

Giant noctule bats face conflicting constraints between roosting and foraging in a fragmented and heterogeneous landscape

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Abstract

The tree-dwelling giant noctule *Nyctalus lasiopterus*, a partially carnivorous aerial-hawking bat, is one of the least known European bats, and more information is needed to evaluate its conservation status. Using radiotracking, we obtained the first data on spatial requirements and habitat preferences for the species in an area critically affected by deforestation. Two breeding populations separated by 60 km, one roosting in a city and the other in a nature reserve encircling a vast coastal marshland, showed marked differences in the size of their home ranges, but both used selectively the marshlands for foraging. Urban bats remained in the city for foraging during pregnancy in spring, but increased largely their home ranges towards the marshland during lactation in early summer. The nature reserve, with few roosting opportunities, was only a marginal roosting site for a population which switched between roosts located up to 90 km apart. Giant noctules had to travel long distances (up to 130 km recorded) to meet both foraging and roosting requirements within the fragmented landscape, exhibiting among the largest home ranges ever reported in Microchiroptera. To promote the protection of this threatened species, a network of artificial roosting options should be provided in good foraging habitats until long-term forest restoration is achieved.

Introduction

Landscape fragmentation, forest clearance and urbanization are important threats to wildlife as they eliminate or reduce suitable foraging or roosting habitats (e.g. Riley *et al.*, 2003; Scott *et al.*, 2006). Understanding the effect of landscape modification on wildlife is a major issue in conservation biology. However, it requires previous knowledge of habitat use by species and how it varies with landscape structure, information that is often missing.

The giant noctule *Nyctalus lasiopterus* is included in the IUCN Red List of Threatened Species as 'data deficient' (IUCN, 2006), and is classified as 'vulnerable' in Spain (Ministerio de Medio Ambiente, 2006). It is a large obligate tree-dwelling species that forms fission–fusion societies spread across multiple trees (Popa-Lisseanu *et al.*, 2008). The only Western-European breeding populations of *N. lasiopterus* occur in the southern half of the Iberian Peninsula (Ibáñez, Guillén & Bogdanowicz, 2004), which is one of the most prominent examples of human-induced, large-scale forest destruction in the world (Arribas *et al.*, 2003).

In south-western Spain, intense deforestation across a vast area confines this large tree-dwelling species to urban gardens. Preliminary radiotracking studies conducted in

1992 and 2000 showed that some giant noctules that roosted in urban gardens traveled at least 25 km from their roosts to forage over a vast coastal marshland belonging to the Doñana complex (C. Ibáñez, unpubl. data). Doñana is one of the most important and largest remaining wetlands in Europe (RAMSAR site information service, <http://www.wetlands.org/RSDB>). It is especially known as a stop-over site for migratory birds, including waders, waterfowl and songbirds, the latter constituting large part of the diet of giant noctules during spring and autumn migration (Popa-Lisseanu *et al.*, 2007). Most giant noctules found in the Iberian Peninsula during the early 20th century were dead or exhausted individuals found on the ground in Doñana (Ibáñez *et al.*, 1995). Available evidence suggested that Doñana could be a crucial foraging habitat for giant noctules in south-western Spain, but where suitable roost sites could not be found.

The occupation of a bat box by a roosting group of giant noctules in the Doñana National Park provided the opportunity to compare the behavior and land use patterns of two populations of this rare species roosting in two extremely different environments, a park of a populated city and a protected environment in the borders of a marshland. Using radiotelemetry, we collected the first data on spatial

requirements and habitat preferences for this species. We investigated the following questions: (1) Is the marshland area of Doñana an important foraging area for giant noctules in southwestern Spain, including those belonging to a distant urban population?; (2) are there differences in space use between the urban population and the one roosting in the protected area?; (3) does season or reproductive period influence space use?; (4) what foraging habitats are preferred?

Materials and methods

Study area

We conducted field work in the provinces of Seville, Huelva and Cádiz, in south-western Spain (Fig. 1). The area has a typical Mediterranean climate, with long dry, hot summers. Most of the land in the Guadalquivir basin is used for extensive agriculture, with few fragmented natural vegetation patches which are mostly shrubby. The Guadalquivir River crosses the city of Seville and the vast coastal marshland complex of Doñana before flowing into the Atlantic. The marshland area lacks forested vegetation and adjacent landscapes have been intensively deforested during centuries of human settlement. Riparian vegetation around the river and in the floodplain is highly modified, and no mature gallery forests exist today.

