The effect of sex on home range in an urban population of European hedgehogs *Erinaceus europaeus* at the southern edge of the species distribution

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Abstract

The effect of sex on home range in an urban population of European hedgehogs Erinaceus europaeus at the southern edge of the species distribution. As the transformation of natural habitats into urban environments increases, some species, such as hedgehogs, are able to adapt and thrive. Six hedgehogs, three males and three females, were tagged with radio—transmitters and tracked for three nights in the University of Alicante campus to study the effect of sex on their home range size, distance travelled per night, and night activity pattern. Time invested in several activities was also analyzed. Males showed larger home ranges than females (mean \pm SD) (\circlearrowleft : 27.7 ha \pm 19.2; \circlearrowleft : 5.5 ha \pm 3.4) and travelled longer distances per night (mean \circlearrowleft : 1,077 m \pm 251.18; \circlearrowleft : 504 m \pm 156.37). Activity rhythm through the night presented a bimodal pattern but differed between sexes. Males tended to be on the move significantly more often than females (\circlearrowleft : 38.7%; \circlearrowleft : 24.8%) while females foraged more often than males (\circlearrowleft : 1.4%; \circlearrowleft : 9.2%).

Key words: Hedgehog, Erinaceus europaeus, Radio-tracking, Home range, Activity pattern, Cat feeder

Resumen

El efecto del sexo en el área de campeo de una población urbana de erizos europeos Erinaceus europaeus en el extremo sur de la distribución de la especie. En la creciente transformación de los hábitats naturales en entornos urbanos, algunas especies como el erizo pueden adaptarse y prosperar. Seis erizos, tres machos y tres hembras, fueron equipados con radiotransmisores y seguidos durante tres noches en el campus de la Universidad de Alicante con el fin de estudiar el efecto del sexo sobre el área de campeo, la distancia recorrida por noche y el patrón de actividad nocturna. También se analizó el tiempo invertido en diferentes actividades. Los machos presentaron áreas de campeo mayores que las hembras (media \pm DE) (\circlearrowleft : 27,7 ha \pm 19,2; \rightleftharpoons : 5,5 ha \pm 3,4) y recorrieron distancias mayores por noche (media \circlearrowleft : 1.077 m \pm 251,18; \rightleftharpoons : 504 m \pm 156,37). El ritmo de actividad durante la noche presentó un patrón bimodal, pero difirió entre sexos. Los machos tendieron a estar en movimiento con una frecuencia significativamente mayor que las hembras (\circlearrowleft : 38,7 %; \rightleftharpoons : 24,8 %), mientras que las hembras invirtieron más tiempo en forrajear (\circlearrowleft : 1,4 %; \rightleftharpoons : 9,2 %).

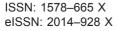
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Introduction

The increasing transformation of natural and semi-natural habitats into urban environments is a major cause of habitat loss (Pickett et al., 2001). Urbanization is generally viewed as deleterious for wildlife, affecting the ecosystem structure and function due to habitat fragmentation, pollution, human activity, and habitat change (Dickman, 1987; Foley et al., 2005). But although residential areas are often unfavorable for wildlife, some species can take advantage of their implicit characteristics (Luniak, 2004). Urban areas also mean low density or absence of potential natural predators (Gering and Blair, 1999; Moller 2012), abundance of alternative shelters, different micro-climatic and hydrological conditions and increase of food availability provided intentionally or accidentally by humans (Rebele, 1994; Cadenasso et al., 2007; Pautasso, 2007). Thus despite their potential disadvantages, urban environments can be successfully colonized. especially by species that exhibit high habitat and dietary flexibility and tolerance to human activity (Crooks, 2002; Bateman and Fleming, 2012). In such resource-rich habitats, species density and survival rates may even increase (Gloor et al., 2001; Prange et al., 2003).

The European hedgehog *Erinaceus europaeus* is a good example of an urban adapter (McKinney, 2006; Bateman and Fleming, 2012). A medium—sized solitary nocturnal insectivore, hedgehogs find semi—urban and urban places an ideal habitat as such areas are free of their main natural predators: eagle owls (*Bubo bubo*) and badgers (*Meles meles*) (Hof et al., 2012). Besides, they hold new food resources, such as pet food (Yalden, 1976; Morris, 1985; Hubert et al., 2011).

