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Spatial segregation of two vole species (*Arvicola sapidus* and *Microtus cabreræ*) within habitat patches in a highly fragmented farmland landscape

Ricardo Pita · António Mira · Pedro Beja

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Abstract Spatial segregation is one of the common mechanisms allowing the co-existence of similar interacting species in heterogeneous environments. Analysing spatial segregation requires information on individual home-range sizes and their degree of spatial overlap. In this study, we used radio-tracking to report for the first time the home-range and core-area sizes of sympatric Cabrera and water voles and to analyse intra- and inter-specific space sharing within habitat patches in a highly fragmented landscape. Results indicated that both species exhibited strong fine-scale site fidelity and reduced variation in range size across sexes and seasons. Monogamous mating system seemed to prevail for both species, although water voles may also exhibit polygynous breeding strategies. Mean home-range

and core-area sizes of water voles (946.3 and 156.6 m²) were about twice that of Cabrera voles (418.2 and 55.1 m²). Within habitat patches, individuals of both species often overlapped their home ranges, particularly during the dry season (May–September), though intra-specific home-range overlap was generally higher than inter-specific overlap. Inter-specific space sharing was restricted to areas outside the centre of activity of animals, as no core-area overlap was ever recorded between Cabrera and water voles. Taken together, results support the view that co-existence of Cabrera and water voles in Mediterranean patchy habitats may in part result from spatial segregation among individuals, which may reflect competitive displacement or small-scale habitat partitioning. Results highlight the need to account for species interactions when designing conservation management strategies for sympatric Cabrera and water voles in fragmented landscapes.

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Introduction

Understanding the mechanisms determining the co-existence of closely related species and their organising dynamics in spatially structured environments has received increasing attention in recent years (Amarasekare 2003; Dammhahn and Kappeler 2008). In particular, co-existence of similar interacting species in patchy habitats has often challenged researchers to meet the predictions from the competitive exclusion principle, especially when niche dimensions at which species differentiate are still to be identified, or life-history trade-offs remain unclear (Hoopes et al. 2005). In this context, spatial segregation is often referred to as an

important mechanism facilitating the co-existence of ecologically similar species because competition for resources is reduced when they occupy different parts of the same habitat patches (Urayma 1996; Amarasekare 2003).

Analysing spatial segregation between interacting species requires primarily information on their spatial ecology and individual life-history traits (Eccard and Ylonen 2003; Brunjes et al. 2009). Because animals tend to defend a certain territory for resting, food gathering or breeding at least during particular periods of their life, information on site fidelity, home-range sizes and their degree of overlap is fundamental to assess eventual segregation mechanisms at the individual level (e.g. Rosenzweig 1991; Borowski 2003; Hillen et al. 2009), which in turn will determine species distribution patterns at the population level (South 1999; Eccard and Ylonen 2003; DeAngelis and Mooij 2005). Studies aiming to describe species ranging behaviour, socio-spatial organisation and inter-specific relations might also have a major practical importance when interpreting habitat size required for keeping viable populations of threatened species, on which decisions about the design and management of protected areas should be based (Simcharoen et al. 2008; Hillen et al. 2009). In particular, the spatial aggregation or segregation within and between closely related, ecologically similar and sympatric species that are threatened by the same processes should be highly informative to determine the appropriate scale for conservation planning (Brunjes et al. 2009; Oro et al. 2009).

The Cabrera vole (*Microtus cabreræ*) and the water vole (*Arvicola sapidus*) are two Arvicoline rodents with reduced and overlapping geographical ranges, occurring exclusively in the Iberian Peninsula in the case of the Cabrera vole and in the Iberian Peninsula and parts of France in the case of the water vole (Palomo et al. 2007). Both species are currently facing serious population declines and in need for conservation and management, mainly due to fragmentation and destruction of the habitats on which both species have specialised (IUCN 2009). Typically, these habitats include little disturbed and often seasonally flooded tall wet meadows and some adjacent shrubby vegetation able to provide food and protection from predators (e.g. Fedriani et al. 2002; Pita et al. 2006; Santos et al. 2006; Luque-Larena and López 2007; Pita et al. 2007; Román 2007). Overall, agricultural development, intensive herbivory by livestock and severe drought episodes are apparently the most important threats across the species' distribution ranges (Fedriani et al. 2002; Fernández-Salvador et al. 2005a, b; Pita et al. 2007; Rigaux and Charruau 2007; Román 2007).

Although the habitat characteristics required for Cabrera and water voles are relatively well known, information on their spatial ecology and hence on some of their basic life-history traits is still scarce, limiting the effectiveness of conservation efforts recommended for these species (Pita et

al. 2006, 2007; Rigaux and Charruau 2007; Román 2007). Moreover, because of their ecological similarities, it has been hypothesised that space use by Cabrera and water voles in sympatric areas might be influenced by competitive interactions and that co-existence might in part result from spatial segregation between the two species (Pita et al. 2006). Because of this, the potential for competitive interactions should be duly considered when designing habitat conservation management strategies to protect these species (Pita et al. 2006).

In this study, we addressed these issues by analysing home-range and core-area size and overlap by Cabrera and water voles within habitat patches in highly fragmented landscapes. Firstly, we assessed the foraging site fidelity of Cabrera and water voles in farmland habitats of southwestern Portugal and quantified their home-range and core-area sizes using radio-tracking techniques. Secondly, we analysed how conspecifics partition their individual home ranges and core areas and assessed the degree of spatial overlap between the two species. This information was then used to test predictions on the spatial ecology of these two species, derived from general ecological theory and previous empirical observations on their life-histories and ecological requirements. Specifically, we predicted that (a) home ranges of water voles should be larger than those of Cabrera voles, due to the much larger body size of the former species (Lindstedt et al. 1986; Swihart et al. 1988), (b) home-range sizes should change across seasons because both the Cabrera and the water voles often cease reproduction during the driest months, when the availability of food resources is presumably much reduced (Ventura et al. 1998; Fedriani et al. 2002; Pita et al. 2007; Román 2007), (c) intra-specific variation in home-range sizes and overlap should be influenced by gender in promiscuous water voles (Román 2007), but not as much in monogamic Cabrera voles (Fernández-Salvador et al. 2001), reflecting differences in mating systems between species (Wolff 2007) and (d) there should be inter-specific spatial segregation of home ranges because this is usually considered essential to enable the co-existence of similar species that apparently show no obvious partitioning of resources (Amarasekare 2003; Brunjes et al. 2009). Results of this study were then used to discuss the role of spatial processes at the individual level in explaining the co-existence of this two species in highly fragmented landscapes and to derive management prescriptions favouring the conservation of sympatric Cabrera and water voles in Mediterranean farmland.

