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Geoffroy's bat, *Myotis emarginatus*, preys preferentially on spiders in multistratified dense habitats: a study of foraging bats in the Mediterranean

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Abstract. In a Geoffroy's bat *Myotis emarginatus* colony in central Iberia, we investigated the foraging behaviour of six lactating females by means of radio-tracking and the diet of 23 individuals by faecal analysis. The bats preferred to forage mainly in pine plantations, riparian woodland, and scrubland, whereas native dehesa (a loose semi-natural oak *Quercus rotundifolia* and *Q. suber* woodland) was not exploited as expected. By far the most important prey type for this bat in the Mediterranean were spiders. We conclude that Geoffroy's bat prefers to forage in multistratified dense habitats, even if these include nonnative plantations. The vertical structuring and especially high cover, along with the combination of both parameters are important for this highly manoeuvrable, clutter-tolerant bat. This is valid even when the vertical component is much reduced as occurs in scrubland, in the first succession steps to woodland creation, and in degraded conditions. Under such circumstances, aerial weaving spiders might be detected and captured when lying in their webs. It is likely that dehesa is too loosely wooded to offer suitable characteristics for orb-weaving aerial spiders to build webs, and thus it may not be as attractive for *M. emarginatus* as more dense habitats.

Key words: Iberia, Chiroptera, foraging, dehesa, Araneae

Introduction

Geoffroy's bat *Myotis emarginatus*, which suffered a significant population decline between the 1960s and 1990s, has recently made an important recovery, populating new areas and forming stable populations, so it is now classified as Least Concern at a European scale (Hutson et al. 2008, Temple & Terry 2009). In Iberia the species is found throughout the peninsula, inhabiting mountainous areas and/or woody landscapes ranging over both the Mediterranean and Atlantic regions. Its status there, however, is irregular and affected by local factors, mostly the loss of roosts (mainly buildings), so overall *M. emarginatus* is considered vulnerable (Quetglas 2007).

Previous studies in non-Mediterranean areas have demonstrated that foraging *M. emarginatus* used predominantly mixed and deciduous native woodland and avoided coniferous plantations (Krull et al. 1991, Brinkmann et al. 2001, Huet et al. 2002, Demel et al. 2004, Zahn et al. 2010). However, in the single study carried out in the Mediterranean region so far, this species was found to select pine forests and planted olive groves (Flaquer et al. 2008). Indeed, regional but also local landscape composition and availability certainly affect a species' habitat use (Goiti et al. 2003). Among the environmental changes witnessed by the Mediterranean area, deforestation can be regarded as one of the most profound consequences. As a result a lack of native wood cover can be observed over vast areas. Nonetheless, a unique habitat type typical of the Iberian Peninsula has survived to the continuous and ongoing transformations, the *dehesa* (known in

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Portugal under the term *montado*). Dehesa is a semi-natural ecosystem resulting from a traditional sylvo-pastoral system and derived from the clearance of Mediterranean woodland. It is described as a loose oak woodland, mainly *Quercus ilex rotundifolia*, but also *Q. suber* and to a lesser extent *Q. pyrenaica*, interspersed with pastureland, and is sometimes referred to as the European savannah (Olea & San Miguel-Ayanz 2006). However, even if dehesa has been identified as a key habitat to the conservation of biodiversity in the Mediterranean (EU Habitats Directive, Natura 2000 sites, Diaz et al. 2003), its relative importance to woodland species is unknown or has been little studied. Close and dim environments, where microclimatic conditions mitigate humidity loss, high temperatures, and direct solar rays, are scarce in the Mediterranean, but could be crucial for a vast number of species. More recently, those characteristics found in the former Mediterranean woodland can nowadays be found in the exotic plantations, which especially consist of coniferous and lately eucalyptus tree species. The role of these new woodlands in areas poor in shade habitats may have been underestimated, as their importance seems to be more than marginal during certain periods or in particular situations (Russo et al. 2005). We tried to identify the degree of importance of these new habitats and thus worked in an area where both the native open dehesa and the dense exotic plantations occurred plenty.

Foraging behaviour in bats is affected not only by structural factors answering to ecomorphological constraints (Fenton 1990, Kalko & Schnitzler 1999) but also by availability of profitable prey (De Jong & Ahlén 1991, Goiti et al. 2006). To date no study about the diet of *M. emarginatus* has been carried out in the Mediterranean, so shedding light on this subject will help reach sound conclusions about the species' ecological requirements (Akasaka et al. 2009).

