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Spatial organization and intraspecific relationships of the southern water vole (*Arvicola sapidus*) in a Mediterranean mountain river: what is the role of habitat quality?

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Abstract An understanding of population dynamics, especially in endangered species that present metapopulation structures, such *Arvicola sapidus*, is important to gain knowledge of the dispersal and patterns of both occupation and space use. Here, we use radio tracking to report for the first time the relationship of the southern water vole with the environment in a Mediterranean mountain riparian area and also the relationships between individuals. Along the Montsant River, the size of the home ranges, the average distance travelled daily, the population density and the habitat quality were contrasted. In the subsection with better quality habitat, both the home ranges and distances travelled were smaller than in the subsection with poorer quality habitat, whilst population density was higher in the subsection with better quality habitat. Interactions (static and dynamic) between individuals reflected low sociality, especially between members of different groups. Within a group, adult males did not interact, but interactions between male and female adults intensified during the reproductive period. The home ranges of individuals changed with the emergence of new available gaps and in response to reproduction needs. Tracking a dispersant young male showed a trajectory in stages and made obvious the high risk of predation during this period. Our results here, and previously, indicate the possible effect of habitat quality on space use and relationships between individuals, emphasising the importance of the quality and structure of habitat in the conservation of the southern water vole.

Keywords *Arvicola sapidus* · Dispersal · Habitat quality · Home range · Intraspecific relationships · Mediterranean riparian environment

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Introduction

The distribution of species in the environment arises due to interactions between the spatial structure of the landscape and behavioural processes that result from individual choices: the setting up of a home range, territoriality, dispersal, mating and reproduction strategies, social system, feeding behaviour, responses to competitors and predators, and life history, amongst others (Rushton et al. 2000). Knowledge of patterns of occupation and the use of space is especially important if we are to specify the space requirements of individuals, to determine the scale of movements involved in daily activities and to evaluate the degree of sociality. Spatial use is influenced by the availability and abundance of resources within the environment (food, mates, shelter and nesting sites) and the ratio between the cost and benefit of maintaining a territory (Ostfeld 1985, 1990; Ims 1987). Social behaviour is another important component of population dynamics. Such behaviour affects variations in birth rates and mortality, limitations on the size of the breeding population, control of the sexual maturation period and the dispersion of individuals (Krebs et al. 2007). Dispersal is related to the connectivity between

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groups and the capacity to respond to loss and fragmentation of habitat (Schooley and Branch 2006). Consequently, it is particularly important for species that show metapopulation structures (Sutherland 1998; Woodroffe 2003).

The southern water vole, *Arvicola sapidus*, is a medium-sized arvicoline species endemic to the Iberian Peninsula and France (Saucy 1999). It is present near flowing or stagnant water, wet meadows and seasonally flooded areas (Ventura 2007; Pita et al. 2013; Rigaux 2015), provided that these places are covered with abundant herbaceous vegetation, mainly helophytes, and the land margins are suitable for the digging of burrows and galleries (Ventura 2007; Mate et al. 2013). Over most of its range, it occupies linear habitats that follow the course of rivers and streams and which are highly sensitive to change, especially anthropogenic changes. Southern water vole populations present metapopulation dynamics (Fedriani et al. 2002; Román 2007; Pita et al. 2013), with natural extinction and recolonization phenomena (due to the *rescue effect* of dispersing individuals) that generally result in low population densities (Telfer et al. 2001). This, along with its limited geographical distribution, makes this species very susceptible to sharp reductions in population as a result of unexpected disturbances (Araújo et al. 2011). The southern water vole is a strict herbivore (Ventura et al. 1989; Garde and Escala 2000; Román 2007), and because of the severe low abundance of water in Mediterranean habitats during summer (aestival drought), seasonality of food availability is considered a key factor that influences its demographic dynamics and patterns of reproduction (Román 2007). Although some aspects of their ecology have been studied in some depth (e.g. Ventura and Gosàlbez 1987, 1992; Ventura et al. 1989; Garde and Escala 1996a, b, 2000; Fedriani et al. 2002; Román 2007; Pita et al. 2011; Mate et al. 2013, 2015), information on their spatial ecology is still limited (Pita et al. 2010), and to the best of our knowledge, there are no studies of this kind concerning Mediterranean mid-mountain riparian environments.

We have previously studied habitat selection and the inter-specific relationships of *A. sapidus* in Mediterranean mountain environments (Mate et al. 2013, 2015, unpublished data). The lack of studies on the occupation and use of home ranges by the southern water vole in Mediterranean riparian environments led us to undertake this work, using the technique of radio tracking to generate the data. Along the study area, we set the following objectives: (a) to determine the size of home ranges occupied and used by southern water voles in a stretch of a Mediterranean mountain river showing a mosaic of different habitat conditions; (b) to relate the size of the home range (area and length) with the mean distance travelled daily (energy expenditure) and the population density (carrying capacity); (c) to estimate the possible relationship between habitat quality and spatial occupation; and (d) to observe and describe patterns of social behaviour both of individuals within a group and between groups. This work aims to provide

evidence to address the hypothesis that the quality and structure of habitat play an important role in the selection, occupation and use of space, and interactions between individuals. This knowledge could be useful to establish what actions could help to preserve the species.

Materials and methods

Study area

The study was conducted along the Montsant River (41°10′–41°18′N and 0°53′–0°45′E, NE Iberian Peninsula), a secondary tributary of the Ebro River (Fig. 1), which crosses the karstic massif of Serra de Montsant (maximum height, 1163 m) from NE to SW. It has a typical Mediterranean regime, with strong fluctuations in flow that cause large seasonal changes; it undergoes severe drought in many places along the watercourse in the summer and sudden floods during spring and autumn. Reservoirs at Margalef and La Vilella Baixa regulate the water flow and act as physical barriers to certain vertebrate species (Orta and Ruiz-Olmo 1987). There is a Mediterranean climate in the area (Pascual 2007), with a mean annual temperature of 11–14 °C and a mean annual rainfall of 450–600 mm. During the study period (July–August 2011), the mean temperature was 23.9 °C (min. 14.0 °C, max. 40.0 °C) and the mean daily rainfall was 0.12 mm. The riparian environments along the valleys that the Montsant River occupies have areas of cropland (orchards, vineyards, olive groves, and fields of peach and hazelnut) alternating with strips of riparian forest, wasteland, dry grassland, scrubland and a few fragments of Mediterranean forest. The region hosts an important range of fauna, with a large diversity of species (Barrull and Mate 2007). Regarding the species susceptible to establish interspecific relationships with the southern water vole, we can highlight predators such as the genet (*Genetta genetta*), the stone marten (*Martes foina*), the red fox (*Vulpes vulpes*), the wild cat (*Felis silvestris*), the grey heron (*Ardea cinerea*), the Bonelli's eagle (*Aquila fasciata*), the eagle owl (*Bubo bubo*), the tawny owl (*Strix aluco*) and the barn owl (*Tyto alba*), amongst others, or potential competitors such as the black rat (*Rattus rattus*).

