Local and landscape habitat determinants of water vole distribution in a patchy Mediterranean environment¹

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Abstract: We studied the distribution of a water-dependent species (southern water vole, *Arvicola sapidus*) in a Mediterranean region (Doñana National Park, southwest Spain) characterized by a complex array of different-sized ponds (where voles were confined) embedded in a mostly unsuitable landscape. For each surveyed pond ($n = 185$), a total of 26 variables related to both local (20) and landscape (6) attributes were quantified, and the presence of voles was evaluated by finding their typical signs (latrines). We found signs of water voles in 60% of ponds, despite the fact that most of them (84%) were totally dried out. A generalized linear model analysis showed that water voles were sensitive to both local and landscape attributes of ponds. At a landscape scale, presence of voles was more likely in ponds located outside the national park, close to other ponds holding voles, and far away from areas rich in potential predators and competitors. At a local scale, ponds with water voles were characterized by abundant grasses, banks well covered by brush, low altitude, and low abundance of rabbits (*Oryctolagus cuniculus*). We also studied the use of microhabitat by voles within four specific ponds and found that they preferred plots of higher vegetation cover; thus, there was consistency in some cues used by water voles at the population/subpopulation scale (among different ponds) and at the behavioral scale (within ponds). Our study strongly supports the notion that the entire vole population is structured in distinct subpopulations, which are affected by a hierarchy of processes ranging from metapopulation dynamics and influenced by the landscape within which ponds are embedded as well as the local habitat quality.

Keywords: *Arvicola sapidus*, habitat selection, patchy distribution, spatial scaling, water vole.

Résumé : Nous avons étudié la répartition d'une espèce aquatique (le campagnol amphibie, *Arvicola sapidus*) au Parc national Doñana, dans le sud-ouest de l'Espagne. Cette région méditerranéenne est caractérisée par un arrangement complexe d'étangs de différentes tailles (où les campagnols sont confinés) entourés d'un paysage plutôt inhospitalier. Pour chacun des étangs étudiés ($n = 185$), un total de 26 variables reliées à des caractéristiques locales (20) ou à des caractéristiques du paysage (6) ont été échantillonnées. La découverte de latrines permettait de confirmer la présence de campagnols dans ces étangs. Nous avons trouvé des indices de la présence de campagnols dans 60 % des étangs, bien que la plupart de ces derniers (84 %) étaient complètement secs. Selon un modèle d'analyse linéaire, les campagnols amphibies sont sensibles à la fois aux caractéristiques locales des étangs et aux caractéristiques du paysage. À l'échelle du paysage, ils se rencontrent surtout dans les étangs situés à l'extérieur du parc national, près d'autres étangs habités par des campagnols, loin des secteurs fréquentés par les prédateurs et compétiteurs potentiels. À une échelle locale, les étangs où l'on trouve des campagnols sont à une altitude peu élevée et sont colonisés par d'abondantes graminées. Leurs berges sont recouvertes d'arbustes et on trouve peu de lapins (*Oryctolagus cuniculus*) dans les environs. Nous avons également étudié l'utilisation par les campagnols de microhabitats dans quatre étangs. Ainsi, les campagnols préfèrent les sites où le couvert végétal est haut, ce qui montre que les caractéristiques recherchées par les campagnols sont similaires, que ce soit à l'échelle d'une population ou d'une sous-population (entre différents étangs) ou encore à une échelle comportementale (à l'intérieur même des étangs). L'ensemble de la population de campagnols serait donc subdivisée en sous-populations distinctes influencées par la structure du paysage entourant les étangs et par la qualité des habitats, mais qui interagissent malgré tout au sein d'une métapopulation.

Mots-clés : *Arvicola sapidus*, sélection d'habitat, répartition en plaques, mise à l'échelle spatiale, campagnol amphibie.

Introduction

Selection of habitat is a critical process by which individual behavioral decisions are translated into local patterns of distribution and abundance (Morris, 1992; Boyce & McDonald, 1999). Nonetheless, the proximate cues used by individuals to select habitat at a local scale do not always match those that govern their presence in a heterogeneous landscape (Wiens, 1985; Orians & Wittenberger, 1991). Therefore, to estimate the relative importance of different levels of spatial heterogeneity in predicting spatial distribution of target species is a main concern of landscape ecology today (Kareiva & Wennergren, 1995; Bowers & Barrett, 1999).

However, distinguishing among the contributions of local and larger-scale explanatory variables to a species' distribution is problematic since they often correlate (Bowers & Barrett, 1999; Mazerolle & Villard, 1999).

Small mammals often have small ranges, limited dispersal distance and ability, relatively short generation time, and rapid responses to small- and large-scale variation in habitat features (Barrett & Peles, 1999). Consequently, their populations usually are not homogeneously distributed across the landscape and, under particular circumstances (e.g., presence of barriers), can be spatially structured in distinct subpopulations (Lawton & Woodroffe, 1991; Lima,

¹Rec. 2001-08-28; acc. 2001-11-20.