Materials and methods

Study area and species

The study was carried out on the coastal plateau of southwestern Portugal (37°57'–37°35' N, 08°51'–08°48' W)

which is included in the thermo-Mediterranean bioclimatic zone (Rivas-Martinez 1981). Mean temperature is about 16°C and mean annual rainfall around 650 mm, of which over 80% falls between October and April (SNIRH, National System of Water Resources Information database, <http://snirh.inag.pt>). The landscape is predominantly flat and devoted to irrigated agriculture and livestock production, with natural and semi-natural habitats occurring marginally in dunes, entrenched stream valleys and cork oak woodlands surrounding the farmed area. Surface waters in this landscape are mostly associated with temporary ponds which flood during the rainy season and dry out in summer, whereas permanent water bodies are scarce and mostly associated with irrigation infrastructures such as concrete channels and reservoirs. Over the past two decades, the landscape has changed considerably as a result of social and land management transformations, with an overall intensification of agriculture, along with the abandonment of some marginal and less productive areas (Beja and Alcazar 2003; Pita et al. 2007, 2009).

As in other regions of the Iberian Peninsula, both the Cabrera vole and the water vole have a highly discontinuous distribution within this agricultural landscape, where they are largely restricted to patches of little disturbed tall grass communities typical of temporary ponds and to narrow herbaceous strips along the margins of small intermittent streams, field boundaries and road verges (Pita et al. 2006, 2007). Although water voles are generally reported to be dependent on permanent and stable water bodies (e.g. Garde and Escala 1993; Ventura 2004), in our study area, they often occupy seasonally flooded or moist habitats (R. Pita, unpublished data), as it seems to be the case in other dry Mediterranean areas (Fedriani et al. 2002; Román 2007). Cabrera voles are also associated with these habitat types and so the two species often occur within the same patches, which tend to be separated from other patches by a largely inhospitable agricultural matrix (Pita et al. 2006, 2007).

Within habitat patches, Cabrera voles are usually organised in monogamic breeding pairs exhibiting relatively high residence times of over 10 months (Fernández-Salvador et al. 2001). Water voles generally mate promiscuously and rarely survive beyond 12 months (Román 2007). Both species tend to exhibit diurnal peaks of activity (Ventura 2004; Fernández-Salvador et al. 2001) and to feed mainly on leaves, stems and seeds of grasses, sedges and rushes (Soriguer and Amat 1988; Román 2007; Rosário et al. 2008). Reeds may also be an important food item for water voles nearly permanently inundated habitats, such as river banks (e.g. Ventura et al. 1989). Because of the severe Mediterranean summer droughts, seasonality in food availability is regarded as a key factor influencing population dynamics and breeding patterns of both species in southwestern Iberia (Pita et al. 2007; Román 2007). In particular, food quality is considerably reduced during the summer, when annual plants are scarce

and voles increase their consumption on perennial plants with lower protein content and higher concentrations of secondary compounds inhibiting digestion and reproduction (Soriguer and Amat 1988; Román 2007; Rosário et al. 2008).

Study design

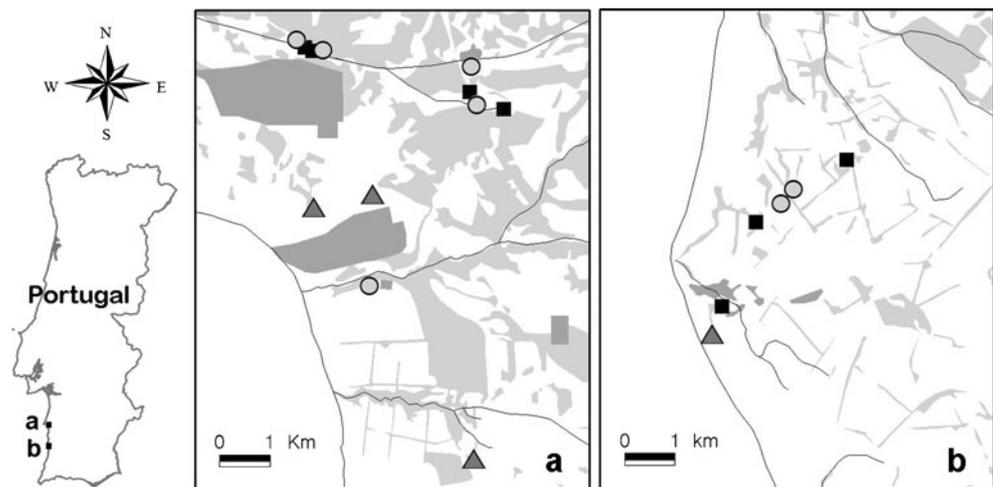
The spatial ecology of Cabrera and water voles was analysed with radio-tracking, from individuals captured within 18 discrete habitat patches distributed across two farmland areas in the Portuguese southwest coast, where agreement with landowners to capture and radio-track voles could be obtained (Fig. 1). Mean (\pm SE) nearest neighbour distance between sampling sites was 1.2 ± 0.3 km (0.12 – 4.0 km). Sampling sites that were relatively close to each other were still treated as distinct units in the context of this study because they were separated by inhospitable matrix (e.g. heavily grazed pastureland or ploughed land), and it was very unlikely that voles crossed such areas within their routine movements. All sampling sites consisted of a mosaic of mixed grasses and forbs, as well as tall wet and riparian meadows, shrubs and trees, embedded in a predominantly agricultural matrix. No site was associated with a water body, although all flooded partly during rainy periods, eventually resulting in small, scattered and shallow surfaces of water, lying beneath the vegetation.