The stretch of the river where we captured southern water voles and radio tracked them is located between Molí del Vilar and Molí del Mig (in the municipality of Margalef, Province of Tarragona), on the western slope of the Serra de Montsant. It is situated approximately 2 km downstream of the Margalef dam (Fig. 1). The study area extended along 825 m of river, with a mean width of the watercourse of approximately 5.3 m (min. 2.2 m, max. 12.5 m). This stretch was chosen for three reasons: (1) the habitual presence of southern water voles (at least for the 5 years prior to the study); (2) the mosaic of different habitat conditions—optimal, suboptimal and hostile (according to categorization in Mate et al. 2013); and (3) good accessibility parallel to the river (along trails and
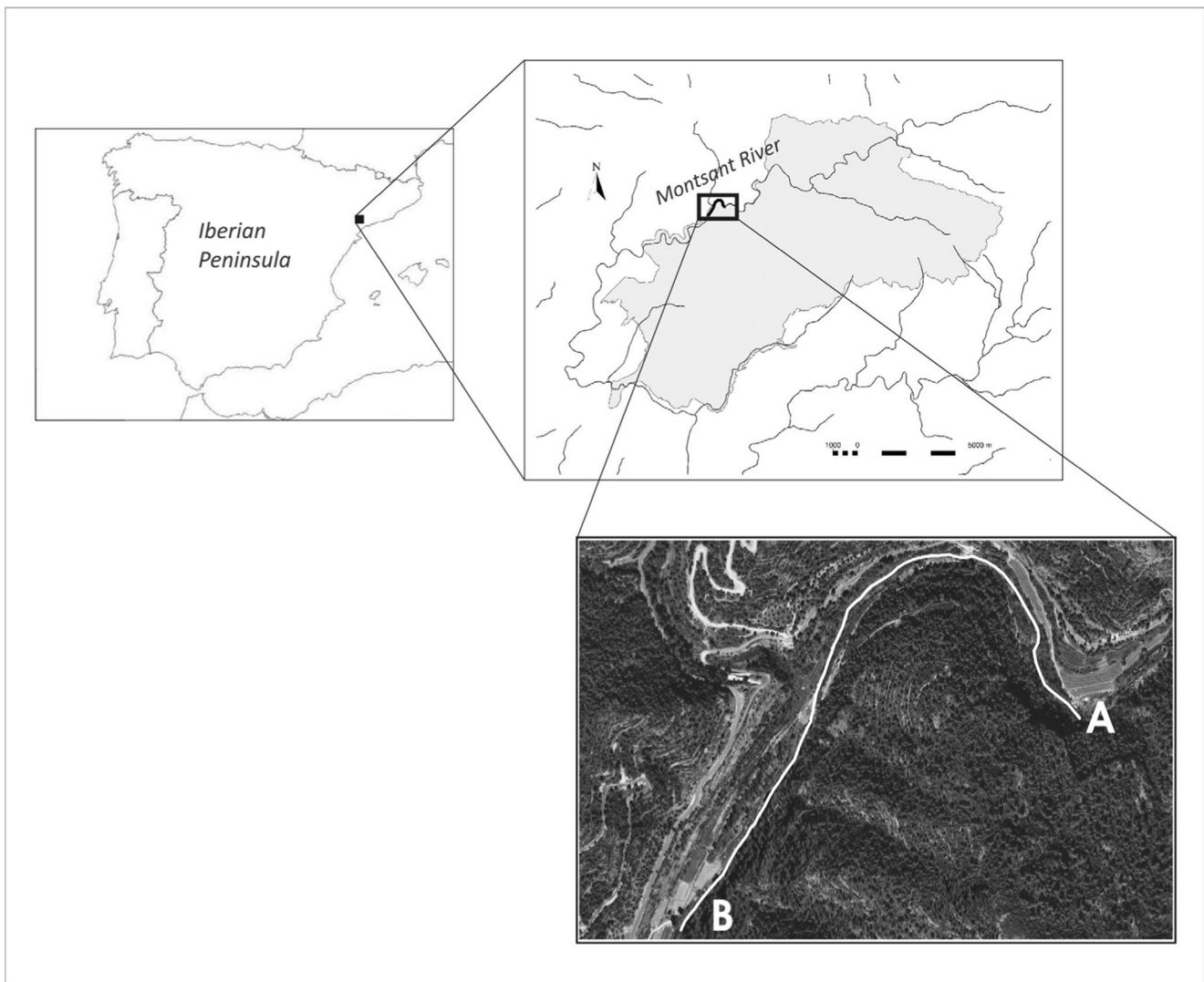
Fig. 1 Stretch of the Montsant River where the study of the spatial ecology of the southern water vole was carried out, between Molí del Vilar (*A*) and Molí del Mig (*B*) (in the municipal district of Margalef, Province of Tarragona, Catalonia, Spain)

paths) which allows minimal interference with the activity of the arvicoline. The stretch includes a series of patches with different features: areas of cliffs where the river flows through gorges with no herbaceous vegetation and only a few trees; areas dominated by trees (*Salix* spp., *Populus nigra*, *Fraxinus angustifolia*) and shrubs (*Coriaria myrtifolia*, *Rubus ulmifolius*, *Rosa* spp., *Crataegus monogyna*, *Cornus sanguinea*, *Viburnum tinus*, *Clemmatis* spp., *Hedera helix*), sometimes interspersed with small patches of megaphorbic vegetation (*Epilobium hirsutum*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Dorycnium rectum*, *Mentha* spp., *Humulus lupulus*); and areas dominated by reeds and rushes (*Phragmites australis*, *Typha* spp., *Scirpus holoschoenus*, *Juncus* spp., *Arundo donax*), sometimes alongside patches of watercress (*Apium nodiflorum*).

The animals were captured and radio tracked along two subsections physically separated by a weir about 3 m high, with a waterfall on the north bank, not an insurmountable obstacle for

voles (it implied a displacement over the ground of some 25 m between the two subsections). Subsection 1 (SS1; watercourse 416 m in length and of 4.9 m mean width), downstream of the weir, consists of a succession of habitat patches with distinct characteristics: areas of flat rocky riverbanks with no vegetation in one bank and trees (*Salix cinerea*, *Ficus carica*) and shrubs (*R. ulmifolius*) on the opposite bank; areas of lush reeds (*P. australis*) with small fragments of cattails (*Typha* spp.) and rushes (*S. holoschoenus*); and shady areas where trees (mainly *Salix* ssp.) and bushes were dominant (*R. ulmifolius*, *C. sanguinea, C. myrtifolia*). Subsection 2 (SS2; watercourse of 165 m in length and 6.8 m of mean width), upstream of the weir, was characterized by a pond about 50 m long and 2.5 m deep, with calm water, surrounded by a broad strip of vegetation (mainly reeds and cattails), and was externally limited by some shrubs (*R. ulmifolius*, *C. myrtifolia*) and isolated trees (*Salix alba*, *F. angustifolia, P. nigra*).

