005), and in temperate regions even sedentary ones often move seasonally from hibernation to reproductive quarters to search for suitable microclimatic conditions. Clearly, this mobility implies a marked tendency to explore the surroundings of roosting areas, a fact which calls for a landscape-scale approach to management.

Managed and unmanaged stands in forested landscapes might function, respectively, as sinks and sources in metapopulation dynamics (Pulliam 1988; Pulliam and Danielson 1991), but no study has so far tested this prediction. Understanding the role of managed patches near unmanaged ones would help in setting up strategies to promote their colonisation, improve their role as biological corridors and ultimately increase population size.

In this study, we used the barbastelle (*Barbastella barbastellus*) as a model species. A typical tree-dwelling bat, the barbastelle mostly roosts in snags (Russo et al. 2004), and exhibits frequent roost switching (Russo et al. 2005). A previous study (Russo et al. 2004) in the same region where the present study was conducted found that roosting *B. barbastellus* prefers unmanaged beech forest (hereafter termed UF) over other lightly managed forest types (shelterwood forest and forest associated with pasture). That study did not address the role of intensively managed stands potentially encompassed in the typically large home range of this species (Hillen et al. 2009).

In fact, *B. barbastellus* also occurs in a nearby managed forest site (hereafter abbreviated as MF), separated from UF by mountain ridges (Fig. 1) and mostly exploited for timber production.

In this study we characterized available roost trees in the two sites and analyzed their closeness to optimal conditions, adopting as a reference point the habitat selection patterns observed in forest areas subject to little or no human alteration (Russo et al. 2004). Moreover, we made the following predictions:

1. Mountains separating UF from MF may be crossed by bats, so bats may travel between areas;
2. If MF is less suitable for roosting, bats should be less frequent there than in UF;
3. If any bats roost in MF, they should exhibit a more flexible pattern of roost selection.

To account for the possible influence of differences in food availability between the two sites on the numbers of bats observed, we also recorded the occurrence of moths (favoured food of *B. barbastellus*: Rydell et al. 1996; Sierro and Arlettaz 1997).

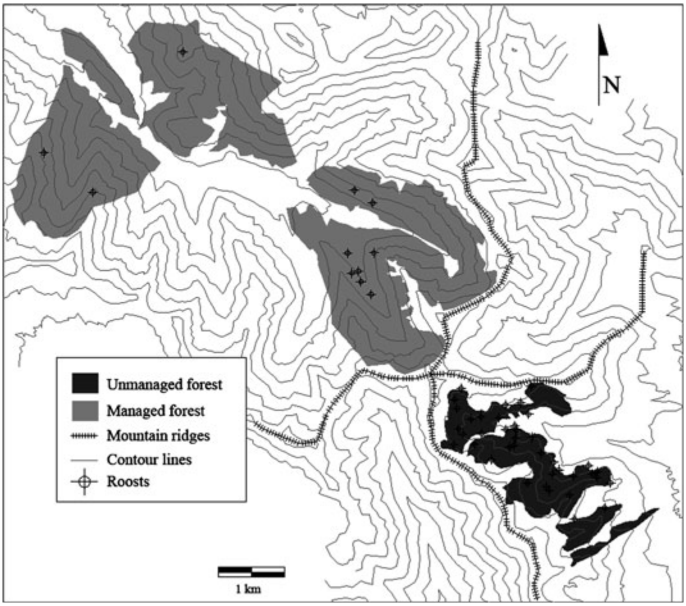

Fig. 1 Land use types and roost location in the study area. Note that unmanaged and managed forest sites are separated by mountain ridges

Materials and methods

Study area

In both UF and MF, the dominant tree species was beech *Fagus sylvatica*. The unmanaged site (UF) considered for this study corresponds to that defined as "unmanaged woodland" in Russo et al. (2004). That study, and others (Russo et al. 2005, 2007) were set in that area, as well as in the neighbouring ones located SE of it (not considered for the present study) and subject to limited disturbance ["pasture + woodland" and "shelterwood—logged" areas in Russo et al. (2004)]. None of these earlier studies included MF, an area mainly characterized by young beech stands largely subject to diameter-limit harvesting, along with some mixed coppice forest including beech and European hop-hornbeam *Ostrya carpinifolia*. Forest was mainly located along mountain slopes and canyons, surrounding a wide grassland area traditionally grazed by cattle (Fig. 1). In this area, forest was periodically logged by plot according to a rotation plan: given plots were chosen in different years and selective logging was applied, i.e. trees logged were those previously selected by a forestry technician based on criteria such as diameter, position and overall timber volume.