Studying a species home range is a basic step towards understanding its ecology because range is related to biological aspects such as number of mates, reproductive strategy, diet, food availability, body weight, and shelter (Clutton-Brock and Harvey, 1978). These aspects can provide information about the quality of the habitat (Harestad and Bunnell, 1979). Hedgehogs' home range in Europe have been studied in environments ranging from arable landscapes to urban environments (Riber, 2006; Haigh et al., 2012; Rautio et al., 2013; Pettett et al., 2017), but data on the ecology of hedgehogs in southern Europe are scarce. Furthermore, little is known about their spatial ecology in these southernmost parts of its range. Only two studies are available about this species in Spain, and both are from the north of the country. One was performed in a peri-urban area with bush and open natural areas (García et al., 2009) while the other investigated hedgehogs released from a wildlife recovery center (Cahill et al., 2011). The aim of the present study was to analyse the effect of sex on the home range and distances travelled per night and to determine nocturnal patterns and activities of hedgehogs in an urban population in southern Spain.

Material and methods

Study area

The study was conducted in the campus of the University of Alicante (38° 23' 7.13" N, 0° 30' 50.27" W) in the southeastern Iberian Peninsula. The campus is a large gardened area (80 ha) located in the city of San Vicente del Raspeig (Alicante) (fig. 1). Half surrounded by buildings and roads, the campus is also connected to natural spaces through natural and man—made corridors.

Despite being located in a region with semi-arid Mediterranean climate with low annual rainfall (300 mm) and warm temperatures (annual mean 18°C), the campus itself has a micro-environment thanks to artificial irrigation. The landscape is dominated by wide open spaces, including pavement and grassy areas, with scattered vegetation such as bushes and garden plants, which provide good shelter. The development of vegetacion contrasts with the typical dry Mediterranean shurbland we find in the surroundings, with scattered Stipa tenacissima and Rhamnus lycioides as predominant species and large percentage of bare soil. Further information about the campus vegetation can be found in UVERDA (http://arbomapweb-accesociudadano.cloudapp.net/ UniversidadAlicante/indexes.html).

As in several public spaces in the cities, we also find several points with cat feeders (n = 14), intentionally placed and maintained by local people to feed stray cats. Cat feeders are permanently located (fig. 1) and food and water are replaced daily. The cat feeders consist of 5L plastic water bottles that have been remodeled for use as feeders through the creation of a lateral opening. This opening allows access of one individual at a time. In contrast with other studies, there is not shortage of food at these sites and they may be visited by several hedgehogs (besides other animals) throughout the night.

Radio tracking

Six adult hedgehogs (three males and three females) from a population that was monitored in the campus of Alicante University were equipped with radio-transmitters. Hedgehogs were captured by hand with the aid of spotlights and individually marked using a unique colour combination of heat shrink plastic tubes (Jones and Norbury, 2006; Young et al., 2006; Haigh et al., 2013). All hedgehogs caught in the campus were sexed according to the urogenital distance (Reeve, 1994; Morris, 2014) and classified as juvenile, subadult, or adult according to body measurements, weight and presence of growing spikes (Reeve, 1994). In order to study the effect of sex on home range, and to take into account the variability associated with body size, we selected for marking the smallest and the biggest individual of each sex known in the monitored population and one medium sized male and female.

The transmitters (Televilt TXH-2) were glued to the hedgehogs' spines with an epoxy putty (Ceys)

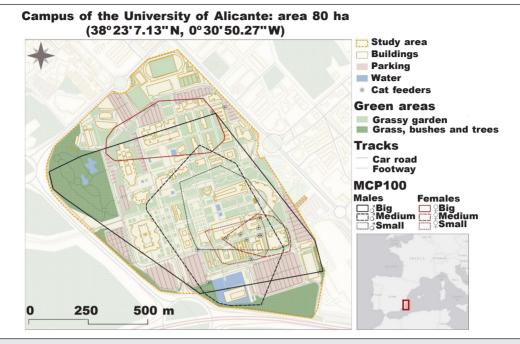


Fig. 1. Location of the study area (inset) and map of its habitat composition, showing cat feeder locations and individual MCP100 of the radio–tracked hedgehogs.