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Marquet & Jaksic, 1996). These subpopulations may form an interacting ensemble or metapopulation system (Hanski & Gilpin, 1997), with a variable degree of communication among them. Small and isolated subpopulations are more prone to extinction than large and better connected subpopulations, and where local extinctions outweigh (re)colonization, the range of the species ends (Hanski & Gilpin, 1997). Besides, once (re)colonized, the persistence of such subpopulations is influenced by key intrinsic attributes of habitat patches, e.g., food, vegetation, patch size (Van Apledoorn *et al.*, 1992; Forsys & Humphrey, 1999). Thus, a comprehensive understanding of the relative importance of both local (*i.e.*, intrinsic to patches) and landscape (*i.e.*, relative to patch context) habitat attributes as determinants of small mammal distributions is fundamental to identifying the processes regulating such populations (Van Apledoorn *et al.*, 1992; Forsys & Humphrey, 1999; Mazerolle & Villard, 1999; Schweiger *et al.*, 1999).

Water voles (*Arvicola* spp.) are represented in Europe by two species weighing about 220 g (Mitchell-Jones *et al.*, 1999). *Arvicola terrestris* L. is distributed from northern Spain to Asia and includes fossorial populations living far from water. *Arvicola sapidus* Miller, restricted to the Iberian Peninsula and France, is considered a strictly water-dependent species (Mitchell-Jones *et al.*, 1999). Both species form discrete and easily recognized breeding colonies (Ventura & Gosalbez, 1987; Lawton & Woodroffe, 1991) and are largely dependent on grasses and other green vegetation, which are a major source of food and nesting material and also allow them to remain hidden from predators (Lawton & Woodroffe, 1991; Garde & Escala, 1993).

In this study, we used *Arvicola sapidus* as a model species to analyze the relative influence on its distribution of several variables concerning both local and landscape levels of spatial heterogeneity. Our study system, located in the Doñana National Park (southwest Spain), includes a complex array of different-sized lagoons and temporarily flooded ponds (overall, 603 water bodies) embedded in a mostly unsuitable macrohabitat (the dry sclerophyll Mediterranean scrubland). Since *A. sapidus* seems to be a water-requiring species, we expected water voles to be confined to water bodies scattered in the scrubland. In addition, we expected that the probability of finding voles in a particular water body would be related to both within-patch quality (*e.g.*, food, shelter) and between-patch conditions of the landscape (*e.g.*, distance to other patches, isolation). Finally, we evaluated the consistency between the distribution pattern of water voles in Doñana and the process of habitat selection made by individual voles.

Methods

STUDY AREA

The study was carried out in and around the Doñana National Park (37° 10' N, 6° 23' W) at the western bank of the Guadalquivir River (southwest Spain, Figure 1). The climate is Mediterranean sub-humid, characterized by dry, hot summers (June–September) and mild, wet winters (November–March). Average annual rainfall is about 600 mm, but there is a high interannual heterogeneity, with periods of several dry years (annual rainfall under 300–

400 mm) alternating with periods of wet years (annual rainfall above 900 mm). The Doñana area (800 km²) was a sea gulf a few thousand years ago. It has been replenished by muddy sediments of riverine origin, forming a very large marshy area (~280 km²) flooded during the winter, and by sandy sediments of aeolian origin, where there is a scrubland (~150 km²; Valverde, 1960). The scrubland-marsh ecotone is a highly productive area (locally known as Vera; Figure 1), where potential water vole competitors and predators are very abundant (Soriguer, 1983; Travaini *et al.*, 1997; Forero *et al.*, 1999). At the aeolian mantle, winter rains and an underground hanged water layer give rise to more than 600 water bodies very variable in shape and size (0.02–33 ha; Bravo & Montes, 1992). Larger lagoons are flooded or wet during all or most of the year, whereas small ponds hold water during rainy winters, but dry out during the summer and in dry years.

Since scrubland has been historically modified by humans, and macrohabitat may influence the distribution of small mammals (Morris, 1987), we used a classification system comprising five macrohabitat types: 1) Mediterranean scrubland: mainly formed by *Halimium halimifolium* L., *Erica* spp., *Pistacea lentiscus* L., and scattered *Quercus suber* L.; 2) pasturelands: open areas of annual herbs (*e.g.*, *Silene laeta* L., *Gaudinia fragilis* L.) and scattered trees (*e.g.*, *Q. suber*, *Olea europaea* L.); 3) tree forests: plantations of *Pinus pinea* L. and *Eucalyptus* spp. with some scrubs of *H. halimifolium* and *Erica* spp.; 4) wetlands: open areas, where trees and scrubs are scarce, that lie flooded during the rainy season; and 5) agriculture lands: tilled areas where native vegetation is practically absent.

