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THE ROLE OF BIOTIC INTERACTIONS IN THE ECOLOGY AND CONSERVATION OF THE LITTLE BUSTARD: FROM NICHE RELATIONSHIPS TO BEHAVIORAL RESPONSES

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A mis padres.

A mis perros.

Presentación

Es un hecho indiscutible que el ser humano está causando profundos cambios en la mayor parte de los ecosistemas del planeta y, debido a las necesidades, cada vez más exigentes, de una población humana en continuo aumento, es previsible que las presiones se incrementen en muchas regiones del planeta. Ante este escenario de cambio global, son muchas las voces que, desde distintos sectores, reclaman medidas efectivas para salvaguardar la biodiversidad actualmente amenazada. Para responder a las demandas conservacionistas de la sociedad, es fundamental determinar cuáles son los factores y mecanismos que afectan a la distribución de las especies y las escalas a las que operan. Mientras que a escala continental son las variables relacionadas con el clima, como la temperatura y las precipitaciones, las que condicionan el rango de distribución de las especies, a escala regional y local adquieren una gran preponderancia el hábitat y las relaciones bióticas. Son precisamente la degradación, modificación, fragmentación o incluso desaparición de los hábitats algunos de los factores más influyentes en el declive poblacional de muchas especies. Además, estas alteraciones en los hábitats pueden conllevar cambios en las interacciones que establecen las especies que conviven en una misma comunidad. Sin embargo, dichas relaciones bióticas raramente son tenidas en cuenta a la hora de proponer medidas de conservación, las cuales se focalizan generalmente en mejorar o reestablecer las condiciones físicas alteradas por el hombre, quizá debido a que los cambios en el medio físico son más fácilmente apreciables y a la falta de conocimiento respecto a la red de interacciones en muchas comunidades. A pesar de ello, es necesario sobreponerse a dichas dificultades si queremos llegar a conocer con precisión cuáles son las interacciones que establecen las especies entre sí y cómo éstas afectan al *fitness* de los organismos y, por ende, a la viabilidad de las poblaciones.

En la actualidad, las aves ligadas a los medios agrícolas se encuentran entre las especies de aves más amenazadas de Europa. Muchas de ellas han sufrido importantes declives poblacionales atribuidos a los drásticos cambios que han tenido lugar en estos paisajes, como consecuencia fundamentalmente de una intensificación en las prácticas agrarias para maximizar la producción agrícola. La intensificación agraria ejerce sus efectos a distintos niveles, desde la disminución en la disponibilidad de alimento para las crías hasta la modificación o pérdida de hábitats para la nidificación. Entre estas aves esteparias, la situación del sisón es particularmente preocupante ya que, tras el importante declive sufrido a lo largo del siglo XX, las poblaciones de la Península Ibérica y Francia, que aglutinan más de la mitad de la población mundial, continúan en progresivo descenso sin mostrar signos de recuperación. Mientras que el conocimiento respecto a la selección del hábitat de los machos de sisón durante la época reproductora es extenso y ha servido para proponer y aplicar medidas de conservación, los estudios que contemplan el papel de las interacciones bióticas son ciertamente escasos y en su mayoría se centran en determinar los mecanismos evolutivos de formación de leks. Por tanto, es un tema aún pendiente determinar qué tipo de relaciones bióticas establece el sisón tanto con otros individuos de la especie como con otras especies de la comunidad de aves esteparias y cómo pueden dichas interacciones afectar a la regulación y dinámica poblacional de esta especie, lo cual permitiría mejorar las medidas de conservación.

La presente tesis doctoral aborda el papel de las relaciones bióticas en el uso del hábitat, la distribución espacial a escala de paisaje y el comportamiento del sisón. A lo largo de los cinco manuscritos que conforman esta tesis doctoral se desgrana cuáles son los efectos de las relaciones establecidas tanto con individuos de la misma especie como con la avutarda, una especie con la que frecuentemente coexiste y con la que, tanto por su proximidad filogenética como por la similitud en cuanto a sus requerimientos ecológicos durante la época reproductora, podría mantener relaciones de competencia. Así, los tres primeros capítulos se centran en esclarecer la posible existencia de competencia entre el sisón y la avutarda y destacar algunas recomendaciones de gestión que promuevan la conservación de ambas especies en aquellas zonas donde se encuentran coexistiendo. En concreto, en el *CAPÍTULO 2* se analiza por primera vez la existencia de relaciones de competencia entre el sisón y la avutarda en el marco de la teoría del nicho ecológico, analizando relaciones de denso-dependencia en el grado de solapamiento de nicho entre las dos especies y si la avutarda induce modificaciones en el nicho realizado del sisón. Tras ello, el *CAPÍTULO 3* ahonda en la existencia de interacciones competitivas y cómo éstas afectan a los procesos denso-dependientes de selección de hábitat tanto del sisón como de la avutarda. En el *CAPÍTULO 4* se evalúa la idoneidad de zonas de uso exclusivo de las especies frente a zonas de coexistencia con el objetivo de proponer medidas de conservación para la gestión local de aquellas regiones donde cohabitan el sisón y la avutarda. El *CAPÍTULO 5* pasa a abordar el efecto de las relaciones entre coespecíficos en el sisón y, en concreto, se centra en evaluar el papel que cumplen los núcleos de machos reproductores establecidos durante la época de cortejo en la posterior distribución espacial de las hembras con crías, considerando además el uso del hábitat de las mismas. En el *CAPÍTULO 6* se estudia si las diversas actividades humanas realizadas en los medios agrarios, con un particular interés en la actividad cinegética debido a su destacada relevancia socio-económica en estas zonas rurales y a los efectos que tiene sobre la fauna, inducen cambios comportamentales a la vez que generan estrés fisiológico en el sisón. Finalmente, los principales resultados obtenidos a lo largo de los distintos capítulos que integran la tesis doctoral se discuten de manera conjunta en el *CAPÍTULO 7*, en el que además se proponen ideas que sirvan de base para investigaciones futuras.

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...each organic being is either directly or indirectly related in the most important manner to other organic beings, we must see that the range of the inhabitants in any country by no means exclusively depends on insensibly changing physical conditions, but in large part on the presence of other species, on which it depends, or by which it is destroyed, or which it comes into competition.

Charles Darwin. On the Origin of Species.

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Chapter 1

Introduction

Nowadays, world biodiversity is facing one of its major challenges in Earth's history originated by the impacts of one species: humans. Although humans caused profound effects on landscapes and brought many species to the extinction early in their history (Diamond, 1989; Wilson, 1992; Prescott et al., 2012), the Industrial Revolution in the 18th century marked the veritable start of a widespread, unprecedented modification of global processes which increased exponentially after the World War II (Steffen et al., 2011). Biodiversity is globally threatened by habitat loss and fragmentation, overharvesting, invasion of alien species, pollution and anthropogenic climate change (Wilson, 1992; Millennium Ecosystem Assessment, 2005). There is increasing awareness among worldwide society and scientists about how biodiversity loss can impact human well-being, bearing in mind the high demanding previsions for an increasing 7 billion human population (Bloom, 2011). Thus, governments adopt conservation policies directed at the preservation of global biodiversity with high emphasis in those species most endangered. But such decisions, ranging from habitat management to species reintroductions, are based on the enhancement of suitable physical or habitat conditions, and frequently ignore the complexity of biotic interactions in nature and their role in community structure and species distribution (Soulé et al., 2005).

1.1 Biotic interactions: the role of competition and facilitation

Organisms do not live in isolation, influenced solely by the physical component of their environment. They interact in many different ways with other beings belonging to their own or different species. Organisms prey in other species, they mate in order to transmit their genes to descendants, modify physical conditions allowing different species to settle while excluding others, or aggressively interfere to defend resources (Begon et al., 1999). Regardless of whether interactions operate in a direct or indirect manner, biotic interactions exert important selective pressures on individuals, shaping communities and driving evolutionary change (Pianka, 2000). There are three main interaction types according to the resulting positive or negative effects for the interacting organisms: competition, predation and mutualism. Among them, competition has been acknowledged as the major force governing community formation and responsible of evolutionary divergence (Darwin, 1859; Diamond, 1978; Keddy, 1989). However, facilitation has been recently recognized to play a significant role influencing species distribution and community structure (Bertness and Callaway, 1994; Bruno et al., 2003; Cavieres and Badano, 2009).

Intra- and interspecific competition

Competition is a ubiquitous biological phenomenon in nature. Organisms require food resources for their growth and to raise their brood, shelter to avoid predation or good quality territories to attract potential mates and reproduce. But most of these resources are often limited during certain moments of an individual's life-span so organisms must ensure the access to enough amount of good quality resources (Begon et al., 1999). Otherwise, their survival and reproductive success can be compromised and their fitness consequently reduced (Watson, 1985; Bolger et al., 2005; Davis et al., 2005). This means that organisms sharing a limiting resource are likely to get involved in competition for its monopolization. In a competitive interaction, all participants are negatively affected by the decrease in resource availability as organisms consume them, which in turn reduces per capita growth rate (Begon et al., 1999). But competitive effects can be unequally distributed among competitors because organisms differ very often in their abilities to consume resources. When asymmetric competition occurs, the superior competitor outcompetes the others. Depending on the mechanisms and the resulting effects of competition, two types can be distinguished: exploitation and interference (Begon et al., 1999). Exploitative competition involves an indirect interaction which occurs when the use of a shared resource by one competitor simply reduces the amount available to another. In interference competition, individuals directly control the access to a limiting resource via aggressive behaviors or chemical weapons which negatively affect the competitors' ability to acquire resources.

The type of limiting resources depends also upon the species' life history and can be grouped basically in space and food (Dhondt, 2012). Space can be a limiting resource during winter in temperate regions, when territory ownership may be crucial for winter survival and may influence juvenile dispersion in territorial species (Watson, 1985; Hakkarainen et al., 2008). In birds, competition for good quality nesting sites in order to avoid predation evidences the scarcity of this resource (Martin and Martin, 2001; Aitken and Martin, 2012). Adults and their offspring can be food limited by the abundance and quality of food resources as well as by a mismatch with food peak (Dhondt, 2012). Food shortage, for instance, decreases clutch size and delays laying date in birds, impoverishes offspring condition and reduces adult survival (Brittingham and Temple, 1988; Simons and Martin, 1990; Davis et al., 2005; Robb et al., 2008; Derbyshire et al., 2015). Competition for limiting resources can therefore impact diverse demographic processes which may translate into changes in population size and distribution (Dhondt, 2012).

Intraspecific competition is widely recognized as a pervasive force regulating population-level processes (e.g. Calsbeek and Cox, 2010). However, the determinant role of interspecific competition in community organization and functioning is a long-lasting central idea in community ecology which has received as much support as criticism (Wiens, 1977; Connell, 1983; Schoener, 1983; Keddy, 1989). In one side, it has been argued that resources are seldom limiting so competition rarely occurs and its relative importance in community assembly is depreciated (Wiens, 1977). In the other side, interspecific competition is considered as a prominent evolutionary force which can result in the exclusion of the inferior competitors or reinforce rapid divergence in resource use allowing species coexistence. Interspecific competition is outlined as a transient force which has shaped communities in the past and no longer operates (Lack, 1944; Brown and Wilson, 1956). Thereby, its role in community organization cannot be empirically tested (Connell, 1980). However, many theoretical and empirical studies support that interspecific competition is indeed an ongoing and regular mechanism dictating community assembly and species coexistence (for an exhaustive review of interspecific competition in birds see Dhondt, 2012). Interspecific competition induces density-dependent effects on demographic parameters (Dhondt, 2010), affects patterns of abundance (Cooper et al., 2007), shifts temporal and spatial patterns of resource and habitat use (Ziv et al., 1993; Martin and Martin, 2001), and even induces rapid evolutionary change on morphological traits (Adams, 2004; Grant and Grant, 2006).

Conspecific and heterospecific attraction

In spite of the great controversy raised around competition, it has been distinguished as one of the main forces governing population and community dynamics. Nevertheless, in many cases, the spatial distribution of organisms is inconsistent with the assumption that competition is the fundamental biological driver structuring populations and communities. This was originally highlighted by the study of territorial bird species in which individuals should compete for limiting resources but often establish in clusters, leaving apparently suitable sites unoccupied (e.g. Lack, 1948). Therefore, co-occurring organisms not only incur in competitive costs but may also obtain mutual benefits because of their proximity (Stamps, 1988; Danchin et al., 2004). By settling close to a conspecific or heterospecific, individuals can reduce predation risk because of two non-mutually exclusive hypothesis: many individuals are scanning the surroundings for predators and time can be allocated to other activities like foraging (Many-eyes hypothesis, e.g. Lima, 1995); and increased density dilutes per capita predation risk (Hamilton, 1971). The presence of other organisms can be also interpreted as cues of site quality (Fletcher, 2007; Sebastián-González et al., 2010). The evaluation of site quality is a time-consuming activity (Slagsvold, 1986) which can delay or even reduce opportunities for the establishment in good habitats if they are already occupied by others (Schmidt et al., 2015). The use of "public information" may aid individual settlement decisions based on valuable information about how well other individuals performed in terms of reproductive success (Doligez et al., 2002; Danchin et al., 2004; Seppänen et al., 2007). Conspecific attraction may have benefits in the sexual function by facilitating mate evaluation and increasing the chance of encounter a potential mate (Höglund and Alatalo, 1995; Melles et al., 2009). However, it is expected that fitness benefits of attraction decrease with increased density, and competitive costs due to foraging exceed benefits of attraction beyond some density (Mönkkönen et al., 1990; Forsman et al., 2008). Future research should face the relative role of facilitation to better comprehend its evolutionary and ecological role in population and community regulation.

1.2 Species distribution: from global to local scale

The spatial distribution of the species is governed by direct and indirect effects of multiple environmental factors, which regulate their presence and abundance (MacArthur, 1984; Peterson et al., 2011). The ecological processes mediating the species-environment relationship act at different spatio-temporal scales, presumably in a hierarchical way (Pearson and Dawson, 2003). It is therefore of capital importance for the conservation of biodiversity to identify and asses the relative role of these factors and the scales at which they operate in a context of global change. It is a well-established premise that climate exerts a dominant role in determining the coarse features of species' natural distributions, supported by evidences from the fossil record (e.g. Davis and Shaw, 2001) and actual trends of extant species (Hughes, 2000; Walther et al., 2002; Chen et al., 2011). Indeed, the impact of climate in shaping species' geographic distribution was early noticed by ecologists (von Humboldt and Bonpland, 1807; de Candolle, 1855; Darwin, 1859) because climate imposes ecophysiological constraints to the distribution of organisms with profound effects on the species' macro-distribution dynamics over time (Kearney and Porter, 2009). Historical events like glaciation periods also condition present species' distributions at large scale (Svenning and Skov, 2007; Hortal et al., 2011). As the resolution is downscaled to regional and landscape levels, other environmental factors like topography and land-use cover become drivers of major importance, in areas where suitable climatic conditions are first satisfied (Pearson and Dawson, 2003; Pearson et al., 2004). Ultimately, biotic interactions and dispersal abilities of species are expected to control population performance at fine resolution, when physical conditions are less severe (Pulliam, 2000; Pearson and Dawson, 2003; Soberón, 2007).

