



Carr, A., Zeale, M., Weatherall, A., Froidevaux, J., & Jones, G. (2018). Ground-based and LiDAR-derived measurements reveal scale-dependent selection of roost characteristics by the rare tree-dwelling bat *Barbastella barbastellus*. *Forest Ecology and Management*, 417, 237-246. <https://doi.org/10.1016/j.foreco.2018.02.041>

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[10.1016/j.foreco.2018.02.041](https://doi.org/10.1016/j.foreco.2018.02.041)

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Original research paper - Forest Ecology and Management - March 2018

Official URL: <https://doi.org/10.1016/j.foreco.2018.02.041>

Title: Ground-based and LiDAR-derived measurements reveal scale-dependent selection of roost characteristics by the rare tree-dwelling bat *Barbastella barbastellus*

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Abstract:

Bats use roosts for protection, sociality and reproduction. Lack of knowledge regarding the specific roost preferences of tree-dwelling bats means that roosts are regularly removed from woodland during felling and thinning interventions, even when woodlands are managed to promote biodiversity. The often-unintentional loss of roosts this way continues to constrain efforts to conserve many rare bat species.

We investigated roost selection by the barbastelle *Barbastella barbastellus* in fragmented oak woodlands in southwest England. Twenty-nine bats were radio tracked to 44 tree roosts between 2007 and 2015. Twenty-four different characteristics of roosts were measured using a combination of ground-based field surveys and airborne light detection and ranging (LiDAR) imagery, and roost characteristics were compared with those of random trees to determine selection.

Bats selected trees in ancient semi-natural broadleaved woodland over other woodland habitat types. Standing dead oak (*Quercus* spp.), while scarce, was positively selected over other tree types and supported significantly more suitable roost cavities. Roost selection was most strongly influenced by the number of cavities present on a tree and the openness of the canopy around the tree. The height of roost cavities and distance to water were also important features that influenced selection. Pregnant and lactating bats switched roosts less frequently than post-lactating and nulliparous bats and selected cavities higher on trees, most likely to facilitate the development of offspring and reduce the risk of predation.

Old growth woodland is vitally important to barbastelles and so the preservation and restoration of these habitats should be a conservation priority. While standing dead trees supported more preferred roost cavities than other tree types, our findings indicate that any tree supporting a suitable cavity may be used as a roost, irrespective of the size, condition or species, and should be retained wherever possible. Promoting the natural succession of younger woodland will help to deliver additional sustained benefits in the future.

Keywords: barbastelle, conservation, radio tracking, roost preferences, tree cavity, woodland.

1. Introduction

The availability of suitable roosts influences the distribution, diversity, social structure and reproductive fitness of bats (Kunz and Lumsden, 2003). Roosts provide protection from predation and shelter from ambient environmental conditions and are important sites for mating, hibernation and rearing young (Kunz and Lumsden, 2003; Lacki et al., 2007; Willis and Brigham, 2007). When woodlands are subject to human intervention i.e. to increase economic yield, promote recreational use or to improve ecological function after degradation has taken place, these interventions can affect the availability and suitability of roosts. By identifying characteristics of tree roosts that are most important to bats a more directed and effective approach to woodland management can be undertaken that delivers improved conservation outcomes.

Meta-analyses have identified a number of habitat features that are typically important to tree-dwelling bats, including tree height and diameter, canopy closure, tree trunk girth and the occurrence of standing deadwood (Lacki and Baker, 2003; Kalcounis-Ruppell et al., 2005; Fabianek et al., 2015a; Nadó and Kaňuch, 2015). The frequency, type and size of cavities has also been shown to influence roost selection (Russo et al., 2004; Lučan et al., 2009). In addition, bat presence within woodlands has been linked to the ruggedness (Froidevaux et al., 2016) and openness (Russo et al., 2004; Cox et al., 2016; Kortmann et al., 2017) of the upper canopy. Favourable microclimatic conditions may increase roost suitability (Boyles, 2007) and the phenomenon of social thermoregulation driven by roost characteristics indicates that bats do not rely passively on ambient temperature while roosting (Willis and Brigham, 2007; Russo et al., 2017a). In certain landscapes, topographical characteristics such as elevation, terrain aspect and distance to water have also been shown to be important (Cryan et al., 2000; Lacki and Schwierjohann, 2001; Lacki and Baker, 2003).

The importance of woodland characteristics can vary according to the sex and reproductive state of bats. Breeding female *Plecotus macrobullaris*, for example, predominantly roost in tree cavities at lower elevations than non-breeding females, while males select roosts in rock cavities and man-made structures (Alberdi et al., 2015). Understanding variability in roost selection by other species during different reproductive stages requires further work (Jachowski et al., 2016).

Many tree-dwelling bat species form fission-fusion societies, whereby individuals roost with one another interchangeably (Fleischmann and Kerth, 2014), and regular roost switching by bats in these societies is well documented (O'Donnell and Sedgeley, 1999; Russo et al., 2005; Trousdale et al., 2008; Ngamprasertwong et al., 2014). The primary function of roost switching remains unclear although reducing parasite load and risk of predation, minimising roost fouling, maintaining social cohesion among individuals, and maintaining knowledge of the locations of available roosts have all been proposed as drivers (Owen et al., 2001; Russo et al., 2005; Kühnert et al., 2016). Maintaining knowledge of existing roosts may be particularly important due to the ephemerality of tree roosts (Trousdale et al., 2008; Russo et al., 2005) and the temporal variation in the thermoregulatory requirements of bats (Russo et al., 2017a). While frequent roost switching is commonly exhibited by some species, these species typically express high inter-annual fidelity to roosting sites, returning to the same breeding site each year (Hillen et al., 2010; Silvis et al., 2014).

The barbastelle (*Barbastella barbastellus*; Schreber, 1774) is classified as 'Near Threatened' by the International Union for the Conservation of Nature (Piraccini, 2016), is listed under Annex II and IV of the EU Habitats Directive and is a UK Biodiversity Action Plan priority species (JNCC, 2010).

Throughout Europe, barbastelles have retained a strong preference for roosting in trees and require old growth broadleaved forests that provide a high number of suitable roost cavities (Russo et al., 2004, 2010). Historic declines in populations have been associated with loss of old growth broadleaved forest habitat (Russo et al., 2004; Piraccini, 2016). To date, few studies have characterised the roosting requirements of the barbastelle. Russo et al. (2004, 2010) and Kortmann

et al. (2017) documented roost preferences in breeding populations inhabiting extensive beech (*Fagus sylvatica*) and mixed upland forests respectively. Only limited data are available for the species within fragmented broadleaved woodlands at lower elevations that are more typical across the species' Europe-wide range.