Fieldwork

The occupation and use of the space by the southern water vole were analysed from data collected by radio-tracking animals that had been captured, fitted with collars and released. Captures and radio tracking were conducted during the summer of 2011, with the pertinent authorizations from the Biodiversity and Animal Protection Service of the Autonomous Government of Catalonia. The presence of individuals along the stretch had been confirmed in previous surveys, which systematically detected typical signs of the presence of the species (faeces, latrines, feeding stations and pathways through the vegetation; Fedriani et al. 2002; Román 2003; Pita et al. 2010). The stretch chosen was pre-baited with chopped apple every 4 days, 3 weeks before the capture period, so the animals become accustomed to these provisioning points (Gurnell 1980; Román 2007). A total of 30 single-entry live cage traps with a tilting door (20, 30 × 15 × 14-cm, and 10, 60 × 15 × 15-cm traps) were used for the captures. The traps were baited with plenty of apple and cattails and covered with vegetation. The cages were positioned every 10–15 m at the sites most visited by southern water voles during the habituation period, as well as at intersections of pathways and points with fresh latrines or feeding stations. This distance was deemed sufficient since the usual displacements of an adult individual range from 15 to 26 m, according to Román (2007). Each cage was left in the same place for 2 days as, after the first day, the number of new captures tends to be small and the number of recaptures large (Garde 1992; Román 2007). The catches spanned 8 days, with a total effort of 208 trap days. Traps were placed on both sides of the riverbank, covering some 570 m of the river. Individuals of non-target species were released immediately at the point of capture. When the radio-tracking period ended, the animals were recaptured to recover the radio collars. Special care was taken with nursing females during this process; we attempted to shorten the recovery period as much as possible and return them to the point of capture as soon as possible.

To fit the radio collars, the animals were sedated with isoflurane (IFL, IsoFlo®, Esteve Veterinaria-Abbott Laboratories, Barcelona, Spain): an inhalant agent that allows good control over the induction and depth of anaesthesia is eliminated through the airways and has fewer side effects than other sedative agents (Laredo et al. 2001; Breck and Gaynor 2003). The anaesthetic reduces stress during handling and minimizes traumatic remembrance (Prout and King 2006; Parker et al. 2008), thus facilitating the recapture of individuals for subsequent recovery of transmitters. The dose (initial, 5.0 % IFL + 5.0 l/min O_2; maintenance with auxiliary mask, 1.5 % IFL + 0.6 l/min O_2) was administered using portable anaesthetic equipment (McKinley type 2 anaesthetic machine, Everest Veterinary Medical Technology, Molins de Rei, Spain). The anaesthetic protocol was supervised by a veterinary surgeon from the Biodiversity and Animal Protection Service of the Autonomous Government of Catalonia and followed the recommendations of Olfert et al. (1993) and Sikes et al. (2011) during anaesthesia and handling of the animals.

A collar with a radio transmitter (Pip Ag393 3g, Biotrack Ltd., Wareham, Dorset, UK; 150.0–150.9 MHz) was fitted to each individual weighing more than 100 g, for which the weight of the collar represented less than 5 % of body weight, so as not to increase necessary energy expenditure excessively (Wilson et al. 1996; Sikes et al. 2011). Individuals weighing less than 100 g were fitted with a transmitter that was stuck directly to the dorsal fur using a tissular adhesive (*n*-butyl cyanoacrylate, VetBond® 3M, St. Paul, MN; Kirk et al. 2000; Lumsden et al. 2002) since a collar could strangle them or prevent feeding as they grow (Sikes et al. 2011). Each individual captured was sexed, weighed and their standard biometric measurements taken (Gosàlbez 1987). Young and adults were distinguished by body weight (adults, >180 g; juveniles, <180 g; Garde 1992) and their reproductive status determined (active or inactive) based on the position of the testis (abdominal or scrotal) for males and on vulva perforation and size of nipples (udder appearance) for females (Román 2007). Pregnant females were identified by abdominal palpation (Barnett and Dutton 1995). The average time for placement or removal of the radio collar and taking biometric measurements ($\bar{x} \pm$ s.e., $n = 20$) was 7.3 ± 0.7 min. Once the handling was finished, the animals we left resting in the same cage in which they were captured (with a cattail bed, food and water ad libitum), in a quiet place and covered with a blanket, and we monitored them as they regained consciousness. Once conscious, the animals were returned to the wild at the same point of capture.

Once the catching period was completed, individuals were radio located at 3-h intervals (eight locations per individual and day: UTC 0530, 0830, 1130, 1430, 1730, 2030, 2330 and 0230 hours), from 9th July to 24th August (47 days). The water voles were searched for along the river using a Sika receiver (model S/N 701W, Biotrack Ltd.) and a handheld rigid three-element Yagi antenna (Lintec Antennas, Goring-by-Sea, West Sussex, UK). Their locations were determined by homing in and then by triangulation, taking bearings at close range from at least three locations (White and Garrott 1990; Macpherson and Bright 2010). The reference positions of the observer (UTM) were measured using a handheld GPS device Garmin eTrex® (Garmin, Romsey, Hampshire, UK). The GPS has a characteristic error of ±5 m, which was considered sufficiently precise since the range occupied by the southern water voles cover a few hundred square metres (Pita et al. 2010). The coordinates of the locations for each individual were estimated and plotted on a digital orthophotomap (1:2500 scale, resolution of 25 cm/px, 2010 flight; Institut Cartogràfic de Catalunya).

Data analysis

Individual home ranges were estimated using the minimum convex polygon method (MCP) and the fixed kernel method (FK) (Knight et al. 2009). The lack of a suitable method to estimate home ranges in linear habitats means that a combination of both methods is recommended (Kernohan et al. 2001; Boyle et al. 2009) to contrast the estimates and acquire an estimate that avoids the worst shortcomings of each (Blundell et al. 2001; Knight et al. 2009). MCP is robust when the available data are autocorrelated (Harris et al. 1990), but the delimited area is strongly influenced by peripheral points, which often only represent places occasionally visited by individuals, leading to an overestimation (White and Garrott 1990; Kenward 2001). Kernel methods are unaffected by peripheral values (Kenward 2001) and may therefore underestimate the area used when there are multiple locations in one place (Pattishall and Cundall 2008), but they provide more information on the occupation and the intensity of space use by individuals (Seaman and Powell 1996). The smoothing parameter h was fixed at 1, in FK, given that least squares cross-validation provides home ranges that undervalue the passageways between the nuclei most commonly occupied by the animals (Blundell et al. 2001; Pattishall and Cundall 2008; Knight et al. 2009).