WATER VOLE SURVEY

The water vole survey was carried out during August–September 1999. The presence/absence of water voles was assessed on the basis of the presence of their typical signs (latrines and scattered feces; see Woodroffe & Lawton, 1990, for *A. terrestris*) in 185 ponds throughout the Doñana area. Surveyed ponds were selected independently of the presumed local status of water voles, but in a way that maximized the overall area covered and that included all types and sizes of existing ponds. Our sample comprises 31% ($n = 603$) of the overall water bodies inventoried by Bravo and Montes (1992) and TRAGSATEC (1993) in the Doñana National Park and a surrounding area (called Abalario; Figure 1), respectively. We restricted our survey to lagoons and ponds because no sign of water voles has been found away from water bodies during our last 20 years of field work in the Doñana area. This pattern was confirmed during 2000–2001 with intensive capture-recapture studies of water voles in six 28.3-km² parcels (three in Doñana and three in Abalario) comprising 202 ponds overall. Latrines inside ponds were found daily, but no sign of voles was found away from ponds. Further, during 1998–1999, we set 4,189 circular plots (50–80 cm diameter) in the Mediterranean scrubland, and after a careful inspection of them, no sign of voles was found. In the survey carried out for this study, an initial effort of 10 minutes of searching was invested at each pond, during which occurrence or absence of signs (latrines, feces) was recorded. For small ponds (< 0.1 ha), searches were always ended after those

FIGURE 1. Sketch map of the study area with locations of surveyed and non-surveyed ponds. Circles represent surveyed ponds (black and open ones with and without water vole signs, respectively) and squares represent non-surveyed ponds. The marshes (muddy sediments) occupy the shaded region, whereas the remaining areas are occupied by the eolian mantle, where there is a scrubland. The ecotone between the scrubland and marshes is a highly productive area locally known as Vera. The dashed line represents the boundaries of the Doñana National Park (37°10'N, 6°23'W), which comprises three local areas (Marismillas, Reserva, and Matasgordas). At the western side of the park is the Abalarío.

initial 10 minutes, but for medium (> 0.1 but < 1 ha) and large (> 1 ha) ponds, up to five and ten additional minutes, respectively, were invested. In 88% of positive cases (overall, 111 positive ponds), signs of water voles were found within the first 10 minutes of survey, and in 78% ($n = 111$), we found latrines composed of flattened masses of feces topped up with fresh ones (*i.e.*, about two months old or fresher), thus suggesting that our sampling effort (up to 20 minutes for large ponds) and procedure were adequate to evaluate accurately the recent presence of water voles in ponds of Doñana.

LANDSCAPE ATTRIBUTES OF PONDS

We identified six variables representing the landscape in which ponds were embedded (Table I). All these variables share the trait that they cannot be measured within specific ponds. Type of macrohabitat (as described in Study Area) in which ponds are embedded, distance to the nearest known pond holding water voles, minimum number of ponds holding voles within a radius of 2 km, and distance to the nearest permanent lagoon were included because they may determine the proneness of ponds to episodes of (re)colonization by migrants (Hanski & Gilpin, 1997; Bowers & Barrett, 1999). Level of human protection (ponds

within versus outside the Doñana National Park) and distance to the Vera ecotone (Lawton & Woodroffe, 1991; Barreto *et al.*, 1998) were included because they may affect the abundance of potential predators and competitors of voles (Soriguer, 1983; Travaini *et al.*, 1997).

LOCAL ATTRIBUTES OF PONDS

We identified twenty variables representing the local attributes of ponds (Table I). These variables were measured within specific ponds. Size of ponds was included because patch size frequently affects the abundance of small mammals (Bowers & Matter, 1997). Because vegetation may be an important source of food and shelter for water voles (Lawton & Woodroffe, 1991), the area of each pond occupied by each type of vegetation cover (open, marshy, canopy, brushes, and grasses; Table I) was included and estimated in the field as the percentage of pond occupied by a specific type of vegetation (estimated visually) $\times$ total area of pond 100^{-1} . Similarly, each main type of vegetation along the pond bank (*Pistacea lenticus*, *Erica* spp., *Halimium halimifolium*, and other brushes; Table I) was quantified as low ($< 25\%$ of the bank occupied), medium ($> 25\%$ but $< 50\%$), or high ($> 50\%$). Altitude was included since it could influence the availability of water and thus also the availability

TABLE I. Independent variables considered in the generalized linear model analysis as potentially affecting the presence of water voles (*Arvicola sapidus*) at ponds of Doñana area. The first group of variables includes those concerning the local attributes of ponds, whereas the second group of variable includes those concerning the landscape in which ponds were embedded.