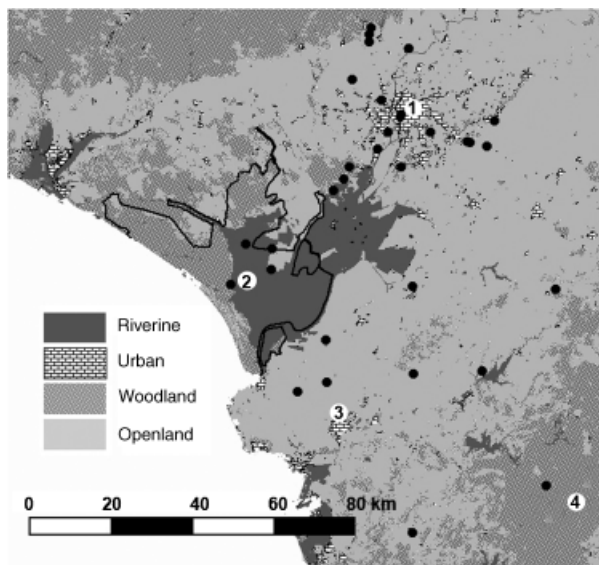


Figure 1 Map of the study area showing the two giant noctule *Nyctalus lasiopterus* populations studied (1: María Luisa park in Seville; 2: bat box in the Doñana National Park, Huelva) and two other giant noctule roosting sites in Southern Spain, (3: Zoological Gardens in Jerez de la Frontera, Cádiz; 4: Alcornocales Nature Park, Cádiz, with suspected roosts), the radiotracking stations (circles) from which bearings were taken and the limits of the Doñana National Park and protected surroundings (black outline). The vast wooded region to the North is part of the Sierra Morena Mountain Range. The study area is limited by the Atlantic Sea in the south-west.

Capture and radiotracking

Bats captured at maternity roosts in the María Luisa Park in Seville (hereafter Seville or urban population) were radiotracked in summer 2003, autumn–winter 2003 and spring 2004. Bats from Doñana National Park (NP) were radiotracked only in summer 2003 (Table 1). Bats were captured with mist-nets as they emerged from their roosts at dusk. Each bat was equipped with a teflon-collared radiotransmitter (Pip Ag392, Biotrack, Dorset, UK) designed to wear off after 1–6 months. Each bat was classified based on age, sex and reproductive status. Lactating females could be identified by the hairless skin around enlarged nipples, and juveniles by the cartilaginous plates in the metacarpal–phalangeal joints (Anthony, 1988). The transmitter was also attached to the back of the neck with surgical cement (Skin-Bond, Smith and Nephew United, Largo, FL, USA), after clipping the fur in this area to prevent the transmitter from rotating around the neck. Total mass of the transmitter, including collar and glue was ~1.85 g, representing <5% of body mass (Aldridge & Brigham, 1988). All radiotracked bats were adult females, as adult males are rarely present in maternity colonies. Capture and marking of the bats were approved by the Environmental Council of the Junta de Andalucía.

Table 1 Female giant noctules *Nyctalus lasiopterus* radiotagged from two study areas, showing the period from date of tagging to date of last observation and number of locations obtained for each bat

Population	Bat ID	Date of tagging	Last observation	Number of locations	
Doñana NP	705	11/06/2003	05/08/2003	27	
	709	11/06/2003	01/07/2003	4	
	707	11/06/2003	19/06/2003	9	
	710	11/06/2003	22/07/2003	7	
	726	1/07/2003	15/07/2003	2 ^a	
	Seville	739	3/07/2003	24/07/2003	31
		740	3/07/2003	25/07/2003	37
742		3/07/2003	12/07/2003	7	
785		21/10/2003	04/11/2003	26	
792		21/10/2003	30/10/2003	7	
793		21/10/2003	04/11/2003	21	
782		21/04/2004	23/06/2004	66	
783		21/04/2004	23/06/2004	58	
795		20/04/2004	13/05/2004	8	
796		20/04/2004	23/06/2004	94	
797		20/04/2004	23/06/2004	112	
798		20/04/2004	27/05/2004	41	
799		21/04/2004	12/05/2004	7	
800		21/04/2004	04/05/2004	15	
801	21/04/2004	13/05/2004	16		
802	23/04/2004	23/06/2004	100		
803	23/04/2004	27/05/2004	70		
804	23/04/2004	10/06/2004	59		
805	23/04/2004	23/06/2004	83		
807	23/04/2004	29/04/2004	9		

^aRoosting locations.

Bats were radiotracked during their nocturnal foraging activity from a total of 30 fixed stations situated on vantage points in the periphery of Seville, Doñana and Jerez (Fig. 1) with handheld telemetry receivers (FT-250 RII, Yaesu Musen Co. Ltd, Sapporo, Japan; Falcon V, Wildlife Materials International Inc., IL, USA) and three-element Yagi antennae (AF Antronics Inc., IL, USA). Bearings were taken each night simultaneously from two or three stations that were selected depending on the initial flight direction of the bats to maximize radiotracking success. Bearings were recorded at 10-min intervals to avoid time-dependent auto-correlation. The position of one of the (2–4) observers was always fixed, 200 m away from the roosting site in Doñana in a 30 m high tower, to detect tagged bats returning to the roosting box. Detection range was very variable (from a few kilometers up to 60 km) and probably depended on terrain and flying heights of the bats.

Analysis of home ranges

Locations of the bats were estimated through cross-triangulation between two or three positions using the software Locate II v1.82 (Nams, Truro, Canada) and entered into ArcView v3.2 (Environmental Systems Research Institute Inc., 1999). When the error was larger than 6 km (8% of all locations), these data were removed from every analysis. To compare home ranges, a minimum convex polygon (MCP) with all remaining locations was created for each population (urban and NP) per tracking period, using the Animal Movement extension for ArcView (Hooge & Eichenlaub, 1997), which was also used for computing the relationship between the number of locations and home range area by bootstrapping. Single locations were buffered by a distance of 2.5 km to account for mean location error and MCPs were calculated to encompass these buffers.

