



## Research Article

## The role of secondary trees in Mediterranean mature forests for the conservation of the forest-dwelling bat *Myotis alcaethoe*. Are current logging guidelines appropriate?

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### Keywords:

bats  
bioindicators  
logging  
chiroptera  
ecological indicators  
roosting behaviour

### Article history:

Received: 9 December 2016  
Accepted: 28 March 2017

### Acknowledgements

Bats were captured, handled and tagged with permits and under the criteria of the Catalan Government (Generalitat de Catalunya). We would like to thank the LEM (Laboratorio de Ecología Molecular) from the EBD-CSIC (Centro Superior de Investigaciones Científicas - Estación Biológica de Doñana) for their support in the DNA identification. This study has received financial support of the Catalan Environmental Ministry (Departament d'Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural), specially from the Paratge Natural d'Interès Nacional de l'Albera. We also thank Laura Torrent, Oihana Eizaguirre, Eloi Ballega, Oriol Mas-sana Valeriano, Josefina Gomis, Andrés Daniel Jiménez, Miriam Carrero, Jaume Justafre, Jaume Geli, Bartomeu Borràs Olivier Galindo and Jérôme Paoli for fieldwork and logistical assistance. This work was supported by the "Consell General dels Pirineus Orientals". Finally, we thank the two anonymous reviewers for their constructive comments.

### Abstract

Forest cover in Europe has substantially increased in recent decades, resulting in extensive secondary forest cover (ca. 10–20 years) that is too young for many specialist forest-dwelling species. In the Mediterranean region, forests have historically been logged with detrimental effects on local biodiversity. Only a few small forest patches remain untouched. Specialist forest-dwelling species are often less studied than other species due to their lower population densities and the inherent difficulties involved in sampling. In fact, some forest species have only recently been discovered or described such as the *Myotis alcaethoe* (Alcaethoe bat) and so there is a remarkable dearth of information regarding their natural history, habitat requirements and conservation status.

A total of 18 *M. alcaethoe* bats were captured and radio-tracked in a 100-year-old Mediterranean forest which led us to locate and describe 18 different tree roosts. The structural traits of each roost and the surrounding habitat were studied to unravel the factors involved in roost selection. Alcaethoe bats were found roosting in a wide variety of sites (holes, cracks and under bark) and tree species. Around 70% of the roosts were found in dead or decrepit trees. However, except for roost height, no special traits were selected. Due to the maturity of some common holly *Ilex aquifolium*, this typically secondary bush species was often used as a breeding roost. Our results provide new insights into how old and small secondary tree species play an essential role in the conservation of certain forest species.

Considering that in 20 years of bat surveys in the region, breeding colonies of this forest species have only been found in this forest characterized by its remarkable maturity (50–100 dead trees/ha), we suggest that current forest management guidelines (recommending densities of 5–10 dead trees/ha), might not be enough to ensure the presence of breeding colonies of these tree-dwelling bats.

## Introduction

Forest cover in Europe has increased by 17 million ha over the last 20 years. However, due to the intensive deforestation that occurred in the past, European forests are usually remarkably young (FAO, 2011). In the Mediterranean region, forests have been exploited and logged to the detriment of local biodiversity, and ecosystems have been driven towards global impoverishment. Only few small forest patches with complex biodiversity ecosystems remain untouched (Reig, 2013), and tend to be threatened by human activities such as the demand for wood for use as biomass and leisure activities. According to Mallarach et al. (2013), 40% of the NE Iberian Peninsula is covered by forest but only 0.3% of this forest is considered as "mature" (Comas et al., 2013). Due to their maturity, these forest patches play a highly relevant role in conservation as ecological islands that offer refuge to certain forest-dependent species (FAO, 2011; Russo et al., 2016).