Code	Description	Type of variable (units)	Range
LOCAL ATTRIBUTES OF PONDS			
SIZE	Size	continuous (ha)	0.02-32.7
ALT	Altitude a.s.l.	continuous (m)	0-69.1
OPEN	Open area within the pond	continuous (ha)	0-22.9
MASH	Marshy vegetation within the pond	continuous (ha)	0-9.9
CANO	Canopy within the pond	continuous (ha)	0.2.5
BRUSH	Brushes within the pond	continuous (ha)	0-14.7
GRASS	Grasses within the pond	continuous (ha)	0-9.4
PIST	Amount of pond bank surrounded by: <i>Pistacea</i> brushes	discrete	1-3
ERICA	<i>Erica</i> brushes	discrete	1-3
HALI	<i>Halimium</i> brushes	discrete	1-3
JUNCUS	<i>Juncus</i> brushes	discrete	1-3
TAMA	<i>Tamarix</i> brushes	discrete	1-3
OTHER	Other brushes	discrete	1-3
TREE	Presence of trees within 50 m from pond bank	categorical	1-2
WATER	Amount of water within the pond	discrete	1-4
LIVEST	Abundance of: Livestock	discrete	1-4
DEER	Red and fallow deer	discrete	1-4
BOAR	Wild boar	discrete	1-4
RABBIT	Rabbit	discrete	1-4
HARE	Hares	discrete	1-4
LANDSCAPE ATTRIBUTES OF PONDS			
MACRO	Macrohabitat in which the pond is embedded	categorical	1-5
PROT	Level of human protection	categorical	1-2
DIS_VE	Distance to ecotone Vera	continuous (m)	0-27756
DIS_P	Distance to nearest pond holding water voles	continuous (m)	100-8989
NP_2	Number of ponds holding water voles within 2 km	discrete	0-11
DIS_L	Distance to nearest permanent lagoon	continuous (m)	46-7015

of green vegetation to voles. Presence of trees within 50 m of the pond bank was also recorded since it could increase the vulnerability of water voles to raptors (Kay *et al.*, 1994). Finally, because potential competitors (livestock, deer, wild boar, rabbits, and hares) could negatively affect vole populations, the use of each pond by those species was roughly assessed on the basis of the relative abundance (none, low, intermediate, or high) of their signs (mainly tracks and feces) within each pond.

STATISTICAL ANALYSIS

Results from vole and pond surveys were analyzed using a generalized linear model fitted using PROC GENMOD from SAS (Stokes *et al.*, 1995). We analyzed a matrix in which the presence or absence (1/0) of the species in ponds and their local and landscape attributes were recorded. Because of the dichotomous nature of the response variable (presence/absence of voles), we assumed that errors followed a binomial distribution (Stokes *et al.*, 1995), and thus we fitted the model with binomial error and a logistic link function. An initial full model was fitted using all 26 factors (Table I). The significance of each factor was assessed by step-wise backwards elimination from the full model. We used "Type 3 analysis" to ensure that our results did not depend on the order in which terms (*i.e.*, explanatory variables) were specified in the model (Stokes *et al.*, 1995). The increase in deviance of the model when a factor was removed was checked against the chi-square distribution with the same degrees of freedom (df) as the increase in df of the model. When the ratio deviance/df of the initial minimum model suggested overdispersion in the data, the

deviance of the model was scaled, and the significance of the final model rechecked.

Neighboring ponds shared several attributes, which could have led to skewed results if our sampling was limited and/or was spatially unbalanced. However, we sampled a high percentage of the existing ponds (31%) homogeneously dispersed over the area (Figure 1), thus minimizing the range of spatial autocorrelation (Sokal & Oden, 1978).

BEHAVIORAL RESPONSE OF VOLES TO VEGETATION WITHIN PONDS

To evaluate the consistency of the patterning of vole presence/absence in ponds of Doñana and the process of habitat selection made by individual voles, we studied the behavioral response of water voles to vegetation cover within ponds. Thus, we compared vegetation cover in circular plots of 80 cm diameter used by water voles (those with latrines or feces, on which the plots were centered; hereafter positive plots, PP) with vegetation cover in randomly chosen plots of the same dimensions without signs of water vole activity (hereafter negative plots, NP). Within a selected pond, a total of 15 PP were set. From the location of each PP, we set two associated NP, at 10 and 20 m respectively, in a random cardinal direction (starting at 0° and consecutively rotating 90° clockwise). Thus, for each pond 15 PP and 30 NP were set. Two indexes of vegetation cover were estimated for each plot: the proportion of an 80-cm segment intersected by vegetation at a height of 10 and 20 cm, respectively. To evaluate the pervasiveness of water vole responses to vegetation cover within ponds, we repeated our

approach in four ponds (two in Doñana National Park and two in Abalario) where the presence of water vole was known, but which were otherwise randomly chosen. Overall, 60 PP and 120 NP were set. Differences in vegetation cover among compared plots (*i.e.*, PP versus NP) were evaluated separately for each pond by Wilcoxon Matched Pair Tests (Siegel, 1956).

Results

OVERALL PATTERNS

We found signs of voles in 60% of ponds sampled ($n = 185$), despite the fact that most surveyed ponds (84%) were totally dried out. Figure 1 reveals that the population of water voles was not homogeneously distributed. Water voles were found in 70% of ponds ($n = 95$) outside the national park but in only 50% ($n = 90$) of ponds inside the park. In addition, none of the surveyed ponds in the northern portion of the national park ($n = 6$), called Matasgordas (Figure 1), hosted the species.