The presence of Cabrera and water voles within each habitat patch was initially confirmed from surveys based on systematic searches for the typical presence signs of each species, mainly droppings and the characteristic pathways on ground vegetation (e.g. Fedriani et al. 2002; Santos et al. 2006; Pita et al. 2007), both of which are about two times larger for water voles (Román 2003; Pita et al. 2006). These preliminary surveys indicated that seven out of 18 sampling sites showed signs of both species, while seven were apparently used by Cabrera voles only and four by water voles only (Fig. 1). Because the number of voles inhabiting each habitat patch was generally very small and we wanted to keep disturbance to a minimum, we restricted sampling to a small number of individuals from each habitat patch. Also, we avoided repeated disturbance to small populations by sampling each patch in a single occasion between April 2006 and April 2008. To account for potential seasonal differences in range use, ten patches were surveyed during the wet season (October–April) and eight during the dry season (May–September), with the later corresponding to the period with high temperature and very low rainfall.

Captures and radio-tracking

Voies were captured using Sherman live traps ($7 \times 23 \times 9$ cm³ for Cabrera voles and $10 \times 37 \times 11$ cm³ for water

Fig. 1 a, b Location of 18 sites sampled in two farmland areas of southwestern Portugal. Squares and triangles indicate the presence of Cabrera voles and water voles, respectively, while circles represent sites where species co-occurred, as revealed from sign surveys. Built-up areas and forestry habitats are shown in dark and light grey, respectively, while white areas represent the agricultural matrix. Lines represent the main streams crossing the study area



voles) baited with apple and supplied with hay and hydrophobic cotton for bedding. Traps were placed at likely capture sites, which were assessed by checking eaten apple trials left in the area during the previous 1–3 days. After setting the traps, these were checked every 8 h (around 0800, 1600 and 0000 hours). A total of 804 traps were used during 108 days of trapping distributed through the study period. The sampling effort varied among sites depending on the evidence for the presence of voles signs, patch size, capture–recapture success and whether radio-tracking was in progress. Mean (\pm SE) sampling effort to capture Cabrera voles was 186.3 ± 63.8 trap nights per sampling site during the dry season ($n=6$; range 50–450) and 195.7 ± 41.3 trap nights per sampling site during the wet season ($n=8$; range 45–315). Sampling effort for water voles averaged 207.8 ± 68.8 trap nights during the dry season ($n=6$; range 42–420) and 244.2 ± 84.3 trap nights per sampling site during the wet season ($n=5$; range 72–540).

All Cabrera and water voles captured were weighed and sexed, and the reproductive status (active or non active) of non-juveniles (>28 g for Cabrera voles, Fernández-Salvador et al. 2005a, b; >94 g for water voles, Román 2007) was assessed based on the testis position (scrotal or abdominal) for males and on vulva perforation and nipples size (small or large) for females. Animals of non-target species were immediately released at the point of capture. Individual Cabrera and water voles were fitted with collar radio-transmitters (Wildlife Materials, Inc., Murphysboro, IL, USA) adding no more than 5% of the animals weigh, so as to ensure no significant additional energetic costs for voles (Gannon et al. 2007). Pregnant females were identified by abdominal palpation, and they were not collared to reduce potential negative effects on vole populations (Mendonça 1999). All animals were lightly sedate with a subcutaneous injection of Dormitor® (0.2 mg/kg) to reduce handling stress. After transmitter attachment, voles were induced out of

anaesthesia using an equivalent dose of Antisedam®, a reversing agent to Dormitor®. Before release, collared animals were kept under observation for at least 2 h to ensure that they were suffering no ill effects or loss of mobility. During this short observational period, uncovered wire cages supplied with hay and hydrophobic cotton were used, and apple and water were provided ad libitum. Radio-tracking started at least 4 h after trap removal and the release of animals at their point of capture (e.g. Gray et al. 1998).

Six different 4-h radio-tracking intervals covering a complete 24-h cycle (0615–1000, 1015–1400, 1415–1800, 1815–2200, 2200–0200, 0215–0600 hours) were alternately surveyed for each animal. Each tracking session started at least 8 h after the previous session and consisted in recording the location of each individual at 15-min intervals, totalling 16 fixes recorded per animal in each session. Whenever possible, tracking was carried out until at least a minimum of 96 locations was reached for each individual, corresponding to the number of locations needed to obtain a complete 24-h cycle. Voles were located using a TRX-100S receiver and an external three-element yagi directional antenna (Wildlife Materials, Inc., Murphysboro, IL, USA). Locations were made by homing and by multiple triangulations when the tracker was close to the animals. At each radio-location, a positioning measurement was recorded using a Garmin eTrex® handheld GPS, except when the animal remained in the same location in successive fixes, for which the coordinates of the previous fix was assigned to minimise global positioning system (GPS) measurement error. GPS typically yielded an error of ± 4 m and was considered sufficiently accurate, as the range used by voles may cover hundreds of square metres (see “Results” section). At each radio-location, we recorded whether the animal was active or inactive, as judged by fluctuating vs. stationary radio-signal. After radio-tracking, each sampling site was re-trapped, so as to remove collars from tracked voles.

Data analysis

The first aspect investigated concerning space use by voles was a test for random movement at fine-scale (site fidelity analysis). This analysis estimated whether voles moved through space at random, or whether the animals made directional choices for particular areas within habitat patches (Shanahan et al. 2007). One thousand random walks were generated for each tracked vole using the Animal Movement Analysis Extension (AMAE; Hooge and Eichenlaub 2000) for ArcView GIS 3.2 (ESRI, Redlands, CA, USA). Each distance travelled between locations was equal to that observed in true vole tracks, and random turning angles substituted all actual angles taken (Shanahan et al. 2007). The parameters used to compare real and random walks were the average straight-line distance each consecutive location moved away from the start point of the track (R^2) and the total linear distance between the start and end points of an animal's path divided by the total length of the path (LI; Spencer et al. 1990). For each individual, observed R^2 and LI values were compared with the range of values given by the random track. If R^2 and LI of an observed animal track was in the lower 5% of the range of values for the random walk tracks, then the observed track was considered significantly more constrained than would be expected by chance, indicating that the animal exhibited site fidelity (Hooge and Eichenlaub 2000), which in turn reveals the existence of a measurable home range (Spencer et al. 1990).

