Hierarchical spatial segregation of two Mediterranean vole species: the role of patch network structure and matrix composition

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1   **Abstract**

2   According to ecological theory, the coexistence of competitors in patchy environments may

3   be facilitated by hierarchical spatial segregation along axes of environmental variation, but

4   empirical evidence is limited. Cabrera and water voles show a metapopulation-like structure

5   in Mediterranean farmland, where they are known to segregate along space, habitat and time

6   axes within habitat patches. Here we assess whether segregation also occurs among and

7   within landscapes, and how this is influenced by patch network and matrix composition. We

8   surveyed 75 landscapes, each covering 78-ha, where we mapped all habitat patches

9   potentially suitable for Cabrera and water voles and the area effectively occupied by each

10   species (extent of occupancy). The relatively large water vole tended to be the sole occupant

11   of landscapes with high habitat amount but relatively low patch density (i.e., with a few large

12   patches), and with a predominantly agricultural matrix, whereas landscapes with high patch

13   density (i.e. many small patches) and low agricultural cover, tended to be occupied

14   exclusively by the small Cabrera vole. The two species tended to co-occur in landscapes with

15   intermediate patch network and matrix characteristics, though their extents of occurrence

16   were negatively correlated after controlling for environmental effects. In combination with

17   our previous studies on the Cabrera-water vole system, these findings illustrated empirically

18   the occurrence of hierarchical spatial segregation, ranging from within patches to among

19   landscapes. Overall, our study suggests that recognizing the hierarchical nature of spatial

20   segregation patterns and their major environmental drivers should enhance our understanding

21   of species coexistence in patchy environments.

22

23   **Keywords:** Cabrera vole; competition; landscape heterogeneity, patchy environments;

24   species coexistence; southern water vole

Introduction

Understanding the mechanisms facilitating the coexistence of potential competitors in patchy environments is a long standing topic in ecology (Hanski 1983; Chesson 2000; Amarasakere 2003; Valladares et al. 2015). Most studies have addressed this problem by evaluating how species segregate along patch-level niche axes such as food, microhabitat or time of activity (Holt 2001; Jorgenson 2004; Leibold and McPeek 2006). However, it is possible that coexistence may also be facilitated by niche partitioning beyond local habitat patches, with for instance variation in patch network structure and matrix composition contributing to determine whether two competitors can coexist at the local and regional levels (Hanski and Ranta 1983; Yu et al. 2001; Nowakowski et al. 2013). Although this idea has been widely addressed theoretically, empirical investigation of landscape-level niche partitioning remains relatively scarce (Amarasakere 2003; Boeye et al. 2014).

In a system with two asymmetric competitors, the most extreme case of landscape-level segregation may occur when the dominant competitor occupies all landscapes meeting its requirements in terms of, for instance, patch network and matrix characteristics, while the subordinate competitor is forced into landscapes unsuitable for the dominant competitor (Schippers et al. 2015). In this case, coexistence would only be possible at the regional scale, because the two competitors would be unable to share the same landscapes. At the other extreme, the two species may always be able to coexist at the landscape-level, which is often judged to result from the interplay between species' limiting factors, competitive and colonization abilities, and the spatial distribution of shared resources (Amarasekare and Nisbet 2001; Amarasakere 2003; Hanski 2008). A situation intermediate between these two extremes may also occur, with some landscape features leading to occupation by either only the dominant or only the subordinate competitor, and others favouring the coexistence of the two species. For instance, the subordinate competitor may be totally absent from landscapes

50   that are optimal for the dominant competitor, but be able to coexist or even be the sole

51   occupant in less favourable landscapes (Durant 1998). However, even in landscapes where

52   both species coexist, the dominant may still influence the subordinate competitor by

53   constraining its distribution or abundance at smaller spatial scales (Amarasakere 2003,

54   Schippers et al. 2015). Overall, therefore, it is possible that segregation may occur over a

55   hierarchy of scales depending on environmental circumstances, with potential competitors

56   using for instance different landscape types, different patch types within landscapes where

57   they coexist, and different space, time and food resources within those patches that are used

58   simultaneously. At present, little information is available to test these ideas, probably because

59   this would require detailed data on species distribution and co-occurrence patterns across

60   landscapes with different properties (e.g. Yu et al. 2001; Richter-Boix et al. 2007; Schmidt et

61   al. 2008), which are often costly to collect and difficult to replicate in natural systems,

62   particularly for vertebrate species.

63   In this study we used a system of two vole species that share similar resources in

64   Mediterranean farmland landscapes, to evaluate whether segregation occurs at more than one

65   spatial scale, and whether segregation at different scales is associated with particular

66   environmental conditions. We focused on two species of conservation concern (Palomo et al.

67   2007), the Cabrera vole (*Microtus cabrerae*) and the southern water vole (*Arvicola sapidus*,

68   hereafter water vole), which in agricultural landscapes exhibit a metapopulation-like spatial

69   structure, occupying similar patches dominated by wet and tall herbaceous vegetation,

70   imbedded within matrices of varying land use types (Pita et al. 2007, 2013). Previous studies

71   have shown that Cabrera and water voles share much the same food preferences, grazing

72   mostly on evergreen annual and perennial monocotyledons such as grasses, sedges and rushes

73   (Soriguer and Amat, 1988; Román 2007, Rosário et al., 2008). However, the species tend to

74   segregate at the patch-level, along axes of space, microhabitat and time of activity (Pita et al.

75 2010, Pita et al. 2011a, 2011b). In the case of time, for instance, there was some evidence that

76 the dominant competitor (water vole) excludes the subordinate competitor (Cabrera vole)

77 from its preferred time of activity (Pita et al. 2011b). Segregation beyond the patch-scale has

78 never been assessed, but this may occur because each species is strongly affected by

79 landscape features such as patch network structure and matrix composition (Pita et al. 2007,

80 2013). Therefore, to test whether segregation occurs over a hierarchy of spatial scales we

81 examined the distribution and co-occurrence patterns of the two species across replicate

82 landscapes with variable habitat amount, patch density and matrix composition, assessing: (i)

83 whether the two species coexist in some landscapes but not in others; (ii) how shared and

84 exclusive use by each species are shaped by landscape features; and (iii) whether the area

85 used by each species within shared landscapes (extent of occurrence) is consistent with a

86 negative impact of the dominant competitor on the subordinate competitor (Guillaumet and

87 Leotard 2015). Results are used to discuss the implications of hierarchical spatial segregation

88 for understanding the coexistence of potential competitors in fragmented landscapes.