Our GLM analysis indicated that three variables concerning landscape attributes and five variables concerning local attributes of ponds significantly influenced the status of water voles (Table II). This model reduced the overdispersion of the intercept model by 33% ($\phi = 1.353$; calculated as the deviance divided by degrees of freedom), thus evidencing a substantial improvement in the goodness-of-fit of the model. The percentage of variance (total sum of squares) in our data explained by this final model was 36.3% (estimated as the change in deviance following this model divided by the deviance following the intercept model).

LANDSCAPE ATTRIBUTES AFFECTING VOLE PRESENCE

Twelve percent of the variance in our data was explained by three variables related to the landscape in which the ponds are embedded (PROT, DIS_P, DIS_VE; Table II). The negative sign of PROT indicates that ponds located inside the Doñana National Park were less likely to hold water voles than those outside the park. There was no

evidence of any response by water voles to the macrohabitat (MACRO) in which ponds were embedded. Our analyses also indicated that ponds neighboring other ponds holding voles were more likely to hold this species than more isolated ponds were (negative sign of DIS_P; Table II). Finally, once controlled for the effect of PROT, ponds close to the Vera ecotone were less likely to hold water voles than ponds away from Vera (Table II).

LOCAL ATTRIBUTES AFFECTING VOLE PRESENCE

Most of the variance (24.3%) in our data was explained by variables related to local attributes of ponds (ALT, GRASS, ERICA, HALI, and RABBIT; Table II). The negative sign of ALT indicates that presence of water voles was less likely in ponds located at higher elevations. The significance of GRASS, ERICA, and HALI indicates that water voles were sensitive to both habitat composition within ponds and vegetation along their banks. The negative effect of RABBIT (Table II) indicates that presence of water voles was less likely in ponds used by this potential competitor. Pond size had no apparent effect on the presence of water voles.

FIGURE 2. Mean indexes of vegetation cover (bars) and SD (vertical lines above the bars) at the four selected ponds within the Doñana National Park (Doñana-1 and Doñana-2) and Abalario (Abalario-1, Abalario-2). Within each pond, 15 plots with water vole signs (PP) were set. From the location of each PP, two associated plots with no water vole signs (NP) were randomly set at 10 and 20 m [NP (10 m) and NP (20 m), respectively]. An index of vegetation cover was estimated twice for each plot, at a height of 10 and 20 cm, respectively (a and b). Note that indexes of vegetation cover at PP were consistently higher than those of NP for all four ponds.

TABLE II. Main results of analysis of parameter estimates and main effects for the final generalized linear model predicting the probability of occurrence of water voles (*Arvicola sapidus*) at ponds of the Doñana area. The model was fit with binomial error and a logistic link function. Mean values and standard error of parameter estimates, *F*-statistics, degrees of freedom (df), and *p*-values for the analysis of each main effect specified in the final model are shown.

Source	Parameter estimates		Analysis of main effects		
	Mean	SE	df	<i>F</i>	<i>P</i>
DIS_VE	0.0002	0.0001	1	5.98	0.0154
DIS_P	-0.0005	0.0002	1	7.81	0.0058
PROT	-3.8624	1.0531	1	16.22	0.0001
ALT	-0.1489	0.0325	1	26.94	0.0001
GRASS	6.1464	1.4675	1	44.90	0.0001
ERICA	0.6058	0.1889	1	11.75	0.0006
HALI	0.4564	0.2073	1	5.21	0.0224
RABBIT	-0.6096	0.1908	1	11.28	0.0008
Intercept	1.22	0.5472			

Scale factor of final model: 0.9496

BEHAVIORAL RESPONSE OF VOLES TO VEGETATION WITHIN PONDS

Our evaluation of the use of habitat by voles within ponds of Doñana indicated that mean indexes of vegetation cover were always much higher within plots containing vole signs (46-67 and 18-49, for 10 and 20 cm of height, respectively; Figure 2) than within random plots located at 10 m (10-24 and 3-16, for 10 and 20 cm of height, respectively) and at 20 m (6-33 and 1-15, for 10 and 20 cm of height, respectively). Differences were significant for all four ponds (Wilcoxon Matched Pair Tests, $Z > 2.2$, $n = 15$, $p < 0.031$; Figure 2). Further, in 65% ($n = 60$) of PP we found both feces and tunnels made through the vegetation and used by voles for movements. Thus, our results indicate that water voles responded to vegetation by focusing their activities on patches of high vegetation cover and that this pattern was consistent throughout the four ponds considered.

