

WINTER HABITAT SELECTION AND PARTITIONING IN TWO SYMPATRIC FARMLAND SMALL MAMMALS: *APODEMUS SYLVATICUS* AND *MUS SPRETUS*V́ctor NOGUERALES^{1,2}, Juan TRABA², Cristina MATA² & Manuel B. MORALES²

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RÉSUMÉ.— *Partage et sélection d'habitat en hiver chez deux rongeurs sympatriques en milieu agricole : Apodemus sylvaticus et Mus spretus.*— Les patrons de sélection d'habitat des mammifères varient selon l'échelle et il existe différentes vues sur le rôle des facteurs agissant à macro- et à micro-échelles dans l'assemblage des communautés. Dans cette étude, nous évaluons si les différents patrons de sélection du macro- et du microhabitat expliquent la coexistence de deux espèces de rongeurs sympatriques, *Mus spretus* et *Apodemus sylvaticus* en milieu agricole au centre de l'Espagne. Nous avons échantillonné les rongeurs des cultures céréalières et des champs non-cultivés (jachères et friches) en utilisant une grille de pièges Sherman. La disponibilité de nourriture et la structure de la végétation (variables à l'échelle du microhabitat), ainsi que la composition du paysage (variable à l'échelle du macrohabitat), ont été mesurées à chaque grille d'échantillonnage. L'abondance de chaque espèce a été analysée en utilisant des Modèles Linéaires Généralisés (MLGs) pour déterminer quelles sont les variables d'échelle associées à l'abondance spécifique. Le poids de chaque échelle dans la formation de l'assemblage a été examiné par une procédure de partition de variance. À l'échelle du microhabitat, *A. sylvaticus* était positivement lié à la couverture de buissons et *M. spretus* était positivement liée à la disponibilité des graines. À l'échelle du macrohabitat, *A. sylvaticus* était négativement associé à la distance de l'arbre le plus proche, alors que *M. spretus* était associée positivement à la même variable. Le macrohabitat explique 39 % de la variance de l'assemblage, alors que le microhabitat n'explique que 8 %. Ces résultats suggèrent une relative ségrégation d'utilisation des ressources par les deux espèces à l'échelle du microhabitat, et un partage de l'espace à macro-échelle, permettant la coexistence des deux espèces conformément aux règles d'assemblage des communautés. Cette étude montre l'importance de considérer l'échelle du macrohabitat pour comprendre la configuration des assemblages de rongeurs.

SUMMARY.— Patterns of small mammal habitat selection vary according to scale, although there are discrepancies about the importance of macro and micro-scale factors in rodent community assembly. We assess whether differences in their micro and macrohabitat selection patterns explain the coexistence of two sympatric rodents, *Mus spretus* and *Apodemus sylvaticus*, in an agricultural area of central Spain. We trapped mice in uncultivated and crop fields using a grid of Sherman traps. Food availability and vegetation structure (microhabitat) and landscape composition variables (macrohabitat) were measured in each plot. We used GLMs to determine the scale predictors related to specific abundance. The importance of each scale in the assemblage was assessed by a variance partitioning procedure. At microhabitat scale, *A. sylvaticus* was positively related to shrub cover and *M. spretus* to seed availability. At macrohabitat scale, *A. sylvaticus* was negatively associated with distance to the nearest tree, whereas *M. spretus* was positively associated with this variable. Macrohabitat explained 39 % and microhabitat 8 % of the variance in the assemblage. Results suggest a relative segregation of food preferences at microhabitat scale, and a habitat partitioning at macrohabitat scale, which may allow spatial coexistence of both species, according to community assembly theory. This study shows the importance of both micro and macrohabitat in the configuration of rodent assemblages.

Small mammal communities are structured on the basis of distinct habitat selection patterns, intra- and interspecific interactions, behaviour, morphology, body size, predation risk, resource partitioning and resource availability (Kotler & Brown, 1988; Kotler *et al.*, 1994; Abramsky *et al.*, 2001; Corbalán & Ojeda, 2004; Traba *et al.*, 2009). Hence, the detection and interpretation of such patterns is affected by the spatial scale of the study (Levin, 1992).

Habitat selection in small mammals has frequently been analysed in terms of the physical and biological characteristics of the space in which the organisms live (Rosenzweig & Winakur, 1969; Morris, 1984). Habitat selection, furthermore, is an active process through which a species selects between available resources (Johnson, 1980). Such a process is hierarchical, including the macrohabitat level – defined as the habitat type and its landscape context i.e. its degree of complexity and heterogeneity – and also the microhabitat level, which is normally studied in terms of vegetation structure (Kotler & Brown, 1988), which is ultimately perceived and selected by the organism concerned (Morales *et al.*, 2008).

Studies of small mammals' habitat selection differ with respect to the importance given to micro- and macrohabitat. Some confirm that small mammals distribution and abundance are determined by microhabitat structure (Bellows *et al.*, 2001; Jorgensen, 2004; Traba *et al.*, 2009; Tarjuelo *et al.*, 2011), whereas others find macrohabitat characteristics to be more reliable predictors of this (Morris, 1984, 1987; Orrock *et al.*, 2000; Corbalán, 2006).