Relying on the key role of climate in species' geographic ranges, models based solely on climate variables have been widely applied to explain macro-distributions and to forecast future trends of species under scenarios of climate change (e.g. Thomas et al., 2004; Jiménez-Valverde et al., 2011). However, global changes threatening biodiversity are not only about shifts on climate regimes. The increasing demands of food supply and housing for a growing human population of 7 billion people have caused devastating changes of land cover in many regions across the world (Millennium Ecosystem Assessment, 2005; Steffen et al., 2011). Habitats have been consequently modified, degraded or even destroyed which may alter the output of biotic interactions in natural communities (Auer and Martin, 2013; Boström-Einarsson et al., 2014). The process of global change also opens the door to the colonization and establishment of invasive species, which can eventually interfere in community functioning and completely alter the structure of communities (Grosholz et al., 2000; Sanders et al., 2003; Fukami et al., 2006). Many criticisms have been postulated against the validity of climatic models because they underestimate the potential impacts of biotic interactions -particularly interspecific competition- in the spatial distribution of species even at broad geographic scale (Hampe, 2004; Araújo and Luoto, 2007; Van der Putten et al., 2010). Certainly, models including the presence of co-occurring species better track the actual distribution of species (e.g. Araújo and Luoto, 2007; Heikkinen et al., 2007). However, ecologists require a solid comprehension on how biotic interactions shape communities in order to elucidate their scaling up effects.

1.3 The ecological niche concept

What are the environmental conditions that allow a species to exist in a given region? This key question intimately links the study of species' geographic distributions with the concept of ecological niche. Since the pioneering works of Grinnell (1917), Elton (1927) and Gause (1934), who first coined the niche concept, a large theoretical body was steadily developed until 1980s (for a review see Chase and Leibold, 2003). However, the disproportioned amount of niche studies also generated many ambiguities around the significance of the ecological niche and its application in community ecology, which likely contributed to the afterward recession and even opposition to the use of the niche concept (Chase and Leibold, 2003). Nowadays, most ecologists reclaim a unified and solid niche-based framework that, together with the recent implementation of powerful computational tools, shed light in a myriad of topics relating to comparative biology, functional ecology, evolutionary ecology and, mechanisms of biodiversity maintenance and species coexistence, among many others (Chase and Leibold, 2003; Araújo and Guisan, 2006; Blonder et al., 2014).

The modern concept of ecological niche was that proposed by George Evelyn Hutchinson in its memorable "Concluding remarks" (Hutchinson, 1957). Hutchinson understood the niche as a quantitative n-dimensional hypervolume constituted by the range of environmental features that enable a species to maintain a viable population indefinitely. Niche dimensions are independent axes with biological meaning for the species, typically physical variables, resource types, habitats and phenotypic traits as proxies of ecological requirements (Hutchinson, 1957; Schoener, 1989). However, Hutchinson differentiated two niche categories influenced by the prevailing view that interspecific competition was a major determinant in community organization (e.g. Darwin, 1859) and, in particular, by the results of Gause's experiments (Gause, 1934). These set of experiments demonstrated one of the most fundamental ideas in ecology, latter called the principle of "competitive exclusion" (Hardin, 1960), which states that two species exerting identical competitive effects one upon another cannot coexist in the same physical space and only the dominant competitor persists. Therefore, the fundamental niche is the n-dimensional space which can be potentially occupied by the species due primarily to its physiological and behavioral characteristics in the absence of competition. The presence of a dominant competitor prevents the species to fully exploit the environmental conditions of its fundamental niche so the portion of the fundamental niche actually occupied by the species under the effects of interspecific competition represents the realized niche.

Because, as stated above, niche theory is rooted in the view that interspecific competition dominates community assembly rules, it constitutes an attractive basis to elucidate one of the most controversial issues in ecology, the relative role of interspecific competition in species coexistence (Chase and Leibold, 2003). Based on the principle of competitive exclusion, niche theory implicitly assumes that niches of co-occurring species must differ to attain a stable coexistence (Hutchinson, 1957; Chesson, 1991) although a certain degree of similarity is permissible (May and MacArthur, 1972; Pianka, 1974). By measuring the extent of niche overlap under different population sizes of putative competitors, ecologists can explore the effects of density-dependent competition on the tolerable upper limit of niche overlap (Young, 2004). Furthermore, the conceptual niche framework allows to test whether competition between sympatric species is actually an ongoing process molding a given species assemblage. In the absence of a superior competitor, a species is released from competitive constrains and can exploit a wider range of resources, which increases its niche breadth ("Ecological release hypothesis" Robinson et al., 2000; Bolnick et al., 2010). Still, many relevant issues about the effects that biotic interactions cause on niche shifts need to be answered and integrated within the theoretical framework. Nevertheless, it is also essential to provide additional empirical support to theoretical models, particularly, those explaining how density-dependent mechanisms modulating niche variation regulate species coexistence.

1.4 Habitat selection: a density-dependent process for species coexistence

The spatial distribution patterns observed in nature are scale-dependent (Wiens, 1989). But at the end, individual choices made at local scale relying on environmental conditions and restrictions tied to species' life histories truly shape the temporal and spatial dynamics of populations (Rosenzweig, 1981; Doncaster, 2000; Morris, 2003*c*; Duckworth et al., 2015). In this context, theories of habitat selection incorporate a variety of ecological and evolutionary mechanisms modulating habitat occupation which provides an adequate basis to evaluate population regulation, community structure and even macroevolutionary patterns (Morris, 2003*c*). A habitat can be defined as "the spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets" (Morris, 2003*c*). This definition highlights several important aspects. First, individuals are capable of recognizing and discriminating among different habitats in the landscape (Fretwell and Lucas, 1969; Morris, 2003*a*). But habitat recognition is a scale-dependent process. For instance, no habitat selection occurs when scale is too small for appreciating habitat boundaries (Morris, 2003*a*). Perceived differences between habitats are necessarily linked to the expected fitness rewards and, because individuals distribute in habitats such as their fitness is maximized, the process of habitat selection represents an evolutionarily stable strategy (Fretwell and Lucas, 1969; Rosenzweig, 1981; Morris, 2003*c*). Finally, habitats must be defined at species and even population level because niche requirements are most likely to vary between species and, species' habitat preferences are susceptible to change with the relative abundance of habitats in the landscapes (Morris, 2003*c*).

Regulating mechanisms of density-dependence play a key role in the process of habitat selection (Morris, 1988). Assuming that individuals are free to distribute in the habitats according to their preferences ("the ideal free distribution model" Fretwell and Lucas, 1969), at low population density all individuals occupy their most preferred habitat where they attain the greatest fitness. As more individuals establish in the same preferred habitat, consumption of resources diminishes their availability and consequently, the expected fitness decays. Therefore, the perceived suitability of a given habitat decreases as a function of density (Fretwell and Lucas, 1969; Morris, 1988). When fitness expectations in the preferred habitat equal those of other habitats, then individuals shift their habitat choice. The resulting habitat distribution is such that the average fitness is equalized in all habitats. However, habitat selection might not be free of costs (Morris, 1992; Lin and Batzli, 2002). The social hierarchy position and differences in the ability to exploit resources or to access high quality sites may restrict individuals' habitat choice ("ideal despotic habitat selection") affecting population regulation in different manners (Morris, 2003*c*).

Habitat preferences may also depend upon the identity and abundance of other species within the community. Therefore, ecologists can use density-dependent habitat selection to infer the outcome of interspecific competition and its implications in community structure, as shown by the elegant experiments designed by Abramsky, Rosenzweig and collaborators (e.g. Abramsky et al., 1991, 1994). When two competing species with shared preference for a common habitat coexist, the inferior competitor is displaced toward less profitable habitats ("shared preference organization", Morris, 1988). Removal of the dominant competitor drastically alters the subordinate's habitat distribution, which redistributes preferentially on the shared and most favorable habitat whereas removal of the inferior competitor does not alter the habitat choice of the dominant species. But when the species have distinct habitat preferences, they segregate in their preferred habitats where they are more efficient consumers than the other ("distinct preferences organization" Morris, 1988). Removal of one competitor allows the other species to also use a less suitable habitat. In populations living at equilibrium, the competing species will be completely separated in different habitats and, even though competition is responsible for the habitat distribution, it cannot be detected except with removal experiments (Abramsky et al., 1991; Higgs and Fox, 1993; Martin and Martin, 2001; Munday et al., 2001). Unfortunately, such removal experiments cannot be accomplished in many species for technical or ethical limitations, particularly in the case of species at risk. Nonetheless, ecologists can still, and indeed should, use the habitat distribution patterns of different wild populations that fluctuate away from equilibrium to evaluate the role of interspecific competition in the dynamics of community assembly (Morris et al., 2000*a*,*b*).

1.5 Theory at the rescue. A necessary link between conservation and theory

As previously stated, the loss of biodiversity has its roots in a myriad of different processes, most of them caused by the widespread anthropogenic impacts. Human society demands effective conservation measures to guarantee the persistence of ecosystems and their species because they might provide invaluable services for human well-being, in most cases still undiscovered (Wilson, 1992). However, successful conservation policies cannot be implemented without a well-developed knowledge on the species biology and, most generally, on the mechanisms and processes operating in nature. The discipline of conservation biology has certainly brought outstanding advances about how human impacts exert direct or indirect effects at different organization levels, also revealing the underlying mechanisms that induce variation in demographic parameters (Primack, 2012). This has helped policy makers to design conservation programs for endangered species.

But most of these conservation measurements deal only with the management of physical or habitat features (very often understanding habitat as vegetation characteristics), either by restoring initial favorable conditions or by preserving unaltered regions, without bearing in mind the effects of biotic interactions (Soulé et al., 2005). Thus, when conservation ecologists fail to understand the capital role of biotic interactions in regulating entire communities, and this should also include interactions with human beings, conservation measurements might not achieve the desired results. The paradigmatic case of gray wolves (*Canis lupus*) in Yellowstone National Park (USA) constitutes an astonishing example illustrating the key role of biotic interactions in regulating communities and ecosystems. After the reintroduction of gray wolves in Yellowstone in 1995, the ecosystem dramatically changed because wolves prompt a trophic cascade (Ripple et al., 2014). Wolves did not only control the number of elks (*Cervus elaphus*), but most importantly, they modified elks' behavior which began to avoid most risky areas (Creel et al., 2005; Fortin et al., 2005). This reduced grazing pressure and allowed for the recovery of plant species like aspen (*Populus tremuloides*) or cottonwoods (*Populus spp.*) (Ripple and Beschta, 2012), which in turn had positive effects for many other taxa (Ripple et al., 2014). Thus, the functional role of species within communities may be unveiled through the outcome of their biotic interactions. Hence, empirical studies in wild communities are needed to improve and validate theories regarding mechanisms of species coexistence and biodiversity maintenance (Morris, 2003*a*). But this should be a feedback pathway. Conservation ecologists must firmly rely on theory to track and predict changes on populations and communities when humans alter ecosystem properties. In summary, theory and conservation should be closely linked to effectively aid in the protection of endangered populations and communities, making a particular effort to fully understand how biotic interactions, including those established with humans, affect population regulation and consequently population recovery.

1.6 Study species: the little bustard

The little bustard (*Tetrax tetrax*) is a medium-sized steppe bird of the *Otididae* family, which inhabits open landscapes, mainly natural steppes and agricultural croplands, across the Paleartic region (Cramp and Simmons, 1980). The species is currently endangered due to the declining trends of its main breeding populations and urgent conservation measures should be adopted to revert the negative population trends (e.g. de Juana, 2009; BirdLife International, 2012).

Distribution and abundance

Although it was once continuously distributed from Iberia to Central Asia, the dramatic declines in its population numbers and the range contraction suffered over the last 50 years caused the separation of its world distribution range in two clearly breeding regions (Del Hoyo et al., 1996). The western breeding populations are concentrated mainly in Spain, Portugal and France, with smaller populations in Italy and Morocco (BirdLife International, 2012). The species became extinct in at least 10 European countries by the mid-20th century (Goriup, 1994). In its eastern range, the little bustard breeds in southern Russia, north-west China, Kazakhstan, Kyrgyzstan, northern Iran, Turkey and Ukraine (BirdLife International, 2012).

Global population estimates indicate that the Iberian Peninsula holds more than half of the world breeding effectives (Spain: 41,482–86,195 breeding males; Portugal: 13,260–21,271 breeding males), followed by Russia (ca 10,000–20,000 individuals, although census may be inaccurate; Iñigo and Barov, 2010). The most important breeding regions in Spain are those of the Southern Plateau (Castilla-La Mancha and Madrid) and Extremadura, which comprise the 49% and 21% of the Spanish breeding population respectively (García de la Morena et al., 2006). Little bustard breeding populations also occur in the Ebro Valley (Cataluña and Aragon), Castilla y León and Andalucía. Residual breeding populations can be found in Murcia and Galicia (García de la Morena et al., 2006). The Spanish little bustards are sedentary or partially migratory (García de la Morena et al., 2015), which implies changes on the species' distribution during the winter period (García de la Morena et al., 2006). The most important breeding regions, the Southern Plateau and Extremadura, concentrate also the vast majority of the winter population (83.3%; García de la Morena et al., 2006). Wintering birds are moderately abundant in the Ebro Valley while the breeding nucleus of the northern plateau almost disappears during winter, probably due to harsher climatic conditions (García de la Morena et al., 2006).

Biological features

The little bustard is a polygynous, sexually dimorphic bird (Cramp and Simmons, 1980). In the Iberian Peninsula, the breeding season begins in early April when winter flocks split up and little bustards arrive to their breeding grounds (Cramp and Simmons, 1980; García de la Morena et al., 2015). The mating system is described as an exploded lek in which males establish breeding territories in a spatially aggregated way (Jiguet et al., 2000). The species' courtship incorporates multiple components differentially involved in the intrasexual and intersexual function. Little bustard males actively advertise and defend territories through territorial calls and chasing behaviors against intruders (Jiguet and Bretagnolle, 2001; Morales et al., 2014). Other behavioral and phenotypic traits serve as cues for female mate choice. Male attractiveness is related with the symmetry of the male nuptial plumage, which consists basically in a complex black and white neck collar, as well as with the rate of wing-flash and jump display (Jiguet and Bretagnolle, 2006, 2014). Although females in lekking species attend leks with the only purpose of mating (Höglund and Alatalo, 1995), it has been largely questioned whether territory quality in exploded lek species plays a critical role affecting females' decision on mate choice (Jiguet et al., 2002; Traba et al., 2008; Morales et al., 2014). Territories of little bustard males are likely to contain resources potentially used by females, like nest sites and arthropods for rearing chicks (Traba et al., 2008; Morales et al., 2013). However, territory quality *per se* does not increase female attraction (Jiguet et al., 2002).

The nesting period occurs during May and June (Cramp and Simmons, 1980). Females lay between 1–4 eggs in the ground and, as a lekking species, males do not provide parental care to their offspring in any stage of the rearing period (Cramp and Simmons, 1980; Höglund and Alatalo, 1995). After hatching, females and their offspring abandon their nesting site and move toward different patches in the search of energetic food resources for chicks (Lapiedra et al., 2011), which feed basically in arthropods (Jiguet, 2002). Two different movement patterns of females with offspring have been described in the species and they correlate with brood survival (Lapiedra et al., 2011). The sedentary pattern exhibited by early broods implies stable rearing areas, whereas late broods show a wandering pattern in which the longer movements increase the rearing area size. The easier access to good quality habitats by early broods might be the process underlying their higher survival (Lapiedra et al., 2011). In spite of the recent insights, the ecology of little bustard females is an issue still poorly understood mainly because of females' elusive behavior. However, such studies are critical to aid in the conservation of the species (Morales et al., 2005*a*).