To test for seasonal differences in the size of home ranges, we conducted a paired *t*-test for those individuals tracked along a 2-month period in 2004. Non-significant deviation from normality was evaluated through Kolmogorov–Smirnov. Two seasons were distinguished: from late April until May 31 (spring) and from June 1 until the signal was lost (early summer, Table II.1), coinciding with the pregnancy and lactation periods, respectively (Popa-Lisseanu *et al.*, 2008). Home ranges were represented by the 95% kernel use distribution (Worton, 1989) of the locations. The same smoothing parameter ($h = 2.5$ km) was used for all bats to allow for comparisons (Bontadina & Naef-Daenzer, 1996).

Habitat selection analysis

Habitat categories were inferred from the digital land-use map of the Andalusian System for Environmental Information (Moreira & Fernández-Palacios, 1995). We grouped the 112 land use categories into four major habitat types: open land (agricultural and farmland, pastures and cleared areas); urban areas; woodland (including Mediterranean shrubs and other types of natural non-arboreal but ligneous vegeta-

tion); and riverine areas (water courses, canals, natural marshland and modified marshland for rice fields).

For habitat selection analysis, roosting locations were not included. As we could not distinguish between foraging and commuting flight, we will use the term ‘activity ranges’ instead of ‘foraging ranges.’ Locations were assigned in the field to one of three accuracy classes (high, medium and low) depending on confidence in the estimated location (see Bontadina, Naef-Daenzer & Schofield, 2002). The true accuracy was then determined from the 95% confidence area of each location, when the triangulation was performed from three fixed stations and the bearing error could be estimated; for locations obtained from two bearings, an averaged overall bearing error was applied (Locate II User’s Guide, Nams, Truro, Canada), obtained from the three-bearing triangulations when two of the telemetry stations were the same. This method was used to minimize differences in bearing error due to topography. The calculations resulted in a mean location error of 2, 4 and 6 km for the three accuracy classes high, medium and low, respectively. Radiotracking locations were buffered by circles with radii of 2, 4 and 6 km depending on their assigned accuracy class to account for location error (Bontadina & Naef-Daenzer, 1996). The MCP for each bat encompassed all the buffered locations.

Habitat selection was investigated to reflect the animals’ choices at two different levels (Johnson, 1980; Porter & Church, 1987). On the first level, the animals selected an activity range within the available landscape, and on the second level, they exploited specific areas within their activity range:

(1) Selection of activity range was analyzed by comparing habitat composition within the overall activity range of each individual with habitat composition within the available landscape. The activity range was measured as the buffered MCP for each individual. The landscape considered available was that area falling inside a circle around the roost with a radius equal to the maximum distance traveled from the roost (MRC or maximum range circle).

(2) Habitat selection within the activity range was analyzed by comparing the proportion of habitats used at buffered locations with the available habitat composition in its individual activity range. Habitat used took into account the intensity of use by measuring the proportion of each habitat type falling inside the buffer area of the individual locations. Habitat available was measured as the proportion of each habitat type within the MCP of the individual buffered locations.

Habitat selection was investigated through compositional analysis (Aebischer, Robertson & Kenward, 1993) using an Excel macro (Smith, 2004) which also accounted for randomization as recommended by Aebischer *et al.* (1993). We analyzed both datasets (urban and NP) together and separately. The first-level activity range selection (MRC vs. individual MCPs) could not be conducted for the NP dataset as we ignored where the bats roosted more than 70% of the time. For the urban dataset, spring (pregnancy) and summer (lactation) periods in 2004 were also analyzed separately.

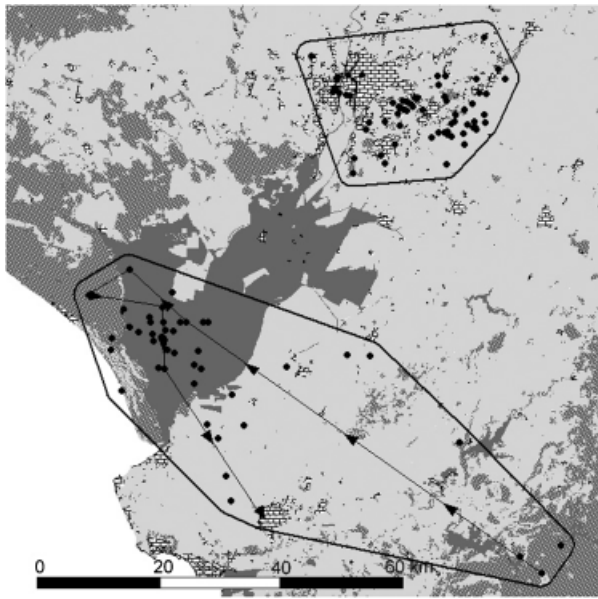


Figure 2 Minimum home ranges of giant noctule *Nyctalus lasiopterus* bats radiotracked in summer 2003, defined by the minimum convex polygon encompassing all buffered locations. Upper polygon represents the Seville population ($n=3$ bats, 75 locations, shown as black dots); lower polygon designates the Doñana population ($n=4$, 48 locations). The arrowed line shows the minimum trajectory of bat 705 in the night of July 14, 2003.