Plant cover and food resource availability are the main factors involved in the process of microhabitat selection in small mammals (Traba *et al.*, 2009; Tarjuelo *et al.*, 2011). At macrohabitat scale, habitat type and landscape complexity are responsible for the structure and dynamics of small mammal populations (Morris, 1984; Millán de la Peña *et al.*, 2003; Fischer *et al.*, 2011). The response to these variables is revealed at a scale of less than 250 m (Bowman *et al.*, 2000; Silva *et al.*, 2005; Butet *et al.*, 2006) due to the limited dispersal capacity of these species (Morris, 1992; Tew & MacDonald, 1994).

Just a few studies of small mammal habitat selection in agrarian environments can be found (Todd *et al.*, 2000; Butet *et al.*, 2006; Michel *et al.*, 2006; Fischer *et al.*, 2011) including Mediterranean Iberia (Díaz *et al.*, 1993; de Alba *et al.*, 2001; Torre & Díaz, 2004; Tarjuelo *et al.*, 2010, 2011). These last works show that the most abundant mouse species (Rodentia, Muridae) in the agricultural landscapes of central Iberian Peninsula are the Algerian Mouse (*Mus spretus*) and the Wood Mouse (*Apodemus sylvaticus*). In this environment the abundance of one species seems to be inversely proportional to that of the other (de Alba *et al.*, 2001; Torre & Díaz, 2004), suggesting possible interspecific competition between them for food or spatial resources (Fons *et al.*, 1988; Khidas *et al.*, 2002).

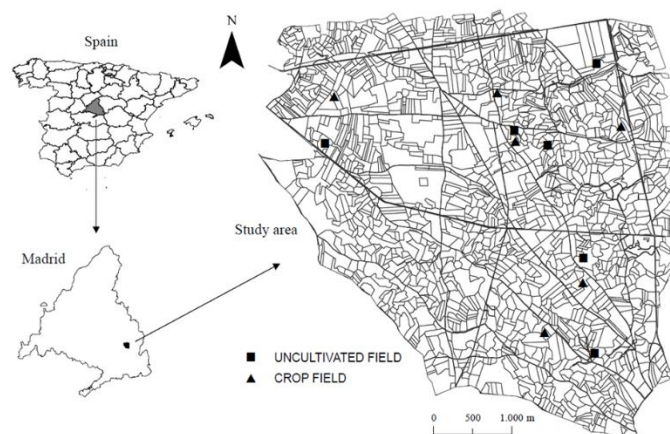


Figure 1.— Location of the study area in the Madrid region. Field layouts are shown including the location of the fallow and crop fields where sampling took place.

From another standpoint, maintaining stable small mammal populations in heterogeneous anthropic systems demands an adequate understanding of habitat and resource use at different

scales by the species concerned. A multiscale approach incorporating both micro- and macrohabitat is thus necessary to determine the habitat selection patterns of rodents, a group whose ecological importance is paramount given their roles as the prey of numerous raptor species (Salamolard *et al.*, 2000) and mammals (Rosalino *et al.*, 2011) and as consumers and dispersers of seeds (Díaz, 1992; Muñoz & Bonal, 2007) as well as in acting as vectors of disease and periodically attaining pest levels of abundance in agricultural systems (Brown *et al.*, 2007).

The overall aim of this study is to describe habitat use and both micro- and macrohabitat selection in the Algerian Mouse (*Mus spretus*) and the Wood Mouse (*Apodemus sylvaticus*) in winter in a region of extensive agriculture in central Spain where both species coexist. The following specific objectives are also addressed: i) analysis of the pattern of segregation or interspecific coexistence, ii) determining the environmental variables at each scale that are associated with the abundance of each taxon, and iii) evaluation of the relative importance of micro- and macrohabitat for the rodent assemblage.

MATERIALS AND METHODS

STUDY AREA

The study area is in the central Iberian Peninsula, southeast of Madrid region (40° 20' 3'' N, 3° 19' 58'' W; Fig. 1). It lies at 770-800 m.a.s.l. and experiences a mean annual precipitation of 500 mm and a mean annual temperature of 13.0° C. The area is dominated by cereal croplands (mainly of barley, *Hordeum vulgare*) under annual crop rotation in which a field is left fallow for one year after a harvest. There are also uncultivated areas dominated by herbaceous annuals and dwarf shrub scrub of *Thymus vulgaris*, *T. zygis* and *Santolina chamaecyparissus*, interspersed with scattered Iberian holm oaks (*Quercus ilex* subsp. *ballota*). Such other crop types as vineyards (*Vitis vinifera*), almond groves (*Prunus dulcis*) and olive groves (*Olea europea*) also form part of the landscape mosaic.

The work was conducted in 12 fields, six of them uncultivated and six sown with barley (Fig. 1), these being taken as the extremes of land management level that fields can experience.