Comparisons of roost tree availability between MF and UF

To assess roost tree availability, we considered only trees whose height above ground and diameter at breast height (hereafter abbreviated as DBH) were, respectively $\geq$3 m and 30 cm, since trees smaller than this are unlikely to bear cavities suitable for *B. barbastellus* (Russo et al. 2004). Available trees were selected by modifying the procedure adopted by Sedgeley and O'Donnell (1999), which was adapted to the study area topography: in this way, we randomly selected locations (point-centres) around which we identified the four nearest available trees (one in each quadrant). The set of four trees around each point-centre was defined as a random plot. From each tree, we recorded the distance from the point-centre to calculate density and measured site.

At each random plot, we measured % terrain slope and aspect (measured as a 0–180° value from north), tree height (m) and DBH (cm).

Trees were categorized as *Fagus sylvatica* classes 1 (live beech trees showing <50% of dead limbs and loss of foliage), 2 (live beech trees with 50–90% of dead limbs and loss of foliage) and 3 (>90% of dead limbs and loss of foliage). Fifteen random plots were selected in each study area, totalling 30 plots (=120 available trees).

Differences in bat relative abundance, sex ratio, roost selection and movements between areas

In both sites, a dozen bat species, including *B. barbastellus*, used cattle troughs for drinking. We sampled bats by erecting 6×2.5 and 12×2.5 m mistnets (50 denier, mesh size = 38 mm) near drinking sites and compared capture frequency—assumed to be proportional to numbers of bats using the sites—between areas. Although in the UF we carried out captures only at one drinking site, others were present in the surroundings, at an average distance of 3.1 km from the one we selected. In the MF, of three cattle troughs present, in most cases only two had water when captures were carried out. In that area, the mean distance between neighbouring water sites was ca. 3.5 km.

Nets were erected at dusk and kept in place for up to 4 h. Captures were carried out in June–August 2001–2008. Subjects were removed from the net promptly, 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. We assessed sex by inspecting genitalia (Racey 1988), and trans-illuminated wings to distinguish juveniles from adults, the former showing cartilage epiphyseal plates in finger bones and more tapered finger joints (Anthony 1988). In females, we diagnosed pregnancy by palpation (Racey 1988), and lactation 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. Sex ratio was calculated as the ratio of males to females in each area.

Roost trees were located by radiotracking bats captured at drinking sites back to their roosts in daytime. Bats were fitted with 0.4 g Holohil LB2 tags applied between the shoulder blades with Skinbond adhesive after partly clipping the fur. We extracted the UF roost sample from the overall dataset used by Russo et al. (2004) and added further roosts (accounting for 47.4% of total) discovered after completion of that study. These also included roosts used by some bats tagged in the MF that moved to the UF after capture.

Roost types were classified as either trees or rocks. The former were further categorized according to the procedure described in Russo et al. (2004). At each roost site, besides measuring terrain slope and aspect, tree height, DBH, and when possible roost cavity position (height from ground and aspect) were also recorded.

Assessing food availability

On two consecutive nights in July 2008 we sampled moths in both UF and MF. In each area, we selected three capture sites (one immediately outside the forest, one along its edge and another in forest interior) in each of which we trapped moths for 1.5 h with a light trap (trapping surface was a back-illuminated 2 m-sided square white sheet). All captured moths were grouped by family.

Data analysis

Random plot (tree density, altitude, slope, aspect) characteristics, as well as variables of available and roost tree (height, DBH, per cent canopy closure, number of cavities) were compared between UF and MF sites with a one-way ANOVA. When residual distribution departed from normality, as assessed with a Ryan-Joiner test, we either square-rooted or log-transformed data before running the ANOVA or, if normality was not achieved after transformation, used a Kruskal–Wallis test instead. ANOVA was also used to compare moth catches between areas. Variable frequencies of both available trees and roosts were compared between areas by either Fisher's exact or chi-square tests (depending on sample size).

