

Habitat selection by *Myotis bechsteinii* in the southwestern Iberian Peninsula

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Bechstein's bat (*Myotis bechsteinii*) is one of the rarest European bat species. In oceanic climates, they appear to be restricted to woodlands, with preference for mature deciduous forests in lowlands. We investigated habitat selection by 20 lactating females belonging to 13 maternity colonies in Mediterranean landscapes. Deciduous forests (particularly *Quercus pyrenaica*) were positively selected, and coniferous forests were opportunistically used, whereas no foraging bouts occurred in evergreen broadleaved woodlands or in non-forested areas. Bats preferred to forage inside the forest rather than in edges or clearings. Stands of high canopy cover were also preferred. The preference for deciduous over evergreen broadleaved woodlands suggests that other variables such as prey availability, rather than structural constraints, drive habitat selection. *M. bechsteinii* might be abundant in well preserved deciduous forests within its Mediterranean range, in which the species' distribution might be limited by habitat loss and degradation related to agricultural practices and deforestation.

Introduction

Bechstein's bat (*Myotis bechsteinii*) ranges from the Iberian Peninsula northwards to southern Scandinavia and eastwards to Iran and the Caucasus (Schlapp 1999) (Fig. 1). Although widespread, it is considered rare over its entire distribution range, even though it may be locally abundant (Červený & Bürger 1989b, Schlapp 1999, Meschede & Heller 2003, Ruczyński & Bogdanowicz 2005, Dietz & Pir 2009). The species is listed as "Least concern" with decreasing populations, thus approaching VU A4c, according to the IUCN (Hutson *et al.* 2008). It has seldom been reported in Mediterranean areas (e.g. Vergari *et al.* 1998, Baagøe 2001). Its present rarity

contrasts with its putative abundance in the late Pleistocene and Holocene (Aellen 1978, Magnin 1989, Morel 1989, Sevilla 1989, 1991).

During the last century, deforestation linked to agricultural practices coincided with declines in bat populations (Walsh & Harris 1996). Its demographically independent small populations (Kerth *et al.* 2008) and habitat requirements (e.g., Greenaway & Hill 2004, Hutson *et al.* 2008, Dietz & Pir 2009) make *M. bechsteinii* especially vulnerable to habitat loss. For this sedentary and short-range species, whose females display a strong fidelity for the colonies where they were raised (Kerth *et al.* 2002, 2003, Kerth & Morf 2004), degradation of local conditions might have an even greater negative impact.

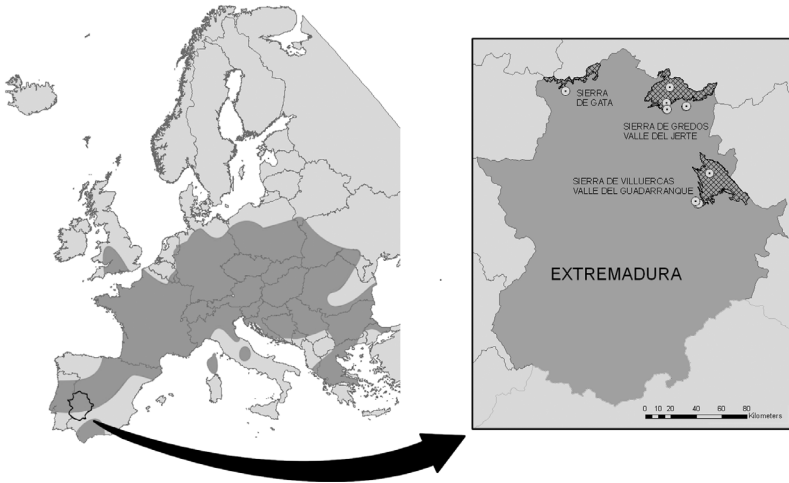


Fig. 1. European distribution of *Myotis bechsteinii* (redrawn from Hutson *et al.* 2008), and locations of the 13 colonies studied (light grey circles). Labels indicate the three SCI areas (cross-hatched).