Forest quality and maturity are essential for some specialist species, including many forest-dwelling bats that have highly specific habitat requirements (Bambini et al., 2010; Russo et al., 2016). The order of bats encompasses approximately 1300 species worldwide, 850 of which roost in trees (Russo et al., 2004). The diversity of forest-dwelling

bat species is mainly influenced by the availability of natural cavities, forest cover and the structural heterogeneity of the habitat (Kunz, 1982; Razgour et al., 2016; Russo et al., 2016). Due to their sensitivity to environmental changes and to anthropic impact upon habitat quality and landscape structure, some forest bats are currently regarded as good biological indicators of the quality and trophic structure of habitats; this is the case of some noctules (*Nyctalus*), the Brown long-eared bat (*Plecotus auritus*), the Barbastelle bat (*Barbastella barbastellus*), the Bechstein's bat (*Myotis bechsteinii*), and the Alcaethoe bat (*Myotis alcaethoe*) (Vaughan et al., 1997; Grindal and Brigham, 1999; Swystun et al., 2001; Kusch and Idelberger, 2005; Menzel et al., 2005; Flaquer et al., 2007; Subirachs et al., 2009; Bohnenstengel, 2012; López-Baucells et al., 2017). However, the number of roost trees that should be protected from logging in order to guarantee local population viability for these species still needs to be further studied (Russo et al., 2016).

The Alcaethoe bat (*Myotis alcaethoe*) is one of the rarest tree-dwelling bats in Europe. It has only recently been separated from the *Myotis* cf. *mystacinus* complex of cryptic species (von Helversen et al., 2001; de Pasquale and Galimberti, 2014) and is now included in Annex IV of the EU Habitats and Species Directive. It is one of the smallest European bats and, despite annual reports of new localities from across Europe, information is still lacking on its range and population size and trends.

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Consequently, it is currently listed as “Data Deficient” in the IUCN Red List of Threatened Species (Hutson et al., 2008).

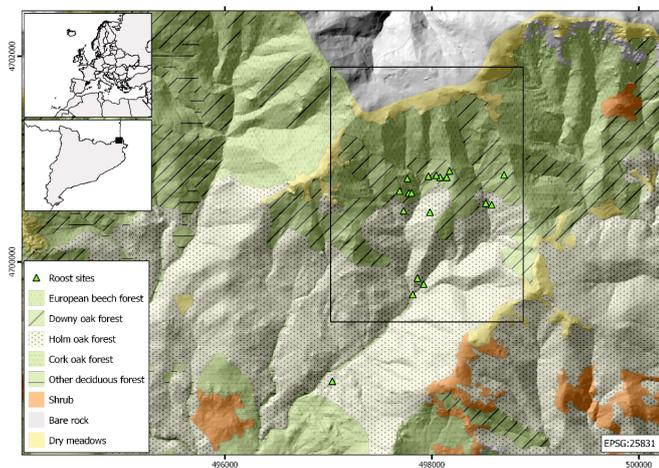
The emerging picture of this bat’s distribution, summarized by Niermann et al. (2007), suggests that the geographical range of *M. alcaethoe* covers a large part of Europe, from northern Spain and France, to central Germany, southern Poland, and Greece and recently in England and Latvia (Niermann et al., 2007; Ohlendorf and Funkel, 2001; Hutson et al., 2008; Anonymous, 2010; Devlin, 2010; Ahlen, 2010). Current records seem to indicate that it is restricted to mountain regions in the south of its range, and that throughout its range it prefers natural, humid deciduous forests with old trees and watercourses. Unfortunately, very little further data on the natural history of this species is presently available (von Helversen et al., 2001).

In the last 15 years, intensive bat inventories have been undertaken in several natural and protected areas across the Northeast Iberian Peninsula, ranging from sea level to 2000 m a.s.l. Although several *M. alcaethoe* have been captured, mainly in riparian forests, only one maternity colony has been reported, in a 100-year-old isolated Mediterranean forest in the Pyrenees (Flaquer et al., 2014). The aim of this study was to contribute to the understanding of the environmental requirements for the Alcaethoe bat by: 1) characterizing its roosts in a 100-year-old forest and 2) determining the structural roost traits that are positively selected.

