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Isodars unveil asymmetric effects on habitat use caused by competition between two endangered species

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In order for competing species to coexist, segregation on some ecological niche component is required and is often mediated by differential habitat use. When unequal competitors are involved, the dominant species tends to displace the subordinate one to its less preferred habitat. Here, we use habitat isodars, an approach which reflects evolutionary stable strategies of habitat selection, to evaluate whether interspecific competition between two competing species with distinct habitat preferences, the little bustard *Tetrax tetrax* and the great bustard *Otis tarda,* modulates their habitat use. Field data on these endangered species demonstrate that unequal competitors can coexist without completely segregating on their preferred habitats. The negatively sloped isodar of the subordinate little bustard unveils its competition with the dominant great bustard. Interference from great bustards in secondary cereal habitats reinforces use of preferred natural habitat by little bustards. Studies of density-dependent habitat selection by a single-species can thus aid in identifying the effects of competition on community composition, and guide the conservation of at-risk species. Isodars, in particular, represent a promising method to gain clear knowledge on interspecific competition for species in which experimental manipulations are not feasible.

Interspecific competition is widely denoted as a prominent mechanism underlying the structure and organization of ecological communities. Competition among sympatric species shapes spatial range boundaries, influences population dynamics, alters local habitat selection and promotes temporal resource partitioning (Ziv et al. 1993, Martin and Martin 2001, Laiolo 2013, Stuart et al. 2014). Competition that reduces availability or access to key resources reduces the fitness of all competing individuals (Begon et al. 2006). However, adaptive behaviors, such as differential density-dependent habitat selection, tend to minimize the fitness loss associated with interspecific competition and act to stabilize species coexistence (Rosenzweig 1981, Morris 2003b). Consequent evolution of closely related competing species reinforces niche divergence and often causes morphological shifts of resource-related traits, favoring speciation and adaptive radiation (Grant and Grant 2006, Stuart et al. 2014).

All organisms require space to live and resources to reproduce and survive but the heterogeneous environments are not equally favorable for all species or individuals. Therefore, the abiotic and biotic characteristics of a given habitat determine the expected fitness that can be attained by individuals of each species or population (Fretwell and Lucas 1969, Morris 2003b). Habitat differences in resource quality and abundance, but also in the way that resources are consumed, affect individuals' reproduction and survival. Organisms capable of perceiving these habitat differences should, if they have the opportunity, occupy those habitats yielding highest fitness (Fretwell and Lucas 1969, Rosenzweig 1981, Morris 2003b). The density and frequency-dependence of fitness thus defines a habitat-selection game in which the distribution of individuals converges on an evolutionarily stable strategy (ESS, Brown 1990, Křivan et al. 2008). The reduction in fitness associated with interspecific competitors alters the ESS, and thereby enables one to use density-dependent habitat selection to evaluate the role of interspecific competition in population and community dynamics (Morris 1989, Morris et al. 2000).

Habitat selection's role in species coexistence is most easily appreciated with reference to the ideal free distribution of Fretwell and Lucas (1969), in which the density-dependent choice of habitats by individuals equalizes their expected fitness in all occupied habitats. In the absence of a competing species, individuals living at low density occupy only their preferred habitat. As density increases, resources are progressively depleted and intraspecific competition intensifies, thus reducing fitness. When the expected fitness in the preferred habitat equals that obtained in other less suitable habitats, individuals shift their habitat choice in order to maximize fitness. The equilibrium habitat distribution of the population is achieved when an individual's expected fitness is the same in all occupied habitats (ESS).

When a competing species is present, however, early theories of habitat selection predicted that stable coexistence of competing species with distinct habitat preferences will occur only when they segregate into their respective preferred habitats (Rosenzweig 1981, Morris 1988). Such spatially segregated species cannot compete with one another even though competition is responsible for their spatial separation (the ghost of competition past, Rosenzweig 1974). Nonetheless, optimal habitat selectors with distinct preferences should overlap in habitat use when species coexist at densities below their jointly stable carrying capacities (Morris 1999, 2003a, 2004, 2009). When this occurs, regressions assessing the species' habitat isodars (the set of densities in occupied habitats such that an individual's expected fitness is equal in each, Morris 1987, 1988) can be decomposed to measure the otherwise hidden competitive interaction (Morris 1999).