89

90 **Methods**

91 **Study system**

92 The study was conducted in south west Portugal (37° 21′–38° 04′ N, 08° 51′–08° 30′ W,

93 Fig.1a), which is characterized by Mediterranean climate with oceanic influence, with mean

94 monthly temperatures about 16 ºC, and average annual rainfall around 650 mm, of which >

95 80 % falls between October and March (wet season) (Pita et al. 2009; Beja et al. 2014).

96 During our study, the mean monthly temperature ranged from 11.2ºC (wet season, 2007) to

97 21.0ºC (dry season, 2006), and mean monthly precipitation ranged from 28.1 mm (dry

98 season, 2008) to 101.0 mm (wet season, 2006) (Table SM1 in Supplementary information).

99   The region is mainly devoted to mixed annual crop-livestock farming (> 65 % of the study

100   area), while woody cover is restricted to a few woodlots (mean ± se = 3.54 ± 0.34 ha) and

101   hedges with planted trees (mainly pines and eucalyptus) delimiting irrigated fields (Pita et al.

102   2009; Beja et al. 2014). Semi-natural habitats occur in dunes, stream valleys, and cork oak

103   woodlands surrounding the farmed area. Despite the overall trend for agricultural

104   intensification since the early 1990s, some areas have been abandoned or maintain extensive

105   agriculture, resulting in many landscape types and ecological gradients that reflect different

106   management options (Pita et al. 2009; Beja et al. 2014).

107   Cabrera and water voles occur in the study area as spatially structured populations, and

108   they are both largely restricted to habitat patches of wet and tall (≈ > 30 cm) herbaceous

109   vegetation dominated by grasses, sedges, rushes and reeds, typically along small streams,

110   temporary ponds, field margins, and road verges (Pita et al. 2007, 2013). Within habitat

111   patches, individuals of both species tend to show strong site-fidelity, with mean ± se (range)

112   home-range sizes of 946.3 ± 126.3 m^2 (198.2 – 2600.2 m^2) for the larger-sized water vole,

113   and 418.2 ± 56.3 m^2 (39.3 – 1075.6 m^2) for the smaller-sized Cabrera vole (Pita et al. 2010).

Sampling design

115   The study was conducted between 2006 and 2008, and was based on 75 landscapes selected

116   across the study area. Each landscape corresponded to a circular area with ≈ 78 ha,

117   encompassing vole habitat patches and the surrounding matrix occupied by a variety of land

118   uses. The mean ± se (range) nearest neighbour distance between centres of landscapes was

119   3.6 ± 0.07 km (2.5-5.8 km) (see Fig. 1b). Landscape size was set to be much larger than the

120   area used by adult breeding voles (i.e. > 800 times larger than their mean home-ranges;

121   Román 2007; Pita et al. 2010), while allowing replication across the region, such that a wide

122   range of landscape types could be sampled (as in Bennett et al. 2006). A total of 20, 37, and

123   18 landscapes were surveyed in 2006, 2007 and 2008 respectively, with a total of 38, and 37

surveyed during the wet (October-March) and dry (April-September) seasons, respectively

(Fig. 1b). In each landscape, a single snapshot survey was conducted to characterize the

patch-network structure and matrix composition, and to assess the (i) presence/absence of

each species in the landscape, (ii) and the extent of occupancy of each species within each

landscape (see below).

Landscape variables

Suitable vole habitats were visually identified through systematic field surveys and mapped

from GPS recordings made along their borders, considering a minimum polygon area of

$50m^2$, and a minimum distance between polygons (ground resolvable distance) of 5m (Pita et

al. 2013). Information was then incorporated in a Geographical Information System (GIS,

ArcView 3.2, Redlands, CA, 1999). Patch networks were described by estimating the total

area (ha) covered by suitable habitat for voles (hereafter referred to as habitat amount), and

the number of potential breeding habitat patches (i.e. patches larger than the minimum area

required for a breeding pair and respective progeny) per square km (hereafter referred to as

patch density) (Fig.1c).

Information on the minimum areas required by breeding pairs of Cabrera and water

voles were unavailable, thus we set the threshold based on the minimum home range sizes for

resident adults of each species observed in our study area (Pita et al. 2010), though excluding

a few very small outliers. We considered that the minimum breeding patch for Cabrera voles

corresponded to one or more habitat polygons distanced from each other by less than 50m

and covering a total habitat area of at least $250m^2$. Breeding habitat patches for water voles

were estimated likewise, by setting the thresholds at 100m and $500m^2$, respectively. After

computing patch density estimates for the two species using these thresholds, we found that

they were strongly correlated (Pearson's $r = 0.88$, 95%CI = 0.81-0.92, p<0.001). Therefore,

in subsequent analysis for both Cabrera and water voles we estimated patch densities based

149   on the threshold for the later species. This was a simplification because the perceptual range

150   of patchiness is species-specific (Swihart et al 2003), but we believe it provides a reasonable

151   basis to assess potential spatial segregation along patch density gradients (as in Basset 1995;

152   Basset and de Angelis 2007). The rationale is that breeding area requirements of the smaller

153   species are nested in those of the larger one (Basset and de Angelis 2007), and that occupied

154   patches we treat as distinct units actually function as independent local breeding populations

155   for both species. This assumption would have been difficult to accept for water voles if we

156   had defined patches based on the threshold for the Cabrera vole. Some caution is needed

157   when interpreting the results, however, as small patches potentially providing breeding areas

158   for Cabrera voles (i.e. those between 250-500m2) are necessarily overlooked. These small

159   patches represented only <5% of the overall patch number, thus excluding them was unlikely

160   to have had major impacts on our results.

161   The main types of land uses in the matrix expected to affect the species were also mapped

162   in the GIS, based on high resolution (0.5 m/pixel) aerial photographs from 2005, and ground

163   validation. These included the cover (ha) by agricultural fields (AGRO, land used for the

164   production of cereals, vegetables and other crops), extensive pastures (EPAST, semi-natural

165   pastures and fallows lightly grazed by cattle), improved pastures (IPAST, sown and irrigated

166   pastures for cattle grazing), and the density (km/km^2) of irrigation structures (IRRIG,

167   irrigation channels and drainage ditches) (Pita et al. 2007, 2013; see Table 1 for summary

168   statistics).