Fig. 1. Localización del área de estudio (cuadro pequeño) y mapa de los hábitats presentes donde se muestra también la localización de los comederos para gatos y los MPC100 de los erizos radio marcados.

directly attached to a mid-dorsal patch of clipped spines (Morris, 1988; Rautio et al., 2013). The six tagged hedgehogs had a minimum weight of 650 g, while the weight of the devices plus epoxy was 31.5 g and represented on average 3.5% of the weight of marked hedgehogs, thus fulfilling the rule of being less than 5% of the animals' weight (MITECO, 2015). All devices were removed at the end of the monitoring period by cutting off the tip of the spines below the epoxy putty (Barthel, 2019).

The radio tracking study was carried out during the mating season, when hedgehogs are most active (May-June 2014). They were tracked using radio receivers (RX98 Followit AB) and a four-element Yagi antenna (Y-4FL A11-0200; 163-165 MHZ) from a distance that allowed visual observation without disturbing the animals' normal behavior (≤ 30 m) (Rautio et al., 2013). The hedgehogs in the study area are familiar with the presence of people and showed no signs of altered behaviour during the radio-tracking periods. Each hedgehog was followed for three nights with 1-28 days interval in between nights. Tracking was begun before the hedgehogs emerged in the evening and ended after the individual reached its nest the following morning (20:00-07:30 approximately) (GMT+2). When possible, locations were recorded every 15 minutes, and an activity category was assigned to each recording showing the hedgehogs' behavior: in motion (locomotion), resting or showing no movement (stationary), looking for natural food (foraging), interacting with other hedgehogs (interaction), and feeding from a cat feeder (feeder). We analyzed the frequency of occurrence of the activity categories assigned to each recorded fix from radio tracking (n = 673). We assumed that the relative frequency with which any particular behavior was recorded reflected the proportion of time a hedgehog devotes to that behavior (Reeve, 1981; Wroot, 1984; Reeve, 1994).

Home range calculations

We calculated the home ranges for the six radio-tracked hedgehogs using radio tracking locations, and we used direct observations obtained during the general study of the university hedgehog population as reinforcement. We calculated three metrics related to home range: MCP100, Kernel 95% and Kernel 50%. The minimum convex polygon (MCP100) involves creating a convex polygon encompassing all locational points gathered for the individual (Gregory, 2017). It is prone to overestimating home range by including outliers and areas never visited by the animal (White and Garrot, 1990; Gregory, 2017), but despite this, it enables a better comparison with previous hedgehog studies in which MCP100 was often used (Reeve. 1982: Boitani and Reggiani, 1984; Kristiansson, 1984; Riber, 2006; Haigh, 2011; Rautio et al., 2013). Kernel methods describe the probability of finding an animal at any one place by centering a bivariate probability density

Table 1. Home range sizes (ha) of all radio-tracked hedgehogs and average home range size of each sex using data from radio tracking plus direct observations: h_{ref}, reference bandwidth estimated by the program; FBw, final bandwidth (bandwidth used to estimate home range after correction described in the text).

Tabla 1. Área de campeo (ha) de todos los erizos radiomarcados y área de campeo media de cada sexo según los datos obtenidos del radioseguimiento y las observaciones directas: h_{ref} ancho de banda de referencia estimado por el programa; FBw, ancho de banda final (ancho de banda usado para estimar las áreas de campeo tras la corrección descrita en el texto).