In this study, we use habitat isodars calculated from field data to investigate the effects of interspecific competition on the habitat use of two coexisting putative competitor species with distinct habitat preferences (the little bustard *Tetrax tetrax* and the great bustard *Otis tarda*; Morales et al. 2006). In particular, we use isodars to evaluate whether the presumed subordinate competitor, the small-sized little bustard, occupies its alternative habitat even when the much larger dominant species is present (Morris 1989). We use the partial regression coefficients from the habitat isodars (Morris 1989, Rodríguez 1995) to infer the effects of interspecific competition in bustard coexistence and to identify the level of asymmetric competition between these species. Although we suspect that interference may occur between these two bustard species, their rarity yields small sample sizes that only allow us to include exploitation competition in the isodar model. Therefore, we also investigate whether isodars can track interference competition when its coefficient is not included in the isodar regression. We follow the approach introduced by Morris (2009) that showed how habitat isodars can inform us about exploitative competitive interactions when data on the competing species are absent (Fig. 1). The isodar slope, which quantifies intraspecific density-dependent habitat selection (Morris 1989), should change from positive to negative sign when competitors are sequentially removed from their preferred habitat (Morris 2009; Fig. 1b). Decreased competition allows individuals of the target species to increase the proportional use of their competitor's habitat (Fig. 1a). We expand the situation evaluated in Morris (2009) to evaluate how the isodar slope responds to statistical removal of interference competition, and whether that effect modifies assessments of exploitative competition.

Revisiting isodar theory

Imagine an ideal-free population of species A that occupies a coarse-grained landscape composed of two habitats (1 and 2). Individuals of species A preferentially select habitat 1 but habitat 2 also harbors resources used by this species. The set of joint densities in each habitat at different population sizes defines species A's habitat isodar (Fig. 1b dotted line):

$$N_{A1} = c + bN_{A2} \qquad (1)$$

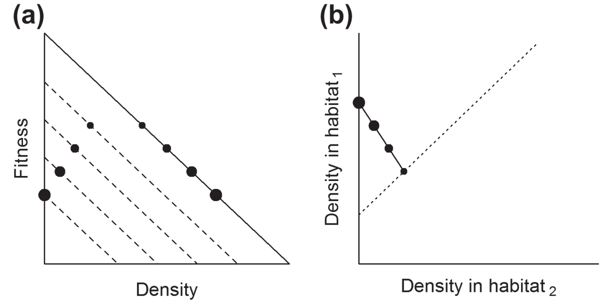

Figure 1. Effect on habitat choice by sequential removal of a competitor while the target species lives at constant population size. Competition between the species only occurs in the alternative habitat 2. Panel (a) illustrates the fitness attained in the preferred habitat 1 (solid line) and in the alternative habitat 2 (dotted lines) for different competitor densities. Point size reflects competitor density in habitat 2 (the smallest point size indicates zero competitor density). Points of equal size indicate joint densities in both habitats for a particular competitor density. Panel (b) illustrates the resulting isodar of the target species with a negative slope (solid line) in comparison with its expected positive isodar when existing in allopatry (dotted line; after Morris 2009).

where N_{A1} and N_{A2} correspond with the density of species A in habitat 1 and habitat 2, respectively. The intercept of the equation, c, corresponds with quantitative differences between habitats (for instance, differences in resource renewal rate; Morris 1988). The isodar slope, *b,* quantifies the difference in the slopes of the underlying density-dependent fitness functions in each habitat. Because density in both habitats increases proportionally with population size, the isodar slope must be positive. Both terms can be easily estimated by linear regression (Morris 1987).

Consider now that species A co-occurs with a second species (B) that prefers habitat 2. Hence, both species may compete for the resources available in habitat 2 and resolve their competition through habitat selection. Although individuals of species A prefer habitat 1, they also occupy habitat 2 when the density of the interspecific competitor is low (Morris 2009; Fig. 1a). The habitat distribution of species A depends upon its intraspecific density-dependent habitat selection as well as the intensity of interspecific competition in each habitat. The effects of this interspecific exploitative competition can be evaluated by including the density of species B in the two-species isodar equation:

$$N_{A1} + \alpha N_{B1} = c + b\,(N_{A2} + \beta N_{B2}) \qquad (2)$$

(Morris 1989, Rodríguez 1995). Rearranging Eq. 2:

$$N_{A1} = c + bN_{A2} + b\beta N_{B2} - \alpha N_{B1} \qquad (3)$$

where N_{B1} and N_{B2} represent the density of species B in habitat 1 and 2. The partial regression coefficients α and β quantify the exploitative competitive effects of species B on species A's fitness in habitat 1 and habitat 2, respectively. We evaluate how interference competition affects species A's habitat use by incorporating the higher order interaction term between both species in habitat 2. Following Morris (1989),

$$N_{A1} = c + b\,(N_{A2} + \beta N_{B2} + \gamma N_{A2}N_{B2}) - \alpha N_{B1} \qquad (4)$$