Home ranges were estimated by MCP considering 100 % of locations (MCP100), and we verified that the number of locations was large enough for the graphic of observations/area to stabilize. Home ranges were estimated by FK using the 95 % isopleth (FK95, the area within which the animals spend 95 % of their time), and the *core area* was considered to be the area delimited by the 50 % isopleth (FK50, the area where the animals spend 50 % of their time). Since the arvicolid mainly occupies narrow river and riverbank strips of variable length within the study area (Mate et al. 2013), the unrestricted home ranges obtained (by MCP and FK) were clipped in order to adapt them to the morphology and the occupation of the river (MCP100$_{clip}$, FK50$_{clip}$ and FK95$_{clip}$). To carry out this adjustment, the river-and-banks surface of the stretch studied was obtained from its delimitation on the Cartographic Institute of Catalonia map of the area (sheets 255-130 and 256-130) using the *Vissir* application (http://www.icc.cat/vissir3/). The reliability of the estimates of home ranges was obtained by considering a sufficient number of locations and by ensuring that autocorrelation between consecutive locations had little influence. For each situation studied (home range/sociability per individual and period), more than 50 locations were used and exceptionally (in tracking week to week) only between 30 and 50 locations were considered, which is the minimum number admissible (Seaman et al. 1999; Millspaugh et al. 2004). We also verified that the 3-h interval used in tracking the animals along the Montsant River was longer than the minimum sampling time interval that ensures low autocorrelation of data

(Schoener 1981; Swihart and Slade 1985). In a complementary manner, the length of the stretch of river occupied (linear range length, LRL$_{max}$) and the daily distance travelled by each individual, as well as the linear population density and the quality of the habitat occupied, were also evaluated. The daily distance travelled was obtained as the sum of the distances between consecutive locations. The linear population density was estimated based on the size of the home ranges during the period when all the individuals were present. Habitat quality was determined from information gained from 33 sampling points distributed linearly over the radio-tracking stretch (one every 25 m). The method used was as follows: (a) for each individual, sampling points within each kernel isopleth were identified; (b) each point was categorized as optimal, suboptimal or hostile, according to the criteria described in Mate et al. (2013), and was weighted by the values 100 (optimal), 50 (suboptimal) and 0 (hostile); (c) the quality of the habitat was defined as the weighted mean of the values of the points included in each kernel. Only data for adults and non-disperser juveniles were included in the analysis. Disperser individuals do not show stable home ranges, and often during the dispersion, they are forced to occupy (as transients) areas of suboptimal or hostile conditions temporarily (Lindstedt et al. 1986; Tedesco 2010; Mate et al. 2013). Moreover, very young individuals occupy small home ranges due to their low energy requirements (Lindstedt et al. 1986) and remain closely linked to their place of birth: near the maternal territory (Myllymäki 1977; Lambin et al. 1992). To relate these variables with the size of the home range, the Pearson's correlation coefficient adjusted for the sample size was calculated.

To determine sociality amongst individuals, we assessed static interactions (home range overlapping) and dynamic interactions (simultaneous use of the same space; Macdonald et al. 1980). To estimate static interactions, the overlapping of home ranges (FK95$_{clip}$) was calculated for each pair of individuals (over the same period of time)

$$\text{Overlap} = \frac{AB}{A + B - AB} \times 100$$

where A is the area occupied by individual 1, B is the area occupied by individual 2, and AB is the overlapping area occupied by both 1 and 2. We also determined the proportional area occupied by each individual within the home range of the other ($S_{A \to B}$ (%) and $S_{B \to A}$ (%)). To estimate dynamic interactions, we used the *coefficient of sociality, S_C* (Kenward et al. 1993), a variant of the index of Jacobs (Jacobs 1974). For each pair of animals, the ratio is expressed as

$$S_C = \frac{d_E - d_O}{d_E + d_O}$$

where d_E is the mean distance between locations (500 random locations for each animal) and d_O is the mean distance observed between locations obtained simultaneously. The

coefficient takes values between −1 and +1: −1 indicates avoidance; 0 indicates that animals move independently and ignore each other; and +1 indicates attraction. The threshold for considering the locations of two individuals as simultaneous was established as within 15 min as this is the mean time between successive locations of two individuals during the radio tracking.

In any dispersive movement, three stages can be differentiated over the time: emigration (the individual leaves its origin site); transience (the individual moves through unknown sites over many days); and immigration (the individual reaches the new site) (Ims and Yoccoz 1997). Thus, the size and evolution of the degree of overlapping of the areas occupied by individuals (FK95$_{clip}$) was calculated using approximately weekly intervals (W1: 09/07–14/07; W2: 15/07–20/07; W3: 21/07–26/07; W4: 27/07–01/08; W5: 02/08–07/08; W6: 08/08–13/08; W7: 14/08–19/08; W8: 20/08–24/08) to detect dispersal. When there is dispersion, the proportion of preserved home range (compared to that of the reference period W1, PRS$_{W1}$) decreases over time and tends to zero when considering extremely long time periods. The tendency to disperse was evaluated in young individuals because these individuals are more susceptible to dispersion (Dobson 1982; Brandt 1992).

Data analysis was carried out, graphs plotted and figures designed using the software RANGES 8 v.2.18 (Anatrack Ltd., Wareham, Dorset, UK) and MiraMon v.7.0 (CREAF, Bellaterra, Spain).

Results

A total of nine individual southern water voles were caught along the stretch of study (five adults: three males and two females; four juveniles: three males and a female). The high rate of recapture ($\bar{x} = 3$; range = 0–7) was probably due to a lack of negative remembrance of catching and handling (Ryder 1962; Prout and King 2006) along with low population densities in the study area (Mate and Barrull 2008; Mate et al. 2013), which seems to ensure that all resident individuals were trapped. The weight of adult individuals ranged between 240 and 286 g ($n = 3$) for males and between 217 and 235 g ($n = 2$) for females. For all the young, the males weighed between 77 and 163 g ($n = 3$) and the females weighed 164 g. Group 1 (G1) occupied SS1 and consisted of four males (two adults, M2 and M3, and two young, M4 and M5) and an adult female (F1). Group 2 (G2) occupied SS2 and consisted of two males (an adult, M7, and a juvenile, M6) and two females (one adult, F8, and one juvenile, F9; Table 1). Each subsection was occupied by an apparently cohesive group of individuals. During the radio-tracking period, two individuals disappeared, probably due to predation: the adult male M3, on 20th July, and the disperser male M5, on 16th August. The female F1 became pregnant and gave birth to twins, which were found in an outside nest on August 26th and had an approximate age of 10 days (they had not yet opened their eyes). The female F8 showed signs of being in advanced pregnancy when recaptured on August 25th. When radio tracking ended, the individuals freed from the collar transmitter were in good physical condition (weight gain, no ectoparasites and no injuries around the neck: no wounds, skin irritation or lack of hair; Gil de Mendonça 1999).