	Individual	W (g)	MCP100 (SD)	K95 (SD)	K50	h _{ref}	FBw
Males	Big	1,195	48.9	40.1	7	150.8	37.7
	Medium	891	23.4	24.9	5.2	64.7	45.3
	Small	794	11.4	12	2.2	43.3	28.2
	Average	960	27.7 (19.22)	25.7 (14.05)	4.8 (2.45)		
Females	Big	1,236	9.4	12.7	3	64.2	35.3
	Medium	764	3.4	4	0.9	29.8	14.9
	Small	663	3.6	3.3	0.5	27.8	11.1
	Average	888	5.5 (3.44)	6.7 (5.22)	1.5 (1.32)		

function with unit volume over each recorded point (Rodgers and Kie, 2010). The 95% kernel (K95: 95% probability to be found in that area) was considered to represent the total home range of the hedgehog (Rautio et al., 2013) and kernel 50% (K50) was used to describe the core area of the home range (areas of intensive use) where the animal spends 50% of its time.

The minimum convex polygon (MCP100) was calculated using QGIS 2.18.25 (Quantum GIS Development Team, 2016), and the fixed kernel (FK) method (Worton, 1989) was used to estimate 95% and 50% isopleths, using Home Range Tools in ArcGIS 10.3 (ESRI Inc., Redlands, CA). The smoothing parameter for the kernels was estimated for each individual as $h_{\rm ref}$ and was reduced in 5% steps until the kernel 95% line broke (Kie, 2013). The smoothing parameter value before the kernel 95% line break was selected as the correct bandwidth.

Although successive locations using radio tracking methods may not have been independent, we used them to calculate home range because we had several tracking nights per home range (Smith et al., 1981) and the time interval between locations was relatively constant (De Solla et al., 1999). Repeated locations due to inactivity or resting periods (daylight nests, mid–night nap places) or continued use of cat feeders were not considered in the home range calculations.

Given that the number of days elapsed between radio-tracking nights varied between individuals (between 1 and 28 days in males, and between 1 and 15 days in females) we checked whether these differences affected home range estimates using all the metrics mentioned. To do so, we calculated the correlation between days elapsed and the increase

in home range (using the three metrics), obtained by adding the locations obtained on the latter day.

We estimated the possible effect of sex on home range size using the three metrics (MCP100, K95 and K50), analyzed using GLM with the Gaussian distribution. In these GLM, the response variable was the home range estimated for each individual. Sex (factor), weight and their interaction were included as predictors.

Night activity pattern

The distance between consecutive radio tracking locations was estimated for each individual. Speed was estimated by dividing this distance by elapsed time and average travel speed within each half–hour period was calculated for each hedgehog. The shape of the pattern of activity was estimated for each sex by averaging travel speeds in half–hour periods and fitting a polynomial regression to these averages. Polynomials of an increasing degree were fitted until the AIC value started to increase; in both sexes this led to the selection of a degree 4 polynomial.

The distance covered by each hedgehog each night was calculated as the sum of the distances of straight lines obtained by radio tracking. The possible effect of sex on distance covered was analyzed using a GLMM with Gaussian family distribution in which the response variable was the distance covered by each individual each night. Individual identity and date were included as random effects and sex and weight were included as fixed effects.

We checked the differences between sexes in the frequency of each type of activity by fitting a Poisson GLM with the number of cases of each activity re-

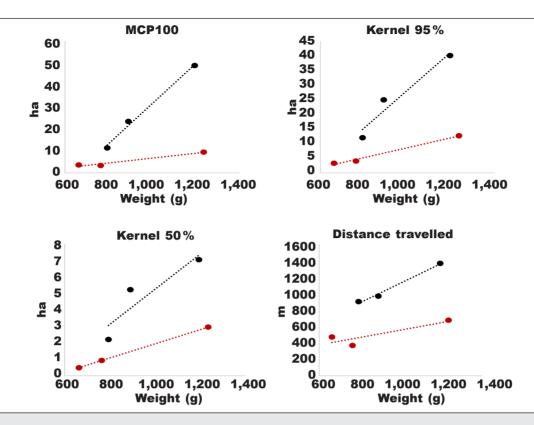


Fig. 2. Home range metrics (MCP100, K95 and K50) and distance travelled per night for radio-tracked hedgehogs in relation to sex and weight: • males; • females.

Fig. 2. Estimas de áreas de campeo (MPC100, K95 y K50) y distancia recorrida por noche de los erizos radiomarcados en relación con el sexo y el peso: • machos; • hembras.

corded for each individual as response variable, and sex as predictor. The logarithm of the total number of activities recorded for each individual was included as an offset. Statistical analyses were performed using the R 3.6.1 program (R Core Team, 2019).