The niche and foraging behavior of insectivorous bat species are strongly constrained by wing morphology and echolocation features (Norberg & Rayner 1987, Crampton & Barclay 1996, Entwistle *et al.* 1996, Racey & Entwistle 2003, Zukal & Rehak 2006). *Myotis bechsteinii* has low wing loading (9.0 N m^{-2}), and medium-span broad wings, which enables slow (4.9 m s^{-1}) but skillful flight (Norberg & Rayner 1987, Jones & Rydell 1994, Siemers & Swift 2006) suitable for flying and foraging in cluttered habitats (Brigham *et al.* 1997). Its echolocation calls, of low intensity and broadband frequency, are also well suited for detecting faint echoes from prey in cluttered environments (Neuweiler 1989, Kaňuch *et al.* 2008). Indeed, *M. bechsteinii* forages within mature, even oak forests (*Quercus* spp.), and prefers areas characterized by closed canopy, with a rich vertical structure and unequal stratification (Meschede & Heller 2003, Kaňuch *et al.* 2008, Dietz & Pir 2009, M. Barataud unpubl. data). Bechstein's bat feeds within the forest, by hawking and gleaning prey from surfaces (Meschede & Heller 2003). The species is considered to be strictly dependent on woodland, with preference for even, mature to aged deciduous forests (Kerth *et al.* 2003, Greenaway & Hill 2004, Kaňuch *et al.* 2008), and forages within small areas around the colonies: maximum reported daily commuting distances approach 1 km (e.g. Kerth *et al.* 2001, Albrecht *et al.* 2002, Fitzsimons *et al.* 2002,

Schofield & Morris 2000) and foraging areas cover no more than 20–40 ha (Kerth *et al.* 2001, Dietz & Pir 2009, M. Barataud unpubl. data).

The Mediterranean region differs from more northern European landscapes where most data about the species have been gathered so far (e.g., Červený & Bürger 1989a, 1989b, Schofield & Morris 2000, Fitzsimons *et al.* 2002, Kerth *et al.* 2003). Global warming after the Pleistocene, reinforced by degradation and overgrazing due to more than 10 000 years of human activities, has resulted in the cumulative decay and desertification of Mediterranean landscapes (Telleria 2001, Blondel 2006). Two distinct, though not mutually exclusive, factors are likely to impose differences in foraging habitat selection and even restrain the species' distribution in the Mediterranean basin. On the one hand, climatic factors such as hot summers may reduce body heat loss, thus mitigating thermoregulation costs, whereas seasonal water shortages increase dehydration risk during the reproduction period. Therefore, environmental features shaping the presence of this species may be different under these conditions; for instance, reduced water availability may limit the location of hunting grounds. On the other hand, characteristic plant associations — loose forests of evergreen broadleaved species devoid of shrubby understory — largely depart from the bat's supposed preferred habitat (Meschede & Heller 2003, Kaňuch *et al.* 2008, Dietz & Pir 2009). If this forces the species to

hunt in suboptimal habitats, we would expect larger foraging areas (e.g. Stephens & Krebs 1986), or other effects on demography aiming to reduce competition, such as smaller colonies or less dense populations (i.e. Goiti *et al.* 2008).

As for many forest bird species, which are adapted to environmental conditions in central Europe (Telleria 2001), the Mediterranean basin may be considered a peripheral area for *M. bechsteinii*, where it may become progressively scarce. Depicting the habitat selection patterns in the Mediterranean range would give us valuable clues about the factors limiting its populations in this area. Thus, in this paper we study habitat selection by *M. bechsteinii* in a Mediterranean region, in order to compare the selection patterns observed with those described for more northern European landscapes, and to elucidate whether habitat requirements may be responsible for the apparent scarcity of *M. bechsteinii* in Mediterranean areas. We focused on maternity colonies, which are especially well suited for habitat selection studies, given their stricter ecological requirements (Kurta *et al.* 1990, Entwistle *et al.* 1996) and their importance for species and population prevalence (Entwistle *et al.* 1996, Sedgely & O'Donnell 1999, Willis & Brigham 2005, Psyllakis & Brigham 2006).

Material and methods

Study area

Our study was conducted in Extremadura, southwestern Spain, at three Sites of Community Importance (SCI): (1) Sierra de Gredos y Valle del Jerte (ES4320038), (2) Sierra de Gata (ES4320037), and (3) Sierra de las Villuercas y Valle del Guadarranque (ES4320039) (Fig. 1). These sites cover an area of 1690 km². Elevation ranges from 400 to 2500 m a.s.l., with an average altitude being ca. 800 m. The climate is meso- to supramediterranean with cold winters (from -5 to 10 °C) and warm (20–35 °C), very dry summers, with high temperature contrast between seasons, and higher annual rainfall (727 mm) than in a standard termomediterranean climate. These conditions allow for the presence

of Pyrenean oak (*Quercus pyrenaica*), a transitional species with humid mesomediterranean requirements (Leco 1997) and tolerating colder conditions than other oaks such as holm oak (*Q. rotundifolia*) and cork oak (*Q. suber*).