We investigated the roosting requirements of female barbastelles in small fragmented broadleaved woodlands in south-west England using radio tracking to locate roosts and examine roosting behaviour. We recorded roost characteristics using a combination of terrestrial field surveys and airborne light detection and ranging (LiDAR) imagery and examined roost selection between early spring and late autumn at three spatial scales: (i) woodland structure and management type, (ii) tree type, and (iii) cavity type. We tested the hypotheses that bats selected roost characteristics at random on all levels by comparing the characteristics of roost features used by bats with those available at random. In addition, we examined whether the selection of roost characteristics and the frequency of roost switching is influenced by the reproductive state of female bats.

2. Materials and Methods

2.1. Study area

Bats were captured and studied between May 2007 and September 2015 in four ancient semi-natural broadleaved woodlands in Dartmoor National Park (3°54'49" W, 50°35'15" N), south-west England (Fig. 1). Each woodland roosting site, hereafter referred to as a 'home wood', was delimited retrospectively using natural features, such as woodland edge and valley ridges, and a maximum distance of 250 m from a roost i.e. the maximum distance that we recorded from a roost to its nearest woodland edge.

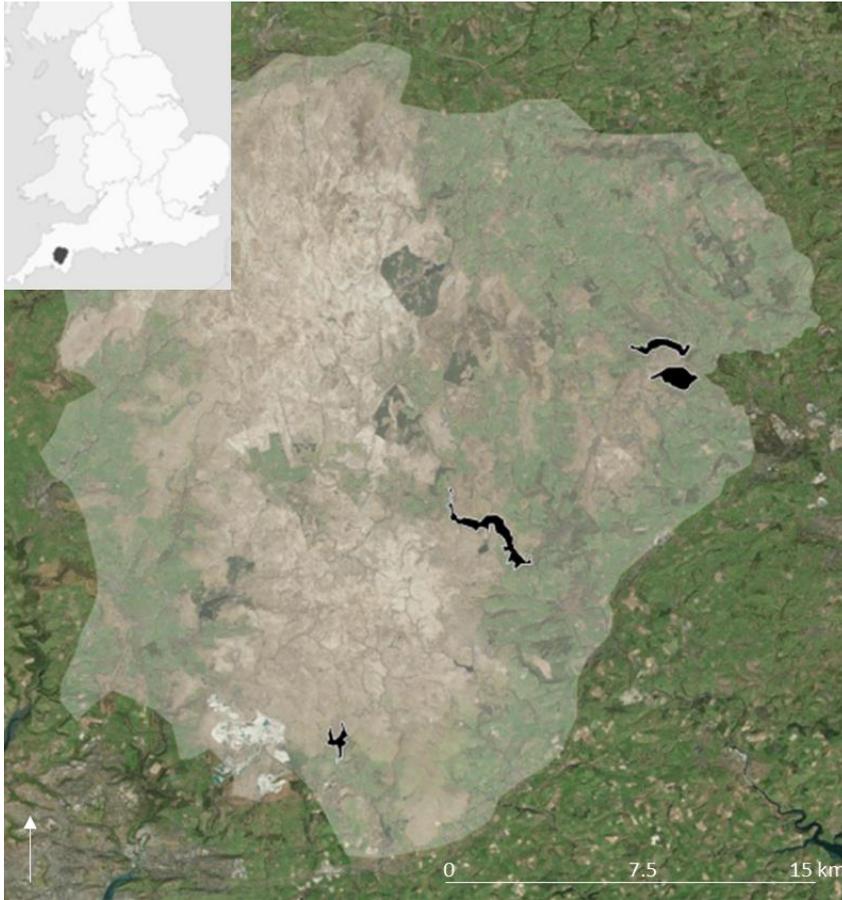


Figure 1. Woodland study sites (black polygons) from top to bottom: Houndtor Wood ($3^{\circ}44'50''$ W, $50^{\circ}36'24''$ N) (71 ha), Yarner Wood ($3^{\circ}43'35''$ W, $50^{\circ}35'41''$ N) (150 ha), White Wood ($3^{\circ}51'40''$ W, $50^{\circ}31'56''$ N) (241 ha), and Dendles Wood ($3^{\circ}56'59''$ W, $50^{\circ}26'13''$ N) (50 ha), in Dartmoor National Park (grey polygon). Inset: location and boundary of Dartmoor National Park within the UK. Adapted from Ordnance Survey open data base map.

Each of the four home wood areas share similar topographic features, including steep Dartmoor intrusion granite slopes and Crackington Formation mudstone valley bottoms covered predominantly with pedunculate oak (*Quercus robur*), sessile oak (*Q. petraea*) and hybrids of these (*Q. x rosacea*). Climatic conditions within the region are wet and mild with mean summer (May-September) precipitation between 260-460 mm and mean temperature between 12-15°C. Historic and current management has resulted in mosaic woodland habitats surrounded by upland heath and agricultural land. For the purpose of this study, habitat types were grouped as (i) ancient semi-

natural broadleaved woodland comprising predominately oak wood but also including ash and wet woodland types, (ii) broadleaved plantation ancient woodland (PAWS) comprising predominantly beech (*Fagus sylvatica*) planted in the 1960s but with remnant oak standards, (iii) conifer PAWS restocked with Douglas fir (*Pseudotsuga menziesii*) in the 1960s, and (iv) woodland scrub with mixed restocked and regenerating broadleaved species.

2.2. Capture, marking, tracking and monitoring

Bats were captured using mist nets (Avinet Inc., Portland, US) and harp traps (Faunatech Austbat, Victoria, Australia) placed along woodland rides, and at roost trees during emergence with large hand nets (net diameter 47 cm, net depth 78 cm) attached to extendable aluminium poles.

Apodemus lures (Apodemus field equipment, Mheer, Netherlands) and Sussex Autobat lures (University of Sussex, Sussex, UK) broadcasting direct recordings and synthesised barbastelle social and echolocation calls, respectively, were used to improve capture success (Hill and Greenaway, 2005; Scott and Altringham, 2014) in open woodland. Acoustic lures were not used at roost trees.

After recording biometric data, caught bats were fitted with lightweight radio transmitter tags (Pip3, 0.45 g; Biotack Ltd., Wareham, UK). Tags were glued between the scapulae using a biodegradable adhesive (Salts Healthcare Ltd., Birmingham, UK) after clipping the fur. All transmitters weighed < 5% of the body mass of the bat to avoid potential load-related changes in behaviour (O'Mara et al., 2014). Bats were fitted with 2.9 mm aluminium wing bands (Porzana Ltd., Sussex, UK) to allow identification of recaptured individuals. All activities were conducted under Natural England licences 2015-8106-SCI-SCI-1 and 20082206.