## Material and Methods

### Study Area

The study was carried out in the Paratge Natural d’Interès Nacional de l’Albera (PNIN Albera) in the Northeast Iberian Peninsula (Lat 42°28’55” N, Long 2°56’46” E) (Fig. 1). This natural area harbors one of the most mature forests in the region that, due to its excellent preservation status, has been classified as “singular” by Comas et al. (2013). The forest has remained all but untouched for more than 100 years. The maximum logging intensity in this forest took place in 1914–1918 during the First World War, and some isolated logging activities were also carried out in 1939–1942 (B. Borràs *pers. comm.*). On average, it has a total of 322 living trees/ha plus 110 dead but standing trees/ha, which makes it unique among mature forests. Its southernmost limit reaches a military base that has been almost completely deforested for training purposes. Despite the prevailing arid Mediterranean coastal climate characterized by only 650 mm of annual precipitation (Orta et al., 1992), this natural area contains several permanent water points, including rivers and temporary watercourses. Our sampling area was situated along a riparian forest near the border with France (2°56’40” E; 42°26’48” N) that was characterized by a notable altitudinal gradient (approx. 400–900 m a.s.l.). Its slopes have obvious vegetation stratification that comprises communities of cork oak (*Quercus suber*), ever-



**Figure 1** – Study area in the Albera Site of Natural National Interest (PNIN de l’Albera) in NE Catalonia (Lat. 42°28’55” N, Long 2°56’46” E). Rectangle: mist-netting and radio-tracking area; Triangles: roosts.

green or holm oak (*Quercus ilex*), downy oak (*Quercus pubescens*), and beech (*Fagus sylvatica*), with common holly (*Ilex aquifolium*) and field maple (*Acer campestre*) as secondary tree species (natural regeneration) (Orta et al., 1992). Due the lack of economic value for these trees species, they reached large dimensions and an important density within the area.

### Mist-netting

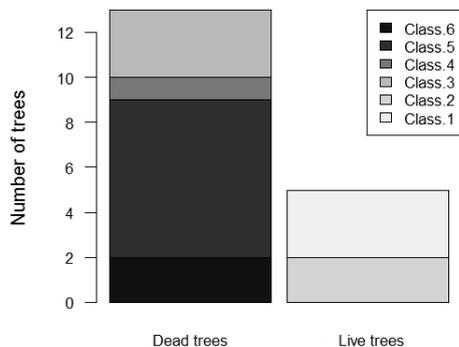
Capture sessions covered as many habitats and forest structures as possible, including tracks, waterways, mountain ridges, and pastures. Bats were captured during the period July–August from 2009 to 2015 (N=26 sampling nights). A maximum of five harp traps and 200 m of mist-nets were simultaneously set. However, nightly effort was site dependent and directly subject to sampling logistics and local circumstances. The identification of the first *M. alcaethoe* that we captured was confirmed by sequencing a DNA mitochondrial fragment of 500 bp from the subunit 1 of the mitochondrial NADH dehydrogenase (ND1) gene (C. Ibañez and J. Juste, *pers. comm.*). All the other captured individuals were identified following Flaquer and Puig (2012) and Dietz and von Helversen (2004). In the study area, they could only be potentially misidentified with *Myotis mystacinus*, as it is the only other whiskered bat reported in the Iberian Peninsula, although not in the study area. However they were separated apart by the smaller size (FA<33), lighter dorsal colouration, short ears and its pinkish shortest muzzle (resembling *M. daubentonii*). The standard measurements — sex, age (juvenile or adult), reproductive status (passive, active, lactating female, or pregnant female), body mass, and forearm length — were taken for all captured specimens. Sex and reproductive status were assessed by inspecting genitalia, while age was determined by trans-retro-illuminating wing joints (Anthony, 1988).

### Radio-tracking

All captured Alcaethoe bats were fitted with transmitters Pip AG337 (Biotrack Ltd., United Kingdom), which represented 5–10% of bats’ weight (Brigham, 1988; Hohti et al., 2011). Transmitters were attached between the scapulae with medical glue, Vetbond (3M S.L., Spain), after shaving the fur from this area (Hohti et al., 2011). After tagging, bats were kept inside capture bags for 10 minutes in order to ensure that the medical glue was completely dry before release. Daily radio-tracking was carried out during the following 7–10 days with radio receivers Antenna-AY/C (TiteleyScientific Europe, United Kingdom) and Icom receptors (Icom S.L., Spain).