At the end of the breeding season (June-July), males, females and juveniles progressively congregate in large postbreeding flocks (Cramp and Simmons, 1980; García de la Morena et al., 2015). In Iberia, some populations stay in their breeding grounds to spend the winter but most of them migrate medium or long distances until reaching their overwintering sites (García de la Morena et al., 2015). Movement phenology is highly variable between populations but displacements may take place from May until October (García de la Morena et al., 2015). Iberian wintering grounds also host little bustards from the last migratory population of western France, which embark in a long-distance journey of 880 km on average (Villers et al., 2010). During winter, little bustards often form mixed flocks with the pin-tailed sandgrouse (*Pterocles alchata*), specially under harsher climatic conditions (Martín et al., 2010).

Habitat selection

There is a well-established research body regarding the habitat requirements of breeding little bustard males in agricultural landscapes and extensive pasturelands of Western Europe. The habitat selection processes have been studied from the microhabitat to landscape and regional scale (Martínez, 1994; Suárez-Seoane et al., 2002; Morales et al., 2008; Delgado et al., 2010). Males set up their breeding territories preferentially in fields of semi-permanent vegetation, namely fallows of different ages, low natural vegetation and pastures (Martínez, 1994; Salamolard and Moreau, 1999; Morales et al., 2005*b*; Faria et al., 2012). Leguminous crops are likewise selected by breeding males when available in the landscape (Wolff et al., 2001). At microhabitat scale, males choose patches of low vegetation height which ensure the conspicuousness necessary for the sexual display and a greater availability of food resources (Morales et al., 2008; Traba et al., 2008). Cereal and ploughed land are often avoided by breeding males because they do not apparently fulfill their ecological requirements (Morales et al., 2005*b*, 2008). When cereals are too high, they do not allow males to successfully perform their sexual display, whereas the absence of vegetation in ploughed lands likely increases predation risk. Additionally, food resources may be lower in these two habitats than in more natural ones (Traba et al., 2015). The processes of habitat selection and territory establishment of breeding males seem to be further density-dependent (Delgado et al., 2010; Morales et al., 2014).

In contrast with the ample knowledge of male habitat preferences, habitat selection by females is less explored due to their cryptic and secretive behavior. Breeding females trade off the need for shelter and the access to food resources by occupying patches with a greater vegetation cover which provide concealment from predators but lower availability of food than patches used by males (Morales et al., 2008; Silva et al., 2014). At landscape level, habitat preferences of nesting females vary with landscape configuration. In extensive systems, old and young fallows are selected in farmlands of Central Spain (Morales et al., 2013), as well as extensively grazed pastures in Southern Portugal (Silva et al., 2010*a*; Faria et al., 2012). In intensively managed systems of Catalonia and France, females often nest in cereals and multi-annual crops respectively (Lapiedra et al., 2011; Bretagnolle et al., 2011). Females with offspring move then to patches with natural vegetation which may offer high supply of good quality food for chicks (Lapiedra et al., 2011).

In winter, the establishment of flocking little bustards is dictated by habitat requirements but also by climatic constraints (Suárez-Seoane et al., 2008). Young fallows, stubbles and grassy vegetation are the most preferred habitats for wintering little bustards (Silva et al., 2004). Winter is a critical period for most bird species because individuals confront harsher conditions like food depletion or extreme climatic conditions which may reduce survival (Watson, 1985; Hakkarainen et al., 2008; Duriez et al., 2012). The vegetation structure of the preferred winter habitats guarantees refugee and may also contain plant species important in adults' diet, mainly *Cruciferae* and *Leguminoseae* (Cramp and Simmons, 1980). However, the analysis of winter habitat selection comes mainly from populations of Southern Portugal so this topic deserves further studies in different regions within the species' winter distribution.

Conservation status and current threats

The world conservation status of the little bustard is certainly worrisome. Since the 19th century, the species has undergone dramatic population declines (Goriup, 1994). It became extinct in at least 10 European countries and its world geographic range has been seriously reduced (Goriup, 1994; BirdLife International, 2012). The species is nowadays included in the IUCN's red list as "near-threatened" worldwide (BirdLife International, 2012), and defined as "vulnerable" in the European context (BirdLife International, 2004). Unfortunately, the declining trend is alarmingly ongoing, with extremely low female productivity in many regions and a sex ratio biased toward males in many populations (Morales et al., 2008, 2015). Several of the most important breeding populations in Extremadura experienced a dramatic 75% decline of census estimates in one decade (de Juana, 2009). But perhaps, the most worrisome trend is that of western France breeding populations which declined a 92% between 1980 and 2004 (Bretagnolle and Inchausti, 2005).

The major threat acknowledged to adversely impact the little bustard is agricultural intensification (Jolivet and Bretagnolle, 2002; Morales et al., 2015). The intensification of agrarian practices backs to mid-20th century in Europe and has caused two simultaneous process of land use change in Spanish cereal farmlands: the intensification of most productive regions and the abandonment of less productive areas (Oñate, 2005). Both of them imply a loss of the most critical habitats for breeding little bustards, i.e. fallows and natural vegetation. The intensification of agricultural practices involves, for instance, increased field size, landscape homogenization and, the use of chemicals to enhance productivity output (Oñate, 2005). These processes may affect little bustards at different levels. The degradation and disappearance of minor agrarian substrates key to foraging and breeding like fallows may compromise reproduction (Morales et al., 2013). The use of chemical products may increase chick mortality by reducing the availability of arthropods (Jiguet, 2002; Bretagnolle et al., 2011). Special conservation efforts should be made to increase female and chick survival, which are fundamental demographic parameters for the species persistence (Morales et al., 2005*a*). The application of agri-environmental schemes in experimental fields excluding mowing and increasing the proportion of good quality habitats have successfully enhanced female productivity in western France (Bretagnolle et al., 2011).

Several other factors may also impact little bustard populations. Spain has suffered a recent and disproportionate process of urbanization and development of infrastructure like high-speed railways, which have contributed to the decrease in the surface of suitable agricultural landscapes for little bustards. In addition, this species tends to avoid the proximity of infrastructures, which may leave suitable habitats unoccupied (Devoucoux, 2014). Collision with power lines is another source of mortality (Silva et al., 2010*b*). As for most extant species, climate change could drive variations in little bustard's distribution range and even threat the persistence of Iberian populations. Precipitations during the breeding season and the previous winter and autumn months positively relate with populations size (Delgado et al., 2009). But forecasts of climate change in Spain predict a decrease in winter and autumn precipitations (Moreno, 2005), which may affect individuals' survival (Delgado and Moreira, 2010). Although illegal hunting does not suppose a significant threat to little bustard populations in the present, the species coexists in the same landscapes with one of the main game species in Spanish hunting estates, the red-legged partridge (*Alectoris rufa*). Indirect effects of hunting have already being detected, like relocation of little bustards in free-disturbance areas (Casas et al., 2009). However, effects of other human activities on the little bustard are unknown but probably relevant due to the increase of human outdoor recreation in farmland landscapes.

As previously mentioned, habitat modification may alter biotic interaction outcomes and affect population regulation (Morris, 2003*c*; Boström-Einarsson et al., 2014). Despite the considerable changes in agricultural landscapes and the decline trend of little bustard populations, no information about how biotic interactions modulate little bustard distribution is available. Among steppe birds, the great bustard (*Otis tarda*) is perhaps the species most prone to interfere with the little bustard due to their phylogenetic proximity and similar ecological requirements (Del Hoyo et al., 1996; Del Hoyo and Collar, 2014). Both species coexist in many regions across their distribution range and are linked to extensive cereal farmlands (e.g. Suárez-Seoane et al., 2002). The species' breeding phenologies also overlap (Cramp and Simmons, 1980) and, although the great bustard's habitat use is not as selective as in little bustard males, both species often occupy the same agrarian habitats like fallows (Lane et al., 2001; Morales et al., 2005*b*). The presence of conspecific has been recognized as a major factor determining great bustard's distribution and abundance (Lane et al., 2001; Alonso et al., 2004) due to its pure lek mating system (Cramp and Simmons, 1980). In addition, little and great bustard females nest in fallows and their chicks feed mainly in arthropods (Jiguet, 2002; Magaña et al., 2010; Bravo et al., 2012; Morales et al., 2013). The great bustard also suffered important population declines in the past, mainly due to hunting (Alonso and Alonso, 1996) but in the last years their Iberian populations are in steady recover, most probably due to targeted conservation measurements (Palacín and Alonso, 2008; Alonso and Palacín, 2010). The current opposite trends exhibited by these species in Iberia may be advertising the existence of interspecific competition between them. Changes caused by processes of agricultural intensification may reduce shared resources and consequently induce or intensify competitive interactions which may negatively impact their populations.

1.7 Thesis outline

Because of the relevant role that biotic interactions plays on multiple processes regulating populations and community dynamics, this thesis pretends to gain new insights in the effects that intra- and interspecific interactions cause on the ecology of the little bustard, with a particular emphasis in the potential relationship established with the great bustard.

As stated before, the outcome of interspecific interactions may change due to habitat modification (e.g. Boström-Einarsson et al., 2014) and, competition can intensify due resource shortage (e.g. Strubbe and Matthysen, 2009). In cereal farmlands, the degradation of agrarian habitats may limit critical resources, inducing interspecific competition. However, no studies have addressed the existence of interspecific competition between the little and great bustards, despite the negative effects that competition may exert on their populations. Therefore, it is necessary to explore whether the little and great bustard compete when co-occurring in order to design integrated conservation schemes favoring these two emblematic steppe birds. Thus, the first three chapters of this thesis focus on determining whether the little and great bustard competitively interact and its implication for conservation. Specifically, *CHAPTER 2* and *CHAPTER 3* evaluate for first time the existence of competition between these bustard species using two different methodological approaches. The ample habitat selection knowledge provides the necessary background to explore in detail the existence of interspecific competition. Based on the ecological niche framework, *CHAPTER 2* explores whether the presence and density of great bustard induce shifts in the little bustard realized niche and if niche variation may be due to competitive processes. This study uses a novel multidimensional niche-based methodology to evaluate the response of three niche components often affected by competition: overlap, breadth and position. Given that habitat partitioning is one of the most relevant mechanisms mediating in the coexistence of competing species (Rosenzweig, 1981; Morris, 2003*c*), habitat data at landscape level are considered as ecological niche dimensions.

Habitat selection is widely recognized as a density-dependent process (Fretwell and Lucas, 1969) with relevant implications for the stable coexistence of competing species (Rosenzweig, 1981; Morris, 2003*c*). The habitat distribution analysis of wild populations departing from equilibrium may unveil the otherwise ”ghostly”interspecific competition (Morris, 1999, 2009). Although intraspecific density-dependent effects are involved in territory establishment and defense in the little bustard (Delgado et al., 2010; Morales et al., 2014) and, conspecific attraction is also a major factor driving great bustard habitat distribution (Alonso et al., 2004), interspecific density-dependent effects in the habitat distribution of these bustard species have not yet been explored. Thus, *CHAPTER 3* uses the isodar theory (Morris, 1988) to evaluate the density-dependent effects of putative competitors in their habitat distribution. This methodology allows to identify in which agrarian habitats competition operates and how the species assembly is structured, which may have important implications for the conservation of these species.

Populations of both species are still threatened in many regions, and thereby, conservation schemes need to be further enhanced. But recommendations to reinforce population recovery are exclusively focused on the ecological requirements of single species, without taking into account the collateral effects that may cause on other coexisting species. *CHAPTER 4* aims to provide valuable guidelines that favor the simultaneous protection of each species’ ecological requirements at landscape scale. Thus, this paper characterizes the environmental features of local areas suitable for being used by both species and areas only favorable for one of them. Their relative adequacy for each species is then compared and conservation measurements proposed.

However, organisms may also obtain benefits by establishing close to others. Attraction to conspecifics may have relevant consequences in population dynamics (Pulliam, 2000; Alonso et al., 2004), and hence, it should be appropriately considered in conservation policies. Because little bustard male territories may harbor resources used by females (Traba et al., 2008; Morales et al., 2013), *CHAPTER 5* studies the spatial distribution of females with offspring in relation to male breeding sites in order to determine whether females may benefit by an aggregated distribution to male displaying sites. The paper also investigates the habitat use of females with offspring in extensive cereal farmlands.

Interactions between wild populations and human beings occur very often in human-originated landscapes like cereal farmlands. Although the species inhabiting these landscapes should be tolerant to human presence, human activity may cause negative effects on wild populations (e.g. Strasser and Heath, 2013). *CHAPTER 6* evaluates the effects of human presence and different activities performed in agricultural landscapes on the behavior and physiological stress levels of wintering little bustards in an extensive cereal farmland. This study puts a major focus on the impacts of hunting activity given its socio-economical relevance but also explores the effects of other recreational activities that are increasingly common in agricultural regions. Levels of physiological stress are measured for first time in the little bustard, using fecal corticosterone metabolites because of its non-invasive nature.

Finally, the main findings of this thesis are discussed in *CHAPTER 7* and recommendations for future researches suggested.

Chapter 2

First evidence of interspecific competition between two endangered steppe birds: little bustard habitat niche shifts in the presence of great bustard.

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Abstract

Interspecific competition has been long acknowledged as a dominant force in animal communities that induces shifts in species' niches in ecological and evolutionary time. The application of new powerful computational tools in empirical studies are likely to improve the theoretical niche framework regarding the effects of competition between coexisting species. Here, we aim to evaluate the potential existence of interspecific competition between the little (*Tetrax tetrax*) and great bustards (*Otis tarda*) using a multidimensional approach to build habitat niches from habitat distribution data. We explored whether the tolerable degree of niche overlap between the species was a density-dependent function of interspecific competition. We then looked for evidences of ecological release by comparing measures of niche breadth and position of the little bustard between allopatric and sympatric situations. Furthermore, we evaluated whether niche shifts could be interspecific density-dependent. Our results suggest that variation in little bustard niche may be the outcome of interspecific competition with great bustard. The habitat niches of these bustard species moderately overlap when co-occurring and, contrary to expectations, niche overlap increased with great bustard density. We also documented widened niche breadth of the little bustard in the presence of great bustard. The displacement from habitats where competition occurs may force little bustards to incorporate low profitable habitats into their habitat choice, thus increasing niche breadth. In addition, we detected that great bustard presence displaced little bustard niche position toward increased use of one of the species' primary habitat, whereas intraspecific competition moved niche position toward a greater use of an unfavorable habitat. Our findings also underline that niche dimension choice is a crucial step in the analysis of ecological niches, which requires detailed knowledge about the species' ecology. The use of powerful computational tools like kernel density estimators to obtain multidimensional niches should bring novel insights on how species' ecological niches behave under the effects of interspecific competition in ecological communities.