The selected fields had a minimum area of 0.3 ha, and were over 200 m apart. In the case of crops, barley grains could be found on ground surface.

SMALL MAMMAL TRAPPING

Small mammals were captured with Sherman live capture traps (20 x 6 x 6 cm) incorporating a wooden end-chamber (10 x 10 x 10 cm) containing a small quantity of cotton wool in order to reduce mortality caused by low temperatures. The capture period extended from 14.XII.11 to 8.I.12. There was no precipitation during this period and temperatures ranged evenly between daily minima of -2°C and maxima of 15°C.

A 5 x 4 grid of 20 traps, 15 m apart, was set up in each field, covering an area of 0.27 ha. Traps were active for three nights in each field, being checked at dawn (08.00 hrs) and sunset (18.00 hrs). They were baited with bread fried in stale olive oil, a bait that has given satisfactory results in capturing small mammals in the Iberian Peninsula (Ruiz-Capillas *et al.*, 2013). The total trapping effort amounted to 720 trap/nights.

Simultaneous paired trapping in crops and uncultivated fields took place in order to avoid biases in capture rates due to differences in small mammal activity due to variation in weather conditions (Vickery & Bider, 1981) or possibly from effects related to the lunar cycle (Price *et al.*, 1984; Díaz, 1992).

Captured individuals were identified to species, noting their breeding condition, sex, weight and capture location within the grid. Each was marked with a temporary colour code (Salvador *et al.*, 2009), in order to detect any possible recaptures, and released at the capture site. The number of different individuals (thus excluding recaptures) captured per grid was used as response variable ('abundance') in habitat selection models (see below). Captures followed the usual protocols for handling animals and occurred under official permit.

CHARACTERISATION OF MICROHABITAT

Five 1 x 1 m quadrats were set up at random in each capture plot in order to determine vegetation structure on a microscale by measuring a series of microhabitat variables (Tab. I), all of which were regarded as descriptors of small mammal presence and abundance (Silva *et al.*, 2005; Traba *et al.*, 2009; Tarjuelo *et al.*, 2011). Each cover variable was estimated independently of the others so total cover could exceed 100 % (Aebischer *et al.*, 1993). A mean value for the variables per plot was obtained from the data from the five quadrats.

Seeds and other plant propagules comprise a significant part of the diet of Algerian and Wood mice, especially in winter (Torre *et al.*, 2002; Khammes & Aulagnier, 2003; Palomo *et al.*, 2009). Hence, three soil surface samples (to 1cm depth) were taken from 25 x 25 cm (0.0625 m²) quadrats (inside of 1 x 1 m quadrats) to determine the availability of

vegetal food resources in each field. After drying, each sample was sifted through progressively finer sieves (diameters 4 mm, 2 mm and 1 mm) in order to extract plant propagules (seeds, inflorescences, caryopses, bulbs, fruits, etc.) in each of these size categories. A maximum sample of 20 propagules in each size category was selected to estimate biomass volume, for each of which the length, width and height were measured with digital callipers (± 0.1 mm). The mean volume of these propagules was calculated by approximating their shape to that of an ellipsoid ($V = 4/3 a.b.c$; where a, b and c are the three perpendicular axes of the ellipsoid). Vegetal food resource availability per field, expressed as mm^3/m^2 , was estimated as the product of the number of vegetal propagules per size category and their mean volume.

CHARACTERIZATION OF MACROHABITAT

The influence of heterogeneity and landscape complexity was analysed in a 200 m diameter circular area (3.14 ha) around the centre of the trap grid, in accordance with the recommendations of other small mammal studies (Butet *et al.*, 2006; Fischer *et al.*, 2011). The following landscape variables were determined in each of these areas: i) length of field margins (herbs, shrubs or trees), ii) number of trees, iii) distance from the trap grid centre to the nearest tree, iv) mean area of fields included within the circular area, and v) substrate diversity within the area. The latter was taken as a measure of habitat heterogeneity and calculated using the Shannon-Wiener diversity index:

$$H' = -\sum p_i \log_2 p_i$$

where p_i is the surface area of each substrate category (uncultivated fields, crop, fallow, olive grove and vineyard) relative to the total area considered (3.14 ha). These variables were all calculated using a geographical information system, ArcGIS 9.3 (ESRI Inc., 2008). Values (mean \pm standard deviation) of micro- and macrohabitat variables used to describe uncultivated fields and crops are shown in Table SI in Supplementary Material.