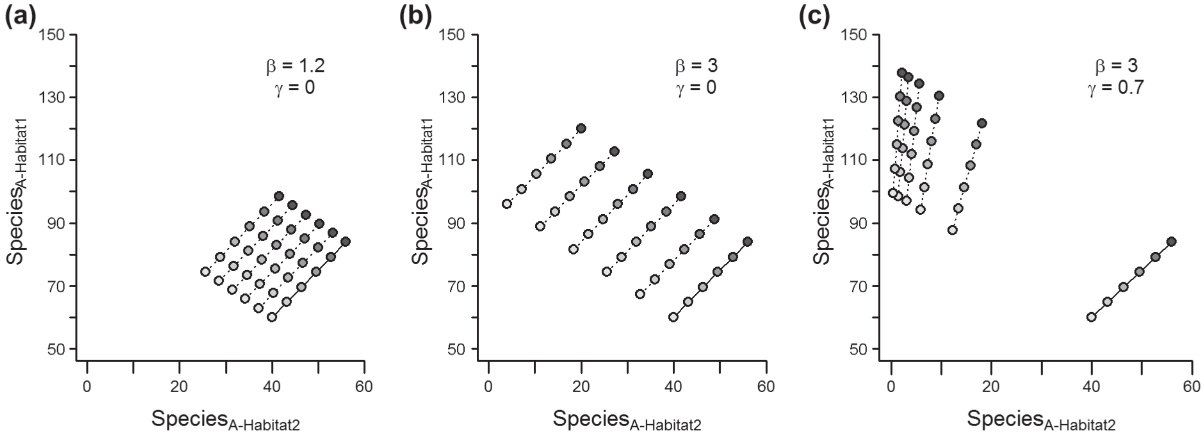

Figure 2. Isodar plots showing the effects of exploitative and interference competition in the habitat use of a subordinate species (A) competing with a dominant species (B) in the subordinate's secondary habitat (2). Increased shading corresponds with increasing density of species A. Circles joined by a solid line correspond with the habitat use pattern in the absence of species B. Circles joined by the same dotted line reflect the habitat use pattern for a single density of species B, which increases from east to west. (a) Isodar in the presence of exploitative competition (β) in habitat 2; (b) the magnitude of exploitative competition increases, reducing the use of habitat 2. The slope remains constant for all species B densities; (c) competition by interference (γ) is also operating between the species. Interference competition steepens the slope of the isodar. The proportional use of habitat 2 is lower for higher species A and B densities. Overall densities of species A ranged from 100 to 140 individuals per unit area, with increments of 8 individuals. Species B densities in habitat 2 were lower, varying from 0 to 20 individuals per unit area, increasing by 4. For simplicity, we assumed that $c = 0$ (habitat 1 and 2 did not differ quantitatively) and $b = 1.5$ (the underlying fitness curves diverge with increasing density). The parameter values guaranteed that the species A occupied both habitats (zero densities bias the isodar intercept).

where γ is the term for interference competition of species B on species A in the secondary habitat 2. We illustrate the joint effects of exploitative and interference competition by calculating the isodar across a range of densities of both species (Fig. 2). Both exploitation and interference induce a gradual displacement of individuals of the subordinate species A towards its preferred habitat. However, the change in habitat use is more drastic for interference than it is for exploitation (Fig. 2b–c).

We now explore how isodars behave when the interference coefficient is removed from the linear isodar regression (parameter values in Table 1). The isodar regression model lacking the interference regression term ($\text{Species}_{\text{A-Habitat2}} \times \text{Species}_{\text{B-Habitat2}}$) yields a significantly negative slope and a significantly positive partial regression term for exploitative competition. It should thus be possible for habitat isodars to unveil interference competition without direct knowledge of competitive interactions or sample sizes large enough to include interference in the regression model. We anticipate that this solution might be widely applicable to studies on rare or endangered species where it is difficult or impossible to achieve sample sizes large enough for a full isodar analysis.

Case study: applying isodars to field data on endangered species

Methods

Study species

We tested the ability of habitat isodars to reveal competition between two members of the *Otididae* avian family that have broadly overlapping Paleartic distributions (Del Hoyo et al. 1996). *Tetrax tetrax* (little bustard) is a medium size steppe bird whereas *Otis tarda* (great bustard) is one of the heaviest flying birds (Cramp and Simmons 1980).

Table 1. Linear regression results of removing the interference competitive term from the isodar model for an unequal competitors community. The subordinate species A prefers habitat 1, but competes by exploitation and interference with the dominant species B in its alternative habitat 2. We compare two models, one with the interference term and other without it (i.e. exploitation and intraspecific effects). Intercept = 0, exploitative competition (β) = 3, interference competition (γ) = 0.7, intraspecific competition coefficient (b) = 1.5. *** and ** indicate $p < 0.001$ and $0.01 < p < 0.001$, respectively. Overall densities of species A ranged from 100 to 140 individuals per unit area, with increments of four individuals ($n = 11$ populations). Species B densities in habitat 2 were lower, varying from 0 to 20 individuals per unit area, increasing by 1 ($n = 21$ populations). We restricted our attention to only one set of competition parameters (β = 3 and γ = 0.7) because we are interested in how isodars respond to the removal of the interference regression coefficient. Other values would reveal similar outcomes.