2.1 Introduction

The role of interspecific competition in structuring ecological communities and evolutionary diversification is a crucial long-standing debate among ecologists which can be addressed within the theoretical framework of ecological niche (Pianka, 1974; Chesson, 1991; Chase and Leibold, 2003; Bolnick et al., 2010). Competition theory postulates that species must differ in their ecological niches in order to attain a stable coexistence (Chesson, 1991; Leibold, 1995). Otherwise, ecologically similar species engage in competition and the species with superior abilities eventually excludes the inferior competitor (Gause, 1934; Human and Gordon, 1996). One of the most prominent ecological mechanisms by which coexisting species resolve their competition is habitat partitioning (Rosenzweig, 1981; Morris, 2003*c*). The process of habitat selection consists of adaptive behaviors by which organisms distribute in habitats according to their preferences on physical conditions, the type of resource consumed and the species' predators (Morris, 2003*c*). These environmental factors are typically considered as independent niche dimensions (Schoener, 1989), even though they are likely to depend on one another. Consequently, habitats can be also visualized as conforming dimensions of hypervolume niches (*sensu* Hutchinson, 1957).

Most theoretical models of habitat selection assume that coexisting species spatially segregate in different habitats in order to avoid the negative cost of interspecific competition (Rosenzweig, 1981; Morris, 1988). This means that species' habitat niches should not overlap when competing species coexist in a stable manner. Certainly, low niche overlap has been documented between coexisting species currently competing (Smith et al., 1978; Young, 2004). However, low values of niche overlap may also indicate evolutionary divergence in the species habitat preferences due to past competition (Connell, 1980). In this case, interspecific competition no longer shapes the habitat distribution of coexisting species, which obeys only to a differential habitat selection. Therefore, the degree of niche overlap does not by itself allow to disentangle whether interspecific competition is currently operating between coexisting species and additional evidences of niche variation are required.

The ecological release from a competitor is also expected to cause niche expansion because new resources previously inaccessible due to competitive constraints can be exploited (Schoener, 1989; Bolnick et al., 2010). Hence, a species living in allopatry may also use habitats which otherwise are only exploited by its competitor (Morris, 1988), consequently expanding its ecological niche. In addition, competitive release may generate displacements of niche position (Adams, 2004), which is often described as the optimum or average value of the species niche (Williams et al., 2007; Barnagaud et al., 2012).

However, it has been theoretically demonstrated that competing species do not necessarily segregate in different habitats when co-occurring (e.g. Morris, 1999, 2009). Rather, the habitat selection pattern balances intra- and interspecific competitive costs on fitness, so competing species can simultaneously use a shared habitat depending upon both species density. Therefore, ecological release from interspecific competition should be a density-dependent process in which niche shifts depend on the intensity of competition (Pianka, 1974; Young, 2004). Certainly, niche segregation is not necessarily absolute and a permissible degree of niche overlap is more likely to occur in nature (May and MacArthur, 1972). In accordance with the "niche overlap hypothesis", this tolerable upper limit of niche overlap between competing species varies inversely with the intensity of interspecific competition (Pianka, 1974). Habitat niche breadth should also decrease with increased density of the competitor due to lower proportional use of the shared habitat (Morris, 2009), although empirical evidence is still lacking. Similarly, movements of niche position should mimic density-dependent adjustments of habitat distribution caused by interspecific competition. Despite the relevant role of habitat selection in regulating community structure (Morris, 1988), little is known about the density-dependent effects of interspecific competition on the species' habitat niche variations (Young, 2004; Benítez-López et al., 2014).

Methods to answer ecological niche inquiries are diverse and have notably improved to overcome significant theoretical and computational issues (Pianka, 1974; Chase and Leibold, 2003; Mouillot et al., 2005; Kearney and Porter, 2009; Geange et al., 2011; Blonder et al., 2014). In particular, the recent development and application of kernel density estimators in the study of ecological niches should bring relevant advances in community and population ecology because they are framed within the multidimensional *Hutchinsonian* niche concept (Mouillot et al., 2005; Geange et al., 2011; Traba et al., 2015). Most community assembly studies deal with the idea that coexisting species segregate along one crucial niche dimension to avoid competitive exclusion (e.g. Kimura and Chiba, 2010; Stuart et al., 2014). However, the niche concept *sensu* Hutchinson (1957) involves a complex set of many different environmental factors conditioning species' presence and abundance. Consequently, it seems more realistic to consider that multiple interacting niche dimensions modulate the process of species coexistence in communities with intricate biotic interaction networks. Therefore, quantification of niche hyperspace may be better understood from a multidimensional niche perspective, as long as niche dimensions are biologically meaningful and non-redundant for the species (Blonder et al., 2014). However, not all possible combinations of niche dimension values are feasible in nature or even comprised within species' fundamental or realized niches. This fact creates complex hypervolumen geometries filled with holes which imposes serious difficulties to the accurate calculation of species' niches (Blonder et al., 2014). Kernel density estimators can easily incorporate complex geometries when estimating ecological niches due to their high flexibility (Mouillot et al., 2005; Geange et al., 2011). However, studies using multidimensional niche approaches that investigate the role of interspecific competition in structuring animal communities are still scarce.

The little bustard (*Tetrax tetrax*) is a medium sized steppe bird which inhabits cereal farmlands in Western Europe (Cramp and Simmons, 1980). This species is currently classified as "near threatened"due to the severe population declines suffered during decades in most of its geographic range (Goriup, 1994) and still maintains negative population trends (de Juana, 2009). Agricultural intensification has been identified as the major threat to little bustard populations, and particularly, the loss of critical non-productive agrarian habitats (Jolivet and Bretagnolle, 2002; Morales et al., 2005*b*). Processes of habitat change may be associated with the intensification of competitive interactions (e.g. Auer and Martin, 2013), but no studies have yet explored the existence of such interspecific interactions between the little bustard and other species within the overall threatened steppe bird community. The great bustard (*Otis tarda*) is an ecologically and phylogenetically close related species which very often co-occurs with the little bustard in many regions across their distribution. During the breeding season, these bustard species show similarities in their habitat selection and spatial distribution patterns. The little bustard is an exploded lek species in which males establishes loosely aggregated territories (Jiguet et al., 2000) preferentially in semi-permanent agrarian habitats like short- and long-term fallows as well as legume crops (Wolff et al., 2001; Morales et al., 2005*b*; Delgado et al., 2010). The great bustard does not show marked preferences among the main agrarian habitats (Morales et al., 2006). This species uses habitats depending upon their relative availability and conspecific attraction seems a major force determining their distribution (Lane et al., 2001; Alonso et al., 2004; López-Jamar et al., 2011; Tarjuelo et al., 2014). Therefore, the simultaneous use of agrarian habitats during the breeding season may induce competition between the species, which may be intensified due to changes in the proportion of habitats within the landscape caused by agricultural intensification.

Here we evaluate the existence of interspecific competition between the little and great bustards on the basis of ecological niche theory. By using a multidimensional approach, we first explore the degree of habitat niche overlap between the species in sympatry and its potential relationship with great bustard density. Our expectation, based on "the niche overlap hypothesis" (Pianka, 1974), is that low values of niche overlap between the species would indicate that interspecific competition has occurred. Furthermore, we expect a negative relationship between niche overlap and great bustard density if the species competitively interact because increased interspecific competition should cause a progressively segregation of the species habitat niches. We then estimate whether little bustard suffers ecological release by measuring changes on niche breadth and position between situations of allopatry and sympatry. Greater niche breadth is expected in the absence of the great bustard due to the removal of competitive restrictions to habitat use. In addition, we evaluate whether interspecific competition induces density-dependent variation in niche breadth and position, controlling for intraspecific competitive effects. We expect narrower little bustard niche breadth at higher great bustard density due to reduced use of habitats also occupied by great bustards. Contrarily, increased intraspecific competition should expand the species' habitat niche because of diversified resource use (Svanbäck and Bolnick, 2007).

2.2 Methods

Study sites

This study was conducted in 9 different sites across Spain between 2006 and 2012. Seven sites were located in central Spain: Campo Real (40°19′N, 3°18′W; study years: 2010-2012); Daganzo (40°34′N, 3°27′W; study year: 2010); Valdetorres (40°40′N, 3°25′W; study years: 2010-2011); Camarma (40°32′N, 3°22′W; study year: 2006); La Solana (38°55′N, 3°13′W; study years: 2010-2011); Calatrava north (38°56′N, 3°53′W; study years: 2007-2011); Calatrava south (38°52′N, 3°57′W; study years: 2007-2011). The remaining study sites were located in the northeast of Spain: Bellmunt (41°47′N, 0°57′E; study years: 2008-2011) and Belianes (41°35′N, 0°59′E; study years: 2008, 2010-2011). All study sites are under Mediterranean climate and dominated by a mosaic landscape of different agrarian substrates typical of extensive cereal farmlands with a two-year rotation system. Dry cereals (mainly wheat *Triticum spp.*, barley *Hordeum vulgare* and oats *Avena spp.*) and ploughed fields represent the main agrarian substrates (ca. 50% of the surface), followed by fallow fields of different ages. Legume crops (*Vicia spp.*, *Pisum sativum* or *Lathyrus sativus*) are also cultivated although not in all the study sites or years. Other minor land-uses are vineyards *Vitis vinifera*, olive groves *Olea europaea*, almond orchards *Prunus dulcis*, pastures and urbanized areas. The little bustard occupies all study sites whereas the great bustard is absent in La Solana, Bellmunt and Belianes. This fact allows for the evaluation of differences in niche breadth and position between situations of allopatry and sympatry.

Bustard and habitat data

Little and great bustard censuses were carried out between April and May, which encompasses both species' reproductive seasons (Cramp and Simmons, 1980). Surveys were conducted by car along routes using the net of roads and tracks available in each study site. The high density and spatial configuration of roads and tracks ensured accurate censuses of both bustard species. Stops were routinely made at every 500 m to scan the surroundings using binoculars and spotting scope, mapping all birds detected. Surveys were made during the first three hours after sunrise and the last three hours before sunset when birds are most active (Cramp and Simmons, 1980). The courtship behavior of little bustard males incorporates ground calls and jumps, which allow them to be also detected acoustically and accurately located. We did not considered little bustard female observations in the analysis since their secretive behavior hinders their detection and leads to an underestimation of their numbers. Great bustards are often found aggregated together in arenas given their lek mating system (Morales and Martín, 2002; Alonso et al., 2004), and the number of individuals of both sexes in each flock was also determined.

Habitat availability was estimated from land-use maps elaborated from field surveys immediately after bird censuses in each study site and year. Each field was assigned to one of the following seven habitat types: 1) cereal; 2) ploughed land; 3) leguminous crop; 4) one-year fallow (hereafter referred to as young fallow); 5) fallow older than two years and short shrub (hereafter referred to as natural vegetation); 6) dry woody cultures, including olive groves, vineyards and almond tree orchards; 7) Others, which encompasses minority substrates avoided by the species like urban substrate, pastures and forest.

Measures of habitat niche shifts and overlap

We generated the multidimensional niche hyperspace of these bustard species using information on habitat cover. Study sites are often arbitrarily delimited and areas falling outside the local distribution of the species may be included within the study site boundaries. This fact can bias measurements of habitat composition or estimates of species density (Aebischer et al., 1993). In order to avoid this, we first delimited the area used by both species in each study site and year using the minimum convex polygon (MCP) created with all bustard observations. A set of random points equal to the sum of little and great bustard individuals was generated inside each MCP. Habitat composition was then determined inside a buffer of 100 m around each random or bustard observation point and the proportion of each habitat type extracted. We selected a radius of 100 m based on previous knowledge on little bustard home range areas (Delgado et al., 2010). Next, we performed a principal component analysis (PCA) with the habitat variables in order to summarize habitat variation within and across all study sites and to attain ecological gradients which could be interpreted as niche dimensions for the species (Morales et al., 2008; Benítez-López et al., 2014; Traba et al., 2015). The PCA was built using the random and bustard points of all study sites and years (see Traba et al., 2015, for a similar approach). PC axes with eigenvalues > 1 and ecological significance as relevant habitats for the species were considered as habitat niche dimensions.

The species' multidimensional habitat niches were defined using a non-parametric kernel density estimator procedure (KDE; Mouillot et al., 2005). KDEs provide smooth functions that do not assume normal distribution for the niche dimensions (Mouillot et al., 2005; Geange et al., 2011). We built niche hyperspaces defined by two-dimensional KDEs for possible combination of pairs of PC axes with ecological meaning for the species instead of the one-dimensional KDEs used in other studies (e.g. Benítez-López et al., 2014; Traba et al., 2015). Our approach might better reflect the process of individual habitat choice than single-variable niche spaces. We fixed a minimum of 5 bird observations per dimension to estimate KDEs (Mouillot et al., 2005). All KDEs were weighted by the number of individuals in the observation. For the subsequent calculation of niche measurements (overlap, breadth and position), we considered two regions within the hyperspace generated by KDEs: the entire niche space and the core area of maximum utilization. The entire niche space was defined as the 95% volume of KDE with the highest probability. We left a 5% KDE region outside the entire niche space in order to avoid the influence of outlier observations. The core area of maximum utilization encompasses the 50% KDE volume of highest probability and it may represent the most conservative strategies of habitat use of each species (Worton, 1989; Cimino and Lovari, 2003).

We calculated niche overlap in the 9 study sites and years (Campo Real 2010-2012; Valdetorres 2010-2011; Daganzo 2010; Camarma 2006; Calatrava North 2008-2009) where little and great bustard co-occurred and the number of bird observations allowed for KDE calculation (see explanations above). The calculation of niche overlap required that the two-dimensional habitat niches of little and great bustard were estimated inside a common niche space and the probability density function evaluated in the same points in order to be comparable. Therefore, we previously defined the coordinates of the two-dimensional niche in which the probability density functions would be evaluated. Because of the volume under the two-dimensional KDE curve sums 1, niche overlap was estimated as the volume under the curve defined with the minimum probability value of each species' KDE in each evaluation coordinate. Zero values indicate no overlap whereas values of 1 reflect complete niche overlap. Niche overlap was determined in the entire niche space as well as in the niche core area.

Little bustard niche breadth was calculated as the number of cells of the two-dimensional KDE falling within the region delimiting the entire niche space and the core area of maximum utilization. Niche position was estimated as the coordinates of niche dimensions which attained the maximum probability value of the kernel density function. Niche breadth and position for the little bustard was calculated for all the study sites and years (n=26). Again, we predefined the coordinates of the two PC dimensions where the probability density function of the little bustard would be evaluated in order to get comparable values of niche breadth and position for the different years-site niche hyperspaces.

Statistical analysis

The effect of great bustard density in the degree of niche overlap between the species was analyzed using generalized linear mixed models (GLMMs) with Gaussian error distribution. The value of niche overlap was the response variable and great bustard density was used as the explanatory one. We included study site as random factor in order to account for potential dependent effects between regions surveyed on several years. We did not include in the GLMMs little bustard density (i.e. intraspecific competition) due to sample size. We evaluated interspecific density-dependent effects in the degree of niche overlap for the entire niche space and for the core area of maximum use. In each case we considered two possible models, one in which great bustard density was left untransformed and other with the density of this species log-transformed, since preliminary explorations pointed out to non-linear relationships between niche overlap and the presumed competitor density. When any relationship was significant, results for the untransformed explanatory variable are shown.