### Roost characterization

Following Lučan (Lučan et al., 2009), all trees with bat roosts were characterized by considering a total of 10 features: species, height, height of canopy basement, height of canopy, tree condition, diameter at breast height (DBH), percentage of bark, distance to a tree with similar DBH, distance to a tree with potential roost, and tree period of sunshine. Tree height and canopy basement height were measured with a clinometer, and canopy height by subtracting the height of canopy basement from the tree height. Tree condition was classified into six classes: 1: alive/healthy (no decomposition); 2: alive with damage (dead or damaged canopy, dead branch and fungi); 3: dead (most branches dead, internal putrefaction and most of the canopy damaged); 4: dead (most branches fallen, damaged canopy, and a large degree of internal putrefaction); 5: dead (part or more of upper third absent, no branches, and an advanced state of decay); 6: dead and fallen (fallen tree and most of the wood decayed). The DBH was measured using a tree caliper. The percentage of bark and tree period of sunshine were classified into four classes: 0–25%, 25–50%, 50–75%, and 75–100%. For each roost, five further specific traits were measured: roost height, type of roost, roost period of sunshine, and the length and width of the entrance. Roosts were classified into five types: natural hole (hollow branches and cavities more than 5 cm wide), bark (usually free spaces under the bark), woodpecker’s nest, crack (hollow branches and elongated cavities less than 5 cm wide) and others. Although there’s no references in the literature of *M. alcaethoe* roosting in woodpecker’s nests, we have con-



**Figure 2** – Tree condition. Class 1: alive/healthy; Class 2: alive with damage; Class 3: dead (most branches alive, some internal putrefaction, and most of the canopy damaged); Class 4: dead (most branches fallen off, damaged canopy, and a large amount of internal putrefaction); Class 5: dead (part or more of the upper third absent, no branches, and in an advanced state of decay); Class 6: dead and fallen (fallen tree and most of the wood decayed).

sidered them as potential roosts as some other tree-dwelling bats such as *Bechstein's* and *Noctule* bats tend to use them (Boonman, 2000; Dietz and Pir, 2009; Dietz and Kiefer, 2016; Kühnert et al., 2016). Roost height was measured using a clinometer and insolation was classified into the same four categories as above.

Potential and available nearby roost sites were also quantified and characterized (Hohti et al., 2011). The five nearest potential roosts were selected and described. For each potential roost tree, we measured the same parameters as previously described. All potential roosts were thoroughly checked by direct prospection (optical fiber viewer) and by searching for indirect signs such as feces at the bases of the trees to ensure that no bats were roosting there.

**Habitat characterization**

The habitat in a 10 m radius buffer around each tree was characterized by measuring four features: number of trees and the amount of tree, shrub, and herbaceous cover. The number of trees were counted and classified into six classes: 0–5 cm, 5–15 cm, 15–25 cm, 25–35 cm, 35–50 cm and ≥50 cm; following Wikum and Shanholtzer (1978), the vegetation cover was classified using the Braun-Blanquet cover abundance scale: 1 (isolated trees), 2 (0–1%), 3 (1–25%), 4 (25–50%), 5

(50–75%), 6 (75–100%). The habitat characterization is summarized in Fig. S1 and S2.

**Statistical analysis**

Preferences in roost selection in *Myotis alcaethoe* were quantified using compositional analysis and Jacobs' preference index for the categorical variable (tree species) (Jacobs, 1974; Aebischer et al., 1993; Kauhala and Auttila, 2010) including selection ratios (% roosts used / % roosts available). Jacobs' index is calculated using the formula:  $D = \frac{(r-p)}{(r+p-2rp)}$ , where *r* is the proportion of used roosts and *p* the proportion of available roosts. *D* varies from -1 (strong avoidance) to +1 (strong preference), and values close to zero indicate that a certain type of roost is used in proportion to its availability. This approach was used to test whether any preference between tree species could be detected. All the different types of roosts were ranked and the significance of bat selection tested using the residuals of a Chi-square goodness-of-fit test, with *p* values corrected with Bonferroni and Westfall confidence intervals.