Model	Adjusted R^2	Coefficient	Estimates
$\text{Density}_{A1} = b\ \text{Density}_{A2} + \beta\ \text{Density}_{B2} + \gamma\ \text{Density}_{A2} \times \text{Density}_{B2}$	1	b	1.500 ± 0.000***
		β	4.500 ± 0.000***
		γ	1.050 ± 0.000***
$\text{Density}_{A1} = b\ \text{Density}_{A2} + \beta\ \text{Density}_{B2}$	0.25	b	–0.604 ± 0.121***
		β	0.628 ± 0.235**

Populations of little and great bustards have declined dramatically and the species are currently classified as near threatened and vulnerable respectively (IUCN 2012). These species' ecological and phylogenetic similarities suggest that they should compete with one another for space and food (Del Hoyo et al. 1996, Horreo et al. 2014). Both species inhabit open grasslands and extensive cereal croplands in western Europe (Cramp and Simmons 1980). The little bustard prefers fallows, legume crops and low natural vegetation (Wolff et al. 2001, Morales et al. 2005) whereas great bustard habitat use is concentrated on cereals but varies with landscape configuration (Lane et al. 2001, López-Jamar et al. 2011, Tarjuelo et al. 2014).

The two species' breeding phenologies also overlap. Great bustard males congregate and display in lek arenas in early April (Cramp and Simmons 1980). Males do not defend territories and females attend the lek with the only purpose of mating, followed by nesting during May (Cramp and Simmons 1980, Morales and Martín 2002). Little bustards initiate their reproductive activity at the end of April throughout May, with females nesting from late May into June (Cramp and Simmons 1980, Lapiedra et al. 2011). Little bustard males actively defend territories (Morales et al. 2014) which may harbor important food resources not only for the territory owner but also for females and their offspring (Traba et al. 2008). Offspring diet of both species is almost entirely arthropods (Jiguet 2002, Bravo et al. 2012).

Study areas

Bustard data were collected in seven different sites dominated by extensive cereal croplands in central Spain between 2006 and 2012: Campo Real (40°19′N, 3°18′W; 2010–2012); Daganzo (40°34′N, 3°27′W; 2010–2011); Valdetorres (40°40′N, 3°25′W; 2010–2011); Camarma (40°32′N, 3°22′W; 2006); La Solana (38°55′N, 3°13′W; 2010–2011); Calatrava north (38°56′N, 3°53′W; 2007–2011); Calatrava south (38°52′N, 3°57′W; 2007–2011). All study sites have a slightly undulating topography with Mediterranean climate and, a traditional cultivation system with a two-year rotation that creates a mosaic landscape of different agrarian habitats (Supplementary material Appendix 1). Approximately 50% of the land surface is covered by dry cereal crops (mainly wheat *Triticum* spp., barley *Hordeum vulgare* and oats *Avena* (spp.), ploughed lands (bare ground), and fallows of different ages. Leguminous crops (*Vicia* spp., *Pisum sativum* or *Lathyrus sativus*) are also sown but not in all regions. Patches of vineyards *Vitis vinifera*, olive groves *Olea europaea* and pastures are also present. The little bustard inhabits all study sites while the great bustard is absent in La Solana.

Bird censuses and habitat data

Little and great bustard censuses were carried out between April and May, corresponding with the species' reproductive periods (Cramp and Simmons 1980). Bird observations were collected by driving along the available network of roads and tracks that ensured complete coverage of each site. Each site was surveyed by two car-teams formed by experienced observers. Each car-team simultaneously covered half of the study area in order to fully census the study site within a single bustard daily activity period. The largest study sites could not be covered in a single-day census period. In such cases, the site was divided in two non-overlapping sectors covered in consecutive days. During the breeding season, individuals of both species are quite fixed to their territories (Alonso and Alonso 1990, Morales et al. 2008), and thus movement of individuals between sectors is unlikely. Censuses for little bustard and great bustard were performed in consecutive days to ensure a reliable mapping of all individuals of the species.

Observers stopped their vehicle every 500 m and scanned the surroundings with binoculars and spotting scopes, mapping all birds detected. Surveys were limited to time when the birds are most active and easier to detect (three hours after daybreak and three hours before sunset, Cramp and Simmons 1980). We counted the number of male and female great bustards in each lekking area (Morales and Martín 2002). Snort calls of little bustard males allowed observers to detect them acoustically and accurate positions were then obtained by a visual search. Little bustard female observations were discarded because their secretive behaviour precludes a reliable estimate of abundance. Maps were revised afterwards in order to remove double counts of the same individuals (bird movements were also drawn in maps). This census methodology enabled a complete map of all birds present in the study site.