STATISTICAL ANALYSIS

Co-occurrence analysis

Null models were constructed by means of Monte Carlo permutations of the matrix of presences and absences of both taxa in the 12 plots analysed, in order to identify and test statistically the pattern of coexistence or segregation of the Algerian Mouse and the Wood Mouse at the field scale. This procedure generated new matrices in which species presences/absences were randomly distributed in the locations (Gotelli, 2000). The C-score index (Stone & Roberts, 1990) was calculated from each matrix, quantifying the mean checkerboard value between all possible pairs of the assemblage. Lack of coexistence of two species (presence of species A, absence of species B, or vice-versa) is identified as a checkerboard. Observed C-score values greater than those randomly estimated indicate patterns of interspecific segregation, whereas values lower than those randomly estimated indicate association (Gotelli, 2000; Gotelli & Entsminger, 2009). This index is relatively robust to 'noise' and variability in the data, minimizing the likelihood of Type 1 errors (Gotelli, 2000; Gotelli & Entsminger, 2009). In this study each sampling plot was considered to be a separate location, assuming that the predicted presences of the species were proportional to the observed presences and that the probability of occupation of locations was proportional to that observed (Gotelli & Entsminger, 2009). This analysis made use of the 'analysis of co-occurrence' module of the ECOSIM software (Gotelli & Entsminger, 2009). The simulation procedure employed 20,000 iterations.

TABLE I

Result of the Principal Components Analysis performed on the transformed variables relating to vertical and horizontal vegetation structure (microhabitat). Correlation coefficients of the variables with the first two components retained are given. Bold type indicates variables with the highest correlation values for each component

Microhabitat variables	Code	PC1	PC2
Stone cover (%)	STCov	-0.896	0.248
Litter cover (%)	LCov	-0.800	-0.036
Bare ground cover (%)	BGCov	0.901	0.222
Herbaceous cover (%)	HCov	-0.767	-0.602
Shrub cover (%)	SCov	-0.899	0.375
Tree cover (%)	TCov	-0.579	0.309
Mean herb height (cm)	MeaHH	-0.259	-0.887
Maximum herb height (cm)	MaxHH	-0.832	-0.484
Mean shrub height (cm)	MeaSH	-0.924	0.311
Maximum shrub height (cm)	MaxSH	-0.922	0.322
Eigenvalue		6.45	1.93
Explained variance (%)		64.50	19.31

Predictive models of habitat selection

The vegetation structure variables (microhabitat; Tab. I) were summarised by means of a Principal Component Analysis (PCA) based on a Pearson correlations matrix. Continuous variables were transformed as $\text{Log}_{10}(x+1)$ and cover percentages were arc-sine transformed. The PCA allows information from a large number of original variables to be summarised, obtaining new components that are independent among them, thus avoiding problems of colinearity detected between the original variables in earlier exploratory analyses. The components that result from the PCA are readily interpreted as ecological gradients among the microhabitat characteristics. The non-rotated components with eigenvalues >1 were retained and used as explanatory factors in later analyses. The PCA was conducted using STATISTICA v.8 (StatSoft Inc., 2006).

The colinearity of the descriptor variables for each habitat scale (Tab. II) was analysed by means of a Pearson correlation test, eliminating those with a coefficient $r > 0.7$ from subsequent analyses (Tabachnick & Fidell, 1996), keeping those variables with a clearer ecological meaning. To conduct the Pearson test those variables that did not fulfil the premises of normality and homoscedasticity of variances were specifically transformed (see Tab. II).

The relationship between the abundance of each species and the descriptor variables at each spatial scale was analysed by means of Generalised Linear Models (GLMs). The GLMs assumed a negative binomial distribution (log-link function) to correct for overdispersion within the data (ver Hoef & Boveng, 2007). The number of individuals of each species per field was used as the response variable and the untransformed original predictors served as explanatory variables (Tab. II). A maximum of two variables was introduced simultaneously in each model to avoid overfitting (Crawley, 2002). The significant variables from each model were retained and analysed once again with the remaining ones, thus testing all possible models (see Delgado *et al.*, 2009, for a similar procedure).

A model was built for each species and habitat scale (micro- and macrohabitat) analysed. The Wood Mouse models only used the captures within the uncultivated fields since only two individuals were caught in the crops (see below). Observations of the Algerian Mouse in both field types were used, introducing substrate type as a fixed factor. The goodness of fit of the models was analysed using their AICc values (Akaike's information criterion, adjusted for small samples). The most plausible model was that with the lowest AICc value (Burnham & Anderson, 2002). The Akaike weight (w_i), was calculated for each model, which represents the relative probability that model i will be the best of those considered. Also, the differences between AICc (Δ_i) were calculated as $(\text{AICc}_i - \text{AICc}_{\text{min}})$. Models with $\Delta\text{AICc} \leq 2$ show the highest fit of the data and have similar empirical support to the best model (Burnham & Anderson, 2002). Hence, in cases where model selection as a function of AICc did not give a single model, an averaging of models with $\Delta\text{AICc} \leq 2$ was performed (Burnham & Anderson, 2002). For this subset of models, the mean of the predictor estimators was calculated together with their unconditional standard errors (USE) and the relative importance of each variable in the final averaged model ($\sum w_i$, the sum of Akaike weights of models in which the variable was present). In this case, the effect of variables was regarded as consistent and significant if the 95 % confidence interval (CI) of its estimator (estimator $\pm t_{0.05} \times \text{USE}$) excluded the value 0 (Burnham & Anderson, 2002). The unconditional standard errors (USE) were calculated using the revised formula of Burnham & Anderson (2004). These analyses were carried out using R 2.14.1 software (R Development Core Team, 2011), employing the *MASS* package (Venables & Ripley, 2002) to construct the negative binomial GLMs and the *MuMIn* package (Barton, 2012) for model averaging.