Bats were tracked daily on foot to roost trees using r-1000 (Communications Specialists Inc., Orange, US), SRX 400 (Lotek Engineering Inc., Ontario, Canada) or Sika (Biotrack Ltd., Dorset, UK) radio receivers and three-element Yagi antennas (Wildlife Materials Inc., Murphysboro, US). Tree cavities were located using a directional antenna and binoculars from the ground, and later confirmed by undertaking dusk emergence surveys using Bat Box Duet bat detectors (Batbox Ltd., Sussex, UK),

Song Meter 2 static detectors (Wildlife Acoustics Inc., Maynard, US) and a bespoke portable CCTV video system (Young et al., In press).

2.3. Ground-based surveys of habitat characteristics

To investigate whether barbastelles selected roosts with particular characteristics, 16 habitat features that were considered to be biologically relevant for tree-roosting bats in the literature (Lacki and Baker, 2003; Kalcounis-Ruppell et al., 2005; Fabianek et al., 2015a; Nadó and Kaňuch, 2015) were measured on the ground or in QGIS (Quantum GIS Development Team 2015, version 2.8.1 Wien) and compared with those recorded from randomly selected trees at the plot, tree and cavity scale (Table 1). Random trees were selected by identifying the nearest potential roost tree to randomly selected point locations within home wood areas. Only trees that were equal to or larger than the smallest roost tree recorded in this study, determined by diameter at breast height (DBH), were selected as random trees. The number of random trees that we recorded data from was equal to the number of roost trees identified in this study ($n = 44$).

Characteristics measured in QGIS at the plot scale for roost and random trees included elevation, distance to water, distance to woodland edge, distance to public footpath and distance to potential sources of disturbance such as roads and buildings. Characteristics measured on the ground at the plot scale included terrain aspect, terrain slope and tree density. Tree density was measured using a point-centre quarter method (Causton, 1988; Russo et al., 2004), whereby the distance from each roost or random tree (point-centre) to its four nearest-neighbour trees (one in each quadrant around point-centres) was recorded and tree density calculated in hectares as $10000/(\text{mean of the distances between point centres and the four nearest-neighbour trees})^2$.

Characteristics recorded at the tree scale included tree type, height, DBH, number of cavities present, and percent canopy gaps assessed visually from the base of the tree. Tree types were categorised as follows: (i) 'Class 1 *Quercus*' live trees (*Q. robur* or *Q. petraea* or *Q. x rosacea*) showing less than 80% dead limbs and loss of foliage; (ii) 'Class 2 *Quercus*' dead trees (*Q. robur* or *Q. petraea*

or *Q. x rosacea*) showing 80% or greater dead limbs and loss of foliage; (iii) 'other broadleaved species' (all live individuals); and (iv) 'conifer spp.' (all live individuals). *Q. petraea* was the dominant oak species within home wood areas.

To investigate roost cavity selection, random cavities were located along transects within woodlands that intersected the areas in which most barbastelle roosts occurred. The identification of cavities as potential suitable roost features for bats was determined by eye using binoculars from the ground and based retrospectively on the structure of roost cavities used by radio tracked bats. To minimise limitations associated with ground-based detection of cavities, cavity surveys were undertaken in winter when leaves were absent. In situations where trees supported multiple cavities, one cavity was selected at random. Variables measured at the cavity scale included cavity type, height and aspect. Cavity types were defined as either (i) bark plates, (ii) splits (including frost cracks, hazard beams and tear-outs, as described by Andrews (2013)), or (iii) rot holes.

2.4. Light detection and ranging imagery

LiDAR measurements (three-dimensional point cloud data) collected in April 2010 were obtained from the UK Environment Agency (open source survey data; <http://environment.data.gov.uk/ds/survey/>). Using QGIS, we created a canopy height model (CHM) at 1 m resolution from a digital surface model (DSM) and digital terrain model (DTM). We derived several structural variables from the canopy height model including canopy gaps, mean canopy height, canopy ruggedness, and standard deviation of canopy height. As we were interested in assessing roost selection at both the tree and the plot scale we defined two buffers of 2 m and 16 m radius, respectively, around roost and random point-centres and recorded each variable at each of these scales. Due to patchiness in the coverage of open-source LiDAR data, comparisons could only be made between 29 roost and random plots, respectively. Following Fabianek et al. (2015b), canopy gaps were defined as being $>2 \text{ m}^2$, with a tree height that was one-third the height of the surrounding mean canopy. Canopy ruggedness, as defined by Froidevaux et al. (2016), was

calculated in QGIS using a terrain ruggedness index (TRI) algorithm (Wilson et al., 2007). Standard deviation of canopy height was used as an additional measure of upper canopy surface variability (Froidevaux et al., 2016).

2.5. Statistical analysis

2.5.1. Selection of woodland habitat type and tree type

To examine whether bats favoured roosts in a particular woodland habitat type or in a particular tree type, we used chi-square analyses to determine (i) whether use of a habitat type (number of roosts in each woodland habitat type divided by total number of roosts located in the study area) departed from that expected (area of corresponding woodland habitat type divided by the overall size of the study area), and (ii) whether the use of a tree type (number of roosts of each tree type divided by the total number of roosts in the study) departed from that expected (number of random trees of each tree type divided by the total number of random trees in the study). The Z statistic was used to calculate Bonferroni's confidence intervals (Neu et al., 1974) and to establish whether bats positively or negatively selected a woodland habitat type or tree type. For the analysis of habitat type selection, only data from Houndtor Wood were used as it was the only home wood area that contained all habitat types. To meet the assumptions of chi-square analysis, woodlands were grouped as 'ancient semi-natural broadleaved woodland' and 'other woodland' that included broadleaf PAWS, conifer PAWS and woodland scrub habitat types, and tree types were grouped as 'live *Quercus* spp.', 'dead *Quercus* spp.' and 'other tree types'.

2.5.2. Selection of roost features

To examine whether roost features differed significantly from random features, first we undertook a series of univariate analyses on the variables. T-tests were performed for parametric data while permutation tests (10,000 randomisations) were performed for non-parametric data. To determine which variables contributed most to explaining differences observed in roost and random features,

we performed a series of generalized linear mixed models (GLMMs) using maximum likelihood estimations with binomial distribution and logit link function (lme4 package; R core team). We considered trees as our sampling units and included bat and site as random effects to control for variation among bats and sites (Bolker et al., 2008). Multicollinearity was assessed prior to model building using Spearman's correlation tests and using a $|r| > 0.6$ coefficient threshold. When correlation between variables was found, the variable with the least statistical explanatory power was removed to achieve model simplification. To provide meaningful comparisons of effect size, data were standardised using mean and standard deviation $((x-\mu)/\sigma)$. To identify the most parsimonious model that also explained the most amount of variance, Akaike's Information Criterion (AIC) adjusted for small sample sizes (AICc) was used. Pseudo R^2 (1-(residual deviance/null deviance)) was also applied for further consideration of model fit. A final set of models with only variables from the best fitting models using delta AICc ($\Delta_i \leq 2$) was selected. For increasing precision in the calculation of estimates and associated standard errors, we applied a model averaging approach on the set of best models (Burnham and Anderson, 2002).