169   **Vole surveys**

170   Cabrera and water vole surveys were based on systematic searches for their typical presence

171   signs, in particular fresh latrines or scattered droppings along runways, which are easily

172   recognizable in the field (Fedriani et al. 2002; Pita et al. 2007, 2013). Searches at each

173   landscape lasted in average (±se, range) 4.1 ± 2.2 days (0.5-8 days), with more effort devoted

8

174   to landscapes with larger amounts of potential habitat. Within each landscape, longer surveys

175   were made in larger patches, with a minimum of about half hour per patch. This sampling

176   effort was judged to have minimised the likelihood of false negatives, as recent studies on the

177   water vole suggest that occupancy may be detected in 80-100% of cases during 30-minute

178   surveys, even in large patches (Fernández et al. 2016, Peralta et al. 2016). Considerable care

179   was also taken to accurately distinguish the dropping of both species, which was mainly

180   based on their sizes: length × width in mm of 4.8-9.6 × 1.8-3.2 in Cabrera voles versus 7.0-

181   16.0 × 3.0-6.9 in water voles (Garrido-Garcia and Soriguer 2014; Román 2014). Reliability in

182   the identification of vole droppings was validated using molecular methods (Barbosa et al.

183   2013; Mira et al. unpublished data).

184   Sign surveys were always conducted in periods with no precipitation during at least

185   the previous two days, to avoid flattening and wetting of faeces. Searches consisted in

186   scanning the whole surface of suitable habitats mapped, starting in preferred microhabitats

187   (i.e. relatively taller and denser vegetation sites) and then expanding to other less suitable

188   locations, so as to maximize the likelihood of detecting the target species (MacKenzie and

189   Royle 2005; Peralta et al. 2016), which are often clustered on a particular portion of the

190   patches. Searches often implied lifting the vegetation, though minimizing disturbance as

191   much as possible. When vegetation density in one particular site was too high to walk

192   through (e.g., bramble *Rubus* thickets), we searched around the edges enclosing that site. The

193   locations of all vole droppings detected were recorded with a GPS with 5 m precision.

194   Surveys were used to estimate the occupancy of each landscape (hereafter landscape

195   occupancy) considering four possible categories: empty, occupied by either Cabrera or water

196   voles, and occupied by both species. We also estimated the extent of the area occupied by

197   each species within each landscape (hereafter extent of occupancy), based on the spatial

198   distribution of droppings. This was done by creating and merging buffers of 20 and 30 m

199   diameters centered on each GPS location of Cabrera and water voles droppings, respectively

200   (as in Pocock et al. 2003; see Fig. 1d). These buffers lengths were defined to provide a circle

201   with an area close to the mean home range estimated in the study area for each species (Pita

202   et al. 2010)

Data analysis

204   Multinomial logit (unordered) generalized mixed effect modelling (Multinomial GLMM)

205   with Bayesian Markov Chain Monte Carlo (MCMC) simulation was used to model the

206   probability of landscape occupancy by each species alone and by both species together in

207   relation to patch-network and matrix covariates, using empty landscapes as a baseline

208   category. Landscapes without suitable vole habitats (i.e. patches dominated by wet and tall

209   herbaceous vegetation) were dropped to avoid trivial results. We used the maximal random

210   intercept structure effects justified by our experimental design, so as to better control

211   variation, increase the power of the analyses, and optimize generalization of the findings (e.g.

212   Gillies et al. 2006; Barr et al. 2013). Therefore, we included in the random component four

213   categorical variables reflecting potential effects of sampling year (three levels), sampling

214   season (two levels) and spatial contagion in the distribution of Cabrera and water voles (four

215   levels each, based on equal class intervals of the proportion of occupied landscapes in a 5-km

216   buffer of each focal landscape). The buffer radius corresponded to the maximum dispersal

217   distance recorded for the larger species, the water vole (Román 2007). Before analysis,

218   covariates were scaled and log-transformed, to reduce the influence of extreme values and

219   improve model convergence. Co-linearity among all covariates was tested using variance

220   inflation factors (VIF), and considering VIFs <2 as indicating acceptable levels of co-

221   linearity (Zuur et al. 2010).

222   In multinomial model building, we first assessed the effect of each covariate alone on

223   landscape occupancy, and then selected as candidate those covariates which yielded deviance

224   information criterion (DIC) values lower than that of the null model (including random

225   effects only). This allowed reducing the number of possible covariates, and avoided the

226   examination of candidate models with too many parameters relative to the number of

227   observations (e.g. Kleinbaum et al., 1998). Candidate models including multiple covariates

228   were then built using all possible subsets of influential variables. Due to limited sample size,

229   only main effects were considered in model building. The best candidate model had the

230   lowest DIC, but we also retained as equally supported all models at < 5 DIC units from the

231   best (ΔDIC). For each model we estimated the 95% credible intervals (CI) and pMCMC-

232   values (significant pMCMC < 0.05) of each covariate. Model fit was estimated using pseudo-

233   R^2 (Johnson 2014). A similar MCMC-GLMM modelling approach based on bivariate

234   Gaussian distribution error was used to relate the extent of occupancy of each species to

235   patch-network and matrix covariates. Empty landscapes were excluded from this analysis.

236   Model posterior distributions were used to estimate the correlation between the two

237   dependent variables; given as $Corr_{Mc,As} = Cov_{Mc,As} \big/ \sqrt{V_{Mc} \cdot V_{As}}$, where $Cov_{Mc,As}$ is the

238   covariance between the extents of occupancy of the Cabrera (Mc) and the water vole (As),

239   and V_{Mc} and V_{As} represent the respective variances (e.g. Hadfield 2010; Wilson et al. 2010).

240   Significant correlations were determined by the 95% credible intervals not overlapping with

241   zero. For simplicity, we present here the results of the model yielding lowest DIC values in

242   each set of analysis. Results regarding alternative models are presented in Supplementary

243   material (Tables SM1-SM6).

244   GLMMs were run in the package 'MCMCglmm' version 2.19 (Hadfield 2010) using R

245   3.0.2 (R Development Core Team 2014), keeping > 1000 posterior samples (Hadfield 2012).

246   Models were run until they reached acceptable low levels of first order autocorrelation

247   (generally < 0.08 for successive iterations) for both fixed and variance components (Plummer

248   et al 2006; Hadfield 2010), and until they reached convergence, as assessed visually using

trace plots for both fixed effects and variance components, and computationally using

Geweke's convergence diagnostic (Plummer et al 2006). For multinomial models we used

1×10^8 iterations, burn-in size of 1×10^5, and sampling every 5×10^4 iterations, whereas for

Gaussian models we used 3×10^4 iterations, burn-in size of 3×10^3, and thinning interval of 10

iterations. Prior specification in multinomial models followed Hadfield (2012), setting

variance at one for all diagonal terms (variances) and 0.5 for all off-diagonal terms

(covariances) in the residual structure. For random effects we specified priors to have a

variance equal to one, with a degree of belief (nu) equal to one. We screened multiple

alternative priors and selected those producing the best trace plots of the variance

components, though model results were largely insensitive to changes in the prior

specification. For Gaussian models we used default uninformative flat priors for the residual

structure, while for the random component we set the variance at one, and the nu at 0.002

(Hadfield 2012). Adjusted pseudo-R^2 were estimated with 'MuMin' (Barton 2014).