Individual home ranges were estimated using both the minimum convex polygon (MCP; Mohr 1947) and the fixed kernel method (FK; Worton 1989) because a combination of polygon and contouring methods is often recommended to account for the potential limitations and shortcomings of each of these techniques (e.g. Kernohan et al. 2001, Boyle et al. 2009). Home ranges based on MCPs were estimated for each animal by connecting the outermost points considering all locations made (MCP100), while checking for home-range asymptotes using the area-observation plots produced in AMAE. Using kernel analysis, we calculated home ranges based on 95% utilisation contour (FK95, the area where animals spend 95% of its time) and defined the core area as the area enclosed by the 50% isopleths (FK50, the area where voles spend 50% of its time; Millspaugh et al. 2006). Smoothing parameters were determined by least squares cross-validation (LSCV), which results in less-biased home-range estimates than other methods (Seaman and Powell 1996), and grid size was selected automatically by the AMAE. In order to ensure that home ranges and core areas better represented the active selection of any particular area, only active fixes were considered in range use estimates (Herr et al. 2009), thereby reducing potential problems of LSCV non-convergence due to identical or spatially closed fixes (Hemson et al. 2005).

This also reduced autocorrelation between locations, although time to independence between locations (Swihart and Slade 1985) was not a main concern in this study, as some autocorrelation might be desirable to add biological meaning in range use analysis, in particular for that of small mammals (Rooney et al. 1998; De Solla et al. 1999; Fieberg 2007). All FK95 and FK50 estimates were based on >30 locations, the minimum number required when using kernel estimates with LSCV for bandwidth selection (Seaman et al. 1999). For each species, the MCP100 and FK95 home ranges were compared using Mann–Whitney U tests (M–W; Siegel and Castellan 1988) in order to determine whether estimates were affected by the analytical technique. Differences in used ranges according to gender and season were investigated likewise for each species, with data pooled across years. Bonferroni corrections for two repeated tests on each species data set were used at the level of 5%, i.e. $p < 0.025$ (Sokal and Rohlf 1995). Analysis were based on data combined for the two farmland areas considered in this study because sample sizes were too small for carrying out separate analysis, particularly in the southern area ($n < 10$ for each species, see “Results” section). Differences between species were compared by M–W after pooling gender, season and year data.

Static intra- and inter-specific interactions were examined using range overlap analyses for those animals radio-tracked within the same habitat patch during the same period. In this analysis, two-dimensional home ranges (HR_i and HR_j) were superimposed, and the overlapped area ($O_{i,j}$) was estimated using the ‘clip’ tool in ArcView GIS project. The measure of space sharing was computed as the proportion of overlap of HR_i on HR_j ($HR_{i,j}$) and HR_j on HR_i ($HR_{j,i}$) for any dyad of ranges (Mizutani and Jewell 1998; Kernohan et al. 2001), i.e.

$$HR_{i,j} = O_{i,j}/HR_i \text{ and } HR_{j,i} = O_{i,j}/HR_j.$$

A mean overlap value was calculated by using all overlap percentages, with a sample size of $2k$ where k is the number of dyads. These procedures were also employed for core-area overlap analysis. Intra- and inter-specific overlaps of home range and core area were compared considering overall data and data from each season separately, using M–W tests (Siegel and Castellan 1988). Inter- and intra-sexual overlaps were compared likewise, whenever the number of dyads within groups allowed statistical testing (i.e. ≥ 5 dyads per group, Siegel and Castellan 1988). Throughout the paper, mean values are presented together with the corresponding standard errors and range of variation.

Results

Altogether, 34 Cabrera voles were captured 53 times in 13 habitat patches, and 43 water voles were captured 78 times

in ten habitat patches, from a total of 239 captures made in the 18 patches surveyed. Although sign surveys suggested the occurrence of both species in seven of the surveyed areas, capture data only confirmed simultaneous co-existence in five of these. Mean (\pm SE) number of Cabrera and water voles captured per sampling site was 2.6 ± 0.5 individuals (1–6) and 4.3 ± 1.2 (1–14), respectively. The Algerian mouse (*Mus spretus*) was also captured frequently (32.6% of the captures), occurring together with Cabrera voles in four sites, together with water voles in three sites and together with both species in four sites. Rats (*Rattus* sp.) were captured less often (9.6% of the captures), occurring in two sites with Cabrera voles, four sites with water voles and three sites with both species. The greater white-toothed shrew (*Crocidura russula*) was rarely captured (2.5% of captures), occurring in two sites with Cabrera voles, one site with water voles and in one site with both species. Finally, a single weasel (*Mustela nivalis*) was captured in a site occupied by water voles only (0.4% of captures).

A total of 31 Cabrera voles and 29 water voles were fitted with collar radio-transmitters. Mean (\pm SE) weight of collared Cabrera voles was 48.4 ± 1.5 g (27–62 g), with no variation between sexes ($U=73$, $df=1$, $p=0.13$), while that of water voles was 175.7 ± 7.9 g (92–261 g), also with no variation between sexes ($U=67$, $df=1$, $p=0.11$). From the 60 animals collared, three water voles and one Cabrera vole were juveniles at the time of collaring, though they were sub-adults by the end of radio-tracking. The mean (\pm SE) number of Cabrera and water voles radio-tracked per sampling site was 2.4 ± 0.4 (1–5) and 2.9 ± 0.8 (1–8), respectively. The percentage of animals radio-tracked during the dry season was 48% for Cabrera voles and 45% for water voles. Females represented 64% of the Cabrera voles radio-tracked and 55% of water voles radio-tracked. Overall, about 87% of the Cabrera voles tracked were reproductively active, with no significant variation between the wet and the dry season ($U=89.0$, $df=1$, $p=0.717$), while the proportion of reproductively active water voles was 83%, also with no variation between seasons ($U=78.5$, $df=1$, $p=0.268$). The number of Cabrera ($n=9$) and water voles ($n=6$) collared in the southern farmland area was relatively small.