Home ranges

During the radio-tracking period, a total of 2727 locations were obtained ($\bar{x} \pm s.e. = 303 \pm 38$ locations/individual; Table 1). The MCP100$_{clip}$ home range estimations provided

Table 1 Summary of data obtained from the capture and 2 months of radio tracking of nine individual southern water voles in the Montsant River

Ind	Sex	Age	w_i	locs	MCP100$_{clip}$	FK95$_{clip}$	FK50$_{clip}$	LRL$_{max}$	Dist$_{day} \pm$ s.e.	VH50	VH95
F1	F	A	217	357	5164.7	6284.6	1774.3	312.6	298.0 ± 25.4	100.0	87.5
M2	M	A	275	371	3276.6	4125.8	1308.3	198.6	284.1 ± 22.5	87.5	85.7
M3	M	A	286	91	4256.2	5366.6	2349.6	276.3	451.2 ± 53.4	100.0	78.6
M4	M	J	77	123	1510.0	928.6	221.2	114.7	140.3 ± 12.8	75.0	66.7
M5	M	J	143	297	6374.5	7192.7	2043.0	413.6	249.1 ± 24.7	83.3	40.9
M6	M	J	163	372	1169.1	549.9	215.5	75.2	87.9 ± 5.9	100.0	100.0
M7	M	A	240	372	2051.5	927.0	336.4	113.8	126.6 ± 8.2	100.0	100.0
F8	F	A	235	372	1731.9	1311.5	508.6	98.1	158.7 ± 9.2	100.0	100.0
F9	F	J	164	372	2186.7	1426.5	396.5	143.4	157.5 ± 12.5	100.0	100.0

w_i (in grams): weight at the time of capture; MCP100$_{clip}$ (in square metres): estimate of the total area of home range by the minimum convex polygon method; FK95$_{clip}$ and FK50$_{clip}$ (both in square metres): estimates of the total area of home range and the *core area*, respectively, according to the fixed kernel method; LRL$_{max}$ (in metres): maximum length of home range; Dist$_{day} \pm$ s.e. (in metres): mean distance travelled daily; VH50: estimated value of the habitat quality of the *core area*; VH95: estimated value of the quality of the habitat of the total area of home range

Ind individual code, *M* male, *F* female (sex), *A* adult, *J* juvenile (estimated age), *locs* number of locations for individual

a mean size ($\bar{x}$ ±s.e.) of 2668.3±503.6 m^2 (range=1169.1–5164.7 m^2) for individuals with stable home ranges (n=8). M5, the disperser, showed a total home range of 6374.5 m^2. However, in the estimate obtained by the kernel method, FK95$_{clip}$ provided a mean size of 2615.0±806.1 m^2 (range=549.9–6284.6 m^2) for individuals with stable home ranges and 7192.7 m^2 for M5. On average, individuals in G1 presented home ranges larger than those of individuals in G2 (p=0.0195; G1=4176.4 m^2, range=928.6–6284.6 m^2; G2=1053.7 m^2, range=549.9–1426.5 m^2). The FK50$_{clip}$ estimates of the *core areas* for individuals with stable home ranges gave a mean size ($\bar{x}$ ±s.e.) of 888.8±289.2 m^2 (range=215.5–2349.6 m^2), whilst for individual M5, the estimated size was 2043.0 m^2. On average, individuals in G1 also presented larger *core areas* than individuals in G2 (p=0.0303; G1=1413.4 m^2, range=221.2–2349.6 m^2; G2=364.3 m^2, range=215.5–508.6 m^2). The *core areas* accounted on average for the 33.1 % (range=23.8–43.8 %) of the total home range. For all individuals with stable home ranges, the time to achieve independence between locations was estimated at 2 h. The reliability of the FK home-range estimations was ensured by setting an interval of 3 h between recorded locations and the use of a sufficient number of locations for each period considered. Meanwhile, the number of locations required to stabilize home ranges estimated by MCP was evaluated as less than 200 locations for F1, M2, M5 and F8; less than 150 locations for M7 and F9; and less than 90 locations for M3, M4 and M6. In the study area, the distance travelled daily by animals correlate strongly with the size of the home range (r=0.93 and 0.94 for FK95$_{clip}$ and FK50$_{clip}$, respectively). For all individuals with stable home-range areas, the mean distance travelled daily ($\bar{x}$ ±s.e.) was 213.0±43.0 m (range=87.9–451.2 m). For individuals in G1, the mean distance travelled daily was 293.4 m (range=140.3–451.2 m), and for individuals in G2 it was 132.7 (range=87.9–158.7 m).

For all the individuals, the main *core areas* were located in the most optimal areas of the home range. The mean habitat quality value of the *core areas* occupied by individuals from G1 at SS1 was 90.6, and the mean value of the *core areas* occupied by G2 at SS2 was 100.0. Regarding the total home range (FK95$_{clip}$), individuals from G1 (except M5, the disperser) occupied patches of unequal characteristics (seven optimum, three suboptimal and two hostile). The mean value of the habitat quality in the space occupied was 79.6 (range=66.7–87.5). Individuals from G2 occupied four patches of optimal quality: 100 was the mean habitat quality value in the space occupied. Regarding M5 during dispersal, this male occupied a stretch of river with an overall habitat quality of 40.9 (two optimal patches, five suboptimal and four hostile; Table 1).

For all the adults and juveniles with stable home ranges, the correlation between the size of FK95$_{clip}$ and the quality of the occupied space was estimated at r=−0.88. The lower quality

of the habitat in SS1 (in relation to SS2) coincided by an increase of +230 % in the mean size of the total home range of individuals from G1. With suboptimal habitat (SS1), the population density was estimated at 0.9 individuals per 100 m, when all the individuals in the group were present (five individuals occupying 575 m of the river). With optimal quality of habitat (SS2), the population density was estimated at 2.4 individuals per 100 m (four individuals occupying 167 m of the river).

Reorganisation of space

The disappearance of the male M3 from G1 led to the reorganisation of the home ranges. In particular, in the absence of M3 (P2: 21/07–24/08), there was a considerable increase in both the total range and the *core area* of the home ranges of the adult individuals in the group—+52.6 % in FK95$_{clip}$ and +16.3 % in FK50$_{clip}$ for F1 and +178.0 % in FK95$_{clip}$ and +197.7 % in FK50$_{clip}$ for M2—as well as a shift in home ranges (Fig. 2). F1 stopped frequenting part of the range she occupied whilst M3 was alive (P1: 09/07–20/07), and M2 occupied 56.3 % of the space left by M3, that with the best habitat quality.

On the other hand, the finding of a nest with two pups belonging to the female F1 (G1) offered us the opportunity to observe differential use of space at different moments of the reproductive period. In particular, despite maintaining the size of home range, the core area of the female moved downstream, around the location of nest site, in the days before the estimated date of giving birth (Fig. 3).

The male M5 gradually left his natal range, showing, over time, distensions and contractions in its home range and a decrease in the degree of overlapping with other occupied areas (preservation of occupied space compared with the reference week W1, which are concordant with dispersant behaviour; Lambin et al. 2012). During the weeks W3 and W4, there were long-distance movements which coincided with crossing a gorge stretch of the river, with nearly vertical cliffs and sparse vegetation (usually shrubby and/or arboreal), clearly hostile to settlement. In weeks W5 and W6, the size of the occupied home range decreased (and, specifically, the size of the core area), coinciding with arrival at a patch of uneven features (three optimal, one suboptimal and two hostile). The percentages of the home range preserved compared to the area of the home range in the reference week, W1, were 82.8 % at W2, 57.8 % at W3, 4.9 % at W4, and 0.0 % at W5 and following weeks (Fig. 4). This behaviour was not observed in the other young individuals of similar age (M6 and F9).