Most characteristic habitats in the area are Mediterranean scrubland, comprising heath (*Erica* spp., *Calluna* spp.) and other shrubs (e.g., *Cytissus* spp.), together with forests of Pyrenean oak and chestnut (*Castanea sativa*). A variety of other land cover types occur as well in *Sierra de las Villuercas*, namely pastures, croplands, *Q. rotundifolia* dehesas, shrublands, and narrow riverside forests of common alder (*Alnus glutinosa*). Dehesa refers to a savannah-like loose oak forest; in general terms, a dehesa is most commonly composed of Mediterranean evergreen broadleaved oaks (*Q. rotundifolia*, *Q. suber*), and to a lesser extent of the deciduous *Q. pyrenaica* and *Q. faginea* (Joffre *et al.* 1999, Blondel 2006). In *Sierra de Gredos y Valle del Jerte*, forests of maritime pine (*Pinus pinaster*) are also common.

Capture and marking

Captures were conducted from 18 June to 12 July 2006. To maximize capture efficiency, and based on thorough forest bat surveys conducted in the area (Schreur 2007) that proved the strict relationship between *M. bechsteinii* and *Q. pyrenaica*, we sampled forest stands with presence or dominance of this tree species in each of the three areas. Sampling points were established next to water sources, considered suitable for drinking (e.g. small irrigation ponds, narrow streams or troughs), where netting has proved more effective. All captures were done with permission of the Extremadura Regional Council. Captures were performed using mist nets placed across water points, i.e. intercepting the trajectory a bat would follow to gain access to water, and at forest borders, hedges, rivers, and vegetation corridors. Each individual was identified and sexed, forearm length and animal weight were measured, and reproductive status and age were determined. Twenty-eight lactating females were fitted with 0.35-g radio-transmit-

ters (PIP II, Biotrack Ltd., Dorset, UK). After the hair between the scapulae was cut with scissors, radio-transmitters were attached using the surgical adhesive Skinbond® (Smith and Nephew, Largo, Florida, USA). The total weight of the transmitter and adhesive never exceeded 5% of the animal's weight (Aldridge & Brigham 1988).

Radio-tracking

Radio-tracking was carried out on foot using four radio receivers (TRX1000S, Wildlife Materials Inc., Carbondale, USA; Yaesu FT-290RII, Andreas Wagener Telemetrielingen, Köln, Germany) and hand-held three-element Yagi antennas. We tagged a total of 28 bats. Nevertheless, some of the tagged bats lost their transmitter or got rid of them before radio-tracking started. In other cases, batteries failed or bats managed to cut off the antenna, hampering emission. Thus, 8 of the 28 tagged bats were excluded, and a total of 20 tagged lactating females belonging to 13 colonies (1–3 bats per colony) were radio-tracked successfully until approximate identification of their hunting areas was achieved (1–2 nights per individual). Whenever possible, tracking was conducted during the entire night. Each animal was tracked as closely as possible to record its commuting route. Locations were preferably obtained by the “homing in” technique (White & Garrott 1990), which involved following the individuals to their foraging areas and identifying their activity points *in situ*. To avoid spatial auto-correlation, successive data recordings were taken 10 minutes apart (Aihartza *et al.* 2003, Russo *et al.* 2005, Goiti *et al.* 2006, Nicholls & Racey 2006). Locations where the bats were at rest or commuting, which might bias further conclusions about the selection of foraging areas, were excluded from posterior analyses, and only active locations were considered. Fixes were either located using GPS or mapped in the field over georeferenced orthophotographs. Field data were transferred to GIS (ArcView 3.2, ESRI, California, USA).

Due to small ranges and commuting distances of *M. bechsteinii*, we were able to track bats on foot. Bats foraged most of the time within the receptors' detection range. As such,

we are confident that the recorded fixes reliably represent the bats' hunting areas.