Altogether, 9,664 locations were obtained during the study, with a mean (\pm SE) number of locations of 148.5 ± 11.9 (48–368) per Cabrera vole and 174.4 ± 18.1 (96–512) per water vole. Loss of signal due to predation, dispersion or discharge of transmitter batteries, prevented us to complete a full 24-h cycle for two of the tracked Cabrera voles, although the number of locations for these animals was still greater than 30. Each individual vole was radio-tracked during a single season. The mean (\pm SE) number of tracking days per Cabrera vole was 10.3 ± 1.1 (5–20 days)

during the dry season and 8.8 ± 1.3 (4–23 days) during the wet season. The mean number of tracking days per water vole was 12.3 ± 1.7 (5–27 days) in the dry season and 8.3 ± 0.8 (5–10 days) in the wet season. Recovery of radio-transmitters was possible for 42% of the Cabrera voles and 65.5% of the water voles tracked. Signs of predation were evident for 16.1% and 3.4% of the Cabrera and water voles tracked, respectively.

Site fidelity

Results from radio-telemetry indicated that for most of animals, the majority of fixes was densely clustered within a particular area. Fine-scale site-fidelity analysis showed that both R and LI values for 90.3% ($n=31$) of tracked Cabrera voles and for all the 29 tracked water voles were significantly lower ($p<0.05$) than those corresponding to random walks. There was thus evidence that generally, the movements by Cabrera and water voles were more constrained than would be expected from random tracks and that individual ranges were sufficiently well defined for their boundaries to be determined with a high degree of confidence. It should be noted, however, that one Cabrera vole male exhibited fine-scale site fidelity only after dispersive movement of 448 m, travelled during one night to a different habitat patch. Therefore, one further habitat patch was considered in the study, totalling 19 patches surveyed for radio-tracking (see [Electronic supplementary material](#)).

Range size

Area-observation curves of individual MCP100 home-range estimates approached satisfactorily an asymptote for all animals showing site fidelity. MCP100 home ranges varied between 57.5 and 987.5 m² for Cabrera voles (mean \pm SE = 375.1 ± 45.7) and between 230.5 and 2,858.5 m² for water voles (mean \pm SE = 828.0 ± 120.2). Although slightly smaller, these estimates did not vary significantly from those produced by 95% kernels (Cabrera voles: $U=370$, $df=1$, $p=0.72$; water voles: $U=366$, $df=1$, $p=0.40$). Therefore, subsequent analyses were based on FK95 home-range estimates, as the kernel techniques are expected to provide a better representation of the internal structure of individuals range use (Harris et al. 1990; Marker et al. 2008). FK95 home ranges of Cabrera voles ranged between 39.3 and 1,075.6 m² (mean \pm SE = 418.2 ± 56.3 m²), while for water voles, it ranged between 198.3 and 2,600.2 m² (mean \pm SE = 946.3 ± 126.3 m²). Core-area sizes (FK50) of Cabrera voles ranged between 1.9 and 182.4 m² (mean \pm SE = 55.1 ± 9.3 m²) whereas estimates for water voles ranged between 21.1 and 562.4 m² (mean \pm SE = 156.6 ± 28.2 m²). The M–W tests revealed that water voles had significantly larger home ranges ($U=174$,

$df=1, p<0.001$) and core areas ($U=164, df=1, p<0.001$) than Cabrera voles. Within each species, there were no sexual or seasonal differences either in home-range or core-area estimates (M–W: $p>0.05$ for all tests, after Bonferroni corrections).