Results

Home range size

The number of locations recorded per hedgehog (mean \pm SD and range) during the three nights of tracking was 112 \pm 10 (99–124). Of these, an average of 69 \pm 14 (41–79) were used to estimate the home range of the individuals after excluding repeated locations while resting or at cat feeders. In comparison, the number of direct observations obtained for each radio tracked hedgehog outside the radio tracking period was only 16 \pm 8 (4–25). The correlation between the days elapsed between tracking nights and the increase in home range was low and non–significant for both sexes for all the metrics used (MCP 100: δ r = 0.132, p = 0.802; φ r = 0.043, p = 0.936; K95: δ r = 0.132, p = 0.803; φ r = 0.158, p = 0.765; K50: δ r = 0.427, p = 0.398; φ r = -0.173, p = 0.743).

GLM results showed a significant interaction between sex and weight for MCP100 ($F_{1,2}$ = 593.03; P = 0.001) and K95 ($F_{1,2}$ = 19.8; P = 0.047). The average home range was thus larger and increased faster with body weight in males (table 1; fig. 2). On the contrary, in the case of the core area (K50), interaction between sex and weight was not significant but the additive model showed sex had a significant effect ($F_{1,2}$ = 10.2; P = 0.0495) and weight had a marginally significant effect ($F_{1,2}$ = 9.07; P = 0.057) (fig. 2).

The GLMM for minimum distance travelled per night detected a significant effect of sex (z=3.42, p=0.0007) but not weight (z=0.33 p=0.739). Therefore, on average, males traveled larger distances per night (mean 1,077 m \pm 251.18; range: 900–1,364 m) than females (mean: 504 m \pm 156.37; range: 367–674 m). Within sex, variability in distance travelled per night was lower than variability in home range.

Night activity pattern

Figure 3 shows the average speed for each hedgehog in 30 minute periods. In general, males moved three times faster than females throughout most of the night (mean \pm SD) (range), \circlearrowleft mean speed: 206 m/h \pm 59.14 (146–265 m/h), \circlearrowleft mean speed:

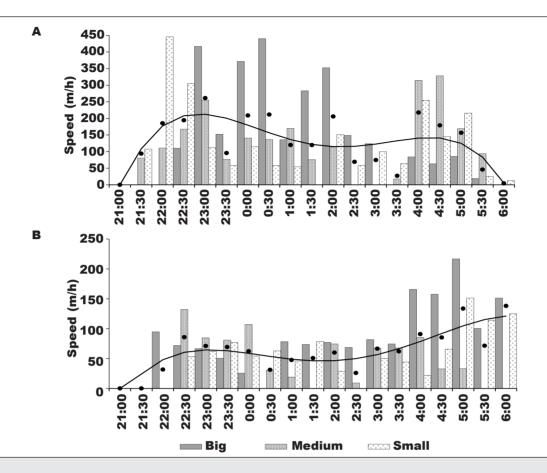


Fig. 3. Activity patterns calculated as the average travel speed within half–hour periods: A, males; B, females. Grey bars show the half–hour average for each radio–tracked hedgehog. The solid line shows the fit of a polynomial regression of degree 4. Black dots indicate the mean speed of the three hedgehogs of each sex for each half–hour period.

Fig. 3. Patrones de actividad calculados como el promedio de la velocidad en intervalos de media hora: A, machos; B, hembras. Las barras grises muestran el promedio de cada media hora para cada erizo radio marcado. La línea continua muestra el ajuste de una regresión polinómica de grado 4. Los puntos negros indican la velocidad media de los tres erizos de cada sexo por cada periodo de media hora.

70 m/h \pm 21.20 (53–93 m/h). Both sexes showed a bimodal night activity but this differed in shape. Males appeared to show a speed peak in the first half of the night (22:00–23:00 h) and a minimum activity between 2:30–4:00 h, while females showed a slight trend to increase speed towards the end of the night (4:00–6:00 h) (fig. 3).