Analysis

Land-use categories and forest types were redrawn from aerial photographs provided by the Extremadura Regional Council. We defined individual habitat availability within a 1-km circular buffer around each animal's diurnal roost (roosts detailed in Napal *et al.* 2009), based on commuting distances measured in the present study (max 908 m), which essentially coincide with currently reported action ranges for this species (e.g., Schofield & Morris 2000, Kerth *et al.* 2001, Albrecht *et al.* 2002, Fitzsimons *et al.* 2002). We placed grid squares (30 m to a side) onto each circular buffer, assigned each cell to a habitat type according to dominant tree species [evergreen coniferous (CONIF), deciduous broadleaved (DECID), or evergreen broadleaved (EVG)], and as non forested (NON F) when trees were not present. To calculate canopy cover, we measured the area covered by vegetation in each cell using orthophotographs. Orthophotographs were masked using generated land cover maps, and calculated cover values were further corrected according to the tree density in each land-use category to avoid overestimating tree cover by including grass or bushes. We further classified the cells according to their position in the landscape as being inside, outside, or at the edge of the forest, or containing loosely placed trees as in dehesa (Table 1).

We determined preferential foraging areas (kernel 95%) following Kernohan *et al.* (2001), considering only active locations. We estimated kernel outlines using ArcView 3.2 — Animal Movement program ver. 2.0.β (Hooge *et al.* 1999), for the fixed kernel method; the smoothing parameter was calculated *ad hoc* (Worton 1989). We plotted individual MCP (Minimum Convex Polygon) sizes against the number of individual locations. MCP sizes were calculated by bootstrapping with replacement — 100 iterations per run — using the software Animal Movement 2.0.β for ArcView 3.2. Small sample size (1–3 individuals per colony) did not allow for the calculation of colony action ranges.

We tested the independence among habitat availability and usage, both individually estimated in the above described way, using χ^2 goodness of fit (log-likelihood ratio G). Habitat categories or features were ranked in order of relative preference according to their selection ratio w_i (Manly *et al.* 1993). To assess the selection or rejection of a given class of habitat, edge or cover, we constructed Bonferroni's confidence intervals, following Neu *et al.* (1974), as adapted by Manly *et al.* (1993) to individually estimated categories' (habitat, position in relation to the edge, and tree cover) availability and use. Selection ratios (w_i) were compared pairwise, and statistical significance of the differences was evaluated by means of Bonferroni's confidence intervals. For all tests, α was set to 0.05, corrected by the number of simultaneous comparisons. The confidence intervals were computed at the 95% level, also corrected by the number of simultaneous comparisons.

Results

We obtained a total of 500 active contacts (mean 25 locations per bat; SD = 9.16), totaling 4826 minutes of activity (mean = 241.3 minutes per bat, SD = 81.17, range = 80–330) (Table 2).

Minimum individual foraging areas averaged 7.69 ha (SD = 7.3, range = 0.26–27.53 ha). All but one comprised less than 20 ha. For 15 of the 20 individuals, MCP size reached an asymptote for the number of active locations considered when MCP size was plotted against the number of locations added. Three of the five MCPs not

reaching an asymptote included fewer than 15 locations. In most of the cases when individuals from the same colony were tracked, we observed notable overlap between individual foraging areas. Bats flew as far as 908 m from their roost (mean maximum distance = 539 m, SD = 197, average distance = 383 m, SD = 211). During the monitoring interval, only one individual was observed to change its roost to another one in close proximity.

When habitats were pooled across all colonies, deciduous forest (DECID) was the most abundant class, followed by scrubland and open space (NON F). Land-cover categories were not homogeneously available across colonies. Regarding the structure of *Q. pyrenaica* stands, individual colonies were found either in forests or in dehesa-like landscapes. Likewise, coniferous and evergreen broadleaved forests were locally abundant though far less available globally (Table 3).

Land cover categories were not used according to availability ($G = 762.03$, $df = 60$, $p < 0.001$; Table 4). Deciduous forests (dominated by Pyrenean oak) were most preferred, followed by coniferous forests, which were opportunistically used where available. No foraging bouts occurred in evergreen broadleaved forests or in open areas (Table 5). Furthermore, animals showed inter-individual differences in resource use ($G = 222.14$, $df = 57$, $p < 0.001$).

The use of edge classes did not depend on availability either ($G = 1151.32$, $df = 57$, $p < 0.001$). Individuals preferred to forage within forests rather than along edges, and positively selected the loose trees of dehesa while avoiding non-forested areas (Table 5).