Results

A total of 142.7 ha of suitable habitat for voles was found in 69 of the 75 landscapes

surveyed, corresponding to ca. 3% of the surveyed area. Overall, 184 patches > 500 m^2 were

identified in 68 landscapes, of which 51 % and 42 % were occupied by Cabrera and water

voles, respectively, and 18 % were occupied by both. In addition, 17 small (< 500 m^2),

isolated (> 100 m from the nearest patch) habitats were identified in 14 landscapes. From

these, 8 patches in 7 landscapes could be considered as potentially providing exclusive

breeding patches for Cabrera voles (i.e. those between 250-500m^2). Presence signs of Cabrera

and water voles were found in three and one of these habitats respectively, with no evidence

for local co-occurrence. Overall, 62 landscapes were occupied by at least one species, of

273 which 26% were occupied exclusively by Cabrera voles, 17% were occupied by water voles

274 alone, and 46% were occupied by both species (Fig. 1b).

275   Co-linearity among covariates was low (VIFs<2, see Supplementary material, Table

276 SM2), and thus they were all considered in the analyses. Multinomial MCMC-GLMM

277 regressions with single covariates provided support for the influence of patch density, habitat

278 amount, and proportional cover by agricultural land and extensive pastures on landscape

279 occupancy status (Supplementary material, Table SM3). These variables were used to build

280 16 candidates models, three of which were roughly equally supported (ΔDIC < 5; Table 2).

281 Among these, the model including habitat amount, patch density, and cover by agricultural

282 land had the lowest DIC and an adjusted pseudo-R^2 of 0.47 (Table 2). Results were largely

283 consistent among the three best supported models (Supplementary material, Table SM4),

284 indicating that landscape occupancy by water voles alone or by both vole species together

285 was very significantly favoured by higher amounts of habitat (pMCMC < 0.001), while

286 exclusive landscape occupancy by the Cabrera vole was significantly (pMCMC < 0.05)

287 favoured by higher patch density. In addition, landscapes with increased cover by agricultural

288 land showed significantly higher probability of being occupied exclusively by water voles

289 (Fig. 2a).

290   The mean ± se (range) extent of occupancy per landscape was 0.72 ± 0.11 ha (0 - 3.98)

291 for Cabrera voles and 1.80 ± 0.26 ha (0 and 9.29) for water voles. Models including each

292 single covariate alone provided support for the influence of habitat amount, patch density,

293 cover by agricultural land, and matrix cover by extensive pastures (Supplementary material,

294 Table SM5). Three of the 16 candidate models built with these variables were equally

295 supported (ΔDIC < 5; Table 3). The model including habitat amount, patch density and cover

296 by agricultural land yielded the lowest DIC and an adjusted pseudo-R^2 of 0.88 (Table 3). This

297 model indicated that the extents of occupancy of both Cabrera and water voles increased very

298 significantly with the amount of habitat (Fig. 2b). For the Cabrera vole, there was also a

299 significant positive effect of patch density and a significant negative effect of agriculture

300 cover, while for water voles there was a very significant positive effect of agricultural land

301 cover (Fig. 2b). These results were consistent among the best supported models

302 (Supplementary material, Table SM6). There was a significant negative correlation between

303 the extents of occupancy of Cabrera and water voles after controlling for the effect of

304 environmental variables ($Corr_{Mc,As}$; posterior mode = -0.39; 95%CI: -0.61 – -0.16)

305

306 **Discussion**

307 This study, together with previous research on the Cabrera-water vole system (Pita et al.

308 2010; 2011a; 2011b), is consistent with the idea that segregation between the two species

309 probably occurs at more than one spatial scale, and that segregation at different scales is

310 associated with particular environmental conditions. Specifically, we found that the two

311 species coexisted in some landscapes but not in others, and that shared and exclusive use by

312 each species were associated with total habitat amount, the density of habitat patches, and

313 matrix composition. Also, we found evidence for a negative correlation between each species

314 extent of occupancy within shared landscapes after controlling for patch-network and matrix

315 variation. Overall, therefore, our study concurs to a growing body of evidence suggesting that

316 segregation between competitors may occur at multiple hierarchical spatial scales, from

317 within-patch to among-landscapes (e.g. Inouye 1999; Gilbert et al. 2008; Laporta and Sallum

318 2014), thus underlining the importance of considering processes operating over a range of

319 spatial scales to understand how competitors coexist in real landscapes (Whittaker et al. 2001;

320 Kneitel and Chase 2004).

321 **Vole segregation among landscapes**

322   Segregation patterns of water and Cabrera voles among landscapes were partly consistent

323   with the idea that the large and putatively dominant competitor tended to occupy all

324   landscapes meeting its requirements in terms of patch network and matrix characteristics,

325   while the smaller and putative subordinate competitor seemed to be partly forced into

326   landscapes unsuitable for the dominant competitor. This was supported by the observation

327   that water voles tended to be the sole occupants of landscapes with large habitat patches (i.e.,

328   landscapes with high habitat amount but relatively low patch density) and high matrix cover

329   by agricultural land, which were shown previously to benefit this species (Pita et al. 2013).

330   Because water voles are relatively large, large patches may provide conditions for a large

331   number of individuals and thus reduce the probability of local extinction (Pita et al. 2013;

332   Sutherland et al. 2014). Agricultural land may be beneficial to water voles because the wet

333   margins that typically appear along irrigated fields are likely to offer habitat and dispersal

334   opportunities across the dry farmland (Telfer et al. 2003; Centeno-Cuadros et al. 2011; Pita et

335   al. 2013). Reasons for the absence of Cabrera voles in landscapes with these characteristics

336   are uncertain, but this may result, to at least some extent, from competitive exclusion by

337   water voles. In fact, previous studies have shown that the probability of patch occupancy by

338   Cabrera voles increase with patch size (Pita et al. 2007), and so they would be expected to

339   occur in landscapes dominated by large patches such as those used exclusively by water

340   voles. It is noteworthy, therefore, that exclusive occupancy by Cabrera voles was associated

341   with landscapes with many small patches (i.e., landscapes with high patch density), which

342   were probably unsuitable for water voles because most patches were too small for sustaining

343   local populations (Pita et al. 2013).