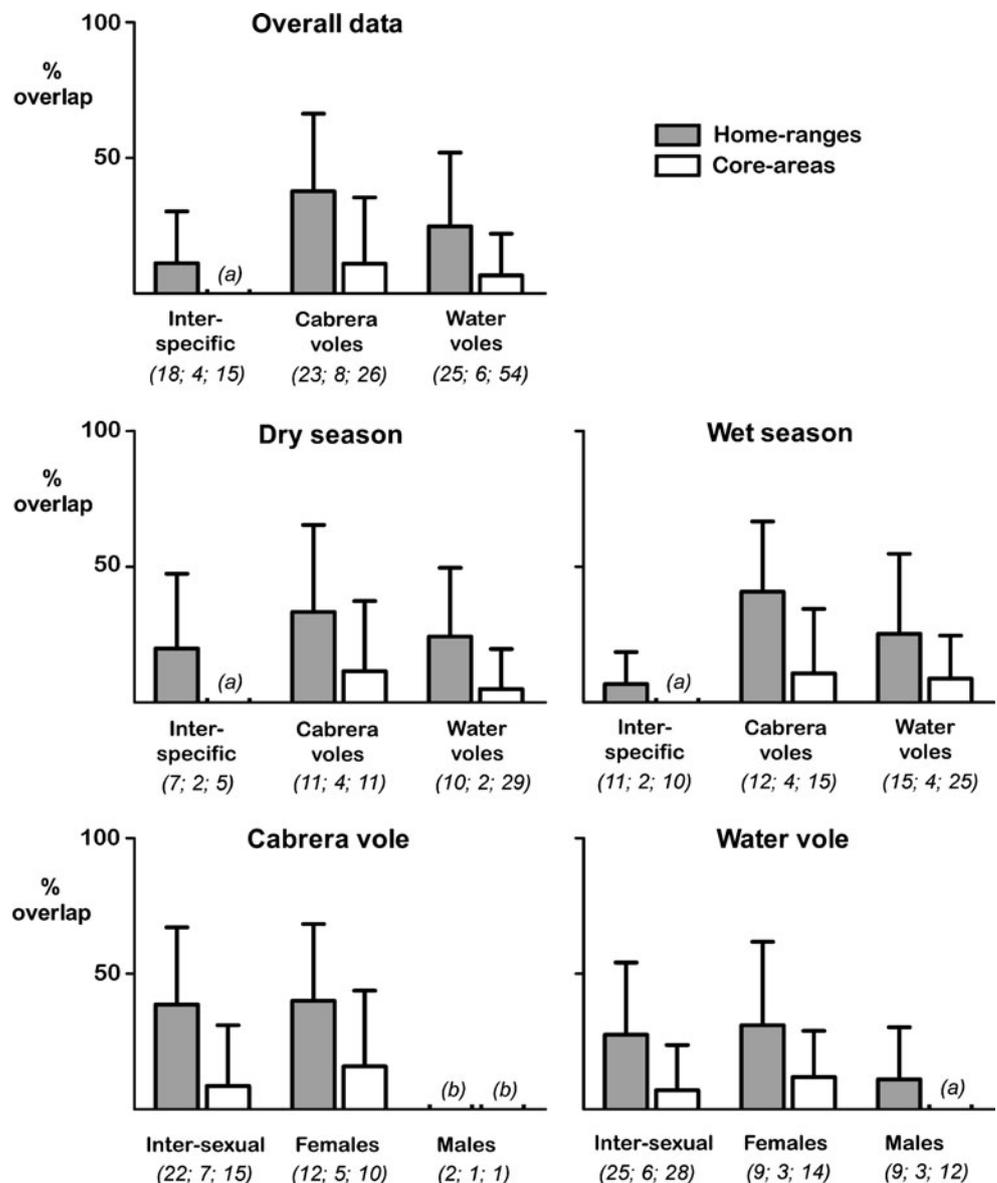
Spatial overlap

Overlap of home ranges was always higher than overlap of core areas for intra-specific space sharing analysis (M–W: $p<0.05$ for all tests), considering either overall data or data from each season separately (Fig. 2). Inter-specific overlap of home ranges was significantly lower than that observed among conspecifics (Fig. 3; [Electronic supplementary material](#)), considering both the overall data ($U=1,431, df=1, p<0.001$) and data from the wet season ($U=398, df=1, p<0.001$; Fig. 2). During the dry season, home-range

sharing by Cabrera and water voles was apparently higher than that observed during the wet season (Figs. 2 and 3; [Electronic supplementary material](#)), reaching up to 60.4%. However, rank-based comparison did not show significant differences between seasonal inter-specific home-range overlap ($U=87, df=1, p=0.588$). Despite this, inter-specific home-range overlap during the dry season was high enough to be considered similar to that observed within conspecifics ($U=308, df=1, p=0.230$). There was no overlap between core areas of Cabrera voles and water voles in either the dry or the wet season (Fig. 2).

Considering the inter-individual static interactions among conspecifics, results suggest a reduced home-range overlap among water vole males (Fig. 2), with significant differences from the overlap measured between males and females ($U=387, df=1, p=0.002$) and nearly significant

Fig. 2 Static interactions showing the mean percentage of spatial overlap between individuals radio-tracked during the same period at the same habitat patch. Error bars show 95% confidence intervals. Sample sizes are given as (number of voles, number of sampling sites, number of dyads). **a** No spatial overlap; **b** insufficient data