When comparing numbers of bats caught over different nights, capture effort differed in terms of net length and capture time. Moreover, captures were conducted from late pregnancy to post-lactation times. Therefore, we used a two-way General Linear Model (GLM) ANOVA to test for difference in the total number of bats (response variable) between areas. First, we entered site (UF, MF) and sex (male, female) as main explanatory factors, and capture effort (expressed as metres of mistnet deployed multiplied by hours of capture/night) and Julian day (first date of capture corresponding to Day 1 = 25th June) as covariates (assumed to be continuous and linear). All between-factors interactions were also included. Because covariates had no significant effect on the response variable, the final model only included site and sex as main factors and their interaction.

All tests were carried out with Minitab rel. 13 (Minitab Inc., State College, PA, USA). Significance was set at $P < 0.05$.

Results

Comparisons of suitability of available trees for Barbastella barbastellus

In both MF and UF areas, dead or dying trees were rare in the available sample but ca. 6 times more frequent in the latter, accounting for 3% and 18% of available trees, respectively ($n = 120$, Fisher's exact test, $P < 0.05$). *Fagus sylvatica* was the dominant tree species in all random plots. Trees other than beech were quite rare: in MF plots, three (*Acer pseudoplatanus*), two in UF plots (*Ostrya carpinifolia*, *Quercus cerris*).

As a result of the higher elevations of the UF, random plot sites differed in altitude ($n = 30$; MF: 1368 ± 91 m a.s.l.; UF: 1552 ± 98 m a.s.l., $F_{1,29} = 28.33$, $P < 0.001$), but neither in terrain aspect ($n = 30$; MF: 93° ± 55°; UF: 68° ± 44°, $F_{1,29} = 1.41$, n.s.) nor slope ($n = 30$; MF: 30 ± 13%; UF: 39 ± 16% $F_{1,29} = 2.81$, n.s.). Available tree density was also equal between areas ($n = 30$; MF: 331 ± 240 trees ha^{-1}; UF: 245 ± 177 trees ha^{-1}; Kruskal–Wallis test, H = 0.87, n.s.).

In MF, trees had a significantly lower DBH (ANOVA on log-transformed data, $F_{1,\ 118} = 44.36$, $P < 0.001$), fewer cavities (Kruskal–Wallis test, H = 20.66, $P < 0.001$) and greater per cent canopy closure ($F_{1,\ 118} = 21.51$, $P < 0.001$) than in UF. However, their heights did not differ significantly between areas ($F_{1,\ 118} = 0.05$, n.s.; Fig. 2).

UF trees had more loose bark (1.67 ± 0.89 cavities) and rot cavities (0.95 ± 1.78) than MF ones (respectively 0.00 ± 0.00 and 0.15 ± 0.48 cavities, $n = 120$, Kruskal–Wallis tests H = 15.6 and 12.6, respectively, $P < 0.001$) while vertical splits and woodpecker holes were similarly rare in UF (respectively 0.03 ± 0.18 and 0.2 ± 1.30 cavities) and MF (0 cavities) for both types (Kruskal–Wallis tests H = 2.02 and 3.05, respectively, n.s.).

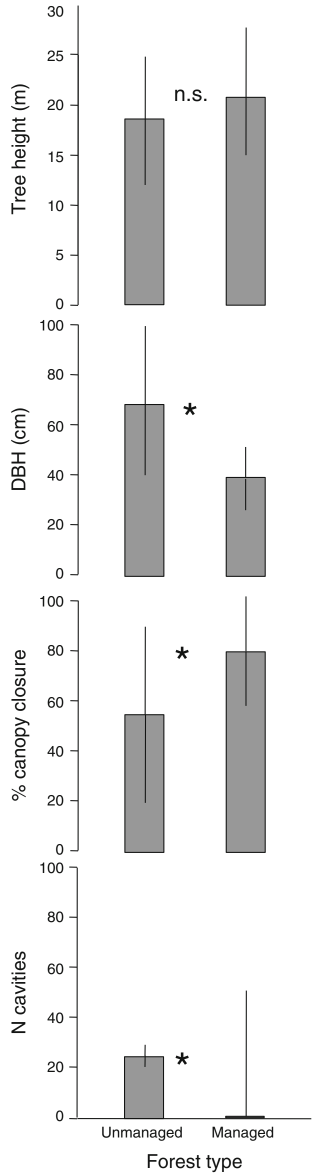

Fig. 2 Available tree height, diameter at breast height (DBH), per cent canopy closure and number of cavities compared between unmanaged and managed forest sites. * $P < 0.001$, *n.s.* = not significant (ANOVA or Kruskal–Wallis tests)

Capture frequencies

In all, we captured 107 bats, 46 for MF and 61 for UF. In MF, the mean number of bats caught/capture effort per capture session was 0.07 ± 0.07 versus 0.19 ± 0.17 in UF, i.e. bats were caught on average 2.7 times more frequently in the latter.