We used GLMMs with Gaussian error distribution to evaluate shifts on little bustard niche comparing first situations of sympatry and allopatry. In order to test the hypothesis of niche release, niche breadth and niche position were used as the response variables and the presence/absence of great bustard was considered as the explanatory variable. Again, we included study site as a random factor in order to control the potential dependency within data surveyed in a given study region. We further analyzed whether intra- and interspecific density-dependent effects caused niche variation, in order to evaluate the existence of potential density-dependent competition using GLMMs. Here, the explanatory variables were the density of little and great bustards inside the MCP. Models of niche breadth were built for both the entire niche space and the core area of maximum utilization. This was unnecessary in the case of niche position because the value of maximum probability does not change with the KDE volume selected.

Observational bird data and land-use maps were processed with ArcGis 9.3 (ESRI, 2007). All statistical analyses and spatial calculations were done with R software v3.1.1 (R Development Core Team, 2014). KDE were built using the "ks" R package (Duong, 2014).

2.3 Results

The lowest little bustard density was found in Camarma (0.50 males/km^2) whereas Bellmunt shown the highest density (7.66 males/km^2). Great bustard density varied more than little bustard density from 0.38 birds/km^2 in Calatrava South to 20.85 birds/km^2 in Valdetorres (Table 2.1).

Habitat niche dimensions

The first three PCA habitat axes retained 80% of the variance. The first two PCA axes reflected a gradient of agrarian intensification, being the

Table 2.1: Mean (± SD) per region density (number of individuals per km^2) of little and great bustards inside the MCP.

Site	Little bustard density	Great bustard density
Campo Real	5.60 ± 0.65	7.48 ± 1.22
Valdetorres	2.56 ± 0.99	20.85 ± 10.76
Daganzo	2.13	5.98
Camarma	0.50	3.39
Calatrava North	3.79 ± 1.23	3.93 ± 4.02
Calatrava South	4.59 ± 0.45	0.38 ± 0.32
La Solana	2.70 ± 0.97	0
Bellmunt	7.66 ± 1.96	0
Belianes	6.06 ± 0.97	0

first axis (PC1) positively correlated with cereal cover, while the second axis (PC2) was positively correlated with the cover of ploughed fields but negatively correlated with the surface of young fallows (Table 2.2). The third axis (PC3) was mainly influenced by the cover of natural vegetation and it can be interpreted as an index of semi-permanent habitat availability (Table 2.2). These three PCA axes reflected the most important agrarian habitats used by the species during the breeding season. Therefore, we built two KDE combining PC1-PC2 and PC1-PC3 to evaluate niche overlap, breadth and position in these three niche dimensions.

Table 2.2: Results of the PCA to summarize original habitat variables. Only PCA axes considered as habitat niche dimensions are displayed.

	PC1	PC2	PC3
Cereal	0.905	-0.006	0.171
Young fallow	-0.280	-0.715	0.468
Natural vegetation	-0.134	0.007	-0.676
Ploughed fields	-0.276	0.698	0.492
Legume crops	-0.057	0.009	-0.133
Dry woody cultures	-0.057	0.012	-0.164
Other	-0.050	-0.006	-0.090
Explained variance (%)	48.4	18.0	13.3

Niche overlap between bustard species

The degree of niche overlap between the little and the great bustard was overall high for the two-dimensional hypervolumes combining PC1-PC2 and PC1-PC3 (PC1-PC2 entire niche: 0.44; PC1-PC2 core area: 0.15; PC1-PC3 entire niche: 0.42; PC1-PC3 core area: 0.14; Fig. 2.1). We found an effect of great bustard density (log-transformed) on the degree of niche overlap for the entire niche space defined by the pair PC1-PC2 although marginally significant (Estimate ± SE = 0.117 ± 0.040; t=2.96; P=0.060). Niche overlap increased with the density of great bustard, stabilizing around 60%. Niche overlap of the entire niche space conformed by PC1-PC3 was not influenced by great bustard density (Estimate ± SE = 0.002 ± 0.003; t=0.60; P=0.592). We did not find any relationship between the degree of niche overlap and great bustard density in the core ares of maximum usage of PC1-PC2 (Estimate ± SE = 0.009 ± 0.004; t=2.01; P=0.138) nor PC1-PC3 (Estimate ± SE = -0.000 ± 0.001; t=-0.25; P=0.825; one observation was discarded from the analysis due to its odd KDE) hypervolumes.

Shifts on little bustard niche breadth and position

The entire PC1-PC2 niche breadth of little bustard was higher in regions with great bustard presence, although the effect was marginally significant (χ^2=2.95, P=0.086; Estimate ± SE = 1064.06 ± 619.80). However, the entire PC1-PC3 niche breadth did not vary between sympatry and allopatry (χ^2=1.84, P=0.175; Estimate ± SE = 564.77 ± 415.89). GLMMs showed that neither great nor little bustard density significantly affected the entire amplitude for PC1-PC2 or PC1-PC3 niches (Table 2.3). For the core area of maximum utilization, great bustard presence did not modify little bustard niche breadth of any two-PC axes niches (PC1-PC2: χ^2=2.43, P=0.118, Estimate ± SE = 301.23 ± 192.93; PC1-PC3: χ^2=2.38, P=0.123, Estimate ± SE = 181.09 ± 117.40). Again, as it happened with the overall niche space, we did not find any relationship between little or great bustard density and niche breadth for any two-dimensional niches (Table 2.3).

Little bustard niche position was only affected by the presence of great bustard for PC3 (PC1: χ^2=0.00, P=0.998, Estimate ± SE = -0.001 ± 0.241; PC2: χ^2=0.67, P=0.415, Estimate ± SE = 0.067 ± 0.082; PC3: χ^2=12.34, P <0.001, Estimate ± SE = -0.38 ± 0.11). We found that niche position was displaced toward lower values of PC3 under sympatry, indicating an increased use of natural vegetation in the presence of great bustard.

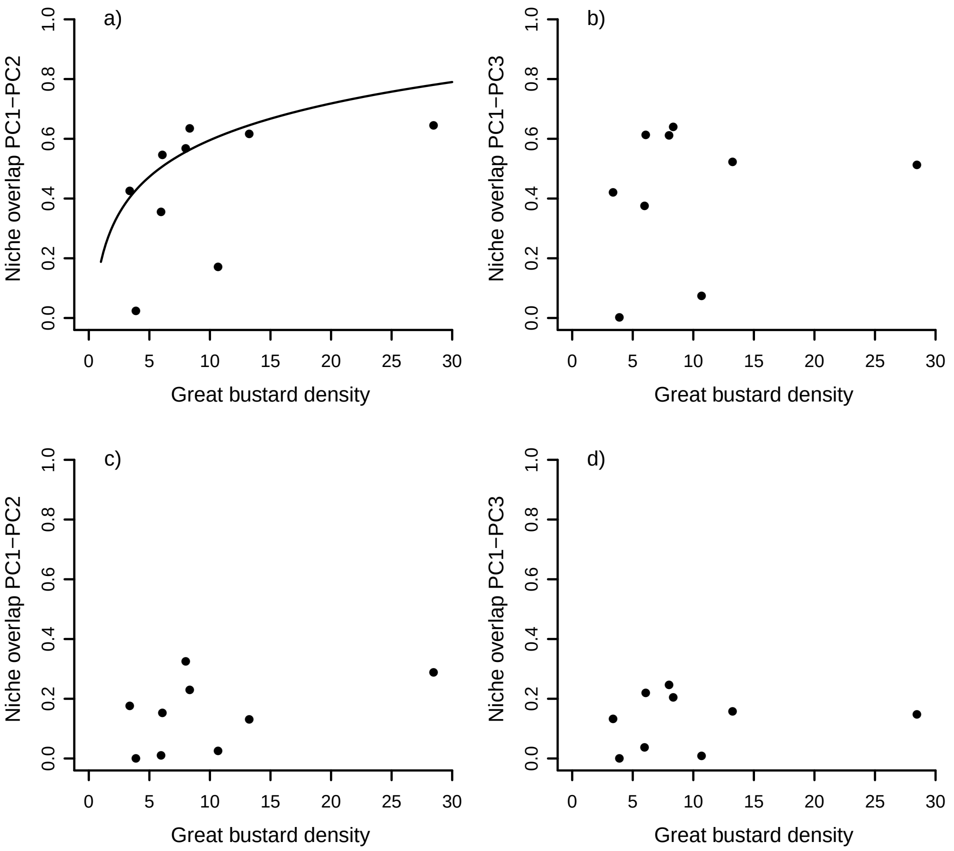

Figure 2.1: Influence of great bustard density in the proportion of niche overlap between little and great bustards in the niche space defined by the combination of two PC axis. a-b) the overall niche space and c-d) the niche region of maximum utilization space.

The density of great bustard did not influence niche position for any PCA axes (Table 2.4). However, little bustard density was significantly related with niche position for the first PCA axes, showing an increased use of cereals with little bustard abundance (Table 2.4).

Table 2.3: Results of GLMMs analyzing intra and interspecific density-dependent effect of competition on little bustard niche breadth. Two-dimensional niches spaces were built using KDE and combinations of PCA axis as habitat niche dimensions. All models included study site as random factor.

		PC1-PC2 niche			PC1-PC3 niche		
	Explanatory variables	Estimates ± SE	*t*	*P*	Estimates ±	*t*	*P*
Entire niche	Great bustard density	-75.96 ± 46.87	-1.62	0.126	-31.61 ± 29.13	-1.09	0.295
	Little bustard density	46.10 ± 134.17	0.34	0.736	14.99 ± 83.16	0.18	0.859
Niche core area	Great bustard density	-14.03 ± 14.46	-0.97	0.347	1.69 ± 8.52	0.20	0.845
	Little bustard density	4.06 ± 41.54	0.10	0.924	-18.58 ± 24.60	-0.76	0.462

Table 2.4: Results of GLMMs analyzing intra and interspecific density-dependent effect of competition in little bustard niche position. Two-dimensional niches spaces were built using KDE and combinations of PCA axis as habitat niche dimensions. We used the maximum probability value of the KDE as a proxy of niche displacement. All models included study site as random factor.

		Dimension 1			Dimension 2		
	Explanatory variables	Estimates ± SE	*t*	*P*	Estimates ±	*t*	*P*
Niche PC1-PC2	Great bustard density	-0.02 ± 0.01	-1.35	0.20	-0.00 ± 0.01	-0.00	0.998
	Little bustard density	0.11 ± 0.04	2.86	0.01	-0.01 ± 0.02	-0.45	0.657
Niche PC1-PC3	Great bustard density	-0.02 ± 0.01	-1.12	0.281	0.00 ± 0.01	0.19	0.853
	Little bustard density	0.13 ± 0.04	3.18	0.006	0.00 ± 0.03	0.11	0.915

2.4 Discussion

Our results based on the analysis of two-dimensional habitat niches lend overall support to the hypothesis that the little and great bustard competitively interact when coexisting and add empirical evidences of the role of interspecific competition driving changes in species' ecological niches.

Habitats have long been considered as potential dimensions of species' ecological niches (e.g. Schoener, 1989; Chase and Leibold, 2003; Young, 2004) probably because habitat selection is a fundamental mechanism mediating species coexistence (Rosenzweig, 1981; Morris, 2003*c*). Theories of habitat selection assume that interspecific competition causes a complete spatial separation of the species in their preferred habitats (Rosenzweig, 1981; Morris, 1988). As a consequence, one would expect no habitat niche overlap due to habitat niche divergence. However, the two-dimensional habitat niches of these closely related species, the little and the great bustard, highly overlapped in those regions where they co-occurred. Most interestingly, niche overlap for the entire niche hyperspace defined by cereal, young fallow and ploughed land increased with great bustard density, following a saturation function which stabilized around 60% of overlap (Fig. 2.1). This result apparently disagrees with current niche theory, which predicts that the upper limit of tolerable niche overlap between competing species should be negatively related with the intensity of interspecific competition (May and MacArthur, 1972; Pianka, 1974). However, current interspecific competition between coexisting species may also cause high values of niche overlap. Experiments conducted by Young (2004) found that asymmetric competition between two salmonid species did not cause reduced niche overlap. Instead, niche overlap increased with competitor density because at high densities the habitat distribution of the competing species converged (Young, 2004). In a similar way, the positive relationship between niche overlap and great bustard density might be explained by a progressive coincidental pattern of habitat use as great bustard density increases. The great bustard is a generalist species with no strong habitat preferences so its habitat distribution depends upon habitat availability (Lane et al., 2001; López-Jamar et al., 2011). At low density, great bustards should occupy basically cereal, the most abundant habitat in cereal farmlands. Meanwhile, little bustards establish their territories preferentially in short- and long-term fallows (Morales et al., 2005*b*; Delgado et al., 2010), which are less abundant habitats. As great bustard density increases, this species will also distribute in other habitats within the landscape like fallows (Lane et al., 2001), and therefore, the habitat distribution of both bustard species may become more similar.

Variation in the little bustard niche breadth and niche position suggests that the species may competitively interact. The little bustard niche breadth was affected by the presence of great bustard for the entire two-dimensional niche space defined by cereal, young fallow and ploughed land gradients. When a species is release from a putative competitor, its niche breadth expands because interspecific competition no longer restrict the exploitation of resources previously monopolized by the competitor (Schoener, 1983; Bolnick et al., 2010). However, we found that little bustard niche breadth increased in the presence of a presumed competitor species. Two facts consistent with interspecific competitive processes may be underlying this result: a lower proportional use of a shared habitat and the incorporation of low-quality habitats into little bustards' habitat choice. Although theories of habitat selection state that coexisting species resolve their competition by complete segregation in different habitats (Rosenzweig, 1981; Morris, 1988), this is not always necessarily true. A species may still use a competitor's habitat even if the competitor is present in the community but its habitat choice is modified as a function of the competitor density (Morris, 2009), indicating that interspecific competition is operating between the species. The proportional use of the common habitat decreases whereas increases in other preferred habitats. Little and great bustards distribute in the same agrarian habitats when they live in sympatry and habitat exclusion is not apparent (authors' unpublished data). Thus, little bustards may reduce the proportional use of the agrarian habitat where competes with great bustard. But at the same time, little bustards should be displaced toward other habitats. Indeed, we found that little bustard niche position differed between allopatry and sympatry in the natural vegetation dimension. Natural vegetation is one of the most preferred habitats by little bustards (Morales et al., 2005*b*; Delgado et al., 2010) and its proportional use was lower in allopatric than in sympatric conditions. Therefore, interspecific competition would likely favor a shift in little bustard habitat niche toward increased use of natural vegetation. This result may also indicate that the species assemblage is governed by a "distinct habitat preference organization" because the little bustard increases the use of a preferred habitat in the presence of a putative competitor (Morris, 1988).

The effects of interspecific competition in the little bustard habitat distribution may also increase levels of intraspecific competition. The limited access to a habitat shared with the great bustard should cause increased density in its preferred habitats and consequently intraspecific competition can intensify. In order to mitigate increased levels of intraspecific competition in the natural vegetation habitat imposed by great bustard presence, some individuals may occupy other low-quality habitats, for instance, ploughed lands and cereals (Morales et al., 2006), thus widening little bustard niche breadth in sympatry. Certainly, results also shown that intraspecific competition caused niche displacement in the cereal dimension. Increased little bustard density displaced niche position toward a greater proportional use of cereals. This may indicate that little bustards diversify their habitat use when reaching high densities. Intraspecific competition constitutes another ecological force modulating species realized niches (Bolnick, 2001; Svanbäck and Bolnick, 2007). Therefore, considering intraspecific competition is necessary to correctly comprehend how species' niches adjust in community organization (Young, 2004; Svanbäck and Bolnick, 2007).