Interactions

The estimation of interactions (static: overlap of home ranges, FK95$_{clip}$; dynamic: S_C) between pairs of individuals showed
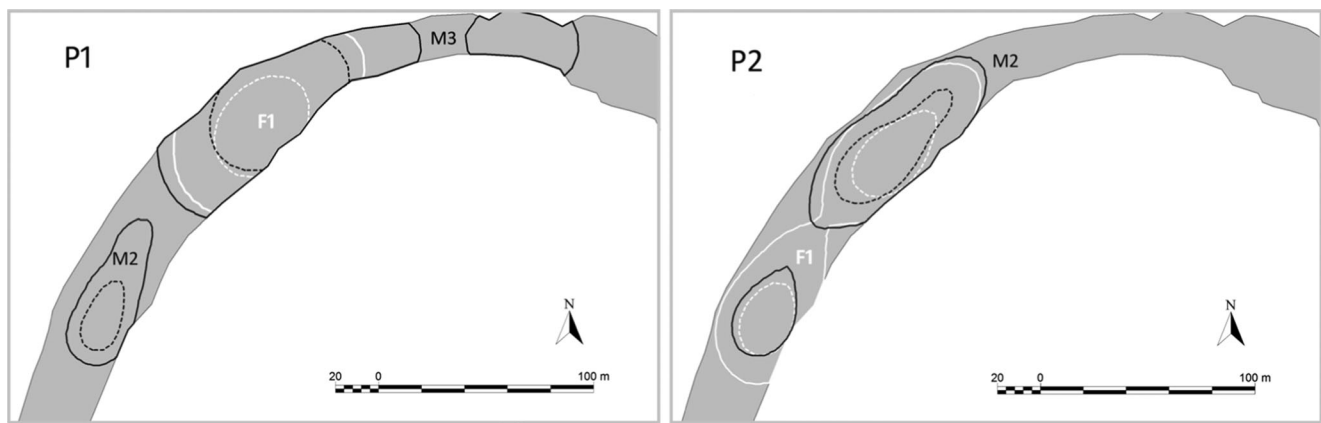
Fig. 2 Home ranges (FK95$_{clip}$, *solid line*; FK50$_{clip}$, *dashed line*) of female F1, male M2 and male M3 (group G1). *P1*: July 9th to 20th (period before the disappearance of M3); *P2*: July 21st to August 24th (period after the disappearance of M3; reorganisation of the home ranges). F1, *white line*; M2, *grey line*; M3, *black line*

nearly no interaction between G1 and G2; the male M3 from G1 was the only individual who showed possible interaction with individuals from G2 (overlap range = 0.2–1.3 %; S_c range = −0.02–0.02). Within G1, interactions were observed between adult couples (F1 and M3 during period P1, and F1 and M2 during period P2) and between M2 and M4 (adult and juvenile males). There was no interaction between the two adult males (M2 and M3). For pairs of individuals from G1 with overlapping home ranges, the static interaction ranged between 65.2 and 68.0 % and the coefficient of sociality ranged between 0.16 and 0.30. Within G2, all the individuals interacted with each other. The mean static interactions and the mean coefficient of sociality were estimated at 53.7 % (range = 32.0–69.8 %) and 0.12 (range = 0.04–0.18), respectively (Fig. 5).

The rate of interaction between the individuals that formed the adult couple from G1 was significantly higher during the reproductive period (W4: estimated week of mating; W7: estimated week of giving birth). The mean area occupied by male M2 within the home range of female F1 was estimated as 88.2 % (range = 58.9–100.0 %) for weeks W4–W7, whilst

the mean coefficient of sociality was estimated at 0.34 (range = 0.21–0.41) for the same period (Table 2). Similar behaviour was observed for the couple F8 and M7 from G2.

In the area of study, adult individuals in both groups were observed to be monogamous: a male defended only one adult female. In G1, the dominant male M3 monopolized female F1 until 20/07 (when M3 disappeared), and from that moment, M2 became the dominant male and was paired with F1 for the rest of the time. In G2, male M7 and female F8 constituted the dominant couple. The young female (F9) remained celibate until the end of the tracking period.

Discussion

Individuals tend to restrict their daily activities to well-defined areas they are familiar with (Leuze 1976; Erlinge et al. 1990). The size of the home ranges (area and length) may vary depending on the size of the animal, its age or its sex (individual energy requirements) and can be driven by several factors, including: (a) differences in habitat characteristics or in the
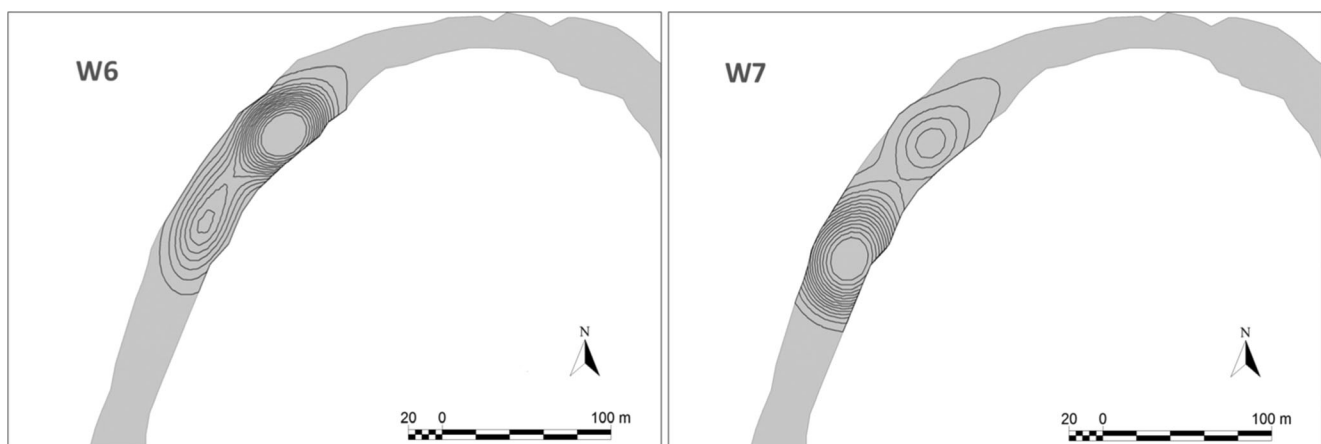