Discussion

Our results confirm that water voles in Doñana are restricted to water bodies, and consequently, their populations are patchily distributed within a hostile matrix composed of dry sclerophyll Mediterranean scrubland. However, the high number of occupied ponds in spite of the dry period chosen for our survey, when most ponds were dried out, challenges the accepted notion of *A. sapidus* as a species strictly dependent on habitats with permanent water (Mitchell-Jones *et al.*, 1999) and suggests that the species is adapted to suffer droughts typical of some Mediterranean areas. Surprisingly, our results indicate that at present the Guadalquivir marshes are not a source of water voles, since ponds close to the marsh were less likely to hold voles than were ponds far from the marshes. This result could be related to the fact that at present the Guadalquivir marshes are an environment invaded by the aggressive and semiaquatic brown rat (*Rattus norvegicus*; Valverde, 1967), which may limit the numbers and distribution of voles. In fact, our limited unpublished data on predation of water voles and brown rats by barn owls at seven independent sites in Doñana (*i.e.*, separated by 4-35 km) show a negative relationship among the numbers of individuals of both species in pellets (Spearman correlation, $r = -0.79$, $n = 7$, $p = 0.036$; overall 46 individuals), suggesting that the abundances of these two rodent species in the field are also negatively correlated, though further work is needed to evaluate this hypothesis.

According to our data, both landscape and local habitat attributes significantly influenced the status of water voles at ponds. Detailed studies carried out in arid and semi-arid regions have shown that the distribution and habitat selection strategies of small mammals are correlated with variations in the availability of resources at a local (microhabitat) scale (Rosenzweig, 1989; Stapp, 1997), whereas in highly productive environments (such as temperate-zone forests), landscape features appear predominant in determining such patterns (Morris, 1987; Harper, Bollinger & Barrett, 1993). In our Mediterranean ecosystem of intermediate primary productivity (Bailey, 1996), we found an intermediate situation in which both local and landscape attributes played an important role. For instance, at the landscape level, we

found a lower presence of water voles at ponds within the national park than at ponds outside the park, which is likely related to the higher abundance of potential predators within the park (Travaini *et al.*, 1997; Forero *et al.*, 1999). Predation has often been identified as an important factor influencing distribution and dynamics of water voles (Spitz & Bourliere, 1975; Barreto *et al.*, 1998); thus, it could also be a limiting factor at ponds of Doñana, where barn owls (*Tyto alba* Scopoli), tawny owls (*Strix aluco* L.), polecats (*Mustela putorius* L.), red foxes (*Vulpes vulpes* L.), and Iberian lynxes (*Lynx pardinus* Temminck) prey on water voles (Valverde, 1967; Delibes, 1980; Fedriani *et al.*, unpubl. data). It is not surprising, therefore, that at the local level, ponds (and their banks) holding voles were characterized by abundant vegetation, which provided voles with a substrate for the extensive tunnels that likely permit them to hide from predators (Lawton & Woodroffe, 1991). Because water voles and rabbits are both herbivores, the negative effect of rabbits on voles could be due to exploitative competition. However, it might also be due to apparent competition (Holt, Grover & Tilman, 1994), since their common predators in Doñana select habitat patches rich in rabbits (*e.g.*, Fedriani, Palomares & Delibes, 1999), which likely enhances predation pressure at ponds where rabbits are more abundant. Patch size is often another local predictor of the presence and abundance of small mammals (see Bowers & Matter, 1997). The lack of effect of pond size in our model suggests that most ponds are large enough to hold voles, and thus pond quality (*i.e.*, vegetation cover, availability of food) was a more critical determinant of vole status at ponds. Interestingly, the proximate cues governing the presence of voles in particular ponds (abundance of grasses and well-covered banks) matched those implicated in the selection of habitat by individual voles (*i.e.*, plots of high vegetation cover), which points to the existence of a link between the habitat selections of individuals and the pattern of vole distribution.

However, distinguishing the role of different levels of spatial heterogeneity is often problematic because local and landscape variables may often be correlated with one another (Mazerolle & Villard, 1999). For instance, the fact that ponds located at low altitudes were more likely to hold voles can be interpreted both at the landscape level (low altitude grounds could act as corridors during the rainy period, and thus ponds within these grounds should be more easily recolonized) and at the local level (lower ponds should be flooded for longer periods and thus grow more grasses). Furthermore, we found a positive correlation between distance to Vera and pond size (Spearman correlation, $r = 0.297$, $n = 185$, $p < 0.0001$); thus, the local effect of pond size could be masked by the landscape effect of distance to the Vera ecotone.

This study can be best described as an instantaneous photographic picture of vole distribution in Doñana. Whereas some of our results can be interpreted in terms of such static situation, for others a dynamic framework is needed. Ponds neighboring occupied ponds were more likely to host voles. Such aggregation may be a result of the distribution of ponds in clusters (*e.g.*, those in Marismillas, Reserva, Abalario, Matasgordas; Figure 1). For instance, no ponds surveyed in Matasgordas ($n = 6$; Figure 1) held water

voles. This could be interpreted in terms of spatial autocorrelation, environmental conditions being more similar within than among clusters. However, we did not detect any effect of macrohabitat, which might be expected in this situation since macrohabitat patches change at a spatial scale close to that of the identified clusters. In this case, it is more plausible to speculate about some kind of metapopulation dynamic (Hanski & Gilpin, 1997), with extinct subpopulations in some ponds being occasionally rescued by migrants coming from neighboring occupied ponds. If so, the fact that ponds in Matasgordas are rather isolated from ponds holding voles (e.g., in the Reserve) should make such rescue difficult. On the other hand, overdispersion in our data indicates that key explanatory variables are missing. Such variables might be related to the recent history of the water bodies (which have been drying out since at least the 19th century; Castroviejo, 1993; Sousa & Garcia-Murillo, 2001) and/or to the dynamics of such fragmented populations, as the persistence of small subpopulations is generally a strong function of highly unpredictable episodes (e.g., arrival of mates, appearance of predators, disease outbreaks; Hanski & Gilpin, 1997). To solve these questions, however, long-term studies are necessary.