Results

Seasonal home ranges

Three bats from Seville and five bats from the NP were radiotracked in summer 2003 (Table 1). Bats from Seville, all lactating females, always returned to the site of capture in the urban park for day roosting. Individual home ranges overlapped to a large extent and its overall size stabilized after 60 (from the 75 available) locations at $\sim 1113 \text{ km}^2$. Bats foraged up to 27 km from their roosts (Fig. 2).

Four of the five bats from the NP were lactating females (705, 707, 709 and 726). Only few locations (2–27) were recorded for each individual (Table 1). From the vantage point near the roost (high tower) from which bats could be contacted regularly up to 40 km distance, none of the bats was detectable most of the time, suggesting that they flew further away from the roost. Although we could confirm that some bats were still wearing their tags during at least 32, 30, five, two and two nights (for bats 705, 709, 707, 710 and 726, respectively; Table 1), only fast changing, very distant bearings could be obtained, and few locations by cross-triangulations were achieved. No activity locations were obtained for bat 726, but it was found roosting in two occasions in the Zoobotanical Gardens, in Jerez, about 42 km from the roost-site where it was captured (Fig. 1). Bat 705 also roosted at this site on at least four different days. The bats returned to the bat box in the NP only occasionally: out of 51 recording days, bat 705 day-roosted

at this site for nine non-consecutive days, bat 707 occupied this roost for 8 days, bat 710 for 6 days, but bats 709 and 726 never returned to the site. After July 3, no radiotagged bat ever returned to the bat box during 33 days of observation.

Bat 705 traveled a minimum of 130 km on the night of July 14 after it was located at dusk (time of emergence) in the Alcornocales Nature Park in Cádiz, 92 km from the Doñana roosting site and 54 km from the roost in Jerez, where it was located the next day (Fig. 2). Bat 710 also foraged on two different nights in the Alcornocales Nature Park.

Home-range size of the NP bats was very large ($\sim 2582 \text{ km}^2$; Fig. 2). Maximum distance that radiotagged bats flew from a roost was 90 km, although only from the small number of locations that we could obtain. In bootstrap re-sampling, the area did not stabilize after the 48 locations available but still increased, suggesting in fact larger activity ranges.

The three bats tagged in Seville in autumn 2003 became inactive after ~ 10 days, so that only between seven and 26 locations could be obtained (Table 1). The bats had a large home range extending to the south of Seville along the Guadalquivir River (Fig. 3b). Individual home ranges overlapped to a large extent and while home-range size reached $\sim 1324 \text{ km}^2$ it did not stabilize even after the maximum number of locations that we recorded (54). Maximum distance traveled from the roosting site was *c.* 40 km, and the bats always returned to the urban park for day roosting.

The home range of the 14 bats from Seville radiotracked in spring 2004 was in marked contrast with the previous results, as the bats always stayed within a radius of ~ 15 km from the roosting site (Fig. 3c). Individual home ranges overlapped to a large extent. Home-range size reached $\sim 704 \text{ km}^2$ and stabilized after 50 of 105 available locations. Seven bats were radiotracked through June, a period when precipitation diminished markedly in the study area (from 64.9 mm in May 2004 to 0 mm in June 2004; data from Doñana Biological Reserve Monitoring Service), and coinciding with the lactation period. Individual home ranges overlapped to a large extent. Overall home range in June (early summer) stabilized after 100 of 195 recorded locations within an area of $\sim 1555 \text{ km}^2$; maximum distance traveled from the roost was ~ 40 km (Fig. 3d). A paired *t*-test confirmed that the increase in size of the bats' seasonal home ranges from spring to early summer was statistically significant (paired *t*-test; $t_6 = -3.132$, $P = 0.02$). In both seasons, bats always returned to the urban park for day roosting.

Habitat selection

Selection of activity range

Percentage habitat composition of individual activity ranges, compared with that of the available landscape within a circle (MRC) with radius of 40 km, was non-random (Seville all: $n = 20$, Wilks' $\lambda = 0.0710$, $\chi^2 = 52.91$, d.f. = 3, $P < 0.001$; Seville spring 2004: $n = 14$, Wilks' $\lambda = 0.0019$, $\chi^2 = 88.10$, d.f. = 3, $P < 0.001$; Seville summer 2004: $n = 7$,