Habitat availability was determined by annual land-use maps obtained from field surveys conducted immediately after bird censuses. Thus, erroneous habitat choice assignments caused by temporal changes in landscape composition were avoided. Each field was classified in one of the following habitats: 1) one-year fallows (hereafter referred as young fallows); 2) fallows older than two years and short shrub-lands (hereafter referred to as natural vegetation); 3) leguminous crops; 4) cereals; 5) ploughed lands; 6) dry woody cultures, mainly olive groves and vineyards; 7) other (fruit tree orchards, urban areas, pastures and forest).

Multispecies bustard isodars

We first analyzed whether interspecific competition influences little bustard abundance at the regional scale by means of generalized linear mixed model (GLMMs), with Gaussian error distribution (density of little bustards = the response variable, density of great bustards = the explanatory variable, n = 20). Study site was included as a random factor in order to account for the dependence of data collected in the same study site over different years.

We then evaluated competition for habitat using multispecies isodars (Morris 1989, Rodríguez 1995). Little and great bustards were most abundant in the three habitats that we used in the analysis: fallows, cereal and ploughed land. Fallows, in this analysis, comprised young and old fallows, as well as leguminous crops. Young and old fallows have been widely denoted as the most preferred habitats for displaying little bustard males (Morales et al. 2005, Delgado et al. 2010). Leguminous crops, although a cultivated habitat, have a low vegetation height and a horizontal structure (Supplementary material Appendix 1 Table A2) that makes them suitable for sexual displays by little bustards (Morales et al. 2008). Based on previous work, we considered fallows as the preferred habitat while cereal and ploughed lands were considered as equivalent secondary habitats (Wolff et al. 2001, López-Jamar et al. 2011).

We were concerned that arbitrarily delimiting study site boundaries might bias our estimates of species density (Aebischer et al. 1993). Therefore, for each study site and year we first computed the area of each habitat type inside the minimum convex polygon (MCP) defined by all bustard observations. We defined each individual's habitat as the habitat of maximum cover inside a buffer of 10 m centered on the bird's observation. Each bird observed was considered as an individual. We then calculated the density of each bustard species in fallows, cereal and ploughed land for each study site and year ($n = 20$ for each habitat and species). To do so, we summed all individuals of the same species using the same habitat category and divided the result by the specific habitat area within the MCP. Both species can move quickly between close plots of different habitats so we assumed that the cost of movements among habitats did not reduce fitness expectations (Supplementary material Appendix 1 Table A1).

We fitted multispecies isodar models with GLMMs with Gaussian error distributions and included study site as a random factor. The GLMMs used a restricted maximum likelihood estimator, the most common procedure for mixed models, to fit the isodars and thus overcome limitations that would otherwise be associated with ordinary least squares solutions (Bradbury and Vehrencamp 2014). Three isodar equations were formulated for each species to test for density-dependent habitat selection between the preferred habitat (fallows) and each of the secondary habitats (cereal and ploughed land), and also between the secondary habitats (cereal versus ploughed land), in the presence of the potential competing species. For the little bustard:

$$\begin{aligned}\text{Density}_{\text{LB-Fallows}} = c &+ b_{c}\text{Density}_{\text{LB-Cereal}}\\ &+ \beta_{c}\text{Density}_{\text{GB-Cereal}}\\ &- \alpha_{f}\text{Density}_{\text{GB-Fallows}}\end{aligned} \tag{5}$$

$$\begin{aligned}\text{Density}_{\text{LB-Fallows}} = c &+ b_{pl}\text{Density}_{\text{LB-Ploughed land}}\\ &+ \beta_{pl}\text{Density}_{\text{GB-Ploughed land}}\\ &- \alpha_{f}\text{Density}_{\text{GB-Fallows}}\end{aligned} \tag{6}$$

and

$$\begin{aligned}\text{Density}_{\text{LB-Cereal}} = c &+ b_{pl}\text{Density}_{\text{LB-Ploughed land}}\\ &+ \beta_{pl}\text{Density}_{\text{GB-Ploughed land}}\\ &- \alpha_{c}\text{Density}_{\text{GB-Cereal}}\end{aligned} \tag{7}$$

where b_c and b_{pl} correspond to the regression coefficients for intraspecific density dependence (isodar slope), the partial regression coefficients β_c and β_{pl} reflect interspecific competition, in cereal and ploughed land respectively, and α_f and α_c are the partial regression coefficients indicating interspecific competition in fallows and cereal, respectively. We then rearranged Eq. 5, 6 and 7 for the great bustard (Rodríguez 1995). Sample sizes ($n = 20$) were too small to include the interaction term ($\text{Density}_{\text{LB-Habitat2}} \times \text{Density}_{\text{GB-Habitat2}}$). We removed the interspecific competitive term from the isodar regression when it was not statistically significant, and rebuilt the equation using only intraspecific competition for habitat.