To examine whether the selection of roost features differed between bats of different reproductive states, bats were grouped as either (i) pregnant and lactating or (ii) post-lactating and nulliparous (i.e. bats showing no evidence of having bred), and differences between groups were compared using t-tests or permutation tests.

All values of central tendency for normally distributed data are presented as mean \pm standard deviation (SD), and for non-normally distributed data as median \pm inter-quartile range (IQR).

2.5.3. Roost switching behaviour

We calculated the frequency of roost switching in individual bats by dividing the number of times a bat switched roost by the number of days the bat was tracked. Bats were grouped as either (i) pregnant and lactating or (ii) post-lactating and nulliparous, and differences in the rate of switching

between groups were compared using permutation tests. All statistical analyses were performed in R 3.1.3 and RStudio 1.0.143 (RStudio Team, 2015).

3. Results

In total 29 adult female barbastelles (Table S1) were radio tracked to 44 roost trees between May 2007 and October 2015. Roost switching behaviour was determined for 27 bats, including pregnant ($n = 4$), lactating ($n = 3$), post lactating ($n = 10$) and nulliparous ($n = 10$) adult females. Bats were located within roost trees over consecutive days for between 3 and 18 days (mean 12 days \pm 4.4 SD). Emergence counts ($n = 59$) revealed that roosts were occupied by 1–23 bats (mean 10 bats \pm 6.5 SD; $n = 36$ roosts). Radio tracked bats expressed high fidelity to home wood areas and only rarely roosted in other woodland sites. Two individual bats caught in 2007 and 2008, respectively, were recaptured in the same home wood in 2015, providing evidence of inter-annual site fidelity to roosting sites.

3.1. Selection of woodland habitat type

Bats roosted in four woodland habitat types, including ancient semi-natural broadleaf woodland ($n = 40$ roosts), PAWS (broadleaf) ($n = 1$ roost), PAWS (conifer) ($n = 2$ roosts), and woodland scrub ($n = 1$ roost). Roosts within Houndtor Wood ($n = 27$) were not evenly distributed across habitat types ($\chi^2_{8.7}$, d.f. = 1, $p < 0.01$) with ancient semi-natural broadleaved woodland positively selected over all other woodland types (Fig. 2).

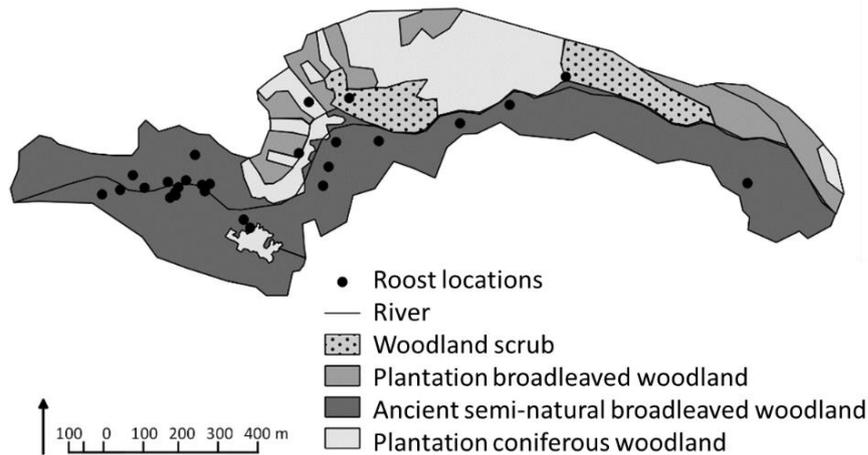


Figure 2. Home wood area within Houndtor Wood in Dartmoor National Park, showing the availability of four woodland habitat types (see section 2.1 for habitat type details) and the locations of 27 barbastelle tree roosts.

3.2. Selection of tree type

Roost trees consisted of live ($n = 23$) and dead ($n = 20$) *Quercus robur*, *Q. petraea* or *Q. x rosacea*, and one live *Fagus sylvatica*. Random trees consisted of live ($n = 26$) and dead ($n = 4$) *Q. robur*, *Q. petraea* or *Q. x rosacea*, 'other broadleaved' species ($n = 9$) and conifer species ($n = 5$). Tree type was not selected at random ($\chi^2_{76.4}$, d.f. = 2, $p < 0.001$) by bats. Dead *Quercus* trees were positively selected, live *Quercus* trees were used in line with availability, and all other tree types (*Fagus sylvatica*, *Betula pendula*, *Acer pseudoplatanus*, *Pseudotsuga menziesii* and *Pinus sylvestris*) were used less than expected. When we examined the number of cavities present on different tree types for the whole dataset that included all roost and random trees ($n = 220$ trees), we found significant differences ($\chi^2_{64.5}$, d.f. = 3, $p < 0.001$), with dead *Quercus* trees having significantly more cavities (median = 5.1, $n = 42$) compared to live *Quercus* trees (median = 1.1, $n = 122$), other broadleaved trees (median = 0.2, $n = 33$) and coniferous trees (median = 0.3, $n = 23$) (Dunn post hoc, $p < 0.001$),

and live *Quercus* trees having significantly more cavities compared to other broadleaved (Dunn post hoc, $p < 0.01$) and coniferous trees (Dunn post hoc, $p = 0.02$) (Fig. 3).