Nocturnal activities

Overall, hedgehogs invested 40.7% of the night resting and 59.3% active. Poisson GLMs showed that both sexes spent a similar amount of time interacting with other individuals and feeding at cat feeders (fig. 4). On the contrary, males tended to be found on the move significantly more often than females (males: 38.7%; females: 24.8%), while females were more often found foraging out of the feeders than males (males: 1.4%;

females 9.2%) (fig. 4). The distribution of activities also changed during the night, with males visiting the cat feeders more regularly but rarely foraging out of them, and females foraging more intensively before visiting the feeders and using them in the second half of the night (fig. 5). The frequency of use of the feeders and interactions throughout the night were highly correlated in females ($r_{\rm s}=0.960$; p<0.001) but not in males ($r_{\rm s}=0.432$, p>0.05), indicating that female interactions with other individuals are especially linked to the visits to the cat feeder sites.

Discussion

Home range sizes obtained in this study are smaller than those obtained in surveys of hedgehogs living in northern latitudes, but they are similar to those repor-

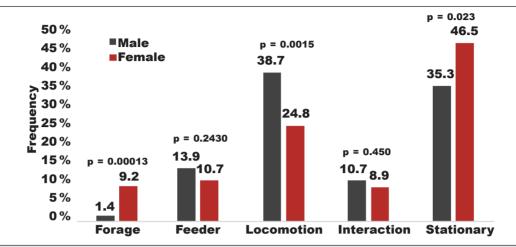


Fig. 4. Average frequency of activity categories recorded for European hedgehogs in an urban area, based on 346 behavioral records of three males, and 327 records of three females. Significance of sex effect on the percentage of each activity according to GLM is shown above the bars.

Fig. 4. Frecuencia media de las categorías de actividad registradas para erizos europeos en un área urbana, basada en 346 registros de comportamiento de los tres machos estudiados y 327 registros de las tres hembras estudiadas. En la parte superior de las barras se muestra el nivel de significación del sexo en el porcentaje de cada actividad según el modelo lineal generalizado.

ted by Garcia et al. (2009) further north in Spain, in Catalonia. Home ranges estimated in other European localities (table 2) are on average 26.1 ha (10–55.2) for females and 64.3 ha (32–97.9) for males, which are about four and twice times larger respectively than average home ranges found in both our study area and in Garcia et al. (2009). Our micro–environment with artificial irrigation and patchy habitat, together with the supplementary food supply for stray cats, may have contributed to the smaller home range. Such an environment likely alters natural conditions by providing greater shelter and more easily accessible food, possibly decreasing the need for hedgehogs to move long distances to cover basic needs.

In natural habitats, receptive females are widely dispersed because of patchy food resources (Kristiansson, 1984), making it difficult for males to predict the location of a female. On the contrary, because cat feeders make food predictable in some urban areas, female home range is reduced, and consequently, male home range was also smaller. The same could have happened in Garcia et al.'s (2009) survey because cat feeding stations are not uncommon in peri-urban areas. However, Rautio et al. (2013) found large home ranges for both sexes in an urban area in Finland with access to food supplies. The shorter breeding season in northern Europe could play a role here as males may try to maximize access to females by increasing their home ranges during a short mating season. This pressure is not a factor at Mediterranean latitudes because the climate is mild all year around, resulting in longer growth seasons (Hails, 1982; Huston and Wolverton, 2009). Furthermore, the difference in climate not only allows the reduction, or even the elimination, of a hibernation period (own data) but also promotes faster sexual maturity and second litters for hedgehogs (Reeve, 1994).

The presence of physical barriers in urban habitats should not be ignored either. Buildings, roads, fences and other human constructions may restrict the movement of hedgehogs affecting spatial use in urban habitats. The campus of Alicante University is not fully fenced and has several corridors connecting the gardened area with its natural surroundings. We have data of some other hedgehogs monitored during the survey that moved in and out the campus, but none of the radio tracked individuals were recorded outside it. However this is a factor that potentially could also affect the spatial use of this campus by hedgehogs.