344   Although these observations provide support for competitive exclusion of Cabrera voles

345   in some landscape types, we cannot rule out the possibility of the patterns observed resulting

346   at least partly from independent and species-specific responses to patch-network, matrix or

347 other habitat characteristics. For instance, the negative association of Cabrera vole to

348 landscapes with high amount of agricultural land may be related to reduced dispersal ability

349 and thus reduced capacity to colonise empty habitat patches (Pita et al. 2007), rather than a

350 negative response to water voles per se. Elucidating this would require experimental studies,

351 manipulating for instance the presence of water voles or the cues of its presence (e.g.,

352 droppings) in landscapes occupied by Cabrera voles, or the density and size of patches at the

353 landscape scale (e.g. Ginger et al. 2003; Brunner et al. 2013). Future studies should also

354 consider the role of other competitors and shared predators, as these have not been examined

355 so far but they can strongly affect the interactions between potential competitors (e.g. Oliver

356 et al. 2009).

Vole coexistence within landscapes

358 Although we found Cabrera and water vole segregation among some landscapes types, the

359 two species actually co-occurred in most of the surveyed landscapes. This was in line with

360 previous observations indicating that both species can coexist within the same patches (Pita et

361 al. 2010, 2011a, 2011b), and suggest that coexistence may be further facilitated by some

362 patch network and matrix characteristics. Specifically, we found that coexistence was most

363 likely where the habitat amount was high but where patch density was also much higher than

364 in landscapes occupied exclusively by water voles, which may reflect landscapes with a

365 diversity of large and small patches. In these landscapes, small patches unsuitable for water

366 voles may serve as refuges for Cabrera voles, and they may provide sources of individuals

367 colonising larger patches temporarily left vacant or only partly occupied by water voles. High

368 patch density may also be related to small inter-patch distance, which may favour dispersal

369 and thus increase colonization ability by the Cabrera vole, which seems to have a much lower

370 dispersal ranges than water voles (Pita et al. 2007, 2013). We also found that landscapes

371 occupied by both Cabrera and water voles had an intermediate cover by agricultural land

372   uses, in relation to those occupied solely by either species. This may be due to the contrasting

373   response of the two species to this variable, with the colonisation ability of Cabrera voles

374   declining with increasing cover by agricultural land (Pita et al. 2007), and the opposite

375   presumably occurring for water voles (Pita et al. 2013). Overall, therefore, it seemed that

376   coexistence was favoured in landscapes that were suboptimal for water voles (relatively small

377   patches and intermediate cover by agricultural land), and that at the same time provided

378   refuges (small patches) and dispersal opportunities (non-agricultural land, short inter-patch

379   distance) for Cabrera voles.

380   As for the segregation among landscapes, it was difficult to assess whether the observed

381   patterns of within-landscape coexistence resulted from independent, species-specific

382   responses to environmental factors, or whether it also involved some kind of competitive

383   interference between species. However, we found that the extent of occurrence of water and

384   Cabrera voles within shared landscapes were negatively correlated after controlling for

385   potentially confounding environmental effects, which is compatible with a negative effect of

386   the putative dominant on the putative subordinate competitor. These results suggest that in

387   the absence of water voles and for constant environmental conditions, the area occupied by

388   Cabrera voles would be larger than that observed in our study. This might be a consequence,

389   for instance, of water voles displacing Cabrera voles from some suitable patches (i.e.,

390   segregation among patches), or by limiting the extent of occupancy of Cabrera voles in

391   patches occupied by both species (i.e., within-patch segregation). Testing these hypotheses

392   should be the subject of future research.

393   **Implications for the coexistence of competitors**

394   The coexistence of competitors occupying habitat patches in fragmented landscapes is

395   generally interpreted as resulting from the partitioning of resources at local scales (classical

396   niche-based mechanisms; e.g. Chase and Leibold 2003; Jorgenson 2004, Leibold et al. 2006),

or from life-history trade-offs for instance in competitive and colonization abilities (e.g.

Amarasakere 2003; Hanski 1983, 2008). The observational studies carried out so far on the

Cabrera-water vole system are insufficient to fully support or contradict either of these

hypotheses, but they suggest that the mechanisms facilitating coexistence may be more

complex than previously envisaged, because different processes may operate simultaneously,

though their relative importance may vary across spatial scales (Kneitel and Chase 2004). On

the one-hand, our previous studies suggest that coexistence within local patches may be

facilitated by segregation along time and habitat axis (Pita et al. 2010, 2011a, 2011b), which

is consistent with niche-based mechanisms (Chase and Leibold 2003). However, the present

study suggests that niche-based mechanisms may also operate at the landscape level, as

segregation versus coexistence appeared to be influenced by species habitat preferences in

terms of patch network and matrix characteristics (Morris 1987; Yu et al. 2001; Westphal et

al. 2006). On the other hand, however, our study also pointed out the possibility of life

history trade-offs facilitating coexistence within landscapes, with the smaller species

offsetting its lower competitive ability by occupying small habitat patches that are hardly

occupied by the larger competitor, thereby enabling a fugitive-like coexistence (Amarasakere

2003; Hanski 1983, 2008). Whatever the mechanism or combination of mechanisms at play

here, our results support the need to account for the hierarchical nature of species spatial

segregation patterns to generate robust hypotheses about the processes that allow their

coexistence (Kneitel and Chase 2004; Szabó and Meszéna 2006; Kneitel 2012). In particular,

because habitat patch-network structure and matrix composition are key landscape properties

in determining scales at which segregation takes place, we suggest that spatial heterogeneity

at the landscape scale should be routinely considered in both theoretical and empirical studies

aiming to understand species coexistence in patchy environments (e.g. Gilbert et al. 2008;

Biswas and Wagner 2012; László and Tóthmérész 2012) This in turn will provide invaluable

422 information to support inferences on possible mechanisms facilitating coexistence across

423 multiple scales, and for improving conservation actions targeting multiple interacting species

424 (Poiani et al. 2000; Tscharntke et al. 2012).

425

436

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607   Figures legends:

608

609   **Fig. 1** – (a) Map showing the location of the study area. (b) Distribution of surveyed

610   landscapes with indication of the sampling occasion and occupancy status. (c) Example of

611   habitat mapping in a landscape occupied by both species. Habitat polygons assigned to a

612   single breeding patch as perceived by water voles, are identified by the same colour (see text

613   for details). (d) Location of Cabrera and water vole droppings in suitable habitat (in grey),

614   and respective 20- and 30-m diameter buffers used to estimate the extent of occupancy of

615   each species (see text for details).

616

617   **Fig. 2** – (a) Posterior estimates of model coefficients and 95%CI for the first ranked

618   multinomial MCMC-GLMM logit model relating landscape occupancy **to** habitat amount,

619   patch density, and cover by agricultural land. Empty landscapes were the baseline category

620   (location of the effects=0) (see Supplementary material, Table SM3). (b) Posterior estimates

621   of model coefficients and 95%CI for the first ranked bivariate Gaussian MCMC-GLMM

622   models relating the extent of area occupied by Cabrera and water voles to habitat amount,

623   patch density, and agricultural cover (see Supplementary material, Table SM6). Effective

624   sample size was > 1000 for all fixed effects in all models run. Asterisks indicate that

625   coefficients are significantly different from zero: * $P<0.05$; ** $P<0.001$.