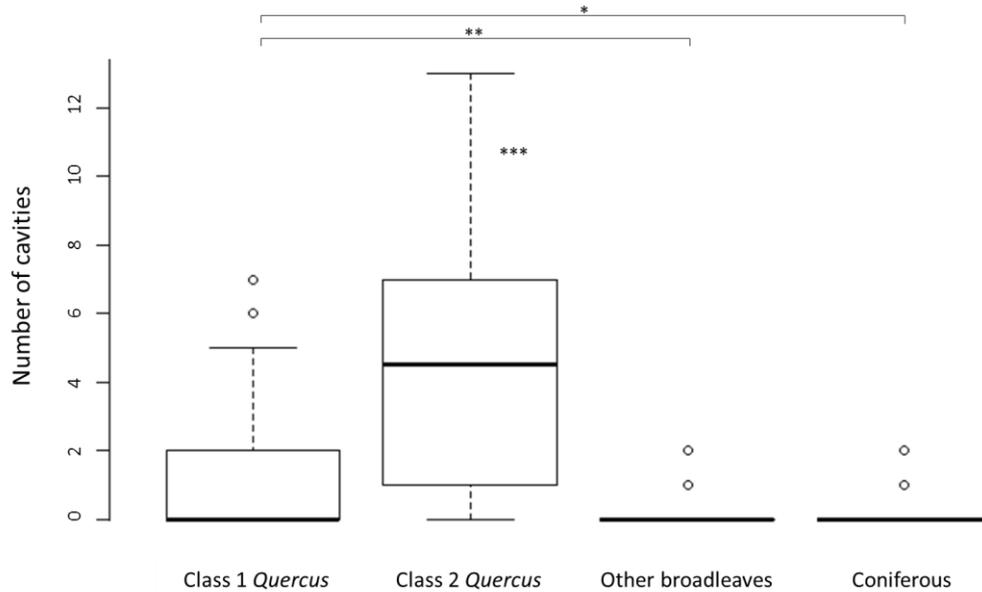


Figure 3. Median and inter quartile range for the number of cavities on roost and random trees ($n = 220$) according to tree type. Class 1 *Quercus* includes live oak trees showing $< 80\%$ of dead limbs and loss of foliage; Class 2 *Quercus* includes dead oak trees showing $> 80\%$ dead limbs and loss of foliage; other broadleaves includes *Fagus sylvatica* (European beech), *Betula pendula* (silver birch), and *Acer pseudoplatanus* (sycamore); Coniferous includes live *Pseudotsuga menziesii* (Douglas fir); and *Pinus sylvestris* (Scots pine). * $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$.

3.3. Selection of roost features

Roost trees had a more open canopy structure at the tree ($n = 44$, perm, $p < 0.001$) and at 0.1 hectare around the tree ($n = 29$, perm, $p < 0.01$), were closer to water ($n = 44$, perm, $p < 0.01$) and had a greater number of cavities ($n = 44$ perm, $p < 0.001$) than random trees. No differences were found for each of the other variables that we examined (Table 1).

Table 1. Habitat variables recorded from roost and random plots ($n = 44$, or $n = 29$ for LiDAR datasets), roost and random trees ($n = 44$) and roost and random cavities ($n = 41$) used by adult female barbastelles ($n = 29$) radio tracked in Dartmoor National Park, Devon, UK. Values of central tendency for normally distributed variables (+) are presented as mean \pm standard deviation, and for non-normally distributed variables (-) as median \pm inter-quartile range. ns = not significant.

Scale	Habitat feature	Roost	n	Random	n	Source	p value	Distribution
Plot	Aspect	Categorical	44	Categorical	44	Field	ns	-
	Canopy gaps 2 m (%)	33 \pm 29	29	33 \pm 63	29	LiDAR	ns	-
	Canopy gaps 0.1 ha (%)	63 \pm 14	29	41 \pm 22	29	LiDAR	< 0.01	-
	Canopy ruggedness 2 m [†]	13820 \pm 7561	29	12323 \pm 7529	29	LiDAR	ns	+
	Canopy ruggedness 0.1 ha [†]	12871 \pm 3799	29	12847 \pm 5559	29	LiDAR	ns	+
	Distance to footpath (m)	87 \pm 133	44	93 \pm 93	44	QGIS	ns	-
	Distance to disturbance (m)	149 \pm 169	44	140 \pm 462	44	QGIS	ns	-
	Distance to water (m)	34 \pm 32	44	72 \pm 92	44	QGIS	< 0.01	-
	Distance to woodland edge (m)	52 \pm 85	44	64 \pm 84	44	QGIS	ns	-
	Elevation (m)	180 \pm 39	44	193 \pm 38	44	QGIS	ns	+
	Mean canopy height 2 m (m)	5 \pm 4	29	7 \pm 7	29	LiDAR	ns	-
	Mean canopy height 0.1 ha (m)	5 \pm 3	29	7 \pm 6	29	LiDAR	ns	-
	SD of canopy height 2 m (m)	4 \pm 3	29	3 \pm 3	29	LiDAR	ns	+
	SD of canopy height 0.1 ha (m)	5 \pm 2	29	5 \pm 2	29	LiDAR	ns	-
	Slope (%)	25 \pm 25	44	25 \pm 25	44	Field	ns	-
	Tree density (ha) ^{††}	145 \pm 189	44	171 \pm 293	44	Field	ns	-
Tree	Canopy gaps at tree (%)	63 \pm 29	44	30 \pm 15	44	Field	< 0.001	-
	DBH (cm)	57 \pm 23	44	22 \pm 6	44	Field	ns	+
	Number of cavities	4 \pm 5	44	0 \pm 0	44	Field	< 0.001	-
	Tree class	Categorical	44	Categorical	44	Field	< 0.001	-
	Tree height (m)	19 \pm 7	44	22 \pm 6	44	Field	ns	+
Cavity	Cavity aspect	Categorical	41	Categorical	90	Field	ns	-
	Cavity height (m)	7 \pm 6	41	6 \pm 9	90	Field	ns	-
	Cavity Type	Categorical	41	Categorical	90	Field	ns	-

[†] Canopy ruggedness score was calculated using terrain ruggedness index (TRI) (Wilson *et al.* 2007)

^{††} Calculated in hectares as $10000/(\text{mean of the four distances to nearest trees in metres})^2$ (Russo *et al.* 2004).

Prior to fitting models, when we checked for correlations among variables we found that tree height, standard deviation of the canopy at 2 m and 0.1 ha, gaps at 2m and canopy ruggedness at 2 m and 0.1 ha were all correlated with one another, and tree type was correlated to canopy gaps and number of cavities. To avoid multicollinearity, tree height at 2 m, standard deviation at 2 m and 0.1

ha, and tree type were removed from models as they were found to be either not significantly different in univariate tests or were less significant than other correlated variables.

When we modelled variables at the plot scale, the model that best explained differences between roost and random trees included canopy gap at 2 m, canopy gap 0.1 ha, distance to water and elevation. At the tree scale, the best model included canopy gap at the tree, DBH, tree height and number of cavities on a tree, and at the cavity scale only cavity height was included (Table 2).

Table 2. List of habitat variables from the best generalized linear mixed effects models ($\Delta_i \leq 2$) at the plot, tree and cavity scale, including effect size, standard error, z statistic and *p* value. See Table 1 for units.