Consequently, we studied simultaneously habitat use and diet in a colony of *M. emarginatus* inhabiting an area with a high diversity of available habitat types, including mainly dehesa, plantations, and open spaces. Our results will help assess the extent to which the observed differences in this species' habitat use correspond to differences in habitat availability between contrasting landscapes, or whether they instead reflect a lack of selectivity for precise habitat types, with foraging habitats being locally chosen as a possible consequence of dietary preferences.

Material and Methods

The study took place in the southeastern part of the province of Cáceres (central Spain). The landscape is hilly with an elevation range of 565–1600 m a.s.l. The climate is typical Mediterranean with a mean annual temperature of 16ºC (lowest mean 8ºC, highest mean 26ºC), and annual rainfall is around 700 mm with a marked summer drought. Vegetation is rather diverse: almost half of the area is open land consisting of pastureland (23% of the total study area) and scrubland (20%), and the remainder is covered by a variety of woody habitats, such as dehesas (24%) dominated by holm oak (*Quercus rotundifolia*); pine plantations (*Pinus pinaster,* 15%); *Eucalyptus* spp. plantations (5%); olive groves (*Olea europaea,* 7%); Pyrenean oak woodland (*Q. pyrenaica,* 3.5%); sweet chestnut woodland (*Castanea sativa,* 2%); and riparian woodland (0.5%). Farther to the southern lowland, cultivated rice paddies and irrigated cornfields dominate. Two years prior to our research, some parts of the area suffered from a wildfire that affected mainly coniferous plantations and scrubland, which were thereafter covered by pasture and shrubs.

The study colony of breeding *M. emarginatus* was located in an abandoned, unfinished railway tunnel and numbered c. 100 bats, sharing the tunnel with breeding colonies of *Rhinolophus mehelyi* and *R. euryale*. Captures were performed on June 21, 2007, under license issued by the Junta de Extremadura. We captured 23 bats using a harp-trap set in the entrance of the tunnel at dawn, when bats returned after foraging. Bats were kept in nylon bags for 1-2 hours. After trimming off the hair between the scapulae, we attached a radio-transmitter (0.35 g, PIP II, Biotrack Ltd., Dorset, UK) using surgical adhesive (Skinbond®, Smith and Nephew, Largo, Florida, USA). After handling the bats, we returned them into the tunnel and gathered the droppings (1-10 per bat) of all captured bats. Pellets were preserved in individual microcentrifuge tubes and later air-dried. Analysis was done in the laboratory using magnifying lens (x40) after moistening the pellets with a drop of water and aided by dissecting needles. Prey remains were identified mainly to order level using Chinery (1977), Barrientos (1988), and McAney et al. (1991). We used the individual bat as the sampling unit (Whitaker et al. 1996). The analysis of diet encompassed 85 faeces corresponding to the 12 radio-tagged females plus 11 other lactating females.

Bats were radio-tracked preferably from dusk to dawn, by means of the 'homing-in' method (White & Garrot 1990). Simultaneous trackers (5-7 at a time) used radio-receiver models TRX1000S (Wildlife Materials Inc., Carbondale, Illinois, USA) and Yaesu FT-290RII (Andreas Wagener Telemetrielangen, Köln,

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Germany) and 3-element Yagi antennas. Locations were noted every 10 minutes, a time interval enough to allow bats fly on average half of their individual foraging ranges. We addressed whether bats were foraging or resting and used only the active locations for subsequent analyses. Foraging locations were recorded in the field on ortophotographs of the area and were later transferred to a Geographic Information System (Arcview 3.2, ESRI, Redlands, California) for measuring spatial parameters (Minimum Convex Polygons -MCP-, flown distances) and habitat use analyses (using land-use maps). The location of the roost was not used in the calculation of foraging areas (individual MCPs). Bats are highly selective in their roost choice, so suitable roosts might not be within or even close to a landscape offering good foraging opportunities, and bats may break off their foraging bouts for night roosting (Goiti et al. 2006). Hence, we chose not to include the roost location and the inactive locations in analysis, as they might bias conclusions about bats' foraging behaviour. Habitat selection was determined by following Neu et al.'s (1974) method (consisting of a Chi square analysis and Bonferroni's confidence intervals). We compared the used habitats to the habitats' availability around the roost in a circular area determined by a radius extending to the farthest recorded location. We also compared the habitat composition within the area limited by this radius with the composition in the global MCP (that formed by summing up all the individual MCPs) in order to address any effect of the local differences in the distribution of habitats.