In conclusion, we found that the distribution of water voles in Doñana was dependent on interacting variables representing several levels of spatial heterogeneity. Landscape variables likely influence the proneness of ponds to be (re)colonized by water voles, whereas local variables likely affect the persistence of voles at ponds. At least for Mediterranean ecosystems, models that do not incorporate both local and landscape attributes of patches under investigation may not reveal the complexity behind species distribution (Mazerolle & Villard, 1999; Schweiger *et al.*, 1999). Our study also provides collaborative evidence linking habitat selection to the pattern of water vole distribution in the Doñana area and strongly suggests that the entire vole population is structured in distinct subpopulations. It would appear that vole distribution is influenced by a hierarchy of factors, including metapopulation dynamics, the landscape within which ponds are embedded, and local habitat quality.

Acknowledgements

We thank R. Alejandro, J. C. Rivilla, and S. Alis for their enthusiastic field assistance. X. Cerdá, D. Morris, S. P. Rushton, and M. Monkkonen critically reviewed early versions and made constructive comments. C. M. Herrera kindly assisted us statistically. H. Abdallah kindly reviewed the manuscript. This study was supported by a Fondo Europeo Desarrollo Regional project (1FD 1997-0789). J. M. Fedriani enjoyed funding from his parents during part of the elaboration of this manuscript.

Literature cited

- Barrett, G. W. & J. D. Peles, 1999. Small mammal ecology: A landscape perspective. Pages 1-8 in G. W. Barrett & J. D. Peles (ed.). *Landscape Ecology of Small Mammals*. Springer-Verlag, Berlin.
- Barreto, G. R., S. P. Rushton, R. Strachan & D. W. Macdonald, 1998. The role of habitat and mink predation in determining the status and distribution of water voles in England. *Animal Conservation*, 1: 129-137.
- Bailey, R. G., 1996. *Ecosystem Geography*. Springer-Verlag, New York.
- Bowers, M. A. & S. F. Matter, 1997. Landscape ecology of small mammals: Relationship between density and patch size. *Journal of Mammalogy*, 78: 999-1013.
- Bowers, M. A. & G. W. Barrett, 1999. Synthesis: A review of the science and prescriptions for the future. Pages 313-337 in G. W. Barrett & J. D. Peles (ed.). *Landscape Ecology of Small Mammals*. Springer-Verlag, Berlin.
- Boyce, M. S. & L. L. McDonald, 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution*, 14: 268-272.
- Bravo, M. A. & C. Montes, 1992. Inventario de las formaciones palustres del manto eólico del Parque Nacional de Doñana (SO España). IV Spanish Workshop of Limnology, Granada.
- Castroviejo, J., 1993. Mapa del Parque Nacional de Doñana. Technical report. Consejo Superior de Investigaciones Científicas / Agencia del Medio Ambiente-Andalucía.
- Delibes, M., 1980. Feeding ecology of the Spanish lynx in the Coto Doñana. *Acta Theriologica*, 25: 309-324.
- Fedriani, J. M., F. Palomares & M. Delibes, 1999. Niche relations among three sympatric Mediterranean carnivores. *Oecologia*, 121: 138-148.
- Forero, M. G., J. A. Donazar, J. Blas & F. Hiraldo, 1999. Causes and consequences of territory change and breeding dispersal distance in the black kite. *Ecology*, 8: 1298-1310.
- Forys, E. & S. R. Humphrey, 1999. The importance of patch attributes and context to the management and recovery of an endangered lagomorph. *Landscape Ecology*, 14: 177-185.
- Garde, J. M. & M. C. Escala, 1993. Predation and intraspecific selection of the barn owl (*Tyto alba*) on the water vole (*Arvicola sapidus*). *Ardeola*, 40: 173-175.
- Hanski, I. & M. E. Gilpin, 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California.
- Harper, S. J., E. K. Bollinger & G. W. Barrett, 1993. The effects of habitat patch shape on population dynamics of meadow voles (*Microtus pennsylvanicus*). *Journal of Mammalogy*, 74: 1045-1055.
- Holt, R. D., J. Grover & D. Tilman, 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist*, 144: 741-771.
- Kareiva, P. & U. Wennergren, 1995. Connecting landscape patterns to ecosystem and population processes. *Nature*, 373: 299-320.
- Kay, B. J., E. T. Lauvie, J. K. Terry & I. N. Helen, 1994. The use of artificial perches to increase predation on house mice (*Mus domesticus*) by raptors. *Wildlife Research*, 21: 95-106.
- Lawton, J. H. & G. L. Woodroffe, 1991. Habitat and the distribution of water voles: Why are there gaps in a species's range? *Journal of Animal Ecology*, 60: 79-91.
- Lima, M., P. A. Marquet & F. M. Jaksic, 1996. Extinctions and colonization processes in subpopulations of five neotropical small mammals species. *Oecologia*, 107: 197-203.
- Mazerolle, M. J. & M. A. Villard, 1999. Patch characteristics and landscape context as predictors of species presence and abundance: A review. *Écoscience*, 6: 117-124.
- Mitchell-Jones, A. J., G. Amori, W. Bogdanowicz, B. Krystufek, P. J. H. Reijnders, F. Spitzenberger, M. Stubbe, J. B. M. Thissen, V. Vohralik & J. Zima, 1999. *The Atlas of European Mammals*. Academic Press, London.
- Morris, D. W., 1987. Ecological scale and habitat use. *Ecology*, 68: 362-369.
- Morris, D. W., 1992. Scales and costs of habitat selection in heterogeneous landscapes. *Evolutionary Ecology*, 6: 412-432.