Observational bird data and land-use maps were processed with ArcGis 9.3 (ESRI 2007). All statistical analyses and spatial calculations were conducted with R ver. 3.1.1 (<www.r-project.org>).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sq135> (Tarjuelo et al. 2016).

Results

Overall, great bustard density was higher and more variable than little bustard density (Supplementary material Appendix 2 Table A3). There was no relationship between the densities of both bustard species (great bustard density coefficient $= 0.07 \pm 0.05$, $t = 1.28$, $p = 0.224$).

In accordance with the species' habitat selection, the little bustard reached its highest density in natural vegetation, followed by young fallow and legume crops (Fig. 3). Great bustard density was highest in cereal, whereas young fallows and legume crops were moderately used (Fig. 3).

The little bustard's multispecies isodars in fallows (Eq. 5) clearly documents competition with great bustards in cereals (significant positive coefficient of great bustard density in cereal, Fig. 4a, Supplementary material Appendix 2 Table A4). Hence, as great bustard density increased in cereals, proportionally more little bustards used fallows (Fig. 4a). Moreover, the negative isodar slope highlighted additional competitive interactions with great bustards in cereal (Fig. 4a). We detected no competition between the species in fallows, the little bustard's preferred habitat (Fig. 4a). The significant intercept of the isodar indicates that the little bustard perceives fallows as quantitatively superior to cereal habitat.

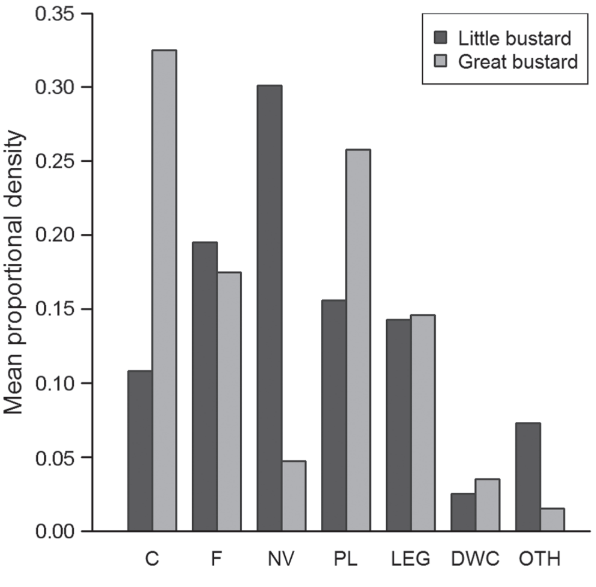

Figure 3. Mean proportion of little and great bustard densities in each habitat (C: cereal; F: young fallows; NV: natural vegetation; PL: ploughed land; LEG: leguminous crops; DWC: dry wood cultures formed by vineyards and olive groves; OTH: pastures, urban areas, fruit tree orchards and forest) using all study sites where the species were present. Means were calculated first obtaining the proportional density in each habitat from the overall density in a given study site and year. We calculated the proportional mean density for each habitat by averaging all study site densities.