Fig. 3 Differential occupation of space by female F1 (FK30-99$_{clip}$) according to the reproductive cycle (W6: 08/08–13/08 and W7: 14/08–19/08, estimated delivery week)
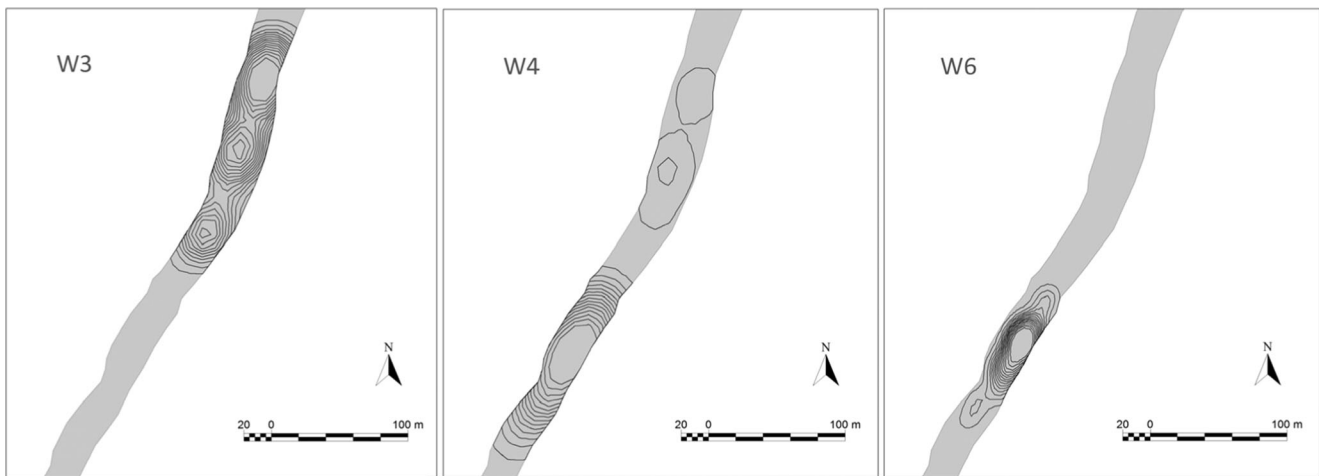
Fig. 4 Weekly evolution (*W3*, *W4*, *W6*) of home range (FK30-95$_{\text{clip}}$) of male M5 exhibiting dispersant behaviour

distribution and abundance of resources (food, shelter, mates); (b) the number of individuals that make up the competitor populations (intraspecific and interspecific); and (c) predatory pressure (Harestad and Bunnell 1979; Ostfeld 1985; Wolff 1985; Erlinge et al. 1990; Lambin 1994; Bond and Wolff 1999; Fisher 2000; Jonsson et al. 2000; Schradin and Pillay 2006; Liesenjohann et al. 2011).

Along the Montsant River, the radio tracking of a small number of individuals (due to the low densities of southern water vole in the study area) allowed us to study the dynamics of two neighbouring groups occupying zones of different habitat quality. Despite the impossibility of generalizing the results obtained from small samples, and recognizing the need to confirm these results in other places with similar characteristics throughout the distribution area, interest in this prospective study is derived from: (a) it allowing us to check our initial

hypothesis against the results obtained, based on the monitoring of two closed and cohesive groups of individuals and (b) it being the first study of its kind conducted in Mediterranean riparian habitats (the natural habitat prevailing in the current distribution area of the species).

With the limitations mentioned above, the results show the relationship between the quality of the habitat in subsections occupied by individuals, and the size of the home ranges and the mean distance travelled daily. Along the subsection of the better quality habitat (SS2: optimal), the area and length of individual home ranges and the distances travelled daily were lower than those along the subsection with poorer quality habitat (SS1: suboptimal). An herbivorous diet rich in cellulose and with a low energy content, and the high energy demand resulting from a semi-aquatic life (Fish 2000), makes the productivity of the habitat especially important for the southern water vole (Ostfeld 1985; Gębczyński 2006; Halle 2006). The selection and preferential use of optimal habitats
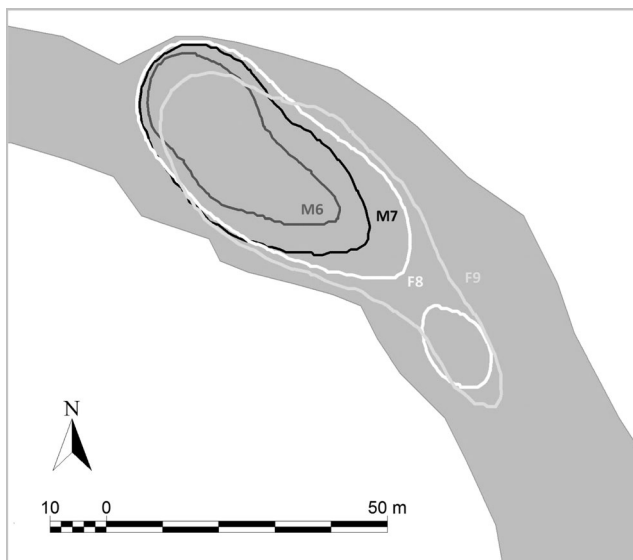

Fig. 5 Home ranges (FK95$_{\text{clip}}$) of individuals from group G2 during the radio tracking. Males: M6, *dark grey line*; M7, *black line*. Females: F8, *white line*; F9, *light grey line*

Table 2 Interactions (static: overlap of home range; dynamic: Sc) between female F1 and male M2 according to the reproductive cycle

Week	Period	Overlap	$A_{F1 \rightarrow M2}$	$A_{M2 \rightarrow F1}$	S_C
W3	21/07–26/07	53.4	89.9	56.8	0.01
W4[a]	27/07–01/08	66.9	69.0	95.7	**0.41**
W5	02/08–07/08	81.9	83.1	98.3	0.21
W6	08/08–13/08	54.4	54.4	100.0	**0.41**
W7[b]	14/08–19/08	48.2	72.6	58.9	**0.33**
W8	20/08–24/08	1.3	2.8	2.2	−0.04

Overlap (in per cent): common area for individuals F1 and M2; $A_{F1 \rightarrow M2}$ (in per cent): area occupied by F1 within the home range of M2; $A_{M2 \rightarrow F1}$ (in per cent): area occupied by M2 within the home range of F1; S_C: coefficient of sociality

Bold entries remarks the periods with higher interaction between F1 and M2

[a] Estimated mating week

[b] Estimated delivery week

could be explained by the fact that if food resources and shelter are closer and more abundant, the arvicoline will cover shorter distances daily in search of food and refuge and, consequently, will minimize both energy consumption and the risk of predation (Owen-Smith 2003). In addition, the territories to defend will be smaller (Fortier and Tamarin 1998). This would also explain why the *core areas* within the home range are located in patches with better quality habitat.

The effect of competition (reducing the size of home ranges) depends on the number of individuals that make up the competitors' populations (interspecific and intraspecific) and available resources (Grant 1972). Regarding interspecific competition, along the Montsant River, the only species that is likely to establish competitive relations with the southern water vole is the black rat (*R. rattus*). The segregation of the two species across the three main niche axes (space: different habitat preferences; time: *Arvicola* is cathemeral and *Rattus* is predominantly nocturnal; resources: their preferences for food and shelter are different) and the low population density in the study area would explain the reduced effect of competition between the black rat and the arvicoline in both the subsections studied (Faus and Vericad 1981; Clark 1982; Cox et al. 2000; Garde and Escala 2000; Pita et al. 2011; Mate et al. 2013, unpublished data).