Variance partitioning

Finally, in order to evaluate the effect of each group of explanatory variables (micro- and macrohabitat) on the structure and abundance of the rodent assemblage, variance partitioning was used (Borcard *et al.*, 1992), employing Redundancy Analysis (RDA) and Partial Redundancy Analysis (pRDA). A *Detrended Correspondence Analysis (DCA)*, (ter Braak, 1995) was previously performed on the response variables to determine the suitable method of canonical ranking as a function of the data structure.

The length of the detected gradient (< 2 SD) suggested the suitability of using an RDA (Lepš & Šmilauer, 2003). The partial RDA allows the effect of variables identified as covariables to be eliminated (ter Braak, 1988).

In this way, using the sum of all the canonical eigenvalues of each analysis (equivalent to R^2 in regression) allowed knowing the variance independently explained by each group of explanatory variables acting on the rodent assemblage.

Those explanatory variables that did not fulfil the premises of normality and homoscedasticity of variances were correspondingly transformed (Tab. II). The number of individuals of each species in each field type was used as the matrix of response variables. The statistical significance of all canonical axes was tested for each RDA and pRDA using a Monte Carlo permutations test, employing 499 unrestricted iterations under the reduced model (Lepš & Šmilauer, 2003). CANOCO 4.5 software (ter Braak & Šmilauer, 2009) was used for this analysis.

RESULTS

ABUNDANCE PATTERNS

Only two species were trapped, the Wood Mouse and the Algerian Mouse. In total 140 individuals of both species were captured. The Wood Mouse was less abundant, with 46

individuals captured, 44 of them in uncultivated fields and two in a crop field (mean captures \pm SD, uncultivated field: 7.33 ± 5.72 ; crop, 0.33 ± 0.82). The Algerian Mouse was the more abundant of the two, with 94 individuals captured, 61 of which were in uncultivated fields and 37 of these within a single uncultivated plot. The number of Algerian Mouse captures in crop fields ranged from 2 to 14 individuals (mean captures \pm SD; uncultivated field: 10.17 ± 13.67 ; crop, 5.50 ± 4.28).

TABLE II

Habitat descriptor variables included in the analyses and the type of transformation employed to meet the criteria of normality and homoscedasticity. Only the variables shown in bold type were used in the analyses, following Pearson correlation tests

Type ¹	Explanatory variable	Code	Transformation	Ecological meaning
MI	Food resources volume	FRV	Log ₁₀ (X+1)	Vegetal food resource availability per field, in mm ³ /m ²
MI	PCA Component 1 ²	PC1	Not required	Horizontal and vertical vegetation structure
MI	PCA Component 2 ²	PC2	Not required	Horizontal and vertical vegetation structure
MA	Tree number	Tree100	Log ₁₀ (X+1)	Number of tree trunks within a 200m diameter circle around the trap grid
MA	Distance to the nearest tree	Distree	Log ₁₀ (X+1)	Distance (m) to the nearest tree from the centre of the trap grid
MA	Plot area	PArea	(1/X)	Extent (ha) of fields included within a 200m diameter circle around the trap grid
MA	Total border length	TBL	(X) ²	Length of field margins (m) of fields included within the 200m diameter circle
MA	Shannon Index of agrarian habitat diversity	H	Not required	Agrarian substrate diversity within the 200m diameter circle
MA	Agrarian habitat type	AgrHT	Not required	Categorical variable with two levels (uncultivated fields and crops)

¹ MI, Microhabitat; MA, Macrohabitat.

² Principal Component Analysis.

TABLE III

Result of the multimodel inference (GLM, negative binomial, log link) for Wood Mouse (Apodemus sylvaticus) abundance as a function of microhabitat and macrohabitat predictors. Details are given for models with $\Delta AICc \leq 2$, showing the deviance and degrees of freedom (df) of each. Crosses indicate the inclusion of that variable in the model. See Table II for key to abbreviations

MICROHABITAT								
Model	FRV	PC1	PC2	AICc	$\Delta AICc$	w _i	Deviance	df
1			X	46.70	0.00	0.61	6.57	4
MACROHABITAT								
Model	Distree	PArea	H	AICc	$\Delta AICc$	w _i	Deviance	df
1	X			48.20	0.00	0.79	6.40	4

CO-OCCURRENCE ANALYSIS

The Algerian Mouse was present in 11 of the 12 plots sampled, being absent from one crop field. The Wood Mouse was present in seven fields: six uncultivated fields and one crop field. The co-occurrence analysis did not allow discarding the existence of a random distribution pattern of both species (simulated C-score = 3.77; observed C-score = 5.00; p = 0.33).