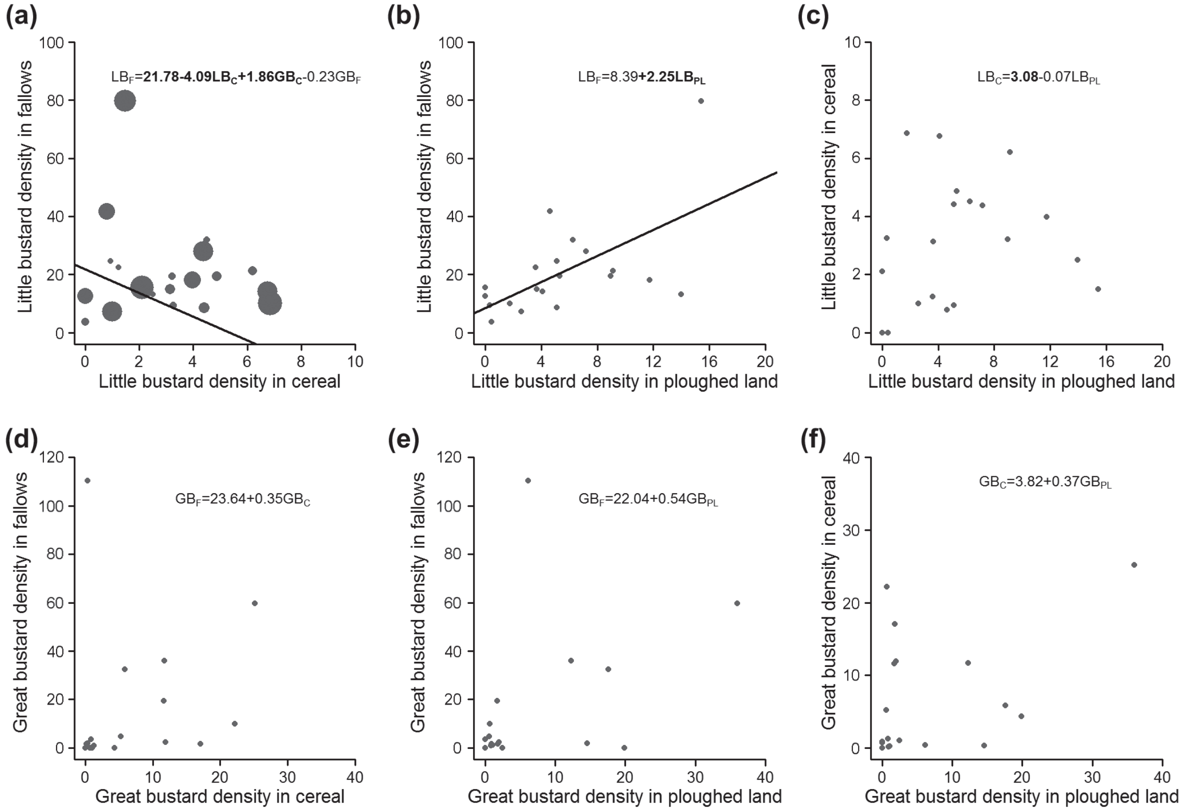

Figure 4. Isodars for little (LB: a, b, c) and great bustards (GB: d, e, f) considering fallows (F) as the preferred habitat and cereal (C) or ploughed land (PL) as the secondary habitat choice. The final regression model is displayed for each isodar graph (with significant $p < 0.05$ coefficients in bold type). Isodars are displayed only for statistically significant slopes (density-dependent habitat selection). Point size reflects the density of the competing species in the secondary habitat in graph (a) because this variable had a significant influence on little-bustard habitat use (Supplementary material Appendix 2 Table A4).

The isodar slope for fallows and ploughed land (Eq. 6) was significantly positive, indicating a density-dependent preference of little bustards for fallows over ploughed lands (Fig. 4b). The intercept was not significantly different from zero, nor was there any evidence of competition by great bustards (Supplementary material Appendix 2 Table A4). According to the habitat isodar, little bustards do not perceive a quantitative difference between these two habitats.

Finally, the little bustard's isodar between the secondary habitats, cereal and ploughed land (Eq. 7), had a significant intercept and a non-significant slope (Fig. 4c, Supplementary material Appendix 2 Table A4). Although little bustards may perceive that cereal is quantitatively superior to ploughed land, their choice of these secondary habitats was independent of density.

Our re-arrangement of the isodar equations revealed no interspecific competition by little bustards on the great bustard's habitat use (Fig. 4d–f, Supplementary material Appendix 2 Table A5). The analyses also revealed that the great bustard had no preference among the three main habitats in these agricultural regions (Fig. 4d–f).

Discussion

Our analyses document that habitat isodars represent an efficient and reliable method to evaluate interspecific competition between coexisting species, even when competitor data are lacking. These intriguing results widen the door for assessment of competitive interactions in systems where data are difficult to acquire, and especially so in systems of conservation concern where densities may be low or far from equilibrium.

Habitat partitioning is one of the most important mechanisms by which competing species coexist (Rosenzweig 1981, Morris 2003b). Although theory often predicts stable coexistence when species segregate into their preferred habitats (Rosenzweig 1981, Morris 1988), our results from field data confirm the prediction that (Morris 1999), when such systems depart from equilibrium, the subordinate species can exploit its secondary habitat while the dominant competitor also uses it. Competition is not resolved by complete spatial separation. Rather, individuals trade off intraspecific competition for interspecific competition by increasing their proportional use of the competitor's preferred habitat when it exists at low density (Morris 1999). If the competitor abundance increases, the balance of intra- versus interspecific competition will be shifted and fewer individuals will occupy their alternative habitat. Competition can thus be equalized by many different combinations of density in different habitats. Despite this, habitat isodars accurately reveal the underlying competitive effects (Morris 2004).

Habitat isodars for the little and great bustards reveal that these coexisting and ecologically similar steppe birds compete asymmetrically. The dominant great bustard is a generalist species with no clear habitat preferences that alters the habitat use of the subordinate little bustard, a species specialized on fallows and legume crops (Lane et al. 2001, Morales et al. 2005, Delgado et al. 2010, López-Jamar et al. 2011, Tarjuelo et al. 2014). The little bustard increases its use of fallows as the density of the great bustard increases in cereals. Great bustard male display arenas or female nesting territories in cereals appear to reduce opportunities for little bustard males to establish territories in this habitat. Meanwhile, neither the presence nor density of little bustards appear to influence habitat choice by great bustards.