The number of bats caught differed according to capture site (ANOVA on log-transformed data, $F_{1,38} = 5.52$, $P < 0.05$) and sex ($F_{1,38} = 35.48$, $P < 0.001$): bats were more frequently captured in UF, where females were more frequent than males. In the model, the "site x sex" interaction also proved significant ($F_{1,38} = 4.73$, $P < 0.05$). In both MF and

UF, males were similarly rare (the mean number of bats caught/capture effort per capture session was 0.01 ± 0.02 and 0.02 ± 0.03, respectively), but females were ca. 3.2 times less frequent in MF (0.05 ± 0.05) than in UF (0.16 ± 0.14). The overall sex (male to female) ratio estimated from captures at both sites (assuming no recapture occurred) was 0.11 in UF versus 0.26 in MF. The larger proportion of females to males recorded in UF explains the significant interaction observed in the GLM.

Movements between areas and differences in roost use

In the MF, we tagged 14 adult bats, five males and nine females (five of which reproductive) which led us to 16 roosts (14 trees, two rock crevices). Of such roosts, five (all dead trees) were found in the UF, confirming that bats move between areas. Four of these roosts were reached on the same night of capture (they were 6852 ± 135 m from capture site), another was reached by a pregnant female that joined a reproductive colony of 20 bats after roosting one night in the MF (in a rock crevice). In the last case, the distance between consecutive roosts was 8203 m.

We tagged 56 bats in the UF, 25 of which led us to 38 roosts in the UF. None of them moved to the MF.

Roost sites in the UF were located at significantly higher altitude than those in the MF ($n = 38, 11$; 1562 ± 70 m a.s.l. versus 1404 ± 98 m a.s.l.; $F_{1,48} = 35.97$, $P < 0.001$) but had similar slope (48 ± 18% and 49 ± 22%, respectively; $F_{1,48} = 0.04$, n.s.) and terrain aspect (72 ± 46% and 83 ± 53%, respectively; $F_{1,48} = 0.17$, ANOVA on square-root transformed data, n.s.).

In the UF, over 85% of used trees belonged to class 3 (snags); no bats used rock crevices. In the MF, despite the limited roost sample obtained, a greater variation of roost types was recorded, including four class 1 (live) trees and two rock crevices—one used by a male, another by a pregnant female (Fig. 3). Snag roosts were more frequently found in the UF (Fisher's exact test, $P < 0.005$).

In the UF, there was greater use of spaces beneath loose bark, a cavity type typically found in snags. In the UF, 28 out of 34 (82%) roost cavities unambiguously identified were of this type versus four out of 11 (36%) in MF (Fisher's exact test, $P < 0.001$).

Food availability

In all, we sampled an identical ($n = 116$) number of moths in MF and UF belonging to ten families (Fig. 4). A preliminary two-way ANOVA (site, moth family) showed no significant influence of site, so the analysis was restricted to family ($F_{9.50} = 15.46$, $P < 0.001$). Of all families observed, only Arctiidae was significantly more abundant than the remainder; no further significant difference was observed (Tukey's post-hoc test) even though Pyralidae and Geometridae showed a tendency towards greater numbers than other families.

Discussion

Our study showed that intensive management alters forest structure so that the main characteristics preferred by *B. barbastellus* (Russo et al. 2004) are either less frequent or missing. As expected, snags were much rarer in managed forest, and available trees had a lower DBH and fewer cavities. Intensive silvicultural practices typically imply a decline in dead wood availability (e.g. Green and Peterken, 1997), so that its amount is directly linked