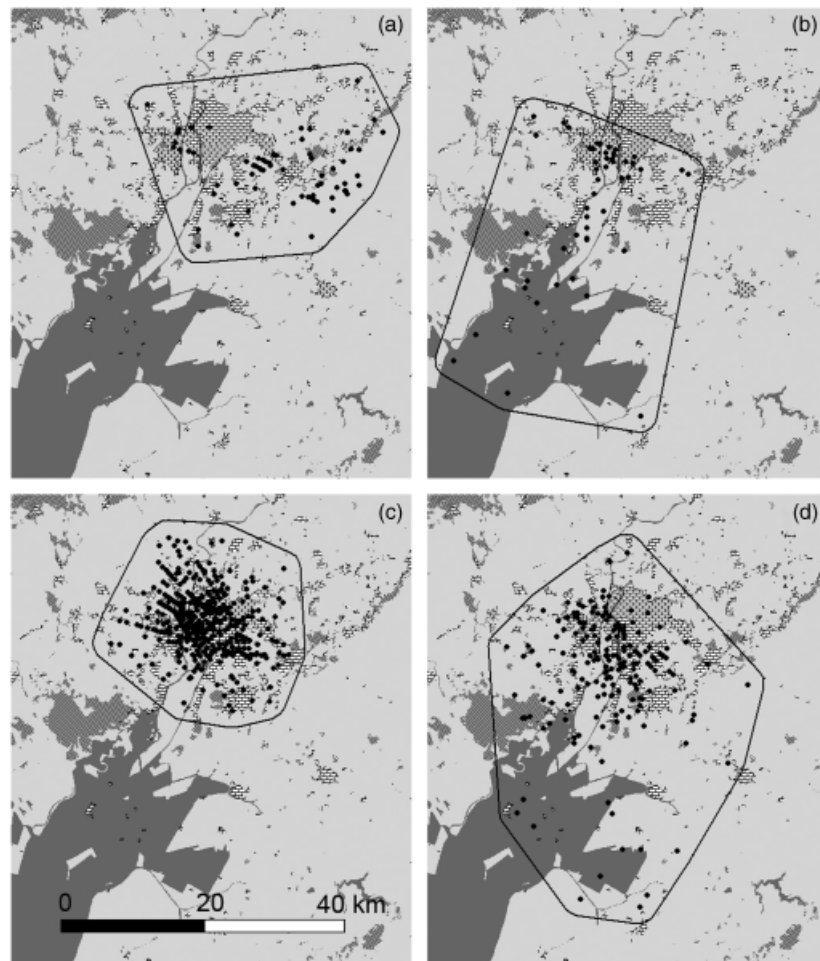


Figure 3 Point locations and overall home ranges of all bats from Seville radiotracked throughout the study period; (a) summer 2003 ($n=3$ bats); (b) autumn 2003 ($n=3$); (c) spring 2004 ($n=14$); (d) summer 2004 ($n=7$).

Wilks' $\lambda = 0.0194$, $\chi^2 = 27.61$, d.f. = 3, $P = 0.015$). Urban areas were on average used more often than they were available; riverine areas were used more often than they were available except for spring 2004 (Fig. 4). Open land and woodland were on average always used below availability. Woodlands were significantly avoided; urban areas and open land were significantly selected over riverine areas, except during summer of 2004 (Table 2).

Habitat selection within the activity range

The selection of habitats within the individual activity ranges of all bats, Seville bats in the spring 2004 and Seville bats in the summer 2004 were significantly different from their availability (all: $n = 24$, Wilks' $\lambda = 0.3866$, $\chi^2 = 24.71$, d.f. = 3, $P < 0.001$; Seville all: $n = 20$, Wilks' $\lambda = 0.3978$, $\chi^2 = 22.13$, d.f. = 3, $P < 0.001$; Seville spring 2004: $n = 14$, Wilks' $\lambda = 0.0852$, $\chi^2 = 44.32$, d.f. = 3, $P < 0.001$; Seville summer 2004: $n = 7$, Wilks' $\lambda = 0.1877$, $\chi^2 = 18.40$, d.f. = 3, $P = 0.005$). Urban and riverine areas were used, on average, more than was available (Fig. 5). Open land and woodland, the first of which was the main habitat type ($\sim 60\%$) within

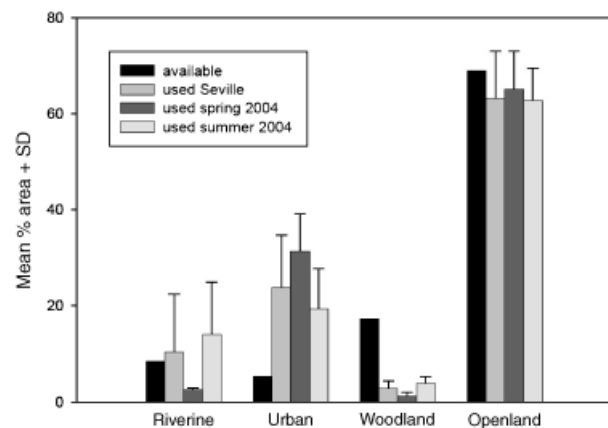


Figure 4 Comparisons of habitat proportions within an MRC with a radius of 40 km (mean percentage area; habitat available) versus habitat proportions within the individual MCPs (mean percentage area + SD; habitat used) for Seville bats, all grouped together and separated by season, that is spring 2004 and summer 2004 (habitat available is the same for all groups). MCP, minimum convex polygon.