Most interestingly, the little bustard's negative isodar slope also documents additional interference competition with great bustards in cereals, an effect that we could not evaluate directly with a higher order interaction term. Our ability to reliably measure interference depended on first accounting for variation in competitor density and potential exploitative competition (Supplementary material Appendix 2 Table A4, Fig. 2c). When we did so, the more acute response generated by interference exceeded the linear exploitative term, and thus a negative isodar slope emerged. Our confidence in this interpretation is bolstered by the significantly positive isodar slope for little bustards in comparisons between fallows and ploughed land that revealed no interspecific competition from great bustards in those habitats.

We interpret the negative slope as originating from the chance of direct encounters between individuals of the two bustard species. Occupation of cereal habitat by little bustard males mitigates intraspecific competition. As the abundance of great bustards increases in cereals, so too does the chance of encounter. Consequently, cereals become less attractive as breeding habitats for little bustard males which increase their use of fallows. The unsuitability of cereals as sexual displaying habitats for little bustard males thus appears not only due to its vegetation structure (Morales et al. 2008; Supplementary material Appendix 1), but also to interspecific competition with great bustards.

One might expect that interspecific competition also occurs in other habitats due to the lack of habitat preference by great bustards. However, the great bustard uses habitats depending on their availability (Tarjuelo et al. 2014) and cereal constitutes the most abundant habitat in these landscapes during spring. Therefore, interspecific competition between the little bustard and the great bustard is more likely to occur in cereals than in any other habitat used by the little bustard.

Others might question whether habitat selection follows something other than an ideal free distribution in the territorial little bustard. Dominance or site pre-emption can often, but not necessarily, create curved isodars (Morris 1994, but see Morris et al. 2000). Although our data are insufficient to rule out alternative distributions, the linear isodar slope for fallows and ploughed land (Fig. 4b) does not support a convincing case for a curvilinear relationship in this species.

Density-dependent habitat selection of bustards has important implications for their conservation. In 2009, the European Common Agrarian Policy abolished the requirement for farmers to leave 10% of their land as fallow (European Commission 2009). Our analyses suggest that the decrease in fallow will intensify intraspecific competition for good quality breeding territories by little bustards. Intensified intraspecific competition will be particularly worrisome in regions with high densities of great bustards because little bustards might not be able to adequately exploit the alternative cereal habitat. This fact may compromise the little bustard's reproductive opportunities and translate into further declines of population size. We caution that this prediction emanates from results derived only from little bustard males. Although males and females might respond differently to competition from great bustards, it is difficult to imagine how reduced opportunities for males to form territories, and similarity between the sexes in habitat preferences at this spatial scale (Morales et al. 2013), would not translate into reductions in population size. Conservation policies that fail to understand the ecological consequences of 'invisible' interspecific competition on community organization can thereby jeopardize the recovery of endangered species.

We acknowledge that negative isodar slopes may emerge from any mechanism that lowers the apparent quality of secondary habitats across space and time, such as differential predation risk or, environmental heterogeneity and stochasticity. This will occur, of course, only if the investigator is collecting comparative densities at those times and places. We also recognize that exploitation and interference cannot be distinguished when any interspecific competitive term is incorporated in the isodar regression because of their similar influence on the subordinate species' habitat selection. We could infer the existence of interference competition between our bustard species because the linear term for exploitation was considered in the habitat isodar. Nonetheless, the important point remains that omitting interspecific competition from the isodar yields a negative slope because the density of the target species in its alternative habitat is lower than expected in the absence of competitors.

Interspecific competition is a crucial driver of community organization and evolutionary change. Understanding these effects requires an ability to evaluate ecological and evolutionary impacts in terms of fitness. Though the effects of interspecific competition on fitness estimates have been traditionally addressed through experimental removals and manipulation of resources (Dhont 2012), doing so is difficult for most species, and particularly so for those of conservation concern. An alternative is to learn to use adaptive behaviors emerging from evolutionary games such as habitat selection as leading indicators of environmental change (Morris et al. 2009). In this sense, our field work with bustards demonstrates that habitat isodars are a particularly promising tool to investigate interspecific competition in species for which experimental manipulations are not feasible. We suspect that they will be valuable tools for any habitat selection study in wild populations that encounters difficulties in gathering data on competitors' density, or even to elucidate the network of species interactions. Although isodars have been criticized for not being able to detect interference competition in gerbil communities (Ovadia and Abramsky 1995), this conclusion was based on the erroneous idea that curved isoclines cannot emerge from constant competition coefficients (Morris 2009). Our results provide conclusive evidence that habitat isodars capture interspecific competition even in the absence of competitor data. The ability of habitat isodars to capture interspecific competition in the absence of competitor data, and the fact that isodars do not require equilibrium dynamics, expand opportunities to gain new insights into the regulation and assembly of real communities from census data on free-ranging populations.

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Supplementary material (available as Appendix oik-3366 at <www.oikosjournal.org/appendix/oik-03366>). Appendix 1–2.