PREDICTIVE MODELS OF HABITAT SELECTION

The first two components of the PCA performed with the nine vegetation structure (microhabitat) variables absorbed 83.81 % of variance (Tab. I). The first component (64.50 %)

was associated positively with bare ground cover and negatively with scrub cover, as well as with its mean and maximum height. The second component (19.31 % of variance) was associated negatively with herbaceous cover and its mean and maximum height and positively, albeit more weakly, with scrub cover (Tab. I). The first component (PC1) may be interpreted as a gradient of intensity of agricultural management, with ploughed fields (sown in winter) with a high proportion of bare ground as opposed to fields with a permanent vegetation layer of dwarf shrubs (uncultivated fields). The second component (PC2) may be interpreted as a gradient of natural vegetation complexity.

TABLE IV

Result of the multimodel inference (GLM, negative binomial, log link) for Algerian Mouse (*Mus spretus*) abundance as a function of microhabitat and macrohabitat predictors. Details are given for models with $\Delta AICc \leq 2$, showing the deviance and degrees of freedom (df) of each. Crosses indicate the inclusion of that variable in the model. See Table II for key to abbreviations

MICROHABITAT									
Model	AgrHT	FRV	PC1	PC2	AICc	$\Delta AICc$	w_i	Deviance	df
1		X			78.70	0.00	0.51	13.36	10
MACROHABITAT									
Model	AgrHT	Distree	PArea	H	AICc	$\Delta AICc$	w_i	Deviance	df
1				X	81.50	0.00	0.23	13.30	10
2		X		X	81.70	0.23	0.20	12.69	9
3			X		82.50	1.04	0.14	13.32	10
4	X				82.60	1.14	0.13	13.34	10
5			X	X	83.10	1.57	0.10	13.05	9

TABLE V

Result of model averaging ($\Delta AICc \leq 2$) performed to analyse the macrohabitat descriptor factors that define Algerian Mouse (*Mus spretus*) abundance. The relative importance of each variable is indicated ($\sum w_i$, sum of Akaike weights of models in which the variable was present), as well as estimators and unconditional standard errors (USE) of the predictors resulting from the final averaged model. Bold type indicates variables excluding the value 0 in their confidence interval (CI). See Table II for key to abbreviations

PREDICTOR	$\sum w_i^1$	β	USE ²	Lower	Upper	CI
				95% CI	95% CI	includes 0?
AgrHT	0.16	-0.61	0.55	-1.70	0.74	Yes
Distree	0.25	0.012	0.01	0.01	0.02	NO
PArea	0.30	0.41	0.29	-0.15	0.99	Yes
H	0.67	-0.99	0.58	-2.14	0.15	Yes
Constant		2.39	0.74	0.93	3.85	NO

¹ Values of $\sum w_i$ are recalculated using only the five models with $\Delta AICc \leq 2$.

² USE calculated using the revised formula of Burnham & Anderson (2004).

TABLE VI

Result of the Monte Carlo permutations test (499 iterations) analysing the statistical significance of all the canonical axes of the Redundancy Analysis and Partial Redundancy Analysis performed. Microhabitat refers to food resource availability and vegetation structure. Macrohabitat refers to landscape complexity and heterogeneity, extent of agrarian plots and diversity of agrarian substrates

Scale	Covariable	F-ratio ¹	p
Microhabitat	-	2.04	0.10
Macrohabitat	-	8.45	0.00
Microhabitat	Macrohabitat	0.80	0.55
Macrohabitat	Microhabitat	3.79	0.08

¹ F statistic obtained via Monte Carlo permutations test

For the Wood Mouse, only one model with $\Delta AICc \leq 2$ was found, both for the micro- and macrohabitat analyses (Tab. III). For microhabitat, the most plausible model for the Wood Mouse included PCA component 2 (PC2) with a positive sign (Tab. III); for macrohabitat, the most plausible model included the distance to the nearest tree variable (Distree) with a negative effect (Tab. III).

For the Algerian Mouse, the only microhabitat model with $\Delta AICc \leq 2$ included availability of vegetal food resources variable (FRV) with a positive effect (Tab. IV). For macrohabitat, the selection process included five models within the $\Delta AICc \leq 2$ range (Tab. IV). Model averaging showed that substrate diversity around the trap grid (H) was relatively the most important variable according to its $\sum w_i$, followed by mean field size (PArea) and distance to the nearest tree (Distree), with substrate type (AgrHT) being the least important variable (Tab. V). Distance to the nearest tree (Distree) was the only variable showing a significant and positive relationship with Algerian Mouse abundance, after excluding the value 0 in the 95 % confidence interval of its effect estimate (Tab. V).

VARIANCE PARTITIONING

A high percentage of the total variance (82.7 %) was explained by both micro- and macrohabitat scales (Fig. 2). After controlling for the effect of the other scale, microhabitat and macrohabitat respectively explained 8.3 % and 39.3 % of variance (Fig. 2). An important fraction of the variability (35.1 %) was explained by the shared contribution of both scales. With respect to model significance, the RDA model employing the macrohabitat matrix proved significant for all its canonical axes (Tab. VI). The partial model employing macrohabitat as the principal matrix and microhabitat as covariable was marginally significant.