- Orians, G. H. & J. F. Wittenberger, 1991. Spatial and temporal scales in habitat selection. *American Naturalist*, 137: S29-S49.
- Rosenzweig, M. L., 1989. Habitat selection, community organization, and small mammals studies. Pages 5-23 in D. W. Morris, Z. Abramsky, B. J. Fox & M. R. Willing (ed.). *Patterns in the Structure of Mammalian Communities*. Special Publication Number 28 of the Museum of Texas Tech University, Lubbock, Texas.
- Schweiger, E. W., J. E. Diffendorfer, R. Pierotti & R. D. Holt, 1999. The relative importance of small scale and landscape-level heterogeneity in structuring small mammal distributions. Pages 175-207 in G. W. Barrett & J. D. Peles (ed.). *Landscape Ecology of Small Mammals*. Springer-Verlag, Berlin.
- Siegel, S., 1956. *Nonparametrics Statistics*. MacGraw-Hill, New York.
- Sousa, A. & P. Garcia-Murillo, 2001. Can place names be used as indicators of landscape changes? Application to the Doñana Natural Park (Spain). *Landscape Ecology*, 16: 391-406.
- Spitz, F. & F. Bourlière, 1975. La dynamique des populations de Mammifères. Pages 77-127 in M. Lamotte & F. Bourlière (ed.). *Problèmes d'écologie: La démographie des populations de Vertébrés*. Masson, Paris.
- Sokal, R. R. & N. L. Oden, 1978. Spatial autocorrelation in biology. 1. Methodology. *Biological Journal of the Linnean Society*, 10: 199-228.
- Soriguer, R. C., 1983. Consideraciones sobre el efecto de los conejos y los grandes herbívoros en los pastizales de la Vera de Doñana. *Doñana Acta Vertebrata*, 10: 155-168.
- Stapp, P., 1997. Habitat selection by an insectivorous rodent: Patterns and mechanisms across multiple scales. *Journal of Mammalogy*, 78: 1128-1143.
- Stokes, M. E., E. Manra, C. S. Davis & G. G. Koch, 1995. *Categorical data analysis using the SAS system*. SAS Institute Inc., Cary, North Carolina.
- TRAGSATEC, 1993. *Inventario de humedales. Proyecto de restauración ecológica del complejo palustre del Abalario, Parque Natural Entorno de Doñana, Huelva*. Technical Report. Junta de Andalucía.
- Travaini, A., M. Delibes, P. Ferreras & F. Palomares, 1997. Diversity and abundance of rare species as a target for the conservation of mammalian carnivores: A case study in southern Spain. *Biodiversity Conservation*, 6: 529-535.
- Valverde, J. A., 1960. An ecological sketch of the Coto Doñana. *British Birds*, 51: 1-23.
- Valverde, J. A., 1967. *Estructura de una comunidad de vertebrados terrestres*. Monografías Consejo Superior de Investigaciones Científicas, No 76, Madrid.
- Van Apeldoorn, R. C., W. T. Oostenbrink, A. van Winden & F. F. der Zee, 1992. Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. *Oikos*, 65: 265-274.
- Ventura, J. & J. Gosálbez, 1987. Reproductive biology of *Arvicola sapidus* (Rodentia, Arvicolidae) in the Ebro Delta (Spain). *Zeitschrift für Säugetierkunde*, 52: 364-371.
- Wiens, J. A., 1985. Habitat selection in variable environments: Shrub-prairie birds. Pages 227-251 in M. L. Cody (ed.). *Habitat Selection in Birds*. Academy Press, Orlando, Florida.
- Woodroffe, G. L. & J. H. Lawton, 1990. Patterns in the production of latrines by water voles (*Arvicola terrestris*) and their use as indices of abundance in population surveys. *Journal of Zoology*, 220: 439-445.