Table 2 Habitat ranking matrix derived from compositional analysis, from most preferred to least preferred, on a first level habitat selection (selection of activity ranges within the landscape) and on a second level habitat selection (habitat selection within the activity range)

Level	Group	Habitat ranking
First level	Seville MRC (40 km)	Urban ^a ≫ Open ^b > Riverine ^b ≫ Wood ^c
	Seville spring 2004 MRC	Urban ^a ≫ Open ^b ≫ Riverine ^c ≫ Wood ^d
	Seville summer 2004 MRC	Urban ^a > Riverine ^{ab} > Open ^b ≫ Wood ^c
Second level	All (Seville and Doñana)	Riverine ^a > Urban ^a ≫ Wood ^b > Open ^b
	Seville	Riverine ^a > Urban ^a ≫ Wood ^b > Open ^b
	Seville spring 2004	Riverine ^a ≫ Urban ^b ≫ Open ^c > Wood ^c
	Seville summer 2004	Riverine ^a ≫ Urban ^b ≫ Wood ^c > Open ^{bc}

Values marked with three signs (≫) indicate significant deviation from zero at $P=0.01$. Habitat categories that are not significantly different from one another are indicated with the same lower-case letter.

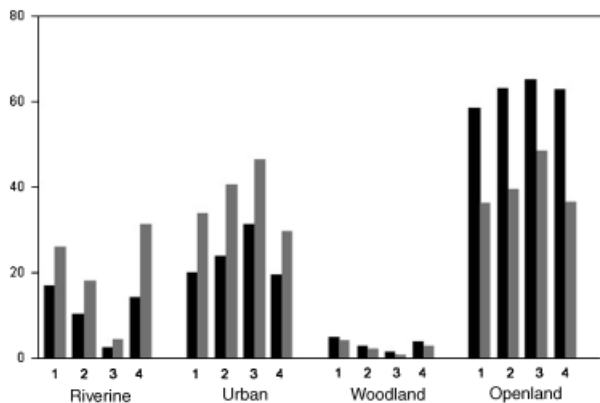


Figure 5 Comparisons of habitat available within the individual buffered MCPs (mean percentage area + sd; black line) versus habitat used defined as mean habitat composition inside the individual buffered locations (gray line). 1: complete dataset; 2: Seville; 3: Seville spring 2004; 4: Seville summer 2004.

the activity ranges of the bats, were used on average below availability. Riverine areas and urban areas were significantly selected over all other habitat types (Table 2). During spring and summer 2004, riverine/marshland was significantly selected over urban areas. Differences in selection of woodland and open land were non-significant.

Discussion

Home-range size varied seasonally and was strikingly different between the two populations studied, urban and NP. Our results support the key importance of the Doñana marshland as foraging grounds for giant noctule populations spread across a vast area. Contrary to our predictions, giant noctules from the NP exhibited the largest home range, almost three times that of urban bats in the same season, and 15% larger than the overall home range of urban bats throughout the whole study period. Its size, larger than 2500 km², is among the largest reported for any microchiropteran species, and represents a conservative estimate as bats were absent from the study area most of the time. One of the radiotagged giant noctules flew an

astounding distance of more than 130 km in a single night. So far, daily foraging movements of over 50 km have only been reported for *Tadarida brasiliensis* (Best & Geluso, 2003).

Home ranges of urban bats showed considerable seasonal variation, being minimal in spring 2004 (within 15 km from the roost) and maximal in late autumn 2003 and early summer 2004 (within 40 km from the roost). Bats enlarged their home ranges southwards during June, coinciding with the lactation period. Energetic demands are higher during lactation than during pregnancy (Anthony & Kunz, 1977; Racey & Speakman, 1987; Kurta, Kunz & Nagy, 1990), and as a response some bats spend more time foraging (Barclay, 1989). However, the opposite was found in several bat species, with the largest distances traveled by non-reproductive females (Entwistle, Racey & Speakman, 1996; O'Donnell, 2001); common noctules in England did not show differences in home-range size relative to reproductive state (Mackie & Racey 2007). Apart from reproductive condition, seasonality in climatic conditions linked to insect abundance in the study area, with negative water balance between May and October (Prenda, López-Nieves & Bravo, 2001) and peak insect abundance in spring (Herrera, 1988; Sánchez-Piñero & Ávila, 2004), could force bats to travel longer distances in search of insect prey during summer. High energetic demands could also result in large ranges during autumn because of the need to accumulate fat reserves before hibernation, or because of low insect abundance due to colder temperatures. The diet of giant noctules experiences a major shift toward nocturnally migrating passerines in autumn (Ibáñez *et al.*, 2001; Popa-Lisseanu *et al.*, 2007). Although the density distribution of this resource is not known at regional scales, its spatial variation, including the concentrations of birds departing from stop-over sites at dusk, could have influenced the foraging movements of this species.