Table 1. Description of the environmental variables measured in this study.

| Variable | Description |
|-----------------|---|
| Land cover type | (EVG) evergreen broadleaved forest (holm oak, cork oak) (DECID) deciduous forest (including Pyrenean oak) (CONIF) coniferous forest (NON F) non-forested space |
| Cover class | Forest cover categories: 0 (NON F), 1 (0%–20%), 2 (20%–40%), 3 (40%–60%), 4 (60%–80%), 5 (80%–100%) |
| Edge | 0: outside the forest 1: within the forest 2: isolated trees (single trees or small groups, as in dehesa) 3: edge [within 25 m of the ecotone between any forest and an open space (non-forested or dehesa)] |

Table 2. Tracking survey data for the 20 radio-tracked lactating females. Body mass (g), forearm length (FAL, mm), tracking effort (tracking nights, number of fixes and total foraging time (TTF) measured in minutes), area (ha) of the foraging area (kernel 95%), and maximum and average commuting distances (m). * too few contacts for distance or area calculations. ** MCP size did not reach an asymptote when plotted against number of locations.

| Code | Body mass | FAL | Tracking effort | | | Foraging area | Distance | | |
|------|-----------|-------|-----------------|-------|-----|---------------|----------|-------|--------|
| | | | Nights | Fixes | TTF | | Max | Mean | SD |
| 56 | 9.70 | 42.45 | 2 | 31 | 270 | 2.70 | 273.5 | 63.7 | 54.86 |
| 93 | – | 41.50 | 1 | 24 | 300 | 0.57 | 396.0 | 358.3 | 22.12 |
| 171 | 9.70 | 41.10 | 1 | 34 | 280 | 6.25 | 431.9 | 286.4 | 127.36 |
| 193 | 10.15 | 41.05 | 2 | 25 | 250 | 2.95 | 448.0 | 361.2 | 54.47 |
| 209 | 9.45 | 41.80 | 1 | 33 | 310 | 2.88 | 319.8 | 92.9 | 57.44 |
| 225 | 9.05 | 42.00 | 1 | 2* | – | – | – | – | – |
| 239 | 10.65 | 42.85 | 2 | 11 | 110 | 1.30** | 665.2 | 551.2 | 47.97 |
| 256 | 11.60 | 42.60 | 1 | 25 | 232 | 0.26 | 548.5 | 505.2 | 18.21 |
| 271 | – | 43.50 | 2 | 17 | 140 | 15.37** | 727.8 | 502.7 | 131.05 |
| 300 | 9.65 | 43.05 | 1 | 33 | 320 | 11.37 | 837.6 | 649.8 | 43.73 |
| 318 | 9.50 | 40.40 | 2 | 33 | 295 | 16.38 | 496.2 | 275.1 | 74.61 |
| 322 | – | 42.80 | 1 | 14 | 206 | 3.33** | 385.3 | 330.7 | 66.85 |
| 355 | 9.95 | 41.50 | 1 | 23 | 210 | 5.72** | 828.5 | 720.7 | 117.51 |
| 373 | – | 42.00 | 1 | 17 | 223 | 12.53 | 449.5 | 199.4 | 193.75 |
| 380 | 10.45 | 42.60 | 1 | 25 | 280 | 10.91 | 603.8 | 432.2 | 117.38 |
| 404 | 10.20 | 41.40 | 2 | 13 | 120 | 27.53 | 665.2 | 263.1 | 160.16 |
| 421 | 9.45 | 41.50 | 1 | 35 | 300 | 0.92 | 908.3 | 808.6 | 24.99 |
| 446 | – | – | 1 | 34 | 330 | 0.47 | 185.1 | 158.3 | 19.19 |
| 451 | – | 40.35 | 1 | 20 | 190 | 16.42 | 453.7 | 323.7 | 125.98 |
| 623 | – | 42.90 | 1 | 11 | 80 | 12.16** | 451.8 | 155.8 | 184.94 |
| 786 | 9.30 | 40.55 | 2 | 42 | 380 | 3.82 | 702.1 | 623.5 | 57.31 |

Table 3. Land cover type availability (%) within 1 km around each colony. SCIs: GA = Sierra de Gata (ES4320037), GR = Sierra de Gredos y Valle del Jerte (ES4320038), VI = Sierra de las Villuercas y Valle del Guadarranque (ES4320039). Categories: NON F = non forested [WATER (stationary water or rivers), SHRUB (Mediterranean shrubland), OTHER (other bare surfaces)]; EVG = evergreen broadleaved stands; CONIF = evergreen coniferous stands; DECID = deciduous broadleaved stands.