Results

We radio-tagged 12 females – one nonreproductive and 11 lactating – and ultimately tracked seven of them satisfactorily. Subsequent recapture of two of the 'lost' bats showed that one had cut off two-thirds of the antenna and the other had discarded it completely. In a third occasion, the signal of a bat previously not contacted was detected at the roost entrance during an emergence event but immediately lost, suggesting a short-range signal presumably due again to partial removal of the antenna. These findings revealed that at least three of the five lost bats were still alive and had experienced no adverse effects following capture and tagging.

Overall we obtained 111 locations of active foraging for six bats, with a range of 10–26 locations per bat (Table 1). For another female we only obtained five consecutive bearings in two locations before the signal was lost, so these data were excluded from analysis. Radio-tracking was extremely difficult due to rapid location shifts and a foraging style characterised by fast and continuous flight, showing a rather low permanence at single foraging sites. However, for most of the times when it was not possible to obtain the exact locations of foraging bats, we were in radio-tracking contact but could not arrive in time to assign a location to a proper habitat, due to the bats' sudden and rapid shifts. Although the presented numbers of locations per bat are rather low, we are confident that they are a good representation of their foraging areas. Distances flown by bats to foraging areas averaged 5 km overall and the farthest individual location was found at nearly 10 km (Table 1). Foraging areas (MCPs) exceeded 100 ha for all the bats, with a range of 120–371 ha. The overall MCP covered 50 km² and extended south to the roost.

Although the use of habitats differed between individuals (Table 2), the bats foraged mainly in two habitats: scrubland and pine plantations. Scrubland was used by all the bats and on average accounted for 35% of mean individual foraging time. Pine plantations averaged 34% of all the individual foraging locations and were used by five of the six bats. Isolated trees (oak, pine, or eucalyptus) summed on average 11%, riparian woods 7%, oak dehesas 6%, and eucalyptus plantations 5%. According to the availability of habitats present within the area encircled by a 10-km radius, bats exploited the resources nonrandomly (chi square = 5774, $P < 0.001$; Table 2), positively selecting pine

Table 1. *Radio-tracking data of six lactating* M. emarginatus *females in Cáceres (Extremadura, Spain).*

Bat code	Total locations	Active foraging locations	MCP 100% (ha)	Maximum flown straight-line distance (km)	Mean flown distance (km)
015	16	10	185	4.6	4.0
242	22	22	220	8.6	6.2
323	31	26	164	6.4	4.6
426	14	14	228	6.1	3.5
521	13	13	120	5.1	4.5
767	26	26	371	9.8	7.0
Total	127	111			

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Table 2. *Habitat use (number of locations) by six lactating* M. emarginatus females *in Cáceres (Extremadura, Spain).*

Bat code	Dehesa	Eucalyptus	Isolated trees	Pine	Riparian	Scrubland	Total
015	1	4	2		1	2	10
242		1	2	14		5	22
323	7		7	5	6	1	26
426				1		13	14
521				11		2	13
767		1	2	8	1	14	26
Total	8	6	13	39	8	37	111
Mean % use	6	8	11	34	6	35	
St dev	10.9	15.8	10.9	33.3	9.2	33.0	

Table 3. *Comparison between available habitats at the foraging MCP (100%) of six lactating female* M. emarginatus *and the area within a 10-km radius around their roost in Cáceres (Extremadura, Spain).*

Habitat	Foraging MCP	10-km radius
Pastureland, crops	24.4	22.6
Scrubland	37.4	20.0
Pine	25.9	14.7
Dehesa	3.0	23.7
Eucalyptus	9.0	5.3
Olive	0.0	7.0
Pyrenean oak	0.2	4.1
Sweet chestnut	0.0	2.3
Riparian	< 0.1	0.4

plantations and riparian woods, whereas scrubland and eucalyptus plantations were opportunistically exploited. Dehesa was not used as expected, even if all the foraging locations corresponding to isolated trees were included within this category for the analysis (owing to the structural similarity of both habitats).

This skewed habitat use was more evident when comparing the relative abundances of habitats within the global MCP to those within the 10-km radius (chi square = 2902, $P < 0.001$). Within the MCP, the main habitats were open, including natural pastures, crops (wheat and vineyards), and scrubland, followed by pine forests (Table 3). Within the 10-km radius, open habitats comprised half of the area as well; dehesas of holm, cork, and Pyrenean oak were 24%, whereas the area of pine plantations decreased. Additionally, this circle included three new habitat types that had not been used by the bats: olive groves, Pyrenean oak woods, and sweet chestnut woods.

In recognition of the varied structure of the foraging habitats, we lumped together those sharing similar characteristics into three categories: close woodland, loose woodland, and scrubland. *M. emarginatus* exploited all of them. A mean of 48% of the individual foraging locations corresponded to close woodland and 17% to loose woodland, indicating the importance of tree cover. However, more than one-third (35%) of the foraging occurred in scrubland, where the tallest vegetation was shrublike regardless of species (for example, thicket oak and pine plantations were also included in this category), thus representing a landscape with a simple vertical structuring that could be described as open.