626 **Table 1 –** Summary statistics of landscape variables recorded per landscape (n=75) sampled

627 for Cabrera and water voles in SW Portugal (2006-2008).

628

Set/Variables	Units	Code	Mean ± se	Range
Patch network				
Habitat Amount	ha	HA	1.90 ± 0.26	0–12.91
Breeding Habitat Patch Density *	# patches/km^2	PD	3.15 ± 0.23	0–8.97
Matrix				
Cover Agricultural land	ha	AGRIC	10.10 ± 1.68	0–65.69
Cover Extensive Pastures	ha	EPAST	16.28 ± 1.85	0–59.42
Cover Intensive Pastures	ha	IPAST	12.49 ± 2.13	0–63.77
Density of Irrigation structures	km/km2	IRRIG	0.34 ± 0.11	0–4.78

629 * based on the perceptual ranges of the larger species, the water vole (see "Landscape
630 variables" for details)

(a) Portugal

N

0 — 100 Km

(b)

Sampling occasion

▲ Dry season - 2006
△ Wet season - 2006
● Dry season - 2007
◐ Wet season - 2007
■ Dry season - 2008
▨ Wet season - 2008

Occupancy status

— Empty
— Cabrera vole only
— Water vole only
— Both species

0 — 10 Km

(c)

0 — 500 m

(d)

● Water vole droppings
● Cabrera vole droppings
— 30 m diameter buffers
— 20 m diameter buffers

0 — 10 m
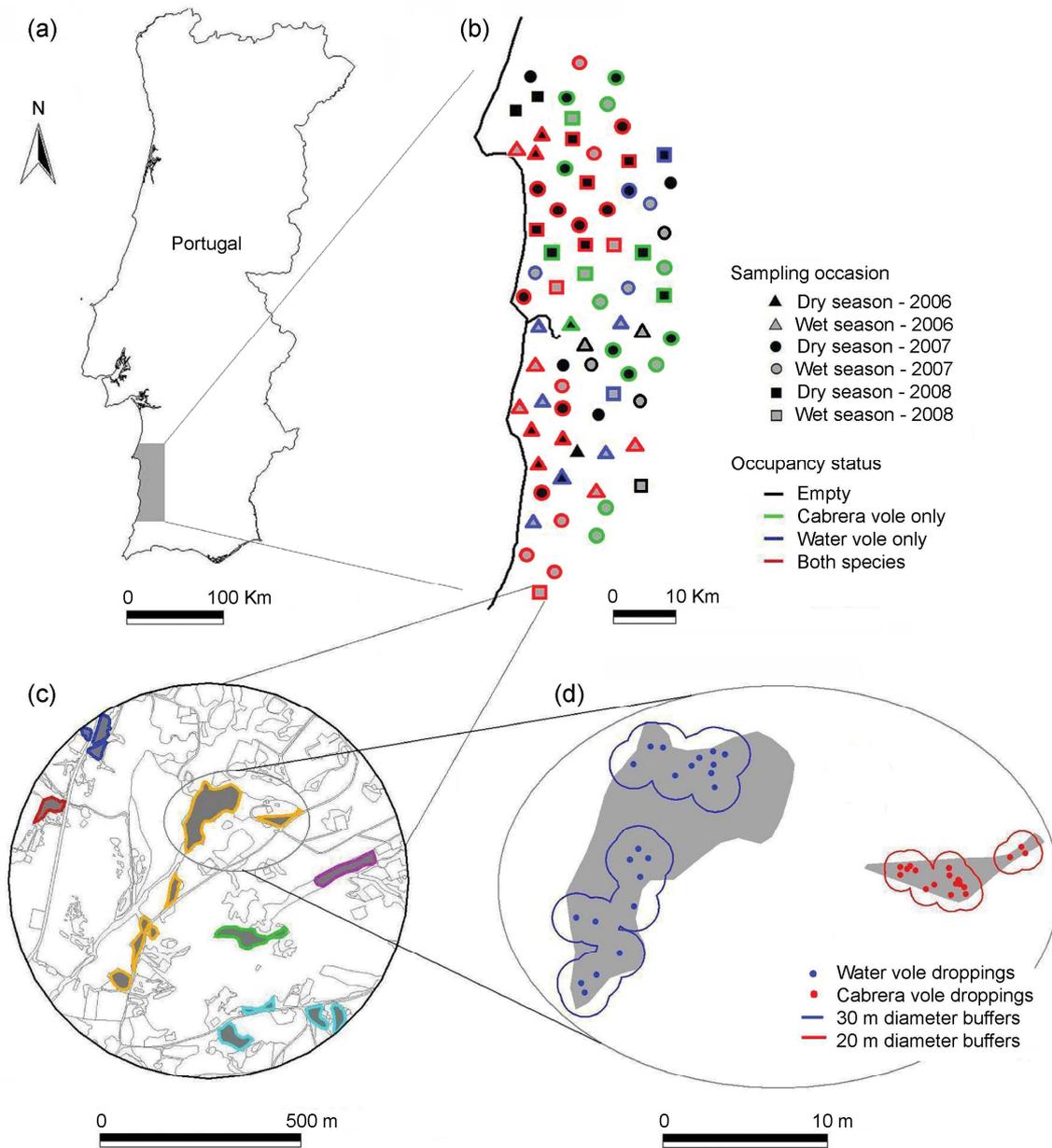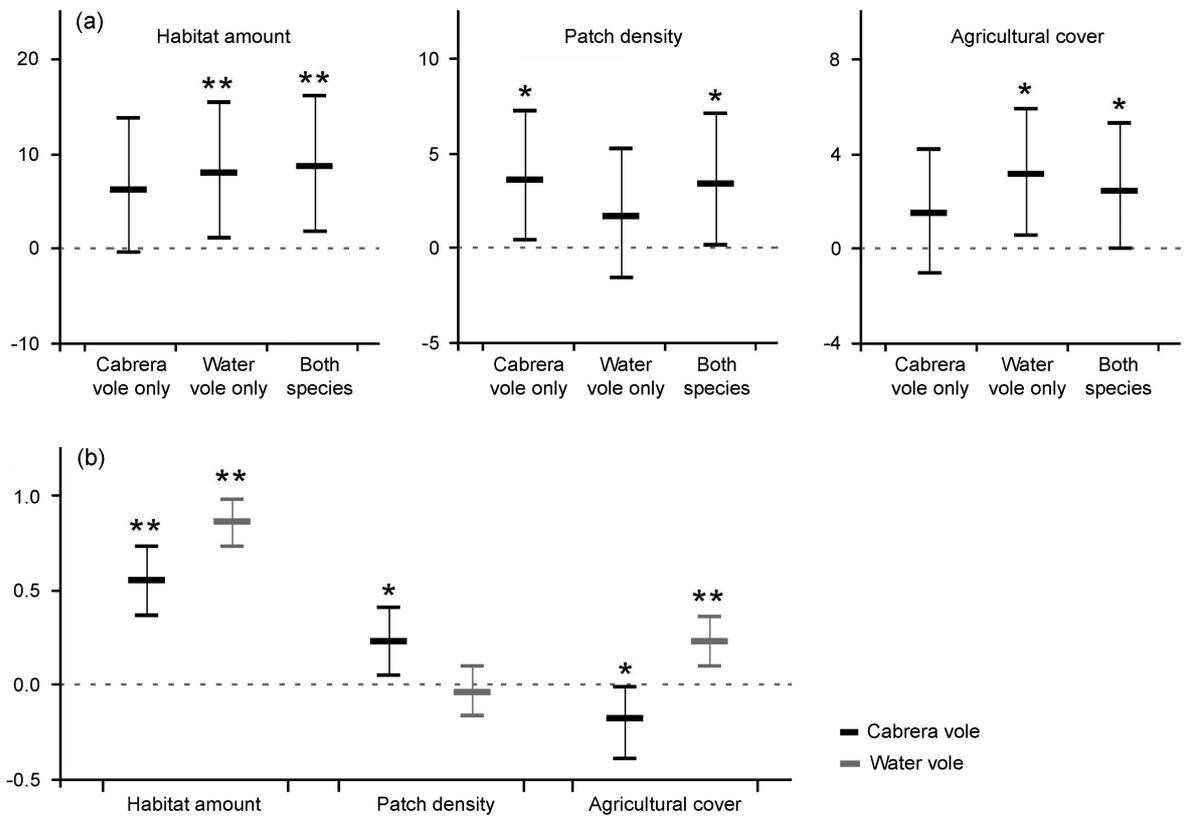
SUPPLEMENTARY MATERIAL