| SCI | COLONY | NON F | | | | | |
|-----|--------------|-------|-------|-------|-------|-------|-------|
| | | WATER | OTHER | SHRUB | DECID | EVG | CONIF |
| GA | HOYOS | 0 | 22.86 | 16.91 | 60.23 | 0 | 0 |
| GR | JARAIZ I | 0 | 21.41 | 22.41 | 56.18 | 0 | 0 |
| GR | JARAIZ II | 0 | 23.88 | 21.41 | 54.71 | 0 | 0 |
| GR | BOYAL I | 0.74 | 12.18 | 16.89 | 29.88 | 0 | 40.32 |
| GR | BOYAL II | 1.86 | 19.25 | 33.14 | 25.92 | 0 | 19.83 |
| GR | CHINATA | 0.75 | 49.66 | 3.90 | 45.69 | 0 | 0 |
| GR | GARGANTA | 0.07 | 27.90 | 22.02 | 50.00 | 0 | 0 |
| VI | CALABAZA I | 0 | 15.21 | 16.73 | 40.02 | 28.02 | 0.02 |
| VI | CALABAZA II | 0 | 14.05 | 21.46 | 40.70 | 22.80 | 1.00 |
| VI | CALABAZA III | 0 | 13.24 | 31.12 | 42.36 | 11.41 | 1.87 |
| VI | BERZOCANA I | 0.04 | 7.55 | 11.22 | 81.20 | 0 | 0 |
| VI | BERZOCANA II | 0.02 | 11.08 | 0.75 | 88.15 | 0 | 0 |
| VI | MAJADILLAS | 0.04 | 6.14 | 13.19 | 80.63 | 0 | 0 |
| VI | Total | 0.27 | 18.77 | 17.79 | 53.47 | 4.82 | 4.89 |

Accordingly, we observed a gradual decrease in preference from more densely covered forests ($G = 1073.48$, $df = 95$, $p < 0.001$) to lower cover classes, with the least covered areas being avoided (Table 5).

Discussion

In general, our results are consistent with previous observations of the species' behaviour. As in more northern conditions, the species preferred

Table 4. Land cover type use (%) by individuals. Abbreviations: see Table 3.

| Code | NON F | DECID | EVG | CONIF | Colony | SCI |
|------|-------|--------|-----|--------|--------------|-----|
| 56 | 0 | 100.00 | 0 | 0 | HOYOS | GA |
| 786 | 0 | 100.00 | 0 | 0 | HOYOS | |
| 93 | 0 | 100.00 | 0 | 0 | JARAIZ II | GR |
| 322 | 0 | 100.00 | 0 | 0 | JARAIZ II | |
| 355 | 0 | 56.52 | 0 | 43.48 | BOYAL I | |
| 421 | 0 | 100.00 | 0 | 0 | BOYAL I | |
| 256 | 0 | 0 | 0 | 100.00 | BOYAL II | |
| 446 | 0 | 100.00 | 0 | 0 | CHINATA | |
| 373 | 0 | 100.00 | 0 | 0 | GARGANTA | |
| 451 | 0 | 100.00 | 0 | 0 | GARGANTA | |
| 623 | 0 | 100.00 | 0 | 0 | GARGANTA | |
| 300 | 0 | 100.00 | 0 | 0 | CALABAZA I | VI |
| 171 | 0 | 100.00 | 0 | 0 | CALABAZA II | |
| 193 | 0 | 100.00 | 0 | 0 | CALABAZA II | |
| 209 | 0 | 100.00 | 0 | 0 | CALABAZA III | |
| 380 | 0 | 100.00 | 0 | 0 | BERZOCANA I | |
| 239 | 0 | 100.00 | 0 | 0 | BERZOCANA II | |
| 271 | 0 | 100.00 | 0 | 0 | BERZOCANA II | |
| 404 | 0 | 100.00 | 0 | 0 | BERZOCANA II | |
| 318 | 0 | 100.00 | 0 | 0 | MAJADILLAS | |

Table 5. Selection of land cover types and habitat features. Selection ratios and Bonferroni confidence intervals follow Manly *et al.* (1993). “>>>” denotes statistical significance of the difference among selection ratios ($p < 0.05$ /number of simultaneous comparisons).