All effects of great bustard presence in little bustard niche variation were found in the entire niche space. We did not find any effect of great bustard in the core area of maximum utilization for any combination of habitat niche dimensions. The core area indicates the most frequent strategies of habitat choice in each bustard species and is likely more conservative than the extremes of the entire niche hyperspace.

Although our findings indicate that these bustard species may compete, our analysis failed to identify any density-dependent effect of potential interspecific competition in little bustard niche variation. The approach followed in this study may be related with this lack of evidence. Raw habitat variables (habitat proportion within delimited region around bird observations) were summarized in PCA axis. This methodology pretends to obtain a reduced number of new variables with ecological meaning that allow to build KDEs. However, the combination of several habitat variables into one new variable may have confounding effects if competition occurs within particular habitats (e.g. Abramsky et al., 1991). Therefore, future studies should explore the role of particular agrarian habitats mediating in the coexistence of these bustard species. Another plausible explanation is that the range of variation in PCA axes is low and it does not allow to detect a possible relationship with great bustard density. Finally, this study has exclusively centered on the potential effects of interspecific competition on little bustard habitat niche. However, interspecific competition may also induce changes on great bustard ecological niches and future research is deserved to elucidate this question at habitat or other finer scale levels (e.g. diet segregation Bonesi et al., 2004).

This is the first study addressing interspecific density-dependent competition, habitat use and species niche adjustments using a multidimensional niche method. Overall, our findings indicate that these bustard species are currently competing, perhaps induce by the recent change on the dynamics of these agricultural landscapes. Our two-dimensional habitat niche approach highlights relevant aspects of the quantification of species niche using kernel density estimators. The selection of niche dimensions is a crucial step for evaluating the role of interspecific competition in niche shifts and must rely on detailed knowledge of the species' ecological requirements. Empirical studies using computational tools which allow to easily obtain multidimensional niches should give more realistic insights on evolutionary and ecological processes shaping communities (Blonder et al., 2014). Studies of ecological niches aiming to improve our understanding of community organization require that intra- and interspecific competition are considered together given their opposite effect on species' niches (Bolnick, 2001; Bolnick et al., 2010).

2.5 Acknowledgements

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Chapter 3

Isodars unveil interspecific competition without competitor's data.

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Abstract

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 evolutionarily stable strategies of habitat selection, to evaluate whether interspecific competition between two competing species with distinct habitat preferences modulates their habitat use. Computer simulations of exploitation and interference competition confirmed that isodars capture the competitive effects and that omitting the dominant competitor's density alters the interpretation of habitat preferences by the subordinate species. Field data on two endangered steppe bird species were consistent with the simulation results and demonstrate that interference associated with increased density of great bustards in secondary cereal habitats reinforces use of preferred natural habitat by little bustards. These results confirmed that study of density-dependent habitat selection can 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.

3.1 Introduction

Interspecific competition has been 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). The 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; Bolnick et al., 2010; Stuart et al., 2014). Regardless of morphological divergence, species in competitor-driven communities often coexist through the differential density-dependent use of habitat (Rosenzweig, 1981; Morris, 2003*c*).

Habitat selection's role in 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, increased levels of intraspecific competition in the preferred habitat cause increased exploitation of other, less-favored habitats. When a competing species is present, however, theories of habitat selection predict that stable coexistence of competing species with distinct habitat preferences will often occur only when they segregate in 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, Morris showed theoretically (Morris, 1999, 2003*b*, 2004, 2009) that species with distinct habitat preferences are capable of occupying their respective competitor's preferred habitat, instead of completely segregating in separated habitats. Different equilibria of species abundance can be attained under different combinations of species population sizes, so that the ghost of competition past (*sensu* Rosenzweig, 1974) can be materialized and, competition evaluated through the study of each species' habitat isodar (the set of densities in occupied habitats such that an individual's expected fitness is equal in each, Morris, 1987, 1988).

In this study, we use computer simulations and field data to investigate the effects of interspecific competition on the habitat use of two coexisting unequal competitor species with distinct habitat preferences (the little bustard *Tetrax tetrax* and the great bustard *Otis tarda*). In particular, we use habitat isodars to evaluate whether the subordinate competitor occupies its alternative habitat even when the 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 exploitative versus interference competition in bustard coexistence.

Habitat isodars can even inform us about competitive interactions when data on the competing species are absent. 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). Decreased competition allows individuals of the target species to increase the proportional use of their competitor's habitat. Consequently, we also use computer simulations to explore how isodars respond to removal of the regression terms for exploitation and interference competition in model communities where competition is responsible for habitat selection. Other ecological mechanisms, like differential predation risk, environmental heterogeneity or stochasticity, may cause a negative isodar slope if they decrease the apparent quality of the secondary habitat across space and time. However, our simulated competitor-driven community is free of such mechanism so we can evaluate how interspecific competition alters habitat selection.

Theoretical context: increased competitors' preferred habitat use when competitors are sequentially removed

Imagine two competing species (A and B) occupying a landscape composed of two habitats (1 and 2). Species A preferentially selects habitat 1. Habitat 2 also harbors resources used by this species, so when the population size of species A increases beyond a threshold, individuals also occupy this alternative habitat. Species B prefers habitat 2. Hence, both species may compete for the resources available in habitat 2 and resolve their competition through habitat selection. However, Morris (2009) showed that in a community in which species A has a fixed population size but the density of species B varies, individuals of species A may still use the alternative habitat in the presence of the competitor. When the density of the interspecific competitor is low, many of the species A individuals occupy habitat 2. But as the density of B increases, fewer and fewer individuals of A occupy their secondary (habitat 2) choice. If one fails to include the density of the competitor in the habitat isodar, then the isodar slope will be negative rather than positive (Fig. 3.1; Morris, 2009).

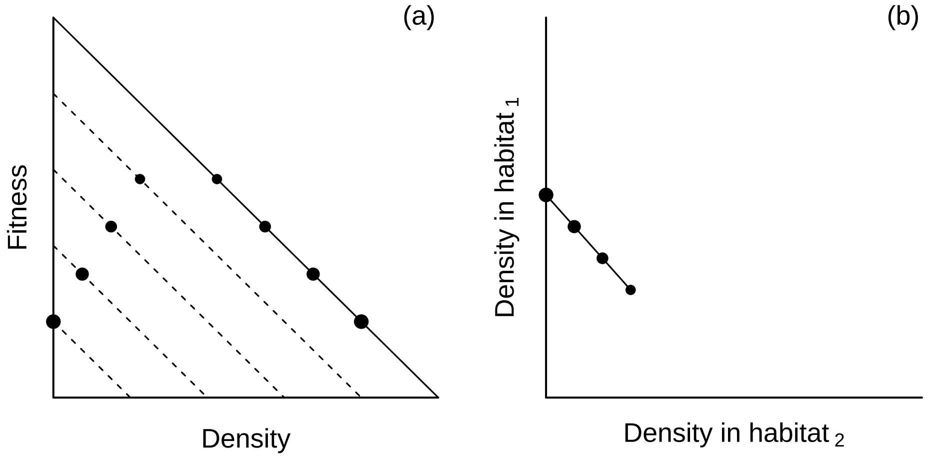

Figure 3.1: Effect on habitat choice by sequential removal of a competitor while the target species lives at constant population size. Competition between the species only occurs in the alternative habitat 2. Panel (a) illustrates the fitness attained in the preferred habitat 1 (solid line) and in the alternative habitat 2 (dotted lines) for different competitor densities. Point size reflects competitor density in habitat 2. Points of equal size indicate joint densities in both habitats for a particular competitor density. Panel (b) illustrate the resulting isodar of the target species with a negative slope. After Morris (2009).

3.2 Methods

Simulation of two virtual competitors

We expanded the situation evaluated in Morris (2009) to include the effects of both exploitation and interference competition on the density of a subordinate species (A). We simulated a dataset with different values for the overall density of species A and the density of species B in habitat 2.

The influence of each form of competition on habitat selection can be inferred by changing the value of the corresponding partial regression coefficient in the two-species isodar equation (Equation 3.1, Morris, 1989). First, we simulated the effect of exploitative competition in the habitat distribution of the subordinate species A. The density of species A in each habitat was thus determined by:

$$N_{A1} = c + b(N_{A2} + \beta N_{B2}) \tag{3.1}$$

where N_{A1} corresponds with the density of species A in habitat 1 and, N_{A2} and N_{B2} reflect the density of species A and B in habitat 2. The intercept of the equation, c, corresponds with quantitative differences between habitats (Morris, 1988, e.g. differences in resource renewal rate), b, the isodar slope, quantifies the density-dependent habitat selection of the target species living in allopatry, and β is the regression coefficient for exploitative competitive effects of species B on species A in habitat 2. Since population density was known for both species we can rewrite equation (3.1) as:

$$N_{A-Overall} - N_{A2} = c + b(N_{A2} + \beta N_{B2}) \tag{3.2}$$

where $N_{A-Overall}$ = the total number of individuals of species A. Rearranging equation (3.2):

$$N_{A2} = \frac{(N_{A-Overall} - c - b\beta N_{B2})}{(b+1)} \tag{3.3}$$

We calculated the number of individuals of species A in habitat 1 and 2 as a function of the competitor density and the strength of exploitative competition. In order to evaluate the effect of competitive magnitude on species A's habitat choice, we used β values ranging from 0 to 5 with increments of 0.2 units.

Next, we incorporated competition by interference in the isodar equation as the higher order interaction term between both species in habitat 2, following Morris (1989):

$$N_{A1} = c + b(N_{A2} + \beta N_{B2} + \gamma N_{A2} \times N_{B2}) \tag{3.4}$$

where γ is the term for interference competition of species B on species A in the secondary habitat 2. Rearranging equation (3.4):

$$N_{A2} = \frac{(N_{A-Overall} - c - b\beta N_{B2})}{(\gamma N_{B2} + b + 1)} \tag{3.5}$$

We calculated the habitat distribution of species A depending on species B abundance and on the magnitude of exploitation and interference competition. We based the range of parameter values on field studies. The set of γ values ranged from 0 to 5 with increments of 0.2 units. Overall densities of species A ranged from 100 to 140 individuals per unit area, with increments of 4 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 simulated all possible combinations of each species densities, β and γ values. We considered only those regression coefficient values of exploitative and interference competition for which species A occupied both habitats for analysis. For simplicity, we assumed that $c = 0$ (habitat 1 and 2 did not differ quantitatively) and $b = 1.5$ (indicates species A's preference for habitat 1).

We used linear regression to explore how isodars behave when exploitation and interference regression terms are removed from the isodar model. First, we analyzed the effects of removing exploitative competition. We built two isodars of equal competitive magnitude, one including the exploitative competitive term and the other without it (i.e. only intraspecific density-dependent effects). The same procedure was followed for interference competition. We compared the isodar including exploitative and interference competition with the isodar lacking interference. We set the strength of exploitation and interference competition at $\beta = 3$ and $\gamma = 0.7$.

Case study: applying isodars to field data

Study species

Our study species are two sympatric members of the *Otididae* family that coexist in many regions across their Paleartic distribution range (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. Populations of both species have declined dramatically and they are currently classified as near threatened and vulnerable respectively (IUCN, 2012). These species are potential competitors given their ecological similarities and phylogenetic proximity (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*b*) whereas great bustard habitat selection concentrates more 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 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 around the end of May and 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). The species may thus compete for space, habitat and food.

Study areas

Bustard data were collected in 6 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 2-year rotation cultivation system that creates a mosaic landscape of different agrarian habitats (See more details on Appendix A). Approximately 50 % of the land surface is cultivated with dry cereals (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 their reproductive periods (Cramp and Simmons, 1980). Bird observations were collected by car along the available network of roads and tracks that ensured complete coverage of each site. Observers stopped every 500 m and scanned the surroundings with binoculars and spotting scopes. Surveys were limited to time when the birds are most active(three hours after daybreak and three hours before sunset, Cramp and Simmons, 1980). Mating calls of little bustard males allowed observers to detect them acoustically. Accurate positions were then obtained by a visual search. Little bustard female observations were discarded since their secretive behaviour precludes a reliable estimate of their abundance. We counted the number of male and female great bustards in each lekking area (Morales and Martín, 2002; Alonso et al., 2004).

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 to 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).

Interspecific competition in bustards

We first analyzed whether interspecific competition influences little bustard abundance at the regional scale by means of generalized linear mixed models (GLMMs), with Gaussian error distributions (density of little bustards = the response variable, density of great bustards = the explanatory variable). 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 multispecific isodars (Morris, 1989; Rodríguez, 1995). Little and great bustards were most abundant in the three habitats that we used in the analysis: fallow, cereal and ploughed land. Fallow, 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 (e.g. Morales et al., 2005*b*; Delgado et al., 2010). Leguminous crops, although a cultivated habitat, have a low vegetation height and a horizontal structure (see Appendix A: Table A2) that makes them suitable for sexual displays by little bustards (Morales et al., 2008). Based on previous work, we considered fallow 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 arbitrary delimitation of study site boundaries might bias our estimates of species density (Aebischer et al., 1993). Therefore, we computed the area of each habitat type inside the minimum convex polygon (MCP) defined by all bustard observations in each study site and year. We defined each individual's habitat as the habitat of maximum cover inside a buffer of 10m centered on the bird's observation. We summed all individuals of the species using the same habitat to estimate density in that habitat. Both species can move quickly from one habitat to another so we assumed that movements among habitats were not significantly costly (see Appendix A: Table A1).

We fitted multispecific isodar models with GLMMs with Gaussian error distributions and included study site as a random factor. Two isodar equations were formulated for each species to test the density-dependent habitat selection between the preferred habitat (fallow) and each of the secondary habitats (cereal and ploughed land) in the presence of the potential competing species. For the little bustard:

$$\begin{aligned}\text{Density}_{\text{LB}\cdot\text{Fallow}} &= c + b_c\text{Density}_{\text{LB}\cdot\text{Cereal}} + \beta_c\text{Density}_{\text{GB}\cdot\text{Cereal}} - \\ &-\alpha\text{Density}_{\text{GB}\cdot\text{Fallow}} \end{aligned} \tag{3.6}$$

and

$$\begin{aligned}\text{Density}_{\text{LB}\cdot\text{Fallow}} &= c + b_{pl}\text{Density}_{\text{LB}\cdot\text{Ploughedland}} + \beta_{pl}\text{Density}_{\text{GB}\cdot\text{Ploughedland}} - \\ &-\alpha\text{Density}_{\text{GB}\cdot\text{Fallow}} \end{aligned} \tag{3.7}$$

where b_c and b_{pl} correspond to the regression coefficients for intraspecific density dependence (isodar slope) whereas the partial regression coefficients β_c and β_{pl} reflect interspecific competition, in cereal and ploughed land respectively. α is the partial regression coefficient indicating interspecific competition in fallow. We then rearranged equations (3.6) and (3.7) for the great bustard (e.g. Rodríguez, 1995). Sample sizes were too small to include the interaction term ($Density_{LB-Habitat2} \times Density_{GB-Habitat2}$). 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 software v3.1.1 (R Development Core Team, 2014).