Interestingly, and independently of either the vegetation type or structure, a mean of 30% of the individual foraging locations occurred in or nearby a creek or a draw, the latter being a watercourse of varied size that fills with water temporarily after rains and is typical of the Mediterranean climate. In the study area, creeks and draws were generally rather narrow, and their vegetation consisted of scrub. This means that a third of the foraging occurred near these water bodies regardless of the main habitat type; e.g., pine plantations may occupy such creeks, and thus bats foraged in the plantation but coinciding with the creek. The elongated shape of individual MCPs depicted the relative importance of these water bodies and most foraging areas matched with them. Only one of the bats foraged rather far from a creek, in a plateau area covered by pine plantations with no such natural drainage elements.

Spiders constituted the bulk of the diet by both volume and frequency. Overall the mean of individual percentages reached 79% (SD = 22.5) by volume for spiders, and the median was 88%. All 23 bats ate spiders, and this prey type appeared in 95% of the faeces. Following far behind in importance were moths, with a mean consumption of 7% of the diet by volume; dipterans (flies and midges) constituted 6.3%; and lacewings (especially the family Hemerobiidae) averaged 4.4%. Four other arthropod categories were found, none reaching a mean of 2%: earwigs, harvestmen, wasps, and beetles.

Finally, although the use of (ground) gleaning cannot be completely ruled out, most of the time the bats

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seemed to use a hawking style, indicated by the quick shifts of the signal.

Discussion

According to our results, pine plantations were the most preferred habitat for *Myotis emarginatus* in central Iberia. This wood type has been disfavoured by this bat in central Europe in favour of native deciduous or mixed woodland (Krull et al. 1991, Huet et al. 2002, Demel et al. 2004, Zahn et al. 2010). However, a notable use of conifers has previously been mentioned for a breeding colony in the Mediterranean (Catalonia, northeastern Iberia), which foraged in Aleppo pine forests (*Pinus halepensis*) (Flaquer et al. 2008) as well as olive groves and, to a lesser extent, deciduous woodland. Aleppo pine is native to the Mediterranean, overlapping with the bat's range (Hutson et al. 2008), and thus it is not surprising for pine forests and plantations to be an important resource for *M. emarginatus* in Catalonia. However, in our study area, pine forests are not native and correspond to plantations during recent decades.

It is noteworthy that dehesa, a typical Mediterranean wooded habitat known to be a 'hot spot' for local fauna (Diaz et al. 2003), was not used as expected from its availability, and was in fact so unused that it was categorised as rejected. The use of scrubland, however, was remarkably high; on average, a third of the individual foraging occurred within this habitat devoid of grown trees, though bats foraged there opportunistically. In contrast, Flaquer et al. (2008) found that the Iberian colony they studied did not use scrubland at all. Furthermore, the bats in our study also made considerable use of isolated trees or small copses (3-4 trees) in open landscape (fields and scrubland) – again, an extremely exposed foraging ground.

The presumed preference of *M. emarginatus* for close wooded habitats (Krull et al. 1991, Demel et al. 2004, Zukal & Řehák 2006, Flaquer et al. 2008) appears challenged by the large variety of vegetation structures exploited by this bat species in our study, and especially by the extensive utilisation of scrubland. In conjunction, these bats seemed to find mostly spiders in their hunting grounds. Although we failed to identify the spider remains (no palps were found in faeces), Bauerová (1986) and Steck & Brinkmann (2006) mentioned that orb-weaving spiders appeared in the diet of Geoffroy's bat. Aerial orb-weavers build webs between vegetation gaps, and thus they may be easily detected and intercepted by a highly manoeuvrable bat species, which fits with our observation of *M. emarginatus* foraging in a hawking style. In this regard, it has been demonstrated that higher vertical vegetation structuring increases the substrates where spiders can build webs (Baldissera et al. 2004), a factor crucial for the establishment of a rich spider community.

Dehesa's traditional use has created a landscape with tree crowns arranged at a mean distance more than 10 m apart to avoid the creation of a dim environment and thus allow the pasture to grow (for details, see Olea & Viguera 1998 and Olea & San Miguel-Ayanz 2006). Dehesa bears two vertical layers, the tree canopy and the ground-level herbaceous layers, with no connection between them but the tree trunk. In this situation, tree branches are possibly too distant from each other and the ground to create a suitable substrate for web-weaving.