Occupancy rate and roost selection were modeled using a binomial Generalized Linear Model (GLM) with the following predictive variables: species, DBH, roost height, entrance roost area (length × width entrance), roost period of sunshine, tree condition, and type of roost. Following Burnham and Anderson (2004), the most parsimonious models were selected using Akaike's Information Criterion corrected for small sample sizes (AICc). The best models were obtained selecting models with an AICc difference from the best model ( $\Delta_i$ ) < 2, using the R package *bestglm* v. 0.34 (McLeod and Xu, 2014). To avoid multicollinearity, the Pearson correlation between the predictors in the models was calculated using the *Corrplot* package (Wei and Simko, 2013) and all predictors with *r* > 0.8 were excluded. Additionally, the Variance Inflation Factor (VIF) of each predictor was calculated; as well, all predictors with VIF > 3 were excluded (Neter et al., 1990). Both entrance length and width were discarded and the entrance section was used as a surrogate variable. All analysis were carried out with R 3.2.2 (R Core Team, 2015); models were built with the *lme4* package (Bates et al., 2015) and plotted with the *effect* and *ggplot2* packages (Fox and Hong, 2009; Wickham, 2009; Bates et al., 2015).

**Results**

Amongst the bats recorded in the study area, 18 *Myotis alcaethoe* were captured (94% in harp traps, Tab. S3). These bats led us to 18 different roosts (Tab. 1, Fig. 3) that included both small and temporary roosts, as well as big maternity colonies. Eight adult passive males, one adult passive female, and eight adult lactating females were radio-tracked during the study period. Of these, seven tagged individuals were found to be roosting in the same maternity colony (roost n° 9 and 13, Tab. 1). Some of the other bats led us to four other temporary roosts. Although three bats shifted from roost to roost during the study period, they stayed on average only 1–2 nights in each different roost (Tab. S3). A single breeding female was found every day in a large *Ilex aquifolium* during 13 consecutive days (Tab. S3).

Most of the roosts were relatively small hollow branches, generally no more than 30 cm deep, in trees with low DBHs (an average of 31.2 ± 20.08 cm, in a range of 10–85 cm), and bat colonies consisted of just a few individuals (1–10, Tab. 1). Due to the difficulty of access to roosts, internal measurements were not taken and were only estimated by direct observation with an optical fiber viewer. Only one roost was found in a relatively large cavity, an 85 cm wide dead hollow tree (Tab. 1). Roosts were found in the following tree species: *Ilex aquifolium*, *Fagus sylvatica*, *Acer campestre*, *Quercus ilex*, *Quercus pubescens*, *Quercus suber* (Tab. 1). Despite the great variety of tree species, the typology of the roosts varied somewhat less: 11 natural holes, 6 cracks in trees, and one under bark. A total of 72.22% of *Myotis alcaethoe* were found in dead trees (in various states of decay, especially in still-standing but completely dead trees) (Fig. 3). Maternity roosts were found in different tree species: *A. campestre* (2), *Q. pubescens* (2), *I. aquifolium* (2), and *Q. suber* (1), plus one in a non-determined



**Figure 3** – Alcaethoe bat roosts found during the present study. Numbers correspond to the roost identity code and match the traits given in Tab. 1.

Table 1 – Roost and tree characterization with structural variables. Numbers correspond to images in Fig. 3.