3.3 Results

Simulations of interspecific competition

In the absence of interspecific competition, the positive isodar slope accurately revealed ideal free habitat selection (Fig. 3.2a). The density of

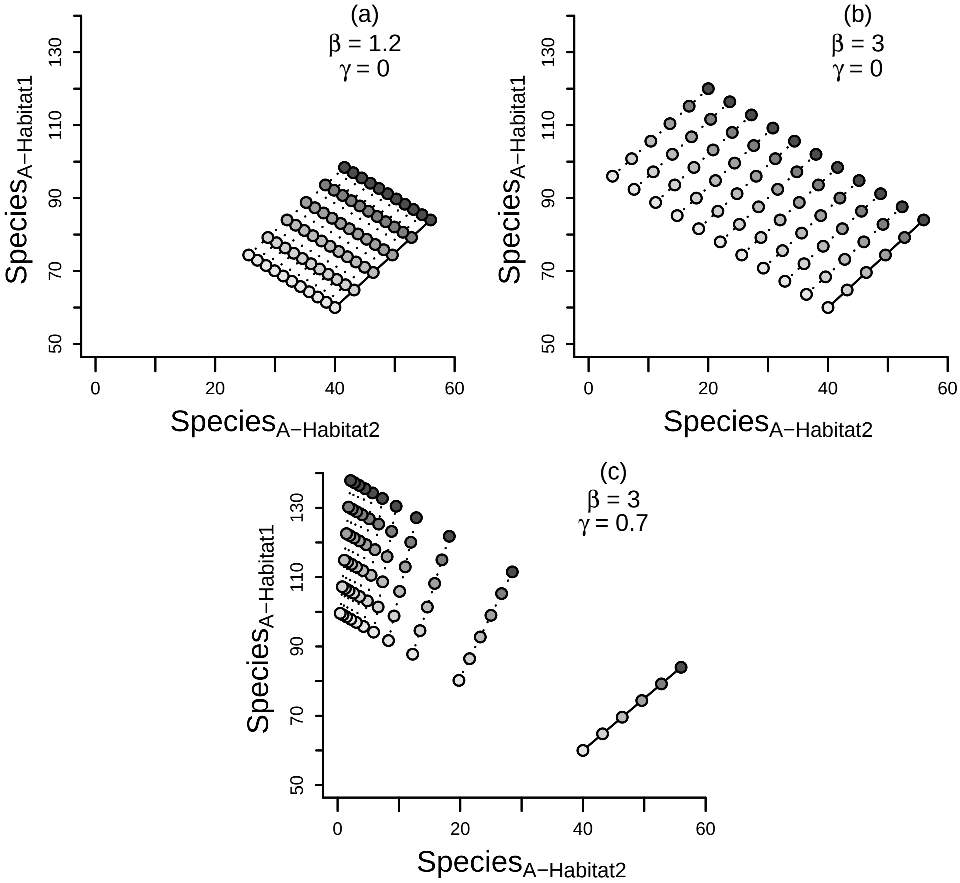

Figure 3.2: Isodar plots showing the effects of exploitative and interference competition in the habitat use of a subordinate species (A) competing with a dominant species (B) in the subordinate's secondary habitat (2). Densities of both species vary. Increased shading corresponds with increasing density 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 single density of species B, which increases from southwest to northeast. 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. c) competition by interference (γ) is also operating between the species. Only a subset of possible species B's densities is depicted in order to facilitate interpretation.

species A in habitat 1 was higher than in habitat 2, and they increased proportionally with population size. Species B gradually displaced individuals of the subordinate species A towards its preferred habitat when we included exploitative competition. Increasing the density of species B induced species A to use less of its alternative habitat. However, the relationship of species A densities between habitat 1 and 2 remained constant for different densities of species B (Fig. 3.2a and 3.2b).

Increasing the strength of exploitative competition caused more individuals of species A to move to habitat 1 and decreased the proportional use of their secondary habitat (Fig. 3.2b). When we then excluded species B density from the isodar regression model, the isodar switched to a negative slope (Table 3.1). This occurred when the range of densities in the alternative habitat was greater than in the preferred habitat (Fig. 3.3). Most importantly, the positive slope was recovered when we included competitor density in the model and the isodar regression accurately estimated all coefficient terms (Table 3.1).

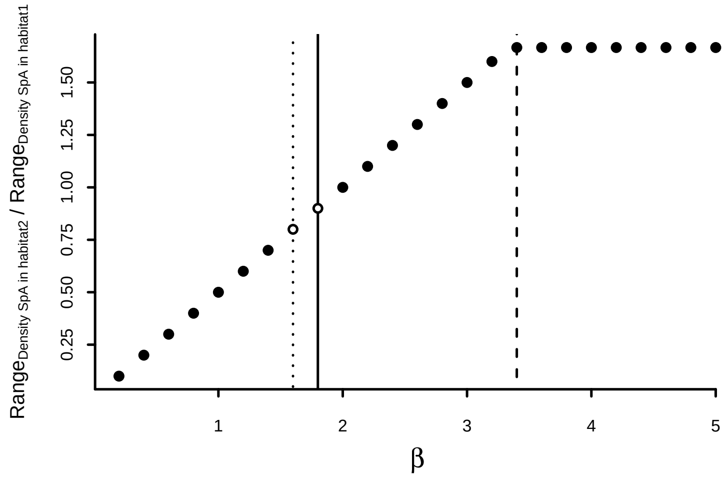

Figure 3.3: Changes in the sign and significance of the isodar slope (b) estimated at different magnitudes of exploitative competition (β) when the exploitative competitive term was not included in the linear regression model. Open and black circles indicate non-significant and significant coefficient estimates respectively. Points left of the dotted line indicate positive isodar slopes while points right of the solid line reflect negative isodar slopes. Points falling to the right side of the dashed line correspond with simulations in which species A used only its preferred habitat.

The isodar slope became steeper with increasing densities of species B (Fig. 3.2c). The proportional use of habitat 1 increased with both species population sizes. Again, as predicted, the isodar model that excluded interference ($\text{Species}_{\text{A-Habitat2}} \times \text{Species}_{\text{B-Habitat2}}$) produced a significantly negative slope (Table 3.1). Additionally, the partial regression term of

Table 3.1: Linear regression results of removing exploitative and interference competition terms in the isodar model. We simulated a community in which the subordinate species A prefers habitat 1, but competes with the dominant species B in its alternative habitat 2. We built two models, one with the competition term and other without it. Intercept = 0, exploitative competition (β) = 3, interference competition (γ) = 0.7, intraspecific competition coefficient (b) = 1.5. *** and * indicate $P < 0.001$ and $0.05 < P < 0.01$, respectively

Competition type	Model	Adjusted R^2	Coefficient	Estimates
Exploitative	$\text{Density}_{A1} = b\text{Density}_{A2} + \beta\text{Density}_{B2}$	1	b	1.500 ± 0.000***
			β	4.500 0.000***
Exploitative	$\text{Density}_{A1} = b\text{Density}_{A2}$	0.25	b	-0.557 ± 0.063***
Interference	$\text{Density}_{A1} = b\text{Density}_{A2} + \beta\text{Density}_{B2} +$	1	b	1.500 ± 0.000***
	$+ \gamma\text{Density}_{A2} \times \text{Density}_{B2}$		β	4.500 ± 0.000***
			γ	1.050 ± 0.000***
Interference	$\text{Density}_{A1} = b\text{Density}_{A2} + \beta\text{Density}_{B2}$	0.25	b	-0.604 ± 0.121***
			β	0.628 ± 0.235***

exploitative competition was significantly positive. As was the case with exploitation competition, all habitat-dependent competitive terms were accurately revealed when we included interference in the isodar regression (Table 3.1).

Interspecific competition in bustards

Overall, great bustard density was higher and more variable than little bustard density (Appendix B: Table B1). There was no relationship between the densities of both bustard species (Great bustard density coefficient = 0.07 ± 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. 3.4). Great bustard density was highest in cereal (Fig. 3.4) whereas young fallow and legume crop were moderately used (Fig. 3.4).

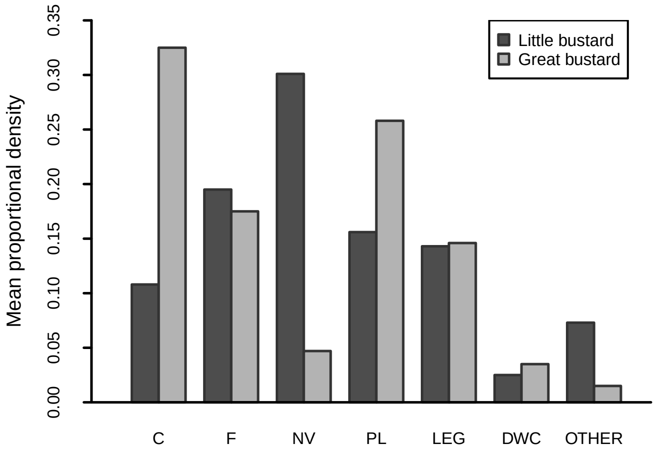

Figure 3.4: Mean proportion of little and great bustard densities in each habitat (C: cereal; F: young fallows; NV: natural vegetation; PL: ploughed land; LEG: leguminous crops; DWC: dry wood cultures formed by vineyards and olive groves; Other: pastures, urban areas, fruit tree orchards and forest) using all study sites where the species were present.

The little bustard's multispecific isodars document competition with great bustards in cereals (significant positive coefficient of great bustard density in cereal, Fig. 3.5a. Appendix B: Table B2). Hence, as great bustard density increased in cereals, proportionally more little bustards used fallows (Fig. 3.5a). Moreover, the negative isodar slope highlighted additional competitive interactions with great bustard in cereal (Fig. 3.5a). We detected no competition between the species in fallows, the little bustard's preferred habitat (Fig. 3.5a). The significant intercept of the isodar indicates that the little bustard perceives that fallow is quantitatively superior to cereal habitat. This species had no preference for ploughed fields (Fig. 3.5b).

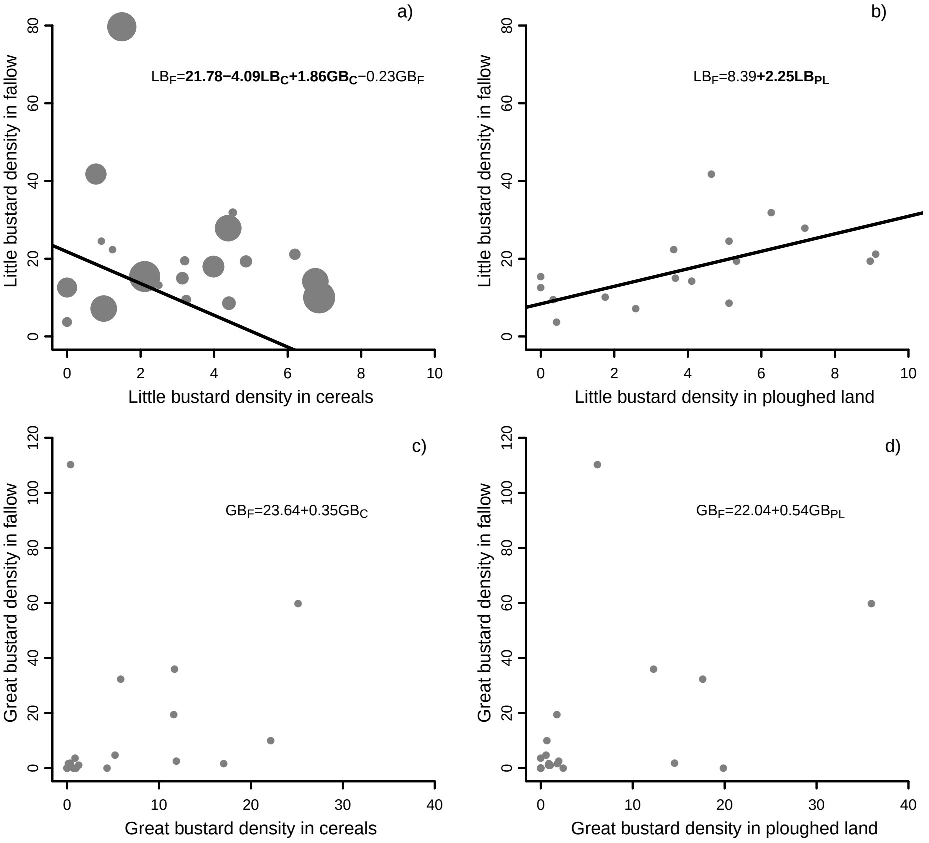

Figure 3.5: Isodars for little (LB: a, b) and great bustards (GB: c, d) considering fallow (F) as the preferred habitat and cereal (C) or ploughed land (PL) as the secondary habitat choice. Black lines correspond with the regression line fitted by GLMM when the coefficients for intraspecific effects (i.e. the isodar slope) were significant. Point size reflects the density of the competing species in the secondary habitat when this variable had a significant effect in the regression model. Regression models with significant ($P < 0.05$) coefficients (bold type) are also displayed.

We detected no interspecific competition by little bustards on the great bustard's habitat use (Fig. 3.5c and 3.5d. Appendix B: Table B3). The analyses also revealed that the great bustard has no preference among the three main habitats in these agricultural regions (Fig. 3.5c and 3.5d).

3.4 Discussion

Our simulations and data 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 far from equilibrium.

Habitat partitioning is one of the most important mechanisms by which competing species coexist (Rosenzweig, 1981; Ricklefs, 1987; Morris, 2003*c*). Bearing this principle in mind, we recreated a competitor-driven community in which two coexisting species with distinct habitat preferences competed for resources in the secondary habitat of the subordinate. Although theory often predicts stable coexistence when species segregate into their preferred habitats (Rosenzweig, 1981; Morris, 1988), our results demonstrate, when such systems depart from equilibrium, that 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). The reduction in fitness caused by intraspecific competition exceeds that of interspecific competition. Increased competitor abundance shifts the balance of intra- versus interspecific competition and fewer individuals occupy their alternative habitat. Competition can thus be equalized by many different combinations of density in different habitats. Even so, habitat isodars accurately reveal the underlying competitive effects (Morris, 2004).

We acknowledge that negative isodar slopes may emerge from any mechanism that lowers the apparent quality of secondary habitats across space and time. This will occur, of course, only if the investigator is collecting comparative densities at those times and places. 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. This is true not only for exploitative but also for interference competition. However, the isodar slope remained positive when exposed to weak interspecific competition because the proportional use of the alternative habitat was barely affected by the abundance of heterospecific competitors.

Bustard habitat selection supports our insights from the simulations. Isodars reveal that these coexisting and ecologically similar steppe birds compete asymmetrically. The dominant great bustard is a generalist species with no clear habitat preferences whereas the little bustard specializes on fallows and legume crops (Lane et al., 2001; Morales et al., 2005*b*; 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 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.

Most interestingly, the negative isodar slope also reflects additional interference competition with great bustards in cereals, which we could not evaluate directly with a higher order interaction term. We interpret the negative isodar 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 that increase their use of fallow habitat. The unsuitability of cereals as sexual displaying habitats for little bustard males may not be only due to its vegetation structure (Morales et al., 2008, Appendix A), but also to interspecific competition with great bustards.