Model	Variable	Effect size	\pm SE	z	<i>p</i>
Plot	Canopy gap at 2 m	-0.5	0.4	-1.4	0.15
	Canopy gap at 0.1 ha	1.2	0.4	2.8	0.005
	Distance to water	-1.1	0.5	-2.5	0.01
	Elevation	-0.5	0.4	-1.4	0.15
Tree	Canopy gap at tree	1.2	0.4	2.8	0.007
	DBH	0.8	0.5	1.6	0.12
	Number of cavities	5.2	1.2	4.2	< 0.001
	Tree height	-0.2	0.4	-0.5	0.64
Cavity	Cavity height	-0.2	0.2	-0.9	0.33

DBH = diameter at breast height

When we fitted the nine key explanatory variables from the plot scale, tree scale and cavity scale models (Table 2) into a single model, three models performed equally well at explaining differences between roost and random trees, with each model containing one or more of the following variables: canopy gap at tree, canopy gap at 0.1 ha, cavity height, distance to water and number of cavities on the tree (Table 3). In the model that included all five variables, canopy gap at the tree and the number of cavities on the tree contributed significantly to explaining differences observed between roost and random trees, with number of cavities having the largest effect size (Fig. 4).

Table 3. Most parsimonious and best fitting generalized linear mixed effects models ($\Delta_i \leq 2$) used to explain differences observed between roost and random trees. Shows the number of estimated parameters (K), differences between model second order Akaike's information criterion for small samples (AICc), the difference in AICc score (Δ_i) compared to the model with the lowest AICc score, Akaike weights (ω_i), and proportion of residual deviance explained by the model (Pseudo R^2). Final models have been averaged. See Table 1 for units.

Model	K	AICc	Δ_i	ω_i	Pseudo R^2
Canopy gap at tree + canopy gap at 0.1 ha + distance to water + no. of cavities	6	42.1	0.0	0.3	0.6
Canopy gap at tree + canopy gap at 0.1 ha + cavity height + distance to water + no. of cavities	7	42.5	0.4	0.2	0.7
Canopy gap at tree + distance to water + no. of cavities	5	42.8	0.7	0.2	0.6

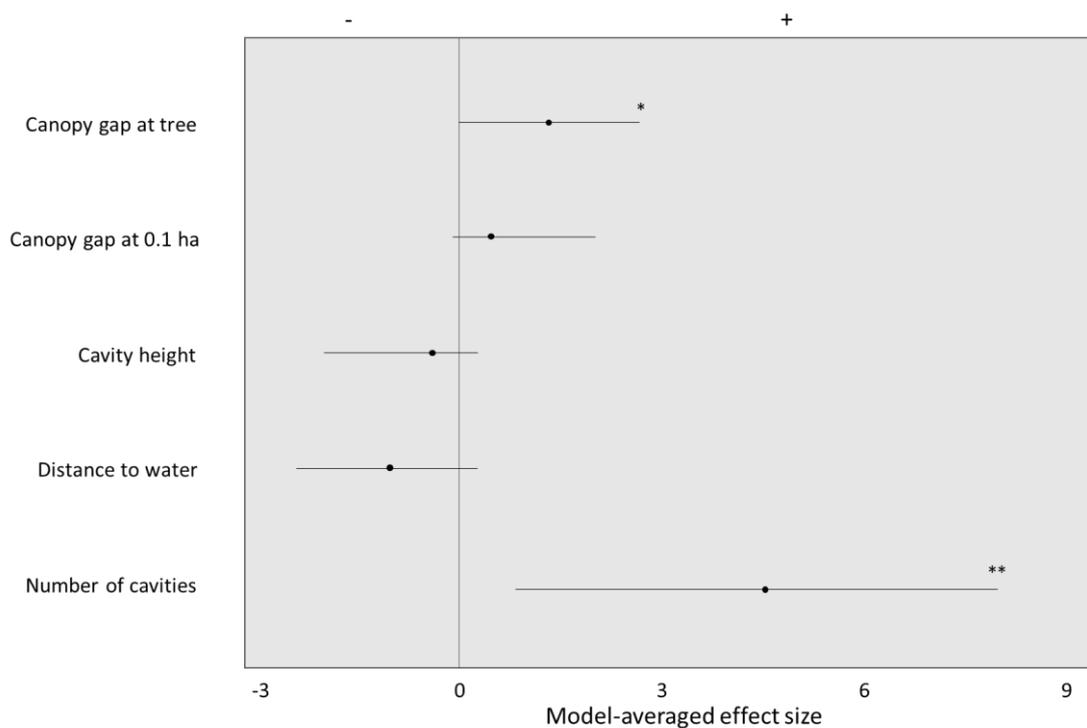


Figure 4. Variables included in the best generalized linear mixed effects models (Δ_i) showing model-averaged effect size (dot) and associated 95% confidence intervals (line) for each variable. Canopy gap at tree and number of cavities show a significant positive effect, and canopy gap at 0.1 hectare shows a non-significant

positive trend on roost use. Cavity height and distance to water show a non-significant negative trend on roost use. * $p < 0.05$; ** $p < 0.01$. See Table 1 for units.

3.4. Effects of reproductive state on selection of roost features

When we examined roost preferences according to the reproductive state of bats we found that pregnant and lactating bats used roost trees significantly further from water ($n = 44$, perm, $p = 0.04$) with fewer cavities ($n = 44$, perm, $p = 0.03$) and in cavities located higher on the tree ($n = 41$, perm, $p < 0.001$) compared to those used by post-lactating and nulliparous bats (Fig. 5). In addition, post-lactating and nulliparous bats roosted under defoliating bark more frequently (65% of roosts used) than pregnant and lactating bats (44% of roosts used), although the difference between the two groups was not significant ($\chi^2_{11.3}$, d.f. = 2, $p = 0.9$). The majority of roosts used by pregnant and lactating bats were roosts of a more solid structure, such as splits and rot holes (56% of roost used). We found no difference for any of the other roost variables that we measured.