On average, the estimated home range size for males was larger than females, in line with findings in previous studies in Europe (table 2). As is common in a promiscuous mating system (Reeve, 1994; Jackson, 2006; Moran et al., 2009), male spatial organization is mostly affected by female space use, while female home ranges are expected to depend only on food and shelter availability. However, the difference between male and female home ranges was higher in our study than in previous studies. On average, in other European surveys, the male home range is 2.7 times greater than that of females (range: 1.8–3.7 times) but the difference was up to five times higher in our study. This finding could also be related to the high availability of predictable food at the cat feeding stations in our study area, which may have reduced more female than male home ranges, that still look

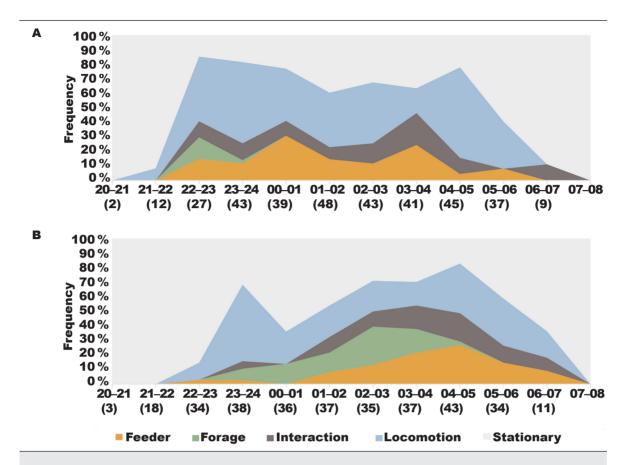


Fig. 5. Percentage of each activity in one-hour periods throughout the night: A, males; B, females. (Sample size, number of locations, in parenthesis under each hour interval).

Fig. 5. Porcentaje de cada actividad en periodos de una hora a lo largo de la noche: A, machos; B, hembras. (Tamaño de la muestra, número de localizaciones, entre paréntesis debajo de cada intervalo de una hora).

out for as many females as possible (Morris, 1988).

Although the presence of cat feeders may be common in habitats studied to date (e.g. suburban areas, golf courses), most studies provide no information about them, and only Rautio et al. (2013) provide some information about their presence. Variation in the abundance of cat feeders or in the amount and time that food is available at these feeders may have important consequences on hedgehogs' spatial use and home range (Cassini and Krebs, 1994). Therefore, more detailed information about the presence of cat feeders and their density should be provided in future studies to better understand hedgehog space use.

Despite the low sample size in our study, our analyses suggest the relation of body weight and home range size (Tucker et al., 2014) is stronger in males than in females. Weight correlated positively with the extension of the home range of males but had little influence on females' territories. The largest female in this study (1,236 g) was as heavy as the largest male (1,193 g), but its range was only slightly higher than the other females. The same occurred with

distances travelled per night, matching other studies where sexually active males ranged more widely and travelled further than females and non-rutting males (Morris, 1988; Reeve, 1994; Riber, 2006). Although hedgehogs have not been classified as a territorial species aggressive encounters between males have been documented (Reeve, 1994). Body mass can thus play an important role in dominance, with larger males being able to restrict smaller hedgehogs' use of space. Access to the feeders may also be restricted in order to avoid fighting with other conspecifics at the site. In such situations, lighter males likely invest more time in foraging in order to keep up with competition, and less time in other activities such as searching for females and wandering, thus accounting for their reduced home range.

Finally, our results showed that the intensity of nocturnal activity presented a bimodal pattern that was more marked in males than in females. This pattern has been described previously in captive (Campbell, 1975) and wild populations of European hedgehogs (Kristoffersson, 1964; Wroot, 1984; Garcia et al., 2009), but no difference between sexes has been

Table 2. Summary of hedgehog home range area (HR, ha) estimated by the minimum convex polygon (MCP100) obtained in several studies using radio tracking. Besides our study, kernels were only calculated by Rautio et al. (2013) who found 81.6 ± 0.2 ha for males and 30.3 ± 7.0 ha for females, so only MCP100 will be used to compare studies: n, number of individuals; * Haigh (2012) estimates \pm SE.