Figure 2.— Result of the partition of variance employing Redundancy Analysis and Partial Redundancy Analysis on the matrix of response variables and captures of Algerian Mouse (*Mus spretus*) and Wood Mouse (*Apodemus sylvaticus*) in an agrarian region in winter. The fraction of the variability explained by each predictor group is shown. Microhabitat refers to trophic resource availability and vegetation structure. Macrohabitat refers to landscape complexity and heterogeneity: distance to the nearest tree, extent of agrarian plots and diversity of agrarian substrates. The overlapping section indicates shared variance between both predictor groups.

DISCUSSION

To our knowledge, this study addresses jointly, for the first time, the analysis of interspecific segregation or coexistence patterns together with habitat selection at two spatial scales of the most abundant rodents of agricultural regions of the central Iberian Peninsula. The results indicate that during winter the observed abundances of the Wood Mouse and the Algerian Mouse could be due to their different habitat selection patterns, in terms of vegetation structure (microhabitat), food resources and various landscape features (macrohabitat). Differential use of habitat and resources at different scales has been described as a mechanism that allows coexistence of similar small mammal species (Brown, 1989; Scott & Dunstone, 2000; Traba *et al.*, 2009). However, we cannot exclude competition as an explanation for the observed pattern, as suggested by Fons *et al.* (1988) and Khidas *et al.* (2002).

The composition and structure of the rodent assemblage could have been biased by the trap type used, whose effectiveness may have differed as a function of the behavioural and feeding

characteristics of each species. Nevertheless, Sherman traps have proved their effectiveness in capturing the various small mammal species of the Iberian Peninsula (Ruiz-Capillas *et al.*, 2013). These authors caught two of the three species (the third one would be the Mediterranean Pine Vole *Microtus duodecimcostatus*) that could make up the rodent assemblage of our study area (Tarjuelo *et al.*, 2010).

ABUNDANCE AND CO-OCCURRENCE

The result of the co-occurrence analysis using null models suggests that Wood and Algerian mice are independently distributed in the two types of agrarian substrates analysed and, therefore, they do not fit any significant pattern of spatial segregation. Nevertheless, the small sample size and single sampling season, together with the existence of other habitat types whose sampling could modify the observed pattern, must be kept in mind when interpreting these results. However, the abundances of each species seem to be inversely related, as detected in previous studies in which a high density of one species appears to be associated with a low density of the other (de Alba *et al.*, 2001; Khidas *et al.*, 2002; Torre & Díaz, 2004; Tarjuelo *et al.*, 2011).

HABITAT SELECTION PATTERNS

The obtained results comprise the first multiscalar approach to the relationship between presence and absence of two sympatric small mammals and the vegetation and landscape characteristics of the cereal croplands of the Iberian Peninsula. They help to understand the role of habitat selection patterns in the coexistence of these species and in the structuring of this rodent assemblage. Despite the low number of different agrarian habitats analysed, the results show that the Wood Mouse and the Algerian Mouse show differential micro- and macrohabitat selection. In the study area, the Wood Mouse in winter seemed to prefer unploughed fields, avoiding laboured agrarian substrates, as already noted elsewhere (Díaz *et al.*, 1993; Todd *et al.*, 2000; Torre *et al.*, 2002). The selection of unploughed fields is interpreted as a dependence on stable burrows to provide refuge from low temperatures (Díaz *et al.*, 1993). The Wood Mouse seems to show a preference for microhabitats characterized by high levels of scrub cover, in accordance with earlier findings (Khidas *et al.*, 2002; Torre *et al.*, 2002). This pattern would be related to the advantages offered by dense woody vegetation in minimizing predation risks by providing secure feeding areas under cover (Díaz *et al.*, 1993; Morris & Davidson, 2000).

The lack of a relationship between Wood Mouse abundance and the volume of vegetal food resources found in this study is noteworthy. This has also been found in other cereal growing areas of the central Iberian Peninsula (Díaz *et al.*, 1993; Díaz & Alonso, 2003). This result may suggest a greater dependence of this species on vegetation structure than on seed availability, as well as a possible dietary preference for non-vegetal resources.

For its part, the Algerian Mouse in winter shows a greater capacity to exploit different habitats of the agrarian matrix, being able to make use of both uncultivated fields and crops (Palomo *et al.*, 2009). The Algerian Mouse selected microhabitats as a function of greater availability of vegetal food resources. The pattern detected in winter could occur regularly, on a temporal scale of days or weeks (Baraibar *et al.*, 2012), as long as a large volume of barley seeds is easily available, since they may comprise a major energy source during this period due to their large size.

Our results reveal the ecological plasticity of the Algerian Mouse, showing that its microhabitat selection varies according to food availability, thus being relatively independent of habitat type and vegetation structure. The absence of a relationship between the Algerian Mouse and microhabitat structural variables contrasts with the results of Khidas *et al.* (2002) in Algerian agricultural landscapes, where the taxon was associated with areas of low woody cover with a high proportion of bare ground. They similarly differ from the findings of Tarjuelo *et al.* (2011), where

there was a significant relationship between Algerian Mouse presence and microhabitats characterised by closed herbaceous vegetation with high availability of food resources.