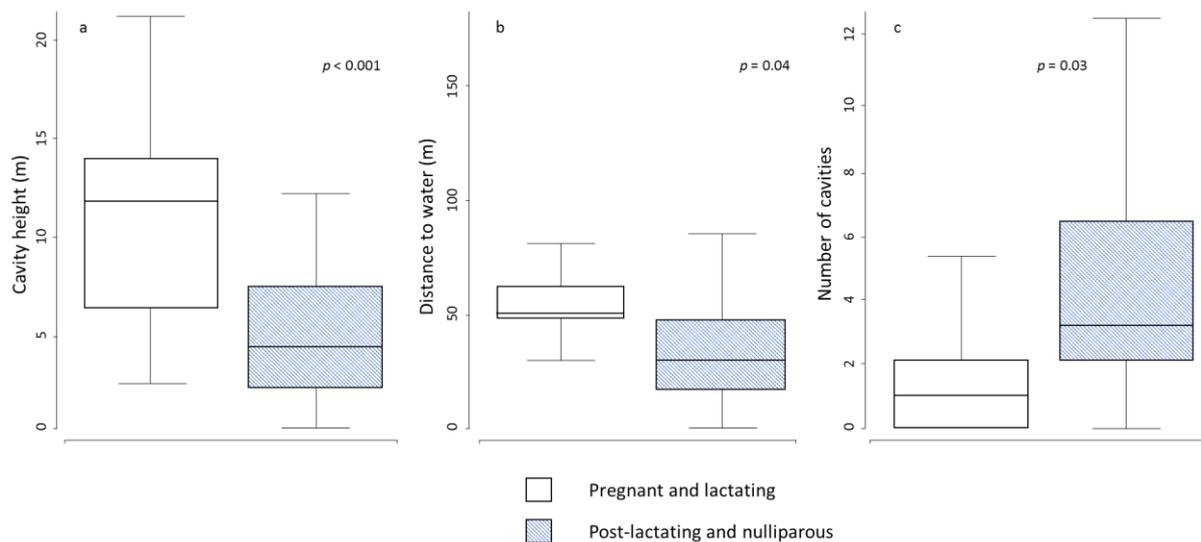


Figure 5. Median and inter quartile range for (a) cavity height ($n = 41$), (b) distance to water ($n = 44$), and (c) number of cavities ($n = 44$) as a function of the reproductive state of radio tracked adult female barbastelles ($n = 29$ bats).

3.5. Roost switching

Most bats (89%) switched roost at least once (median 0.4 ± 0.1 IQR switching frequency per day; range 0.3-0.6) during their respective tracked period, and occupied roosts for an average of 3.3 days (± 2.5 IQR; range 1-11 days) before moving. Pregnant and lactating bats ($n = 7$) switched roosts significantly less frequently (median 0.3 ± 0.1 IQR roost switches per day) than post-lactating and nulliparous bats (median 0.4 ± 0.1 IQR roost switches per day) (perm, $p < 0.05$).

4. Discussion

4.1. Selection of woodland habitat type

Selection of ancient semi-natural broadleaved woodland is common among insectivorous bats (Walsh and Harris, 1996; Russ and Montgomery, 2002; Russo et al., 2010), and roosting barbastelles significantly selected this habitat over other woodland types. Despite other studies finding a preference for roosting in beech forests (Russo et al., 2004), only one roost in this study was located in broadleaved plantation ancient woodland stands dominated by beech, despite its considerable availability within home wood areas, probably due to limited roosting opportunities as a result of the relatively young age of trees and ongoing harvesting within these stands. Indeed, Russo et al. (2010) recorded larger numbers of barbastelle roosts in unmanaged beech forests compared to stands that were periodically logged.

Our findings, in agreement with those of Russo et al. (2004), demonstrate that minimal and non-intervention semi-natural woodland provide considerably higher roosting opportunities for barbastelles than other woodland types and so should be a focus for conservation efforts to protect the species. Initiatives to restore functioning old growth woodland such as the restoration of plantations on ancient woodland sites (Thompson et al., 2003) and rewilding (Monbiot, 2013) should

be viewed as beneficial, and specific objectives to retain features associated with ancient woodland, in particular dead or decaying trees, should be a priority in all woodland types.

4.2. Selection of tree features

Bats selected roosts in trees that had a more open canopy structure than random trees, as has been observed elsewhere for barbastelles (Russo et al., 2004; Kortmann et al., 2017) and other echolocating tree-dwelling bats (Kalcounis-Ruppell et al., 2005; Fabianek et al., 2015b). Much of this effect, however, may result from the strong selection by barbastelles of roost cavities in standing dead trees that had little or no canopy at all. Indeed, if accessibility is not hindered by branches, dense canopy may in fact be beneficial to barbastelles by facilitating earlier emergence times at night and hence earlier foraging (Russo et al., 2007), and so the opportunity to select roost trees with specific canopy features may be limited by the availability of suitable roost cavities.

Roosts were more often located in oak trees (98%) than in other broadleaved or conifer species. Dead oak trees had significantly more cavities than other tree types, and the number of cavities on a tree had the largest effect on roost selection. This strong preference for roosting in dead oak trees has also been documented in Germany (Hillen et al., 2010), although roosts in other broadleaved tree types are not uncommon. Use of conifer species by barbastelles has been documented only rarely, such as in dead spruce trees killed by the spruce bark beetle *Ips typographus* (Kortmann et al., 2017). While the presence of a single suitable roost cavity on a tree may be sufficient, we propose that for barbastelles the overall value of a tree is likely to be positively correlated with the total number of cavities present because (i) more cavities on a tree increases the probability that at least one of them is suitable as a roost site at a particular moment in time, (ii) effort associated with searching for new roost options is reduced, and (iii) it is less risky to relocate to an alternative roost that is close during the day following stochastic events such as degradation of fragile bark plates in poor weather.

Pregnant and lactating female bats were located in trees with significantly fewer cavities compared to those used by post-lactating and nulliparous bats, probably because pregnant bats and bats with dependent young used solid cavity structures such as rot cavities and splits more frequently than post-lactating and nulliparous bats, which use bark plates more frequently (Russo et al., 2004). When bark plates develop on dead or decaying trees often many individual plates develop, providing numerous roosting opportunities for bats. Due to the low sample size ($n = 9$) for pregnant and lactating bats in this study, we recommend that further work be undertaken to identify with greater confidence the influence of reproductive state on roost selection in barbastelles.

4.3. Cavity selection

In this study, roost cavities were located lower on trees compared to random cavities. In contrast, in Italy Russo et al., (2004) described roost cavities that were higher on trees compared to randomly sampled cavities and suggested that bats may select higher cavities that benefit from higher roost temperatures as a result of increased exposure to solar radiation. While Russo et al. (2004) radio tracked mostly pregnant and lactating females, we studied mostly post-lactating and nulliparous bats. Indeed, when we compared groups in this study, we found that pregnant and lactating bats typically roosted in cavities that were higher on trees compared to post-lactating and nulliparous bats, supporting the hypothesis that females select higher cavities with greater exposure to solar radiation during pregnancy and lactation to benefit offspring development both *in utero* and *in situ* while in the roost (Russo et al., 2004). Indeed, at other times of year, when bats are neither pregnant nor have dependant young, it may be advantageous for females to roost in cavities that are cooler to facilitate torpor and conservation of energy (Willis and Brigham, 2007).