Tree	Tree																				
	ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
Species	A. cam	F. syl	F. syl	F. syl	F. syl	I. aqu	I. aqu	I. aqu	Q. ile	A. cam	A. cam	I. aqu	I. aqu	Q. pub	Q. pub	Q. sub	Und.	I. aqu	I. aqu		
Height (m)	5	10	10.6	6	10.55	X	X	x	x	6	14	5	5	10	9	5	X	X	7	8.42	
Height of canopy base (m)	2.5	2.25	2	X	2.5	X	x	x	x	4	4	2.5	x	6.3	2	X	X	x	x	2	
Height of canopy (m)	5	10	10.6	6	10.55	X	x	x	x	6	14	5	x	10	9	5	X	X	7	8.42	
Condition	6	2	1	5	5	1	4	5	5	6	3	1	5	3	2	5	5	5	5	3	
DBH (m)	25	52	50	30	45	15	25	20	20	10	30	10	15	85	35	20	60	15	15	20	
Bark (%)	50-75	75-100	75-100	25-50	75-100	75-100	75-100	75-100	75-100	0-25	75-100	75-100	75-100	75-100	75-100	75-100	0-25	75-100	75-100	75-100	
Dist. to similar DBH tree (m)	3	2.4	10	2.5	1.5	5	0.3	2.5	2.5	1.5	3	0.2	1	>20	5	1	8	2	2	2	
Dist. to a potential roost (m)	6	2.4	4	2	1	1	0.3	2.5	2.5	1	13	0.2	1	>20	10	5	8	2	2	6	
Insolation (%)	25-50	50-75	75-100	50-75	0-25	0-25	75-100	75-100	25-50	0-25	0-25	0-25	0-25	75-100	50-75	50-75	0-25	0-25	X	25-50	
<b>Roost</b>																					
Height (m)	3	4	8	8	3.5	8	1.5	7	0.5	2.5	7	2.5	4	8	4	3	4	2.5	3	3	
Type	Crack	Hole	Hole	Hole	Crack	Hole	Hole	Hole	Bark	Hole	Hole	Hole	Hole	Crack	Hole	Hole	Crack	Crack	Crack	Crack	
Insolation	50-75	50-75	50-75	50-75	0-25	0-25	0-25	75-100	50-75	0-25	0-25	0-25	0-25	75-100	0-25	25-50	0-25	0-25	0-25	0-25	
Length (cm)	15	2	4	4	15	5	4	3	20	20	3	10	30	1	4	3	15	35	50	50	
Width (cm)	1	2	2	2	5	4	3	4	5	5	3	5	5	1	3	3	2	5	5	4	
<b>Bats</b>																					
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	1♂3♀	♀	♀	♀	1♂2♀	♀	♀	♀	♀	♀	♀	
Reproductive status	Pas	2 Lact	Lact	Lact	Lact	2 Lact	Lact	Lact	Lact	Pas	Pas	Pas									
Individual	1	2	3	3	4	5	6	6	6	7, 8, 9, 10	11	12	13	1, 14, 15	16	12	17	18	18	18	
Year	2013	2014	2013	2013	2014	2014	2014	2014	2014	2012	2015	2014	2014	2013	2009	2014	2014	2013	2013	2013	2013

A. cam: *Acer campestre*; F. syl: *Fagus sylvatica*; I. aqu: *Ilex aquifolium*; Q. ile: *Quercus ilex*; Q. pub: *Quercus pubescens*; Und.: undetermined

**Table 2** – Tree species selected by *Myotis alcaethoe* calculated using Jacobs' index and ranked with Westfall and Bonferroni confidence intervals.

Tree species	Occupation (%)	Availability (%)	p-value (Bonferroni)	p-value (Westfall)	Jacobs'	Selection
<i>Ilex aquifolium</i>	37.5	10.7	1	0.922	0.67	Positive
<i>Quercus suber</i>	6.25	1.78	1	0.992	0.57	Positive
<i>Fagus sylvatica</i>	25	21.43	1	0.922	0.10	Neutral
<i>Acer campestre</i>	12.5	17.86	1	0.325	-0.21	Neutral
<i>Quercus ilex</i>	6.25	10.71	1	0.987	-0.29	Neutral
<i>Quercus pubescens</i>	6.25	16.07	1	0.922	-0.48	Neutral
<i>Alnus glutinosa</i>	0	3.57	1	0.922	-1.00	Negative
<i>Quercus petraea</i>	0	1.78	1	0.922	-1.00	Negative

dead tree; the typology of these roosts was as follows: natural holes (6) and cracks (2), most (66.67%) in dead trees (class 3–6) (Fig. 2).

A total of 52 available potential trees for harboring roosts were selected in the same area and characterized. *M. alcaethoe* positively selected *Ilex aquifolium* and *Q. suber* (Tab. 1). However, adjusted p-values with Bonferroni confidence intervals provided no evidence that this selection had a significant effect on the general probability of bat occupancy (Tab. 2).

The best model predicting bat occupancy in available tree roosts only included the height of the roost as a predictor variable (Occupation ~ Height of roost, following a binomial distribution). This variable significantly influenced bat occupancy, and gave higher probabilities for occupied bat roosts at greater heights, with probabilities of over 50% at above four meters.