On a landscape level, urban bats avoided woodland habitats during their nocturnal flights. On a core area level, all bats used riverine and urban areas more intensively within their MCPs. The selection of urban areas might be an artifact owing to the location of roosting sites, and because we could not differentiate between commuting and foraging. Hunting around city lights, a behavior commonly

reported for several bat species living in urban areas (e.g. Kronwitter, 1988; Lee & McCracken, 2002; Haupt, Menzler & Schmidt, 2006), has never been observed for giant noctules. Riverine areas were in all cases the most used habitat type relative to their availability. Bats followed the river when moving south (Fig. 3b and d), and the marshlands in Doñana were used by both urban and NP populations. A preference for this habitat could respond to the high insect availability of riparian environments compared with all other habitats in semi-arid ecosystems (Gregory *et al.*, 1991). The arid conditions during the Mediterranean summer could be the cause why bats from the urban population enlarged their home ranges toward the marshes. Lactation could also motivate bats to search for more productive habitats such as marshes to meet increased energetic demands (Anthony & Kunz, 1977; Racey & Speakman, 1987; Kurta *et al.*, 1990). Both woodland and open areas, the latter being the most abundant habitat type within the MCPs of the bats, were negatively selected. The avoidance of woodland as foraging habitat by giant noctules contrasts with the preference for this habitat type by common noctules in Great Britain (Mackie & Racey, 2007). Open areas, mostly agricultural, were used with low intensity, suggesting that agricultural landscapes do not represent optimal foraging grounds for *N. lasiopterus* in the study area.

The low fidelity shown by bats in the NP to their roosting areas compared to the urban population can be explained by the roosting dynamics and social organization of giant noctules. This species forms fission–fusion colonies dividing every day into smaller roosting groups that experience continuous re-mixing (Popa-Lisseanu *et al.*, 2008). In fact, the population of Seville used at least 73 roost trees during the course of this study. Likewise, bats using the box in the NP constituted a ‘roosting group’ belonging to one or to several colonies whose main roosts were most likely located outside the area of Doñana. This is supported by the fact that some of the radiotracked bats roosted on several occasions in a known giant noctule roost in Jerez 42 km away, and at least once in the area of the Alcornocales Nature Park (around 90 km away). Our results suggest that the larger home ranges of giant noctules from the NP compared with those from the urban are a consequence of the roost-switching behavior typical of this species, in an area where foraging is optimal but where roosts are a scarce and dispersed resource.

The availability and distribution of resources is likely to affect the activity of giant noctule bats on two fronts: (1) roosting sites; (2) adequate foraging grounds. In south-western Spain, these two resources are segregated, as (1) the area around Doñana and the Guadalquivir marshlands, which were positively selected by the bats during their foraging activity, currently lacks sufficient roosting sites for a tree-dwelling bat that exhibits roost-switching; (2) the city of Seville, where a historic park offers a high density of roosts for giant noctules, is not an optimal foraging ground throughout the year. For this reason, this species must travel long distances on a daily basis to reach its foraging grounds or for moving between alternative roosting sites. This might

not be optimal, as flying involves increased energetic costs for bats (Racey & Speakman, 1987).

South-western Spain, with the largest populations known worldwide of giant noctules, is a crucial geographical area for this threatened species and thus deserves attention and concerted conservation efforts. However, current park management practices that cut down old and hollow trees are seriously menacing the last shelters of these bats in this urban environment (Popa-Lisseanu *et al.*, 2008). We recommend the creation of a network of artificial roost sites in Doñana within the limits of the NP. This would reduce commuting distances between potential tree roosts and between roosts and foraging grounds, presumably reducing fitness costs as well as the subsequent risks of mortality during long flights. As the NP is banned to human access, it would also provide safe roosting sites for the bats. This would be a temporary solution until the natural vegetation in Doñana has recovered and mature forests with suitable cavities become available for the bats. Given the importance of Doñana as foraging habitat for the largest known giant noctule populations, these measures could have significant implications for the conservation of this rare species.

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References

- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–1325.
- Aldridge, H.D.J.N. & Brigham, R.M. (1988). Load carrying and maneuverability in an insectivorous bat: a test of the 5% ‘rule’ of radio telemetry. *J. Mammal.* **69**, 379–383.
- Anthony, E.L.P. (1988). Age determination in bats. In *Ecological and behavioral methods for the study of bats*: 47–58. Kunz, T.H. (Ed.). Washington: Smithsonian Institution Press.
- Anthony, E.L.P. & Kunz, T.H. (1977). Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* **58**, 775–786.
- Arribas, A., Gallardo, C., Gaertner, M.A. & Castro, M. (2003). Sensitivity of the Iberian Peninsula climate to land degradation. *Clim. Dyn.* **20**, 477–489.
- Barclay, R.M.R. (1989). The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. *Behav. Ecol. Sociobiol.* **24**, 31–37.
- Best, T.L. & Geluso, K.N. (2003). Summer foraging range of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) from Carlsbad Cavern, New Mexico. *Southwest. Nat.* **48**, 590–596.