Hierarchical spatial segregation of two Mediterranean vole species: the role of patch network structure and matrix composition

Ricardo Pita, Xavier Lambin, António Mira, Pedro Beja

Table SM1 – Mean monthly values and standard deviations of temperature (ºC) and precipitation (mm) in each year and season of surveys (data from the gauging station of 'Grândola' Sistema Nacional de Informação de Recursos Hídricos, Agência Portuguesa do Ambiente, Lisbon, available at: http://snirh.pt, accessed on 01-04-2016).

Year/season	Temperature (ºC)		Precipitation (mm)	
	mean	**sd**	**mean**	**sd**
2006	16.2	6.0	66.4	67.5
Wet season	12.4	4.5	101.0	72.2
Dry season	21.0	4.0	25.0	30.5
2007	15.9	5.2	33.5	18.4
Wet season	11.2	4.0	38.2	14.2
Dry season	19.0	3.2	30.4	21.5
2008	14.8	4.5	39.7	25.6
Wet season	11.7	2.6	49.3	18.4
Dry season	18.5	3.0	28.1	34.7

Table SM2 - Variance inflation factors (VIF) among patch-network and matrix variables tested for their effects on landscape occupancy (dataset 1, n=69), and voles extent of occupancy (dataset 2, n=62).

Variable	Code	VIF	
		dataset 1	**dataset 2**
Habitat amount	HA	1.40	1.03
Patch density	PD	1.09	1.31
Agricultural cover	AGRIC	1.33	1.35
Extensive pastures cover	EPAST	1.69	1.66
Improved pastures cover	IPAST	1.32	1.35
Density of Irrigation structures	IRRIG	1.36	1.34

Table SM3 – Multinomial GLMM's relating landscape occupancy to patch network and matrix variables in single covariate models. Variables used in multiple covariate model building are underlined. For each model we present the deviance information criteria (DIC), the distance in DICs between the model and the null model (ΔDIC), and the posterior parameter estimates for the model coefficients (Coef), 95%CIs, effective sample sizes (Eff. Samp) and pMCMC values. See Table SM1 for variable codes.

Fixed effects (code)	DIC	ΔDIC	Landscape occupancy	Coef.	95%CI	Eff. Samp	pMCMC
Null	164.93	0.00	-	-	-	-	-
HA	135.69	29.24	Cabrera voles only	6.96	1.32—12.61	1929	0.001
			Water voles only	7.98	2.60—13.97	1806	<0.001
			Both species together	8.99	3.24—14.82	1928	<0.001
PD	147.05	17.88	Cabrera voles only	3.73	1.27—6.33	1778	<0.001
			Water voles only	2.83	0.57—5.39	1719	0.001
			Both species together	4.49	1.98—7.17	1757	<0.001
AGRIC	158.60	6.33	Cabrera voles only	0.77	-062—2.58	1998	0.336
			Water voles only	2.30	0.70—4.05	1998	0.003
			Both species together	1.51	0.08—3.11	1998	0.024
EPAST	154.28	10.65	Cabrera voles only	0.95	-0.23—2.12	1998	0.097
			Water voles only	0.88	-2.27—2.11	1998	0.149
			Both species together	2.16	0.93—3.47	1998	<0.001
IPAST	167.75	-2.82	Cabrera voles only	0.64	-052—1.82	1998	0.276
			Water voles only	0.33	-0.89—1.53	1830	0.591
			Both species together	0.09	-0.96—1.22	1998	0.905
IRRIG	168.30	-3.37	Cabrera voles only	0.12	-1.87—2.36	1998	0.962
			Water voles only	1.09	-0.50—2.99	1998	0.178
			Both species together	0.84	-0.70—2.75	1998	0.342

Table SM4 – Summary of the fixed component of most supported candidate multinomial models relating landscape occupancy to patch-network and matrix variables. For each model we present the posterior parameter estimates for the model coefficients (Coef.), 95%CIs, effective sample sizes (Eff. Samp) and pMCMC values. See Table SM1 for variable codes. The 95%CI credible intervals of posterior estimates of the proportion of variance explained by each random effect are also present ('Year', 'Season', and proportion of landscapes occupied by Cabrera and water voles within 5 km-radius around each landscape, 'PLOC5K' and 'PLOA5K', respectively).