### Discussion

Our study area (in which maternity colonies were detected annually from 2009 to 2015) represents the only known breeding area for *M. alcaethoe* in the Northeast Iberian Peninsula. This area is unique as it has been all but untouched by forest management for at least a century due to the difficulty of access that has prevented logging both in the past and the present (Comas et al., 2013). Similar natural areas with such mature forests are very scarce in the Mediterranean region (Comas et al., 2013), which led to a lack of knowledge about the characteristics that make these old forests so special for these forest bats. Our data help the unravel the structural traits that make trees suitable roosts for this rare forest-dwelling bat species, and suggest that current regional guidelines might be unappropriated for bat conservation.

### Tree-species selection

One of the few existing studies of roost ecology in *Myotis alcaethoe* was performed in the Czech Republic (Lučan et al., 2009) and suggested that *Alcaethoe* bats select mature forests of oaks (*Quercus* sp.), hornbeam (*Carpinus* sp.), silver birch (*Betula pendula*), and small-leaved lime (*Tilia cordata*). Their forests were well developed and mature, with numerous tall trees in advanced states of decay, and harbored nearby water points and/or patches of riverside vegetation. The roosts used in the Czech Republic by this bat generally consisted of small cracks or cavities in tree trunks or in canopy branches, at about 16 m above ground level in dying or decaying trees. This study revealed positive selection for the tallest trees. In England, *M. alcaethoe* was also found in alder forests (*Alnus glutinosa*), especially in ravines and on steep slopes, in protected areas (Dietz et al., 2009; Jan et al., 2010). In Italy *Alcaethoe* bats were found in mature beech forests (*Fagus sylvatica*) (de Pasquale and Galimberti, 2014), while the first maternity roost in the NW Iberian Peninsula was recently reported by Hermida et al.

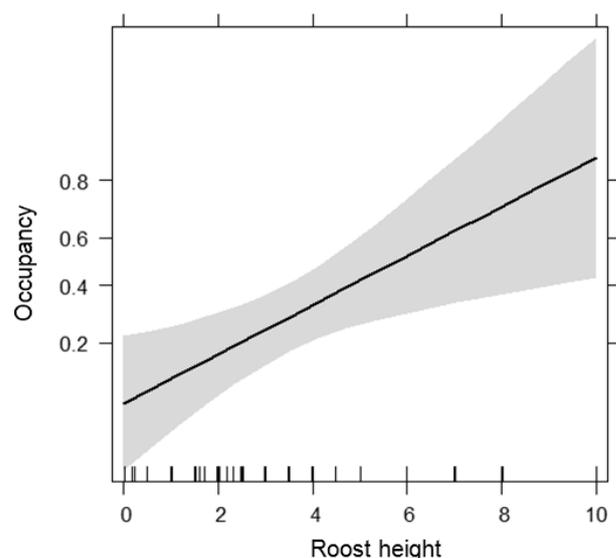
**Table 3** – Results of the occupancy model using a Generalized Linear Model fitted to a binomial distribution.

Coefficients	Estimate	Std. Error	Z value	p> z
(Intercept)	-2.7134	0.7248	-3.744	0.0001*
Height	0.6055	0.2143	2.825	0.005*

(2013) in a crack in a pedunculated oak (*Quercus robur*) at 14 m above ground level in a trunk with no bark. Other radio-tracked bats in this latter study roosted in smaller oaks (*Quercus pyrenaica*) in natural holes, up to 4 m above ground level, in trees with a DBH around 30 cm. Although some positive preference has been reported elsewhere for some tree species, in our study this factor had no significant effect on the probability of the roost to be occupied by *M. alcaethoe* (Fig. 4, Tab. 3). Also, unlike in most of the previously mentioned studies, the roosts in our study area were not generally found in particularly large trees (average DBH=31.22 cm) although centennial trees with DBHs>1 m do exist in the sampling area (Orta et al., 1992). In fact, most of our bats were found in small holly trees (*Ilex aquifolium*) (Peterken and Lloyd, 1967) (Fig. 3 and Tab. 1). However, despite being “small”, many of these trees were very old, and some were dead and in various states of decay. These findings highly correspond to what is usually expected for strictly forest-dwelling bat species in Europe (Lučan et al., 2009). The fact that larger trees were not apparently selected might be a result of competition with other bat and non-bat species. Tree species composition in forests where *M. alcaethoe* have already been reported greatly differ both across Europe and within single localities. This variability indicates that despite being a forest-dwelling specialist bat, roost selection by *M. alcaethoe* is not restricted (or only minimally driven) by certain tree species. The only common factor identified amongst all sites is the high maturity of the forests in which they were found, characterized by the abundance of old trunks and high roost availability.