- Bontadina, F. & Naef-Daenzer, B. (1996). Analysing spatial data of different accuracy: the case of greater horseshoe bats foraging. In *Wildlife – biotelemetry*. Le Maho, Y. (Ed.). Strasbourg: CNRS-CEPE <http://www.rhinolophus.net/wildtele.pdf>.
- Bontadina, F., Naef-Daenzer, B. & Schofield, H. (2002). Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *J. Zool. (Lond.)* **258**, 281–290.
- Entwistle, A.C., Racey, P.A. & Speakman, J.R. (1996). Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philos. Trans. Roy. Soc. B* **351**, 921–931.
- Gregory, S.V., Swanson, F.J., McKee, W.A. & Cummins, K.W. (1991). An ecosystem perspective of riparian zones. *BioScience* **41**, 540–551.
- Haupt, M., Menzler, S. & Schmidt, S. (2006). Flexibility of habitat use in *Eptesicus nilssonii*: does the species profit from anthropogenically altered habitats? *J. Mammal.* **87**, 351–361.
- Herrera, J. (1988). Pollination relationships in southern Spanish Mediterranean shrublands. *J. Ecol.* **76**, 274–287.
- Hooge, P.N. & Eichenlaub, B. (1997). *Animal movement extension to ArcView ver. 1.1*. Anchorage, AK: Alaska Biological Science Center, US Geological Survey.
- Ibáñez, C., Guillén, A. & Bogdanowicz, W. (2004). *Nyctalus lasiopterus* (Schreber, 1780) – Riesenabendsegler. In *Handbuch der Säugetiere Europas*, Vol. 4: 695–716. Krapp, F. (Ed.). Wiesbaden: AULA-Verlag.
- Ibáñez, C., Guillén, A., Juste, J., Migens, E., Pérez, J.L. & Ruiz, C. (1995). Quirópteros del Parque Nacional de Doñana: Especies, y Tamaño y Métodos de Estima de sus Poblaciones. ICONA-CSIC, Sevilla 114.
- Ibáñez, C., Juste, J., García-Mudarra, J.L. & Agirre-Mendi, P.T. (2001). Bat predation on nocturnally migrating birds. *Proc. Natl. Acad. Sci. USA* **98**, 9700–9702.
- IUCN. (2006). *Red list of threatened species*. <http://www.iucn.org/themes/ssc/redlist2006/redlist2006.htm>
- Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.
- Kronwitter, F. (1988). Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. *Myotis* **26**, 23–85.
- Kurta, A., Kunz, T.H. & Nagy, K.A. (1990). Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. *J. Mammal.* **71**, 59–65.
- Lee, Y.F. & McCracken, G. (2002). Foraging activity and food resource use of Brazilian free-tailed bats, *Tadarida brasiliensis* (Molossididae). *Ecoscience* **9**, 306–313.
- Mackie, I. & Racey, P. (2007). Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): implications for conservation. *Biol. Conserv.* **140**, 70–77.
- Ministerio de Medio Ambiente. (2006) Catálogo Nacional de Especies Amenazadas http://www.mma.es/portal/secciones/biodiversidad/especies_amenazadas/catalogo_especies/acceso_catalogo.htm.
- Moreira, J.M. & Fernández-Palacios, A. (1995) *Usos y coberturas vegetales del suelo en Andalucía. Seguimiento a través de imágenes de satélite (Land-use and land-cover in Andalusia. Monitoring from satellite imagery)*. Junta de Andalucía, Consejería de medio ambiente.
- O'Donnell, C.F.J. (2001). Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand. *J. Zool. (Lond.)* **253**, 253–264.
- Popa-Lisseanu, A.G., Bontadina, F., Mora, O. & Ibáñez, C. (2008). Highly structured fission–fusion societies in an aerial-hawking, carnivorous bat. *Anim. Behav.* **75**, 471–482 (Online DOI: 10.1016/j.anbehav.2007.05.011).
- Popa-Lisseanu, A.G., Delgado-Huertas, A., Forero, M., Rodríguez, A., Arlettaz, R. & Ibáñez, C. (2007). Bats' conquest of a formidable foraging niche: the myriads of nocturnally migrating songbirds. *PLoS ONE* **2**, e205 (Online DOI: 10.1371/journal.pone.0000205).
- Porter, W.F. & Church, K.E. (1987). Effects of environmental pattern on habitat preference analysis. *J. Wildl. Mgmt.* **51**, 681–685.
- Prenda, J., López-Nieves, P. & Bravo, R. (2001). Conservation of otter (*Lutra lutra*) in a Mediterranean area: the importance of habitat quality and temporal variation in water availability. *Aq. Conserv.: Mar. Freshw. Ecos.* **11**, 343–355.
- Racey, P.A. & Speakman, J.R. (1987). The energy costs of pregnancy and lactation in heterothermic bats. *Symp. Zool. Soc. Lond.* **57**, 107–125.
- Riley, S.P., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C. & Wayne, R.K. (2003). Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conserv. Biol.* **17**, 566–576.
- Sánchez-Piñero, F. & Ávila, J.M. (2004). Dung-insect community composition in arid zones of south-eastern Spain. *J. Arid Environ.* **56**, 303–327.
- Scott, D.M., Brown, D., Mahood, S., Denton, B., Silburn, A. & Rakotondraparany, F. (2006). The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. *Biol. Conserv.* **127**, 72–87.
- Smith, P.G. (2004). Automated log-ratio analysis of compositional data: software suited to analysis of habitat preference from radiotracking data. *Bat Res. News* **45**, 16.
- Worton, B.J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168.