As for intraspecific competition, in the area of study, both groups showed the same effective number of individuals (if we do not consider the dispersant male from G1) and the same mating pattern, so it would be expected that competitive pressure is manifested in similar individual spatial behaviour in both groups. However, individuals from G2 occupied home ranges of smaller size, despite having some patches of suboptimal quality available that would have allowed them to expand their home range. In addition, the effect of competitive pressure should be more evident in patches of habitat with a higher density of individuals (SS2). This effect would be evident in the relegation of non-dominant individuals (young and subordinate adults) to patches of habitat of lower quality, in the reduction of the size of their home range and the lack of overlap with the areas of dominant individuals, or in the obligation to disperse (Leuze 1976; Myllymäki 1977; Lindstedt et al. 1986; Shahrul 1998; Krebs et al. 2007). Nevertheless, in the study area, individuals from G1 (but not individuals from G2) showed evidence related to possible increased competitive pressure: (a) whilst M3 was alive, the other males in the group (M2, M4 and M5) were relegated to suboptimal patches of smaller size and showed no overlap with areas occupied by the dominant male and (b) the young male M5 showed dispersal movements downstream. Thus, in the study area, it is not plausible to attribute the reduction in the size of the home ranges to intraspecific competition.

Predators are one of the main regulators of the populations of microtines (Korpimäki 1993; Hanski et al. 2001; Sundell 2006). In the study area, one would expect that in the two juxtaposed subsections, the effect of predator pressure would be similar, and in the event of a differential effect, we would expect that the intensity would be higher in SS1 (due to features that make the habitat apparently less safe and the disappearance of individuals M3 and M5 to predation). Contrary to our expectations (a reduction in the size of home ranges to minimize the risk of predation), the home ranges in G1 were larger than those in G2.

Therefore, the cause–effect relationship between habitat quality (structural features of the environment and the availability of food and shelter) and the size of the home range presents itself as the most plausible hypothesis to explain the results obtained in the study area. Competitive pressure and group structure did not show important differences between the two subsections, and the predatory pressure cannot explain the differences observed in the study area.

The population density along the subsection with suboptimal habitat (occupied by G1) was lower than that along the section with optimum habitat (occupied by G2). This result was related to the differential requirements with regard to the size of home ranges (due to habitat quality) in order to meet the needs of individuals. The population density can increase when there is more food availability since the carrying capacity of the environment is higher (Turchin and Batzli 2001). The population density along the stretches of the Montsant River studied here is lower than densities traditionally reported for linear habitats (e.g. five individuals per 100 m of river; Le Louarn and Saint-Girons 1977), but it is consistent with the results of recent studies (e.g. two individuals per 100 m; Rigaux and Charruau 2009). The lower densities found in these more recent studies along the area of distribution are indicative of a decline in the species since the 1970s, and they could be explained by the synergistic effect of the destruction and fragmentation of habitat and the effect of predation caused by the invasion of the American mink (*Neovison vison*; Melero et al. 2012; García-Díaz et al. 2013) and/or competition with other alien species such as the coypu (*Myocastor coypus*) and the muskrat (*Ondatra zibethicus*) (Rigaux and Charruau 2009). Similar results have been observed in Britain for *Arvicola amphibius*, a species with similar ecological requirements to those of *A. sapidus* (4–16 individuals per 100 m, Strachan and Jefferies 1993; 0.3–3.3 individuals per 100 m, Strachan 1997; 0.5–3.5 individuals per 100 m, Neyland et al. 2010).

Another noteworthy aspect regarding the limits of home ranges is their modification by individuals over time, which can result in the gradually adding of land on one edge of their home range and the removal of land from another edge, without leaving completely the area habitually occupied (Lidicker and Stenseth 1992; Moorhouse and Macdonald 2005). This behaviour was observed in the study area with the appearance of a vacant space and also during the reproductive period. The emergence of an unoccupied gap of equal or better quality

could motivate the reorganisation, especially if there is a sexual resource available (Moorhouse and Macdonald 2008). During the pregnancy period, the shifting of the boundaries of the *core area* would be related to the selection of the best breeding area and would be justified by the importance of cattails (*Typha* sp.) as a source of nourishment (Mason and Bryant 1975; Neyland et al. 2010; Mate et al. 2013), especially when energy requirements are higher for females (Ostfeld 1985). Moreover, the shift downstream of the male M5 from G1, moving away from its native area to a maximum distance of almost 390 m, allowed us to observe two of the three stages that characterize dispersal (emigration and transience). It also highlighted the high risk of predation during dispersion as individuals go through unfamiliar places, sometimes with low-quality habitat, and are more exposed to predators (Tedesco 2010).

Finally, the overlap of home ranges and the coefficients of sociality showed the interaction between individuals along the studied area. The minimum interaction between the groups could be interpreted as indicative of territorial behaviour of the dominant individuals, defending a scarce and valuable resources: access to the only receptive female available for the males and, for the females, access to the stagnant ponds with abundant helophytic vegetation (food and shelter) where the water is more persistent during severely low water flow. The tendency to avoid the overlapping of home ranges of adult males has also been observed in the SW of Portugal (Pita et al. 2010). In contrast, the greater dynamic interaction observed in couples of adult individuals that coincided with certain phases of the reproductive cycle would be concordant with a greater proximity of individuals during the periods of mating and giving birth (postpartum oestrus; Ims 1987; Steinmann et al. 2005). The lack of interaction during lactation would be consistent with little or no involvement of males in caring for offspring (Ostfeld 1985; Wolff 2007).

In the conservation and recovery of endangered species, it can be extremely useful to understand the factors that affect habitat selection, the occupation and use made of space and relationships between conspecifics, as well as to assess the effects caused by predators and competitors (interspecific relationships). Such knowledge may allow better targeting of actions aimed at protection, conservation and recovery (Primack and Ros 2002). Understanding the relationship between the species and its environment and knowing the effect of environment on the population dynamics are all useful in predicting the response of populations when faced with environmental changes (Bowler and Benton 2005). For *A. sapidus*, habitat selection and interspecific relationships have previously been studied by us in Mediterranean riparian environments (Mate et al. 2013, 2015, unpublished data). The occupation and use of space and the interactions amongst individuals presented in this prospective study complete the relational framework. The results obtained in this study, and in previous studies, contribute to the understanding of the ecology and behaviour of *A. sapidus* whilst demonstrating a common denominator: the importance of the quality and structure of habitat in the viability of the southern water vole, especially taking into consideration that the regional dynamics of their populations exhibit characteristics of metapopulations (Fedriani et al. 2002; Román 2007; Pita et al. 2013). The persistence of local populations is dependent on their size and rates of extinction, as well as recolonization, which are greatly influenced by isolation and habitat quality (Telfer 2000). The conservation of optimal habitats and the recovery of suboptimal habitats improve habitat productivity and, consequently, may favour survival and reproductive success, as well as providing better protection against predators. Moreover, the recovery of suboptimal and hostile habitats may reduce habitat fragmentation and restore connectivity between patches of good quality. This decrease in the degree of isolation is especially important during dispersal as the costs of the movement (energy expenditure and exposure to predators) increase with distance and time of displacement (Woodroffe 2003; Bowler and Benton 2005).

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