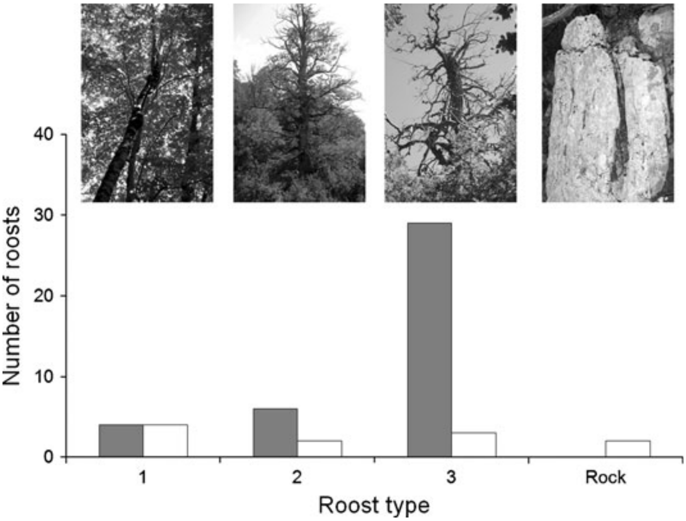

Fig. 3 Number of roosts ($n = 49$) in the unmanaged (grey) and managed (white) forest areas categorized according to roost type. Class 1 = live beech trees showing <50% of dead limbs and loss of foliage; 2 = live beech trees with 50–90% of dead limbs and loss of foliage; 3 = snags, >90% of dead limbs and loss of foliage

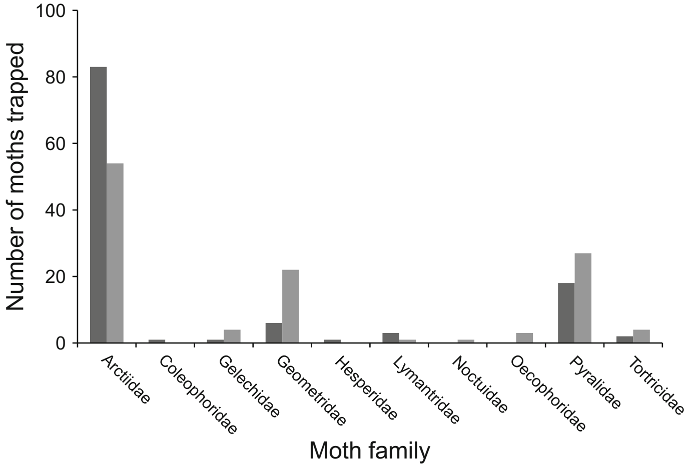

Fig. 4 Composition of light-trapped moth samples taken at the two study sites. Sampling provided an identical number of moths ($n = 116$) at each site. Dark grey: managed forest; light grey: unmanaged forest

with the time since last harvest, as seen in beech forests designated as reserves at different times (the longer the time since designation, the more abundant the dead wood). The reduced diameter of MF trees is a clear consequence of the kind of silvicultural practice (diameter-limited harvest) which removes all trees above a certain DBH value and has a double impact: it prevents natural mortality of trees, leading to fewer available snags, and also reduces available cavities, because trees of a smaller diameter often bear fewer cavities, a relationship valid for both live trees and snags (Smith et al., 2008). Another remarkable difference is that in MF canopy closure is greater, as a result of reduced competition between trees and the even structure reached after several years from logging determined by intensive silviculture. Reproductive groups of *B. barbastellus* select roosts exposed to the sun to decrease the energy costs of thermoregulation (Russo et al. 2004), so open canopy around roost trees may improve roosting conditions. However, a range of roost trees characterised by different degrees of canopy closure may be beneficial, given that *B. barbastellus* often switch roosts (Russo et al. 2005) and that when roosting in closed forest sites, they tend to emerge earlier probably gaining a foraging advantage (Russo et al. 2007). In all, the structural evenness imposed by intensive silviculture decreases the quality of the roosting environment at different spatial scales.

In agreement with our prediction, capture rates were much lower in MF, reflecting the poorer roosting environment found there. The availability of water sources in the two areas was substantially similar. We can therefore exclude that bats were more numerous at the UF capture site because water there was scarcer than in the MF, leading to higher frequencies of drinking events. Although capture rates may also be influenced by some visiting bats roosting elsewhere, we are confident that most bats in the catches were from local roosts. In fact, the difference in sex ratio we found proves that any site-dependent local variation in group composition was genuinely estimated by capture (if bats continuously mixed between areas we would expect the same sex ratio to be recorded at both sites). Neither the difference in the overall capture rate nor that in female frequency could be explained in terms of different food availability, since moths were equally available in both areas. However, because we did not sample moths over the entire study period, we cannot rule out that prey availability may have sometimes changed, and perhaps differed significantly between areas influencing bat foraging, so our data should be taken cautiously. In studies carried out by conventional (i.e. non-molecular) analysis of bat dropping contents such as those available for *B. barbastellus* (Beck 1995; Rydell et al. 1996; Sierro and Arlettaz 1997) the various moth families featuring in diet are usually not recognised from prey remains. However, in both study sites we dealt with, two families (Pyralidae and Geometridae) rated second and third in frequency after the dominant Arctiidae. Sierro and Arlettaz (1997) found that such families were also abundant at a *B. barbastellus* foraging site in Switzerland; as the authors put it, in that case Pyralidae might constitute an important prey item because of their small size.