| | π_i | Bonferroni confidence intervals | | | w_i |
|------------------------|---------|--|--------|-----------|--------|
| | | Lower | Upper | Selection | |
| Land cover type | | DECID > CONIF >>> EVG = NON F | | | |
| NON F | 0.3682 | 0.0000 | 0.0000 | – | 0.0000 |
| EVG | 0.0489 | 0.0000 | 0.0000 | – | 0.0000 |
| CONIF | 0.0482 | 1.0460 | 1.3227 | prefer | 1.1843 |
| DECID | 0.5347 | 1.5785 | 1.9663 | prefer | 1.7724 |
| Position (edge) | | Interior >>> isolated > edge >>> non f | | | |
| 0-non f | 0.2612 | 0.0024 | 0.0126 | avoid | 0.0075 |
| 3-edge | 0.2640 | 0.7245 | 1.0886 | – | 0.9066 |
| 2-isolated | 0.1668 | 1.1422 | 1.2692 | prefer | 1.2057 |
| 1-interior | 0.3080 | 1.6266 | 1.9425 | prefer | 1.7845 |
| Canopy cover | | 5 > 3 > 4 > 2 > 1 > 0 | | | |
| 0 | 0.3561 | 0.0003 | 0.0107 | avoid | 0.0055 |
| 1 | 0.0878 | 0.5649 | 0.7957 | avoid | 0.6803 |
| 2 | 0.1423 | 0.9629 | 1.1795 | – | 1.0712 |
| 4 | 0.1274 | 0.9923 | 1.3217 | – | 1.1570 |
| 3 | 0.1038 | 1.7989 | 2.1301 | prefer | 1.9645 |
| 5 | 0.1825 | 2.0965 | 2.6944 | prefer | 2.3955 |

closed areas in the interior of deciduous forests. Though most likely slightly underestimated, the flown distances to and sizes of foraging grounds (< 1 km and < 20 ha, respectively) resembled those reported in oceanic European forests (e.g. Schofield & Morris 2000, Kerth *et al.* 2001, Albrecht *et al.* 2002, Fitzsimons *et al.* 2002, Dietz & Pir 2009). Furthermore, colony sizes (6–37 individuals; Napal *et al.* 2009) are no smaller than reported for central European populations (15–40 bats; Kerth & König 1999). Assuming that the species reaches its ecological optimum in central Europe, where most of their colonies and larger populations have been reported to date, these similarities suggest that the study area is not marginal or suboptimal in terms of habitat quality for the species.

The particularities of Mediterranean landscapes — seasonal water shortage, hot summers, and an abundance of open evergreen tree assemblages — did not appear to promote a distinct pattern of habitat selection. The species seems to be affected in the sense that it is displaced or nearly restricted to deciduous areas, whose distribution in the area is limited. Yet, the above-mentioned conditions did not completely apply to our study area, characterized by a meso- to supramediterranean climate, which supports forests of deciduous species such as *Q. pyrenaica* and is somewhat more humid than standard termomediterranean, though subject to the same seasonality. Under seasonal water shortages and high temperatures, water could have been expected to act as a limiting factor. In fact, all the colonies were found within 1 km of a water source (Napal *et al.* 2009). However, water was scattered throughout the study area even in summer as small ponds and open tanks, thus minimizing the importance of water as a limiting resource.

In oceanic woodlands, *M. bechsteinii* forages within mature oak forests with closed canopy, high vertical structure of secondary trees, and unequal stratification (Meschede & Heller 2003, Kaňuch *et al.* 2008, Dietz & Pir 2009), and forages to a lesser extent in other deciduous trees, e.g., birch (*Betula pendula*) and beech (*Fagus sylvatica*) (Wolz 1986, Meschede & Heller 2003). Similarly, individuals in our study showed an indisputable preference for Pyrenean

oak woodlands, the main deciduous woodland type in the area, and the substitute for common oak in the Mediterranean climate. Our results confirm the perception of *M. bechsteinii* as a forest species (Kaňuch *et al.* 2008), as no foraging occurred in non-forested areas (but *see* Wolz 1988). Indeed, they preferred higher canopy cover classes, in agreement with their wing morphology and echolocation characteristics. Moreover, *M. bechsteinii* also avoided forest edges (Kaňuch *et al.* 2008), unlike many other forest bat species that successfully exploit such prey-rich ecotones for both commuting and foraging (Crampton & Barclay 1996).

Nevertheless, it is noteworthy that in our study, tracked bats used a wide range of wood structures, from loosely placed trees in meadows — dehesa — to closed stands with a dense understory. These facts contradict Albrecht *et al.* (2002), who claimed that structural richness rather than species composition determined habitat suitability for *M. bechsteinii*.