Tabla 2. Resumen de las áreas de campeo (HR, ha) de erizos europeos estimadas con el mínimo polígono convexo (MPC100) en varios estudios de radioseguimiento. Además de nuestro estudio, los kernels solo fueron calculados por Rautio et al. (2013), quienes estimaron un área de $81,6\pm0,2$ ha para los machos y $30,3\pm7,0$ ha para las hembras, por lo que solo se utilizará el MPC100 para comparar entre estudios. n, número de individuos; * Haigh (2012) estimas \pm EE.

Sex	HR±SD	Range	n	Country	Latitude	Habitat	Study
3	97.9±6.1	88.3–111.2	4	Finland	63°N 29°E	Urban area	Rautio et al. (2013)
2	55.2±17.1	23.6-82.2	3				
8	96±24		4	Denmark	56°N 10°E	Arable land,	Riber (2006)
2	26±15		4			forest and	
						grassland	
3	46.5±15.8	25-67.7	5	Sweden	55°N 13°E	Abandoned	Kristiansson (1984)
2	19.7±8.4	8.1–29.5	6			farmland	
3	56±0.7*		4	Ireland	51°N 8°W	Rural area	Haigh (2012)
9	16.5±0.5*		3				
3	32±8.9	15.5–41.5	6	UK	51°N 0°W	Golf course	Reeve (1982)
	10±2.2	5.5–12	7				
3	57.1±36.6	5.5-102.5	9	Italy	42°N 11°E	Mediterranean	Boitani and Reggiani
2	29.1±20.1	10-56.2	5			maquis region	(1984)
3	23.8±6.0	19.5–28.01	2	Spain	41°N 2°E	Mediterranean	García et al. (2009)
2	6.8 ± 3.2	3.47-9.89	3			forest near	
						peri-urban area	
3	27.7±19.2	11.3-48.9	3	Spain	38°N 0°W	Urban area	Present study
\$	5.5 ± 3.4	3.4-9.4	3				

reported. Peaks of activity are usually associated with periods when hedgehogs are actively foraging and feeding (Reeve, 1994), so the resting pause necessary to digest their meals will only occur if they are able to fill their stomach quickly (Wroot, 1984). This will depend on the food supply and the individual characteristics, making bimodality not always obvious (Reeve, 1994). Presence of predictable food at cat feeders in the study area may have contributed to making the bimodality of the activity pattern clearer.

Cat feeders attract individuals and therefore increase the probability of encounters of both sexes. This may alter the pattern of activity of females. Males were found near the feeders during most part of the night until 4:00 a.m., after which they used these sites less frequently. On the other hand, females used the feeders infrequently before midnight and were found searching for prey in the lawn. Females increased their presence at cat feeders after 1:00 a.m. in the morning and used them most frequently between 4:00 and 5:00 a.m., the time when males were rarely

found there. The frequency of female interaction with other individuals was strongly correlated with the use of the feeders, while interactions were more uniformly distributed throughout the night in males. When several hedgehogs meet at a cat feeder, agonistic interactions are frequent and females are usually disturbed by males (pers. obs.). This limitation in access to easy food translates into females spending more time foraging throughout the night.

In summary, despite maintaining a bimodal pattern, male and female hedgehogs showed differences regarding activity peaks, with males being most active in the early hours after dark and females being more active towards dawn. The females' pattern of activity during the night appeared to be conditioned by the presence of males at cat feeders, as they seemed to avoid frequent interaction with them. In natural landscapes, without artificial food supplies, the probability of encounter of males and females is lower and the two sexes maintain more similar activity patterns (Campbell, 1975; Wroot, 1984).

Conclusion

Home ranges of hedgehogs in the Mediterranean tend to be smaller than those of hedgehogs in northern latitudes. Sex had a major effect on home range, with males having larger ranges than females. The presence of cat feeders altered females' spatial use, and also influenced activity patterns and social behavior. Despite this is a preliminary study with a small sample size, our observations may be useful to understanding how hedgehog populations will perform in northern latitudes in a changing environment with temperatures rising due to climate change. Our results also raise concern on how artificial food supplies in urban areas may alter the population dynamics of a species, the ecological consequences of which we are only starting to disentangle.

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