We propose that the sex ratio difference found between areas can be explained by different thermoregulatory requirements of the two sexes. Daily torpor is an effective way to save energy and water in bats, but reproductive females tend to remain homoeothermic to favour pregnancy and lactation (e.g. Lumsden et al. 2002; Dietz and Kalko 2005): selecting warmer roosts may thus reduce thermoregulation costs (McNab 1982). Dead trees lack most branches and foliage, often occur in small, sunny forest gaps, and have no living wood tissue, all features determining warmer roosting conditions (Law and Anderson 2000). In the UF, "optimal" for *B. barbastellus*, selection of snags by reproductive females is best explained as a result of bats seeking warmer conditions (Russo et al. 2004). In the same period, however, males roost separately from females (Russo et al. 2005) and might make a larger use of daily torpor, as seen in other tree-dwelling bats (Dietz and Kalko 2005). Cooler roosts (where daily torpor is more profitable) such as cavities in live trees or crevices in limestone rocks were largely available in both areas, so while males would have more roosting opportunities, reproductive females would be mostly confined to the snag-rich UF. Daily torpor in male *B. barbastellus* in the reproductive season is probable: unlike reproductive females which form groups and may in that way save energy by clustering together (Kurta 1985), males roost alone (Russo et al. 2005).

Overall, we found that *B. barbastellus* proved more flexible in roost choice than expected, utilizing roost types in MF that were never recorded in UF, including rocks. This behaviour helps explain why, in areas where forest is rare or absent, or tree cavities are scarce (such as in conifer forests), this bat may even occasionally roost in buildings. In fact, although *B. barbastellus* should be regarded as a tree-dwelling species, before radiotracking was applied to studying roosting ecology, most available records referred to buildings (Harrington et al. 1995; Schober and Grimmberger 1997). However, the small numbers of bats and the rarity of breeding individuals observed in the MF suggest that even though forests where preferred trees are scarce may be used by *B. barbastellus*, they cannot support a viable population of this species.

In an optimal forest area such as UF, lactating *B. barbastellus* tend to switch roosts within forest patches apparently delimited by mountain ridges (Russo et al. 2005). The latter are unlikely to act as a significant physical barrier, rather they may have been used to recognize roosting quarters used by different social groups of lactating females (Russo et al. 2005). In this study we found that bats were actually capable of crossing the mountain ridges separating the two study sites. Some of them may have been visitors, since the day after the capture in MF they were found roosting in UF. However, at least in one case we recorded one bat occupying a temporary roost in MF that moved to UF to join a reproductive group in a “typical” roost tree. Besides, we also recorded the occurrence of a small reproductive group in MF for two consecutive years. We interpret this behaviour as a tendency to explore even intensively managed forest sites when they are comprised within the colony home range of bats reproducing in optimal areas. Unmanaged areas can therefore act as source areas for surrounding forests, regardless of the characteristics of the latter. Clearly, the likelihood that new groups will establish, persist and increase over time thanks to this process will depend on the presence of key habitat features.

A main outcome of this study is that harvested areas are still of conservation interest and should not be deemed as irreversibly inhospitable even for snag-dependent species such as *B. barbastellus*. We thus emphasize that such areas, especially when buffering unmanaged stands used by sensitive tree-dwelling bats, should receive more conservation efforts since they are subject to colonization attempts, and that there too management should pay more attention to this critical potential for conservation.

In our case, although no significant range or population expansion is forecast under the current MF management regime, the application of some environmental improvement strategies might imply significantly positive consequences for the overall population. For instance, designating small groups of trees, or even single ones some hundred m apart (the average distance covered by switching bats: Russo et al. 2005) as snag replacement (Moorman et al. 1999) would encourage colonization and movement across the territory, connecting more effectively optimal reproduction areas.