### Structural roost traits selection

Of all the structural variables that could affect roost selection, only height had a significant positive influence. In general greater heights provide bats with better protection from predators during the day (Vonhof and Barclay, 1996). Nonetheless, our bats were found at signific-



**Figure 4** – Effect of “roost height” upon the probability of finding a *Myotis alcaethoe* in a roost.

antly lower heights than those reported in previous studies (e.g. Hermida et al., 2013) in which roosts were located 14 m above ground level. These differences might be due to the fact that the sampled forests in Italy and the Czech Republic simply had generally taller trees than those in our study area, where maximum tree heights were only 10–20 m depending on the species (Comas et al., 2013). As in the Czech Republic (Lučan et al., 2009) and Castilla y León (Hermida et al., 2013), roosts were mainly found in cracks and natural holes, but no typology was positively selected. Another variable that was not targeted in our study but that is globally assumed to be an important factor for roost occupation is roost temperature (Sedgeley, 2001; Flaquer et al., 2014). This might be especially relevant in maternity roosts (specially in Mediterranean regions), where low temperatures reduce offspring survival rates (Harbusch and Racey, 2006) and high temperatures threaten offspring survival due to dehydration (Monsalve-Dolz, 2014).

### Maternity versus temporal roosts

Bearing in mind that we radio-tracked both reproductively passive individuals (males and females,  $n=9$ ) and lactating females ( $n=9$ ), we expected that the characteristics of the roosts chosen by each group would vary (Flaquer et al., 2007). However, no significant differences were found between the two groups, being most of the roosts small and temporary. This uniformity may be due to the fact that radio-tracking was undertaken during the final stage of lactation (as we tried to avoid disturbance during the most sensitive periods of pregnancy). Thus, juveniles were already able to fly and so they did not depend on maternity colonies, thereby favoring colony dispersion as a means of minimizing predation pressure. This would explain why we only found 1–2 lactating females in most roosts (with the exception of the roosts 9 and 13, Tab. 2), while maternity colonies of *M. alcaethoe* and similar species are known to consist of 10–20 individuals (Buckley et al., 2013). In the maternity colonies more than one male were present — probably segregated — which has been rarely reported in the literature for whiskered bats. According to Altringham and Senior (2005), Papadatou et al. (2008) and Angell et al. (2013), this could be a result of the thermoregulatory benefits to the females.

### Implications for conservation

*M. alcaethoe* is a recently described (2001), strictly forest-dwelling bat species that has historically been confused with the sibling whiskered bat (*Myotis mystacinus*), which has led to a general lack of information regarding its natural history. Specialist forest-dwelling species depend on the preservation of natural mature forests as they usually have strictly limited foraging areas and poor dispersal power. Fragmentation and isolation of subpopulations are major issues for forest species that in many cases may negatively affect their survival rates (Subirachs et al., 2009; Camprodon and Guixé, 2013).

Providing information of natural history for those species is essential to understand their conservation status in order to apply an accurate model of conservation management (Jones et al., 2016). Forest logging, tourism, local usage, as well as species conservation must be on top of management priorities. This study shows the importance of maintaining a large number of old trees in forested areas, and especially emphasizes the important role of certain secondary species of shrubs (small trees) such as *Ilex aquifolium*, which can minimize the long-term effects of logging upon bat species like *Myotis alcaethoe* (Hohti et al., 2011).

Considering the fact that in 20 years of continuous bat surveys in the Northeast Iberian Peninsula, breeding colonies of *M. alcaethoe* have only been found in this particular old forest (with 50–100 dead trees per hectare), current forest management guidelines (which recommend a minimum density of 5–10 dead trees/ha as an appropriate logging practice), might be insufficient for accommodating breeding colonies of this tree-dwelling bat. More research is thus essential to further test and improve management logging practices (Russo et al., 2016).

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Associate Editor: D. Russo

## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Figure S1** Percentage of cover within a 10 m radius around roost trees.

**Figure S2** Distribution of tree size classes within a 10 m radius around roost trees.

**Table S3** Data of tagged bats.