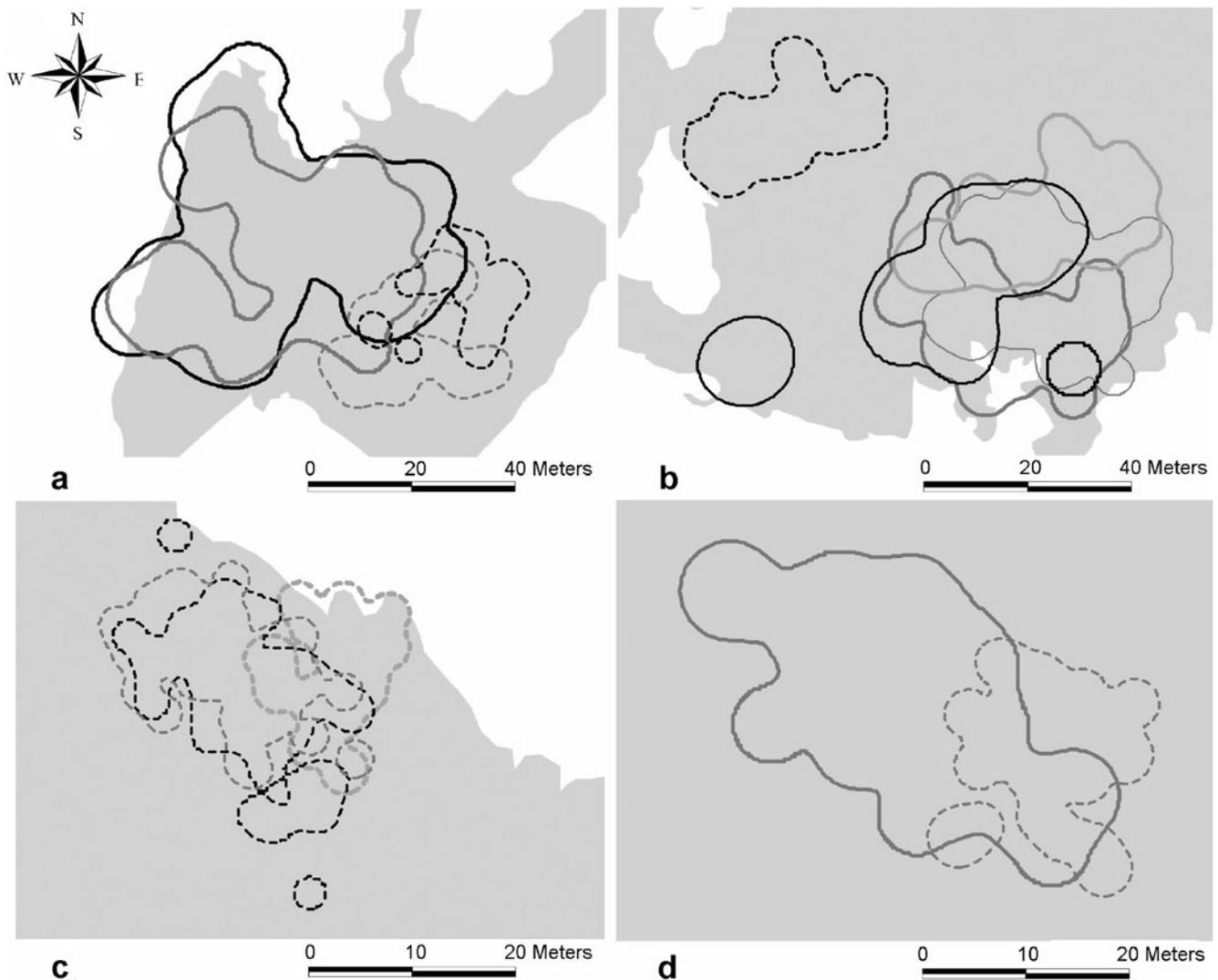


Fig. 3 Examples of individual home ranges and spatial overlap of Cabrera (*dashed lines*) and water voles (*solid lines*), based on 95% fixed kernel (FK95), during the wet (**a**, **b**) and dry (**c**, **d**) seasons (see also [Electronic supplementary material](#)). Sampling site **a** is located at

the southern farmland area, while **b–d** are located in the northern farmland area. For both species, males are represented by *black lines* and females are represented by *lines with different scales of greys*. Suitable habitat patches are shown in *light grey*

differences in relation to female overlap ($U=239$, $df=1$, $p=0.061$). Maximum home-range overlap observed among water voles was high, reaching over 86% in all groups compared. Water vole males never shared core areas (Fig. 2), while females did and in a greater extent than the core-area sharing between sexes ($U=169$, $df=1$, $p<0.001$). Despite this, maximum inter-sexual core-area overlap observed for water voles reached 100%, while among females, it was 66.2%. In the case of Cabrera voles, only two males were followed simultaneously in the same sampling site, showing no spatial overlap. Because of this, only female and inter-gender overlaps were compared for Cabrera voles, with no differences observed both in the case of home ranges ($U=293$, $df=1$, $p=0.890$) and core

areas ($U=280$, $df=1$, $p=0.617$). Maximum home-range and core-area overlap observed for Cabrera voles reached over 87% and 100%, respectively, for both groups considered (between sexes and among females).

Discussion

To the best of our knowledge, this is the first study describing from radio-tracking the use of space by wild ranging Cabrera and water voles and to document the spatial interactions among individuals of the two species. The study provided important novel information regarding the spatial ecology of each species, allowing inferences on

several relevant and still understudied traits of their life histories. Also, our results evidenced that the distribution of Cabrera and water voles may be driven, at least partially, by spatial processes reducing inter-specific encounters, which in turn may reflect eventual competitive displacement or niche differentiation at small scales of habitat heterogeneity (Mouquet et al. 2005). These findings have important implications for the conservation management of habitats of the two species in areas of sympatry.

Range use and spatial organisation within species

This study revealed that both Cabrera and water voles tended to limit their movements to a circumscribed home range, at least during tracking periods of up to about 25 days. Such strong fine-scale site fidelity probably reflected the relatively high seasonal association of individual voles to a particular habitat patch, as reported for both species based on long-term capture–recapture studies (Fernández-Salvador et al. 2005a, b; Román 2007). Faithful behaviour of Cabrera and water voles to an area may be related with the very demanding habitat characteristics required by animals from both species to fulfil at least some of their basic life-history traits (e.g. foraging, resting, thermal regulation, mating). In addition, because habitat patches may be crossed either by other potential competitors, such as the more aggressive *Rattus* sp. (Fernández-Salvador 1998; Fedriani et al. 2002; Ventura 2004; Román 2007), or by predators specialised on voles, such as the weasel (Brandt and Lambin 2007), fine-scale site fidelity might be particularly important for voles by providing knowledge of escape routes to secure sites within the home range.

In general, home-range and core-area sizes estimated for both species agree with those expected according to the allometric relationship between body size and home-range size in mammals (Swihart et al. 1988), with water voles moving over ranges about twice that of Cabrera voles. Despite this, home ranges estimated for Cabrera voles were larger than those inferred for the species from capture–recapture data (between 80 and 100 m²; Fernández-Salvador 1998). Similar comparisons concerning water voles were not possible because no other studies reported quantitatively on their home-range sizes. However, our results suggests that apparently, home-range sizes of water voles in our study area might be slightly larger than those usually referred for its congener *Arvicola terrestris* along narrow (1- to 2-m) linear habitats of northern Europe (length ranges <300 m, e.g. Moorhouse and Macdonald 2005). Results on home-range and core-area sizes of Cabrera and water voles also revealed that variation between seasons was reduced, which could be related with the fact that most of the collared voles were reproductively active at the time of tracking, irrespective of the seasonality

trends in reproductive cycles referred for both species (Fernández-Salvador et al. 2005a, b; Román 2007).

Home-range and core-area sizes of Cabrera and water voles showed also little variation among sexes and considerable inter-sexual overlap, reaching over 85% for home ranges and up to 100% for core areas in both species. Low inter-sexual variation in range sizes together with high inter-sexual overlap and reduced sexual dimorphism in body size are typical traits of monogamous species (Gaulin and FitzGerald 1988; Roberts et al. 1998; Wolff 2007). Although this could not be fully confirmed from our data, monogamous mating system was suggested for the Cabrera vole (Fernández-Salvador 1998; Fernández-Salvador et al. 2001). Monogamy in water voles was referred to occur only in small habitat patches with reduced chances of being occupied by more than one couple of reproductive animals, otherwise prevailing the promiscuous mating system (Román 2007). It is also worth noting, however, that space sharing among the water voles studied here was relatively high between females, while males apparently avoided overlapping their ranges with other males, particularly at the core-area scale. Thus, our data concerning water voles could also fit the resource-defence polygyny models, in which males defend one or more females or a critical resource that will give them access to the females using that resource, as opposed to promiscuous tactics (Wolff 2007). There are thus reasons to hypothesise that water voles may exhibit some plasticity in the mating system according to local variations in quality and abundance of habitat patches. The high spatial segregation among water vole males tracked in this study further suggests that this species may have a tendency for a male-biased dispersal in our study area, as also suggested for the species in other regions (Román 2007).