4.4. Distance to water

We found that roost trees were located significantly closer to water than random trees. The association with water has been shown elsewhere for barbastelle roosts using habitat suitability (Gottwald et al., 2017) and has also been observed in several other temperate forest-dwelling bats

(Kalcounis-Ruppell et al., 2005; O'Keefe et al., 2009; Culina et al., 2017). Rivers that flowed through each study site were prominent features in the landscape and are probably used as flight corridors and drinking sites by bats. In contrast, barbastelles roosting in beech woodlands in Italy, which are regularly devoid of flowing water in summer, rely on cattle troughs as sources of drinking water (Russo et al., 2017b). Post-lactating and nulliparous bats were found in roosts significantly closer to water than pregnant and lactating bats, probably because pregnant bats and bats with dependant young primarily select roosts based on characteristics that benefit the development and safety of offspring rather than distance to water, which was easily accessible and not a limiting factor in each of the study areas.

4.5. Roost switching behaviour

As has been recorded elsewhere for barbastelles (Russo et al. (2004, 2005) and other tree-dwelling bats (Ngamprasertwong et al., 2014; Kühnert et al., 2016), we found that the frequency of roost switching during summer is lowest when bats are pregnant and lactating. Risk associated with moving non-volant dependant young between roosts is likely to be an important factor during lactation (Kühnert et al., 2016) that overrides other potential advantageous associated with roost switching, such as minimising roost fouling or parasite loads within roosts. As bats are more sedentary during pregnancy and lactation, the use of more solid cavity structures is significant in that they provide greater protection against stochastic weather events that can remove ephemeral roost types such as bark plates and reduce risk of predation inside the roost itself. Indeed, we recorded a tawny owl *Strix aluco* on infrared video landing on the exit to a maternity roost inside a deep cavity in an oak tree when the colony was present there, presumably in an attempt to prey on the bats inside. Similar attempts at bark plates could easily result in the fragile plates becoming dislodged and exposing adult and young bats.

The overall rate of switching that we observed among bats radio tracked in this study highlights the large number of roosts that are likely to be required to support a colony of barbastelles within a

woodland. We expect that at least 50 different roost cavities are used each year by the colony at Houndtor, which comprises between 20-30 adult female bats. A high annual turnover of new roost options is also likely to be important, as most roosts we found were under bark plates that may not remain intact over winter and be available for use again in the following summer.

4.6. The efficacy, application and limitations of LiDAR

Investigating habitat and roost use by bats in woodland has traditionally been explored through the use of terrestrial field measurements only (Lacki and Baker, 2003). Measuring three-dimensional vegetation structure such as upper canopy heterogeneity (Jung et al., 2012) at the stand or woodland scale is, however, either impossible using traditional survey methods (Davies and Asner, 2014) or requires substantial resources (Müller and Brandl, 2009). Here, we show that LiDAR-derived measures of canopy structure provide an additional level of insight into roost selection that cannot be achieved easily through traditional survey methods. The use of bespoke airborne LiDAR datasets remains a barrier to some due to cost and lack of expertise needed to process raw data. However, it is notable that LiDAR surveying can be achieved at 5-10% of the cost of equivalent large-scale field surveying (Müller and Brandl, 2009) and in the UK processed open-source datasets have become more readily available in recent years. Several studies have derived informative variables from canopy height models that describe important habitat associations of animals (Hinsley et al., 2006; Müller and Brandl, 2009; Jung et al., 2012), and similar use of LiDAR datasets can be applied to bats to predict suitable roosting areas within woodland. While pairing temporally disparate LiDAR and wildlife survey datasets may present problems in some studies due to changes in habitat characteristics over time, effects of data lag in relatively slow changing habitats, such as woodland, is minimal over periods of up to six years (Vierling et al. 2014), which is longer than the time difference between LiDAR and barbastelle roosting datasets used in this study.

5. Recommendations for management

Old growth woodland is vitally important to barbastelles and other tree-roosting bats and the preservation and restoration of these habitats should be a conservation priority. Intervention that removes maturing and standing dead trees is expected to significantly reduce the carrying capacity of a wood for cavity roosting bats and should be avoided wherever possible. In abandoned plantation broadleaved woodland, bats will benefit from non-intervention management to allow the natural maturation of the woodland and the gradual development of old growth characteristics, in particular standing dead wood and a more heterogeneous canopy structure. For plantation woodlands in production, when thinning interventions are planned we advise the promotion of positive selection (i.e. removing trees that directly compete with neighbour trees that are marked to remain) over negative selection (i.e. removing all undesirable trees including badly shaped trees such as those that are forked, bent, heavily branched or damaged) (Kerr and Haufe, 2011) to ensure that as many roosting opportunities for bats are retained as possible. Standing dead trees do not compete for resources and should not affect the health or growth of the economic stock through direct competition, although we acknowledge standing dead trees can provide suitable habitat for tree pest species that could reduce the timber quality of neighbouring trees.

While standing dead trees typically provide more roosting opportunities for bats than other tree types, our findings demonstrate that roost selection by barbastelle bats occurs principally at the cavity level rather than on the characteristics of the tree, and so any tree supporting a suitable cavity may potentially be used by bats irrespective of the size, condition or species of the tree. As such, when undertaking thinning interventions within woodland it is important to identify the presence of potential roost cavities on all tree types prior to felling to ensure that as many of these features as possible can be retained. Indeed, we located roost cavities on young trees with small girths that would ordinarily be removed during thinning interventions. Tree age can be considered a unidirectional habitat filter (Pereira et al., 2004; Burgar et al., 2017) for tree-dwelling bats and so the

value of young trees should be considered carefully in management plans to encourage the natural succession of veteran and standing dead trees and to provide sufficient turnover of suitable cavities over time. The use of artificial roosts such as bat boxes may be appropriate in young woodland to increase roosting opportunities for bats while waiting for the wood to mature naturally, although consideration should be given to the type of box and scale of use to ensure that rare species such as barbastelles are not unintentionally disadvantaged.

Acknowledgements: We thank David Rickwood of the Woodland Trust, James Mason, formerly of the Woodland Trust, and Miriam Glendell of the Dartmoor National Park Authority for their considerable support throughout this project. We also thank numerous volunteers who helped with the fieldwork, in particular Tom Williams and Mike Treble. We also thank the two anonymous reviewers for their comments and suggestions on this manuscript.

Funding: This work was supported by the Scottish Forestry Trust (59 George Street, Edinburgh, UK), the Forestry Commission (231 Corstorphine Road, Edinburgh, UK), the Woodland Trust (as part of the Moor than Meets the Eye Heritage Lottery Fund partnership) (Kempton Way, Grantham, UK), and the SITA Trust (Eastwood Park, Falfield, UK). JSPF was funded by the Biotechnology and Biological Sciences Research Council through the South West Biosciences Doctoral Training Partnership.

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