This result could be achieved more quickly by deliberately creating snags by girdling, injecting or inoculating large stems (Moorman et al. 1999). Bat boxes, and especially wooden slots (which mimic loose bark, the species’ preferred cavity type) would also prove effective to temporarily encourage population expansion, but they cannot be seen as a long-term strategy because they will deteriorate after a few years. Such practices might also be seen as a form of environmental compensation for harvesting. They seem more economically sustainable than saving entire forest patches from logging, although a combination of these approaches would clearly maximize conservation benefits.

On a larger scale, maintaining diversity in forest structure by applying ad hoc harvesting plans, prolonging rotations and when possible converting coppice into harvested mature forest would improve the overall carrying capacity for the species.

A final management remark concerns the time of year when forest is harvested. In general, in Italy mature stands can be logged all year round. As a result of the EC/79/409 "Birds" Directive, in some regions in Special Protection Areas designated for birds such operations are postponed to avoid disturbance to the nesting avifauna. At least in Italy, no mention of bats is made on the harvest timing even for Special Areas of Conservation (SACs) specifically designated for the protection of these mammals too according to the EC/92/43 "Habitats" Directive (including some typical forest bats such as *B. barbastellus* and *Myotis bechsteinii*). We highlight that the Directive, even outside SACs, prohibits deliberate disturbance of Annex IV species (including bats), particularly during the period of breeding, rearing, hibernation and migration, as well as deterioration or destruction of breeding sites or resting places. Therefore, according to law forestry plans should always take the impact on bats into account.

In the course of the present study, we managed to delay logging where we found the only MF reproductive roost thanks to support from the Park Direction. Of course many similar situations will remain completely unnoticed. We urge forestry managers and responsible authorities to include timing of bat reproduction in their logging schedules, whenever possible delaying harvesting operations at least to the end of August, when juveniles have become fully volant.

If forests were managed more sustainably, e.g. by increasing standing dead wood availability, the expansion of *B. barbastellus* occupied areas to managed forest would possibly imply a highest direct mortality risk, at least out of tree groups and areas specifically designated to preserve the species. In such cases, detailed information on year-round presence of *B. barbastellus* would be crucial to plan logging more safely and avoid turning the sites into habitat traps for this species. Although winter logging is probably safer because *B. barbastellus* mostly hibernates in caves (e.g. Sachanowicz and Zubb 2002), this is rarely done because in many beech forests snow makes forestry operations difficult or impossible.

It is worth mentioning that so far studies on *B. barbastellus* have focused on "natural" forest ecosystems, but especially in the Mediterranean the species may also occur in semi-natural woodland whose persistence relies on active human management, such as chestnut woodland grown for sweet chestnut production and olive groves (Russo and Jones 2003): when managed traditionally, these habitats feature large trees with many cavities that may be suitable for bats, and sometimes significant amounts of dead wood. Studies focused on such habitat types are needed to define the best management practices instead of applying the knowledge acquired in natural forest situations to such special cases. We also remark that, although in our study we referred to managed beech forests of Italian Apennines as to "managed forests" for simplicity, the implications for forestry we discussed may not be valid for some intensively managed forests found in Europe, such as *Eucalyptus* or conifer plantations, where roost and/or prey availability might be more limiting and sustainable forestry more difficult to achieve.

Bats are often deemed effective environmental indicators (Jones et al., 2009). At least as far as forest integrity or structure are concerned, our results call for prudence. The mere observation of *B. barbastellus* in a forest area does not suffice to regard the latter as characterised by a high environmental quality because the species may in fact roost there with very low numbers or may originate from other forest sites found even several kilometres away. A landscape, or regional, scale is therefore needed to correctly interpret the conservation status and needs of barbastelles.

On the other hand, significant amounts of standing dead wood reflect a high probability that the species is present. Not all bats use snags for roosting, but forest featuring many snags certainly also exhibits large, old or defective trees offering excellent roosting opportunities to virtually all tree-dwelling bats. Therefore, in analogy with what has been done for other groups of organisms (Juutinen et al. 2006), we recommend considering standing dead wood as a surrogate for overall bat richness to designate reserves but also, as this study highlights, carrying out habitat improvements to surrounding exploited forest areas to encourage their role of continuous biological corridors or stepping stones.

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