Spatial interactions between species

This study confirmed that, at least in habitat patches with no permanent surface waters, Cabrera and water voles might not only co-exist nearby but also share the same areas within patches. In addition, the strong fine-scale site fidelity of co-existing Cabrera and water voles suggests that none of the species appeared to be actively driving the other out of the area, supporting the view that spatial co-existence was stable. However, overall spatial overlap between species was relatively low at the home-range scale, and there were even evidences for a considerable spatial segregation between species at the core-area scale across all seasons. Therefore, space sharing among species was in practice limited to foraging areas outside the centre of activity of individuals (exploitative competition), and species may thus co-exist via spatial segregation. Because core-area overlap indicates a greater potential for competition than home-range overlap (Brunjes et al. 2009), non-

overlapping core areas between species suggests that inter-specific competition influenced the spatial distribution of voles more than intra-specific competition. However, during the dry season, when the availability of food resources was presumably lowest (Ventura et al. 1998; Román 2007; Rosário et al. 2008), the potential for exploitative competition was the highest, as indicated by the increased inter-specific home-range overlap. This suggests that the strength of competition concerning space sharing between Cabrera and water voles may vary locally according to the quality and abundance of habitat patches (Amarasekare et al. 2004), which in turn suggests that other mechanisms of co-existence besides spatial segregation might occur. These may include spatial partitioning on a temporal scale or habitat partitioning at finer spatial scales than can be detected by our home-range overlap analysis (Amarasekare 2003; Brunjes et al. 2009). Spatial segregation between Cabrera and water voles may indeed result from differences in the way species utilise their habitat at small scales rather than direct competition between species. The discrepant spatial range sizes between Cabrera and water voles suggest that differences in the scale of resource perception might in part explain the co-existence of species (Christopher and Barret 2006; Cromsigt and Olff 2006) and should be accounted in habitat selection studies aiming to investigate habitat differentiation between species.

The higher body size of water voles suggests that this species may be a superior competitor, which in the context of source-sink meta-population dynamics might indicate that Cabrera voles are superior at colonising empty patches (Amarasekare and Nisbet 2001), irrespective to dispersal-range abilities of species. Although this could not be checked from our data, results on fine-scale site fidelity analysis revealed that the only individuals showing no site fidelity ($n=3$) or dispersive movements ($n=1$) were Cabrera voles, which could be indicative of their higher propensity to move away from a habitat patch than water voles. Eventual differences in trade-offs between competitive and dispersal abilities might thus contribute as a further mechanism allowing Cabrera and water voles co-existence in fragmented farmland. Therefore, although our study suggests an effective spatial segregation among Cabrera and water voles, it also reinforces that further research on specific life-history traits and niche differentiation is needed in order to fully understand co-existence of these species within patches in Mediterranean farmland.

Management implications

The southern water vole and the Cabrera vole are globally vulnerable and near-threatened species (IUCN 2009), respectively, and so securing their populations within farmland landscapes may be considered a conservation priority (Pita et al. 2007; Rigaux and Charruau 2007). Previous studies suggested that achieving such goal

requires a network of little grazed and well-connected tall herb humid habitat patches (Pita et al. 2007; Fedriani et al. 2002), which might be protected even in intensively managed landscapes through agri-environment and cross-compliance schemes promoting the retention of grass margins and other interstitial habitats (Stoate et al. 2009). This view is supported by the present study, which showed that individuals of both species circumscribe their routine movements to small areas of suitable habitat, where they likely find adequate foraging and breeding conditions. Based on estimates of home-range size and maximum inter-sexual overlap, the study suggests that areas of about 500 and 1,100 m² might be sufficient to support one Cabrera and one water vole breeding pair, respectively, which underlines the importance of even relatively small habitat patches. However, larger areas should be considered to increase the chances of local population persistence because the likelihood of extinction is generally higher when population units are small (Legendre et al. 2008). In the case of Cabrera voles, Pita et al. (2007) showed that population persistence was indeed higher in larger patches, recommending that conservation programmes in fragmented landscapes should strive to maintain patches of about 2,000–5,000 m². The area requirements estimated in this study suggests that about four to ten breeding pairs may inhabit patches of this size, corresponding to very small populations with a presumably high risk of stochastic extinction (Hanski 1999; Legendre et al. 2008). This strengthens the need to maintain the connectivity among habitat patches, thereby increasing the chances of meta-population persistence, despite the frequent extinction of local populations (Fernández-Salvador et al. 2005a, b; Pita et al. 2007).

Results of this study also support the view that species interactions may need to be accounted for when designing conservation management strategies for Cabrera and water voles in fragmented landscapes (Pita et al. 2006), given the significant levels of inter-specific spatial segregation observed. Although both species appeared to co-exist within the same habitat patch, it is possible that local spatial segregation resulted from larger water voles displacing Cabrera voles from potentially favourable habitats, as it has been found elsewhere for species of different sizes exploring the same or similar resources (e.g. Oro et al. 2009 and references therein). Therefore, the presence of water voles may effectively reduce habitat availability and thus Cabrera vole population size at local habitat patches, thereby increasing the probability of meta-population extinction at the landscape scale (Pita et al. 2007). This possibility requires further investigation, for the conservation of asymmetric competitors in fragmented landscapes is a challenging task, which should be based on a detailed understanding of the spatial and temporal mechanisms of resource partitioning that allow species co-existence in areas of sympatry (e.g. Oro et al. 2009).

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