These factors may also explain the observed preference of Geoffroy's bats for scrubland, where the shrub layer is usually not homogeneous and the plants often form dense patches. Zukal & Řehák (2006) also recorded *M. emarginatus* foraging in woodland edges densely covered with shrubs.

The bats' rejection of the deciduous native woodlands of Pyrenean oak and sweet chestnut could simply be due to their relatively low availability. Olive plantations, an important habitat for the Catalonian population of Geoffroy's bat (Flaquer et al. 2008), were not used by the bats in our study area in Cáceres. The possible cause could be the use of biocides, as the olive groves in our area were intensively managed, arranged in large patches, and subjected to regular chemical treatment, contrary to the olive groves in the area studied by Flaquer et al. (2008), which were in the process of being abandoned. Again, local characteristics seem to modify the behaviour of a species beyond any theoretical assumption.

From a conservation perspective, another important conclusion can be drawn from the observed trend to forage near or along creeks and draws, regardless of whether trees or shrubs formed the vegetation. Riparian habitats are known to be key foraging sites not only for bats (Russo & Jones 2003, Rainho 2007) but also for spiders (Laeser et al. 2005), the main prey of *M. emarginatus*. Even if many of the draws had dried up for the study period, they may have served as a refuge for invertebrates during the dry Mediterranean summer, constituting a perfect foraging ground for *M. emarginatus* in search of spiders. Therefore, even the smallest of rivers, creeks, or draws may be an important orographical element for preservation.

M. emarginatus shows an unusual dependence on spiders, according to our results in the Mediterranean (present study) and others from Europe (Bauerová 1986). Among the handful of studies on the diet of this

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species, two publications reported flies to be the main prey but noted that spiders were the greatest complementary item (Beck 1995, Steck & Brinkmann 2006). These fly-rich diets were though linked to a particular foraging ground of cattle sheds, and to a foraging style of gleaning flies off the walls or other surfaces (Krull et al. 1991, Brinkmann et al. 2001). These would appear to be cases of opportunistic behaviour. In our study area, animal husbandry is an activity of low importance or held extensively, and the only relatively abundant large dung-producers are wild red deer and wild boar. Therefore, a diet based on spiders may be closer to the bat's original, natural situation. This conclusion is supported by Bauerová (1986), who found spiders to account for 70% of the diet by volume. Another study (U. Goiti, unpublished data) found that spiders were significantly important (45% by volume, with the other 55% being flies) in the diet of eight *M. emarginatus* in an Atlantic climatic region in northern Iberia, where cattle and sheds were abundant (c. 80 cattle/km^2 and 45 sheep/km^2) – a case falling between the spider-dominant and fly-dominant diets.

None of the other European bat species has been reported to depend on this prey type to such a degree (Beck 1995). Geoffroy's bat's congener *M. nattereri* has been found to eat spiders but with a greater dependence on flies, possibly in accordance with its superior gleaning ability compared to *M. emarginatus* (Swift & Racey 2002, Siemers & Schnitzler 2004). However, extraordinary local food supply conditions, such as a superabundance of flies where livestock is kept, may lead *M. emarginatus* to change its otherwise favourite prey, spiders, to a more easily capturable one. In conclusion, we consider that *M. emarginatus* prefers well-developed, multistratified, close habitats, but that it can also cope with situations of reduced vertical vegetation structuring. This flexible behaviour suggests that the species is a generalist. Therefore, actions aimed at increasing biodiversity and the conservation of this bat species in the Mediterranean should focus on the creation and maintenance of close, dim habitats as a primary goal, also allowing the growth of vegetation along permanent or temporal watercourses. This action would undoubtedly benefit other bat species as well. Dehesa, a habitat recognised as having primary importance in the conservation of Mediterranean fauna, has shown low importance to *M. emarginatus* at least from a structural viewpoint, though not from a biological one. This landscape covers vast areas in central Iberia, which implies that a structural homogeneity occurs over hundreds of square kilometres. The understorey in dehesa is usually cut off, and sometimes even ploughing is used to maintain its typical structure and objectives. Again, patches without any such management should be encouraged within dehesas – but always keeping the patches sufficiently far apart to prevent the creation of fire corridors, one of the most dangerous environmental threats in this part of Europe.

Finally, the foraging distances found in the present study are in accordance with others observed elsewhere to date (Krull et al. 1991, Brinkmann et al. 2001, Huet et al. 2002, Demel et al. 2004, Flaquer et al. 2008), showing that *M. emarginatus* is fully capable of flying each night to sites at a straight-line distance of around 10 km, though most efforts should be directed toward the preservation of quality habitats within the first half of that range.

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