Model	Variable	Landscape occupancy	Coef.	95%CI	Eff. Samp	pMCMC
1	HA	Cabrera voles only	6.21	-0.41—13.85	1531	0.056
		Water voles only	8.06	1.17—15.45	1557	0.001
		Both species together	8.77	1.87—16.14	1538	<0.001
	PD	Cabrera voles only	3.63	0.45—7.24	1998	0.012
		Water voles only	1.67	-1.56—5.23	2523	0.344
		Both species together	3.40	0.19—7.13	1998	0.030
	AGRIC	Cabrera voles only	1.52	-1.01—4.20	1667	0.270
		Water voles only	3.15	0.59—5.90	1643	0.010
		Both species together	2.44	0.02—5.29	1761	0.044
	Posterior estimates of random effects variance (95%CI):					
	Year=0.02—0.42; Season=0.03—0.49; PLOC5K: 0.02—0.31; PLOA5K: 0.05—0.44					
2	HA	Cabrera voles only	7.80	-0.06—17.06	1395	0.031
		Water voles only	9.98	2.01—18.75	1543	<0.001
		Both species together	10.26	2.50—19.50	1543	<0.001
	PD	Cabrera voles only	4.80	0.65—9.36	1998	0.007
		Water voles only	3.03	-1.16—7.61	1998	0.167
		Both species together	4.58	0.30—9.24	1998	0.017
	AGRIC	Cabrera voles only	2.98	-0.44—7.78	2009	0.103
		Water voles only	4.61	0.50—8,68	1971	<0.001
		Both species together	3.90	0.05—8.29	2096	0.015
	EPAST	Cabrera voles only	-1.20	-3.56—0.88	2218	0.305
		Water voles only	-1.82	-4.45—0.66	1998	0.135
		Both species together	-0.97	-3.45—1.41	1931	0.451
	Posterior estimates of random effects variance (95%CI):					
	Year=0.02—0.40; Season=0.03—0.51; PLOC5K: 0.02—0.33; PLOA5K: 0.05—0.41					
3	HA	Cabrera voles only	4.45	-0.77—10.53	1998	0.066
		Water voles only	6.03	1.11—12.34	1998	0.001
		Both species together	6.86	2.29—13.61	1998	<0.001
	PD	Cabrera voles only	3.24	0.32—6.48	1998	0.020
		Water voles only	1.56	-1.30—4.65	1767	0.280
		Both species together	3.12	0.14—6.24	1786	0.027
	Posterior estimates of random effects variance (95%CI):					
	Year=0.02—0.46; Season=0.03—0.53; PLOC5K: 0.02—0.31; PLOA5K: 0.06—0.50					

Table SM5 – Bivariate Gaussian GLMM's relating the extent of occupancy of each vole species to patch network and matrix variables in single covariate models. Variables used in multiple covariate model building are underlined. For each model we present the deviance information criteria (DIC), the distance in DICs between the model and the null model (ΔDIC), and the posterior parameter estimates for the model coefficients (Coef.), 95%CIs, effective sample sizes (Eff. Samp) and pMCMC values. See Table SM1 for variable codes.

Fixed effects (codes)	DIC	ΔDIC	Extent of occupancy	Coef.	95%CI	Eff. Samp	pMCMC
Null	341.65	0		-	-	-	-
HA	229.74	111.91	Cabrera vole	0.60	0.41—0.78	3081	<0.001
			Water vole	0.82	0.68—0.95	2700	<0.001
PD	339.47	2.18	Cabrera vole	0.30	0.08—0.55	2700	0.013
			Water vole	0.07	-0.18—0.33	2700	0.619
AGRIC	340.19	1.46	Cabrera vole	-0.25	-0.49—0.01	2700	0.062
			Water vole	0.11	-0.15—0.37	2700	0.376
EPAST	335.43	6.22	Cabrera vole	0.31	0.08—0.54	2700	0.011
			Water vole	0.33	0.09—0.56	2700	0.005
IPAST	345.69	-4.04	Cabrera vole	-0.11	-0.38—0.13	2700	0.392
			Water vole	-0.03	-0.31—0.22	2700	0.806
IRRIG	343.76	-2.11	Cabrera vole	-0.11	-0.36—0.12	2928	0.381
			Water vole	0.13	-0.12—0.38	2700	0.287

Table SM6 – Summary of the fixed component of most supported candidate bivariate Gaussian models to explain the variation in the extent of occupancy of Cabrera and water voles. For each model we present the posterior parameter estimates for the model coefficients (Coef.), 95%CIs, effective sample sizes (Eff. Samp) and pMCMC values. See Table SM1 for variable codes. The 95%CI credible intervals of posterior estimates of the proportion of variance explained by each random effect are also present ('Year', 'Season', and proportion of landscapes occupied by Cabrera and water voles within 5 km-radius around each landscape, 'PLOC5K' and 'PLOA5K', respectively).

Model	Variable	Species	Coef.	95%CI	Eff. Samp	pMCMC
1	HA	Cabrera vole	0.55	0.37-0.73	2123	<0.001
		Water vole	0.86	0.73—0.98	2700	<0.001
	PD	Cabrera vole	0.23	0.05—0.41	2700	0.014
		Water vole	-0.04	-0.16—0.10	2700	0.587
	AGRIC	Cabrera vole	-0.18	-0.39—-0.01	3085	0.041
		Water vole	0.23	0.10—0.36	2700	<0.001
	Posterior estimates of random effects variance (95%CI): Year=0.01—0.33; Season=0.01—0.57; PLOC5K: 0.001—0.29; PLOA5K: 0.001—0.32						
2	HA	Cabrera vole	0.58	0.38—0.77	2700	<0.001
		Water vole	0.85	0.73—0.97	2700	<0.001
	AGRIC	Cabrera vole	-0.17	-0.38—-0.04	2395	0.051
		Water vole	0.24	0.12—0.37	3214	0.002
	Posterior estimates of random effects variance (95%CI): Year=0.01—0.38; Season=0.01—0.61; PLOC5K: 0.001—0.31; PLOA5K: 0.001—0.39						
3	HA	Cabrera vole	0.56	0.35—0.75	2700	<0.001
		Water vole	0.87	0.73—1.00	2700	<0.001
	PD	Cabrera vole	0.23	0.11—0.37	2700	0.002
		Water vole	-0.04	-0.17—0.09	2700	0.554
	AGRIC	Cabrera vole	-0.18	-0.38—-0.01	2700	0.049
		Water vole	0.23	0.11—0.37	2700	0.002
	EPAST	Cabrera vole	-0.01	-0.22—0.20	2700	0.893
		Water vole	-0.04	-0.17—0.11	2700	0.611
	Posterior estimates of random effects variance (95%CI): Year=0.01—0.35; Season=0.01—0.59; PLOC5K: 0.001—0.31; PLOA5K: 0.001—0.35						