Due to their open physiognomy, dehesas might be considered a blend of forest and open habitat (Telleria 2001, Diaz *et al.* 2003), where prey availability may be high due to the concurrence of species belonging to both habitats. Dehesas are most commonly composed of holm or cork oak, both evergreen broadleaved species; dehesas of deciduous trees such as Pyrenean oak are much scarcer. Nevertheless, we must stress that all our data on *M. bechsteinii* foraging in open structures refer to deciduous dehesas, and no foraging occurred in evergreen broadleaved assemblages. On the other hand, coniferous forests were opportunistically used in the sole locality where they were available, in a particularly small stand where pines were interspersed with deciduous species and the understory was composed of abundant, lush ferns. These results suggest that even though the dominance of deciduous trees may play an important role, the species composition of woodland may not be a key factor determining habitat quality for *M. bechsteinii* — as Albrecht *et al.* (2002) pointed out — and that within limitations imposed by wing and call design (Neuweiler 1989), the distribution and abundance of catchable prey might have a strong influence on the particular habitats in which these bats forage (Brigham *et al.* 1992,

Saunders & Barclay 1992, Crampton & Barclay 1996, Zukal & Rehak 2006).

Low nitrogen and higher lignin content in both coniferous and broadleaved evergreen leaves (Brändle & Brandl 2006) are related to lower litter decomposition rates and fungal biomasses (Virzo de Santo *et al.* 2002, Hobbie *et al.* 2006) and contribute to higher soil acidity. In such acidic conditions, the activity and abundance of meso- and macrofauna are lower (Giller 1996, Geissen & Brümmer 1999). Consequently, we should expect poorer diversity and abundance of ground invertebrates upon which *M. bechsteinii* preys in coniferous or evergreen forests than in deciduous ones (Entwistle *et al.* 1996, Walsh & Harris 1996). However, the abundance of insects in woodlands is affected by other factors such as structural diversity and forest management (Tews *et al.* 2004, Veteli *et al.* 2006). Consequently, we cannot discard the fact that properly managed and well preserved coniferous assemblages with an abundance of decaying wood and rich understory, both ensuring prey abundance and hunting opportunities, may as well constitute suitable habitats for *M. bechsteinii*.

In the study area, *M. bechsteinii* seemed to depend on humid mesomediterranean deciduous oak woodlands, fairly irrespective of their structure, and this is most likely related to both foraging and roosting opportunities (Napal *et al.* 2009). The observed foraging and commuting within forest, avoiding edges and open areas, implies the need for a minimum area of continuous woodland. However, representation of deciduous forests in the Mediterranean range is constrained by a number of ecological — climatic, edaphic, and topographic — and historical variables. Throughout the Pleistocene, forests concentrated in the mild Mediterranean, but as global warming progressed, they shifted northward, producing the drawback of optimum forests to central Europe (Telleria 2001). In the Iberian Peninsula, climatic changes are coupled with strong human pressure (Baquero & Telleria 2001, Telleria 2001). The dehesa, the dominant landscape in the southwestern Iberian Peninsula, results from clearing of former forests, and subsequent grazing and plowing to maintain extensive grass cover (Telleria 2001). Long-last-

ing man-made deforestation aided the transition from deciduous to sclerophyllous species and imbalanced water relations (Blondel 2006), and at present dehesas are mainly dominated by scattered evergreen oak species (Joffre *et al.* 1999, Pereira & Pires da Fonseca 2003), which appear to be a non-suitable habitat type for both *M. bechsteinii* and other forest bats (Schreur 2007). Moreover, progressive abandonment of traditional agriculture and husbandry is leading to the invasion of previous dehesas by shrubs (Diaz *et al.* 2003) and their conversion into extensive plantations, mostly monospecific. Consequences are the further reduction, fragmentation, and isolation of optimal habitats, together with the loss of spatial diversity and prey availability (De Paz 2006). Metapopulation extinction probabilities increase in broad, short, low aspect ratio winged bats, such as *Myotis bechsteinii* (Siemers & Swift 2006), because increased commuting costs, resulting in smaller foraging areas and low intercolony exchange, are likely to hinder recolonization of empty or vacated patches (Jones *et al.* 2003, Safi & Kerth 2004).

The relatively high number of captures and small core areas suggest that *M. bechsteinii* could be more abundant in the Mediterranean than previously thought (Baagøe 2001), albeit dependent on deciduous forests — particularly oak — and thus limited by their restricted and decreasing distribution. Given the bat's relative flexibility and unexpected local abundance, we suspect the species' rarefaction in the Mediterranean range is directly related to severe deforestation due to secular agricultural practices, which are decimating potential optimal habitats in the range. Preservation of extant patches of deciduous forests interspersed within the matrix of dehesas should be given high conservation priority.

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