With respect to macrohabitat, the results indicate that proximity to trees was an important influence on habitat selection by the Wood Mouse. In the study area trees were mainly Iberian holm oaks and olives, whose fruits with high lipid content could be part of the diet of this rodent (Torre *et al.*, 2002; Khammes & Aulagnier, 2007; Muñoz & Bonal, 2007). This preference for tree proximity would be related to its arboreal habits (Buesching *et al.*, 2008) and its affinity for forested habitats (Rosalino *et al.*, 2011). Arboreal behaviour may have originated as a strategy for minimizing predation risk (Montgomery & Gurnell, 1985) or for foraging in the upper tree canopy (Montgomery, 1980). Branches and tree cavities offer the Wood Mouse secure refuges that are less accessible to predators. Besides, its capacity to climb trees in search of food has been identified in open woodlands as Wood Mouse strategy to avoid resource competition with the Algerian Mouse (Rosalino *et al.*, 2011).

The Algerian Mouse showed an opposite pattern at the macrohabitat level, selecting open areas distant from trees. Earlier studies have described the Algerian Mouse as a species typical of open Mediterranean habitats that are relatively dry and with limited woodland presence (de Alba *et al.*, 2001; Palomo *et al.*, 2009), avoiding even open woodlands as found also by Gray *et al.* (1998) and Tarjuelo *et al.* (2011). Hence, the macrohabitat descriptor variables included in the best three predictive models (larger fields within a matrix of less diverse substrates and at a greater distance from tree trunks) would explain its preference for such environments.

EFFECT OF MICROHABITAT AND MACROHABITAT ON THE RODENT ASSEMBLAGE

Our results show that macrohabitat was more important than microhabitat in the formation of this assemblage (Morris, 1984; Orrock *et al.*, 2000; Corbalán, 2006). The important fraction of the variability explained by macrohabitat variables and the significant relationship with the species matrix indicate the major effect of landscape variables relating to field size, habitat heterogeneity and tree proximity on the assemblage in the study area in winter. The lesser variability explained by microhabitat supports the assumption that these species specifically select macrohabitats at the landscape scale and particular microhabitats within these (Kotliar & Wiens, 1990) according to their spatial structure and the availability of food resources. This result further supports the hierarchical nature of habitat selection (Johnson, 1980).

It is worth noting that 82.7 % of the total variance was explained by the joint effect of micro- and macrohabitat, indicating the suitability of the quantified predictors for describing variation in the assemblage. The high level of shared variance (35.1%) could indicate the difficulty in identifying the spatial limits of the scales in a heterogeneous landscape matrix. This would suggest that landscape complexity (macrohabitat) is revealed on a spatial scale greater than 200m (Butet *et al.*, 2006; Fischer *et al.*, 2011).

In conclusion, our work indicates the need to look more closely into the effect of scale on small mammal habitat selection patterns. It shows the importance of macrohabitat in structuring the rodent assemblage. The disagreement regarding the importance of macro- and microhabitat thus seems to be resolved under the conditions of this study. Our work has shown that there is a degree of segregation in the micro- and macrohabitats selected by the two species, which helps to explain their spatial coexistence during winter. However, it is not possible to determine whether this variation in habitat preferences could be caused by competition processes.

In view of all this, it seems necessary to consider rodent ecology more deeply, given the importance of such organisms to the function of agrarian ecosystems. Long-term studies accounting for the cyclical variability of rotational agrarian systems, and considering more types of agrarian substrates (Jorgensen, 2004) are needed.

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SUPPLEMENTARY MATERIAL

TABLE SI

Values (mean \pm standard deviation, SD) of micro- and macrohabitat variables used to describe uncultivated fields and crops analysed in this study. Only the variables shown in bold type were used in the analyses. See Table I and Table II for key to abbreviations

		UNCULTIVATED FIELDS		CROPS FIELDS	
		Mean	\pm SD	Mean	\pm SD
MICRO HABITAT	STCov	22.17	14.93	2.73	3.58
	LCov	46.20	5.79	10.43	12.50
	BGCov	12.87	6.70	96.67	4.89
	HCov	60.33	19.12	12.93	10.51
	SCov	24.53	18.48	0.00	0.00
	TCov	2.67	4.32	0.00	0.00
	MeaHH	6.37	5.89	3.20	2.50
	MaxHH	46.67	16.06	6.33	3.83
	MeaSH	7.17	5.27	0.00	0.00
	MaxSH	11.17	9.02	0.00	0.00
	FRV	31,796.97	45,531.83	2,084.90	3,558.78
MACRO HABITAT	Distree	38.02	25.36	123.52	54.30
	PArea	1.52	0.94	1.68	1.01
	H	0.83	0.51	1.76	0.33
	Tree100	71.17	73.84	5.50	5.92
	TBL	685.17	101.94	383.17	268.00