Density-dependent habitat selection of bustards has important implications for their conservation. Since 2009, the European Common Agrarian Policy no longer protects 10% of arable land as fallow. 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 will not be able to exploit the alternative cereal habitat. Conservation policies that fail to understand the ecological consequences of "invisible" interspecific competition on community organization can thereby jeopardize recovery of endangered species.

Although isodars have been criticized for not being able to detect interference competition in gerbil communities (Ovadia and Abramsky, 1995), our simulations and bustard data demonstrate their ability to evaluate interspecific competition. Habitat isodars are particularly promising tools to investigate interspecific competition in species in which removal experiments are not feasible. Habitat selection studies in wild populations often encounter considerable difficulties in gathering exhaustive data on competitors' density, or even to elucidate the network of species interactions. The ability of isodars to capture interspecific competition in the absence of competitor data expands opportunities to use free-ranging populations in order to gain new insights into the regulation and assembly of real communities.

3.5 Acknowledgements

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3.6 Appendix A. Vegetation structure description

The traditional cultivation system on the study areas consist in a two-year rotation system. One year the field is cultivated with dry cereals and the next year is set-aside or sometimes planted with legumes which naturally enrich soil nitrogen content. During the first autumn, fields which will be cultivated are ploughed and prepared for sowing in winter. Cereal cultivated fields are left until summer when fields are harvested and become stubbles. The next autumn, stubbles can be ploughed several times until the following year so no vegetation is allow to grow. Alternatively, they can be left without tilling so cereal and weed seeds germinate and grow until the next year, forming fallow lands. This traditional system creates a dynamic mosaic of different substrate, together with the presence of olive groves and vineyards, characteristics of dry climatic regions, and pastures to feed livestock (Table A1).

Here, we present data describing the vegetation structure of the agrarian habitats included in the isodar analysis (i.e. cereal, legume crops, young fallows and old fallows. Because ploughed land is bare ground no information on vegetation structure is provided). Vegetation structure variables were measured between April and June, in three study sites in which bird censuses were carried out: Camarma in 2006; Campo Real 2005 and 2006; Valdetorres in 2005, 2006 and 2013. Control locations falling inside the study area were randomly established over georeferenced cartography using ArcGis. Five sampling points were defined at each random location,: one at the exact point corresponding with the ArcGis generated coordinates and the other four were settled at N, S, W and E side of the central point, separated by 10 m. The agrarian habitat type was determined in each random location and seven variables related with the structure and cover of the vegetation were measured inside a quadrat of 1 x 1 m (Table A2). The mean value of the five sampling points was assigned to each corresponding control location.

Table 3.2: **Table A1** Mean (± SD) surface (km^2) and proportion (percentage) of each agrarian habitat inside the MCP built with all little and great bustard observations for each study site and year (CC=Campo de Calatrava). DWC (Dry woody cultures) includes olive trees and vineyards. Other includes pastures, urban substrate, forest and fruit tree orchards.

	Campo Real	Valdetorres	Daganzo	Camarma	CCNorth	CCSouth	La Solana
Study years	2010-2012	2010-2011	2010-2011	2006	2007-2011	2007-2011	2010-2011
Surface	8.41 ± 0.3	5.73 ± 3.33	5.73 ± 1.57	41.99	11.19 ± 2.25	11.82 ± 3.24	14.33 ± 8.58
Cereal	42.27 ± 3.09	37.83 ± 16.81	38.02 ± 25.16	25.24	49.56 ± 6.95	35.92 ± 8.43	22.86 ± 4.30
Ploughed land	18.28 ± 2.57	26.48 ± 10.35	20.9 ± 15.11	22.03	17.78 ± 6.00	7.93 ± 5.91	13.36 ± 2.20
Young fallow	9.87 ± 1.82	21.28 ± 8.28	19.13 ± 11.33	10.51	13.30 ± 1.58	16.46 ± 16.28	8.52 ± 6.10
Old fallow	8.17 ± 0.64	7.21 ± 0.83	14.3 ± 7.15	11.53	1.83 ± 2.00	14.12 ± 4.86	3.84 ± 0.92
Legume crop	8.15 ± 4.3	0	0	1.64	1.74 ± 1.79	7.00 ± 8.94	0.24 ± 0.34
DWC	5.59 ± 0.95	0	0	0.36	6.86 ± 0.63	5.35 ± 3.63	37.52 ± 7.99
Other	1.98 ± 0.24	2.21 ± 1.31	0.74 ± 0.99	9.78	1.38 ± 0.50	11.09 ± 2.11	3.67 ± 2.01

Table 3.3: **Table A2** Mean (± SD) of the vegetation structure variables. The number of contacts were measured using a rod of 0.5 cm diameter place vertically in the center of each sampling point.

	Cereal	Young fallow	Old fallow	Legumes crop
Modal vegetation height (cm)	59.31 ± 28.96	25.73 ± 19.40	50.49 ± 28.17	27.54 ± 14.86
Number of contacts below 5 cm height	1.03 ± 0.72	1.49 ± 0.92	1.44 ± 0.87	1.43 ± 1.63
Number of contacts from 5 to 10 cm height	1.05 ± 0.66	1.29 ± 0.70	1.10 ± 0.63	1.97 ± 1.94
Number of contacts from 10 to 30 cm height	2.25 ± 1.15	2.82 ± 2.40	1.77 ± 1.62	2.74 ± 2.04
Number of contacts over 30 cm height	2.95 ± 2.08	0.69 ± 1.15	1.05 ± 1.41	0.54 ± 0.98
Green vegetation cover	60.05 ± 31.84	43.00 ± 39.62	32.54 ± 39.52	58.50 ± 38.69
Weed vegetation cover	4.19 ± 8.57	57.65 ± 25.34	54.78 ± 34.08	5.14 ± 9.97

Young fallows and legume crops had a similar vegetation height and density. Both substrates presented the lowest vegetation height but their horizontal structure was denser (Table A2. Fig. A1 and A2). This vegetation structure favored the conspicuousness necessary for little bustard displaying males (Morales et al., 2008, Fig. A3 and A4). Cereal had the highest vegetation height, followed by old fallows (Table A2. Fig. A5 and A6). The high height of old fallows can be explained by the presence of shrubs, which can increase the mean vegetation height (Fig. A5). The height of cereal and old fallows was more variable than the height of young fallows and legume crops, which indicates greater variation in cereal and old fallows between fields within the same study area or between regions. Although cereals have been identified as a habitat avoided by little bustard due to its vegetation height (Morales et al., 2008), its great variability (due to differences on the precipitation regime between years, soil nutrient conditions or the date of data measurements) allows that some cereal fields can be suitable for little bustard use (Fig. A3). Contrary to little bustards, it is unlikely that the vegetation height or density limits the habitat use of great bustards due to its big size.

These measurements were not collected with the purpose of determining the microhabitat characteristic chosen by the bustard species. Therefore, direct application to bustard microhabitat use should be done with caution, although they served us to illustrate differences on the horizontal and vertical structure among these agrarian habitats.

Figure 3.6: **Figure A1.** Young fallow vegetation structure with cereal and several weed species.

Figure 3.7: **Figure A2.** Legumes fields.

Figure 3.8: **Figure A3.** Little bustard male in a) a young fallow and b) a cereal of low vegetation height.

Figure 3.9: **Figure A4.** Little (a) and great (b) bustards occupying a legume crop.

Figure 3.10: **Figure A5.** Old fallow covered with annual species and shrubs (*Retama sphaerocarpa*).

Figure 3.11: **Figure A6.** Cereal fields of high vegetation height.

3.7 Appendix B. Density and isodars of little and great bustards

Table 3.4: **Table B1** Mean (± SD) overall and regional density (number of individuals per km^2) of little and great bustards inside the MCP. Overall great bustard density was calculated without the “La Solana” study area.

Site	Little bustard density	Great bustard density
Campo Real	5.60 ± 0.65	7.48 ± 1.22
Valdetorres	2.56 ± 0.99	20.85 ± 10.76
Daganzo	2.29 ± 0.21	5.22 ± 1.07
Camarma	0.50	3.39
Calatrava North	3.79 ± 1.23	3.93 ± 4.02
Calatrava South	4.59 ± 0.45	0.38 ± 0.32
La Solana	2.70 ± 0.97	0
Overall	3.71 ± 1.51	5.52 ± 6.93

Table 3.5: **Table B2** Results of the little bustard's habitat isodars evaluating interspecific competition. Little bustard density in fallow (preferred habitat) was fitted to GLMM with Gaussian error distribution. The density of the little bustard in this habitat was considered as the response variable given the habitat preferences of these bustard species. Cereal and ploughed land were considered as alternative habitats. All models included "study site" as random effect. Densities of great bustard in the preferred and alternative habitats were removed from the models when no effect of interspecific competition was detected.

Secondary habitat	Variables	Estimate ± SE	df	t-value	*P*
Cereal	Intercept	21.78 ± 9.18	10	2.37	0.039
	Little bustard in cereal	-4.09 ± 1.68	10	-2.43	0.035
	Great bustard in cereal	1.86 ± 0.49	10	3.82	0.003
	Great bustard in fallow	-0.23 ± 0.18	10	-1.31	0.220
Ploughed land	Intercept	8.39 ± 5.06	12	1.66	0.123
	Little bustard in ploughed land	2.25 ± 0.71	12	3.15	0.008

Table 3.6: **Table B3** Results of the great bustard's habitat isodars evaluating interspecific competition. Great bustard density in fallow (preferred habitat) was fitted to GLMM with Gaussian error distribution. The density of the great bustard in this habitat was considered as the response variable given the habitat preferences of these bustard species. Cereal and ploughed land were considered as alternative habitats. All models included "study site" as random effect. Densities of little bustard in the preferred and alternative habitats were removed from the models when no effect of interspecific competition was detected.

Secondary habitat	Variables	Estimate ± SE	df	t-value	*P*
Cereal	Intercept	23.64 ± 15.47	12	1.53	0.152
	Great bustard in cereal	0.35 ± 0.36	12	0.99	0.344
Ploughed land	Intercept	22.04 ± 14.89	12	1.48	0.165
	Great bustard in ploughed land	0.54 ± 0.25	12	2.16	0.052

CHAPTER 4

Are species coexistence areas a good option for conservation management? Applications from fine scale modelling in two steppe birds.

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Abstract

Biotic interactions and land uses have been proposed as factors that determine the distribution of the species at local scale. The presence of heterospecifics may modify the habitat selection pattern of the individuals and this may have important implications for the design of effective conservation strategies. However, conservation proposals are often focused on a single flagship or umbrella species taken as representative of an entire assemblage requirements. Our aim is to identify and evaluate the role of coexistence areas at local scale as conservation tools, by using distribution data of two endangered birds, the Little Bustard and the Great Bustard. Presence-only based suitability models for each species were built with MaxEnt using variables of substrate type and topography. Probability maps of habitat suitability for each species were combined to generate a map in which coexistence and exclusive use areas were delimitated. Probabilities of suitable habitat for each species inside coexistence and exclusive areas were compared. As expected, habitat requirements of Little and Great Bustards differed. Coexistence areas presented lower probabilities of habitat suitability than exclusive use ones. We conclude that differences in species habitat preferences can hinder the efficiency of protected areas with multi-species conservation purposes. Our results highlight the importance of taking into account the role of biotic interactions when designing conservation measurements.

4.1 Introduction

The distribution of species is the result of evolutionary, ecological or anthropogenic processes that operate at different spatial and temporal scales (Gaston, 2003; Wiens and Donoghue, 2004; Ricklefs, 2007; Braunisch et al., 2011). Climate has been described to play a major role in shaping the distribution of the species at continental and regional scales, while biotic interactions are generally considered secondary (Pearson and Dawson, 2003; Hampe, 2004) but see (Araújo and Luoto, 2007; Heikkinen et al., 2007). Land use and biotic interactions become relevant at local scale, at which they exert a major effect in the configuration of population and community dynamics (Martin, 2001; Pearson et al., 2004).

The presence of heterospecifics has been proposed as a factor influencing the habitat use of organisms at local scale (Morris, 2003*c*). Coexistence of sympatric species may be mediated by the segregation of shared resources (Chesson, 2000), for example, the differentiation of habitat preferences at landscape or at microhabitat scale (Kotler and Brown, 1988), or changes in a species' behavioural and food resource-use patterns (Martin and Martin, 2001). Thus, direct or indirect interactions may condition the occurrence of heterospecifics in space and further, the fitness of the individuals (Martin and Martin, 2001). This may be especially relevant for species subject to conservation efforts, since potential changes in habitat use patterns due to biotic interactions may affect their distribution at local scale (Morris, 1989; Martin, 2001; Delgado et al., 2013).

In recent years, conservation issues from both theoretical and applied approaches have been increasingly addressed by the use of species distribution models (SDMs) (Araújo et al., 2004; Martínez-Meyer et al., 2006; Titeux et al., 2007; Kremen et al., 2008; Braunisch et al., 2011). SDMs use species occurrence records to infer the environmental conditions under which a species exists in a particular context and further, they allow to predict potential geographic distribution areas. Despite the potential importance of biotic interactions in determining the spatial distribution patterns of species at fine scale, SDM studies usually focus on single, often keystone or umbrella species (Braunisch et al., 2011; Wilson and Roberts, 2011). However, the efficacy of umbrella and flagship species as conservation tools for protecting other species in the community has been questioned (Andelman and Fagan, 2000; Caro et al., 2004), and several studies have highlighted the importance of considering more than one species in designing successful conservation measures (Carroll et al., 2001; Zipkin et al., 2010). Conservation efforts should be directed towards groups of interacting species, focusing on areas that encompass species assemblages despite the lack of information about interaction networks (Peterson et al., 2011).

In this context, the present study focuses in two steppe bird species which coexist in many areas of their distribution range: The Little Bustard (*Tetrax tetrax*) and the Great Bustard (*Otis tarda*). The two species are of high conservation concern since both are globally endangered and classified as near threatened and vulnerable respectively (IUCN, 2012). Nowadays, Spain holds more than half of their global population (García de la Morena et al., 2006; Palacín and Alonso, 2008), being agricultural intensification and the increase of infrastructure development two major causes of population decline and distribution shrink (Morales and Martín, 2002; García de la Morena et al., 2006). The Little Bustard is a medium sized steppe bird, which prefers heterogeneous agricultural landscapes that maintain a high proportion of fallows and short natural vegetation (Wolff et al., 2001; Morales et al., 2005*b*). The Great Bustard is one of the heaviest flying birds and shows preference for stubbles, leguminous crops and fallows, although its habitat selection pattern changes seasonally and differs greatly between regions (Lane et al., 2001; López-Jamar et al., 2011). Both species avoid man-made structures, such as buildings, roads and tracks (Lane et al., 2001; Suárez-Seoane et al., 2002; Silva et al., 2004). To the best of our knowledge, no studies have been conducted at local scale on the Little and the Great Bustards together in order to integrate their habitat preferences for the management of areas in which both species coexist.

Therefore, the aim of this study is to provide useful guidelines for the conservation of these two sympatric species with different habitat preferences through the identification and environmental characterization of coexistence areas at landscape scale. The delimitation of areas in which species are more likely to coexist might help focusing management efforts on the benefit of both species. We discuss the implications of using coexistence areas to conserve species that differ in their habitat preferences.

4.2 Methods

Ethics Statement

The present study did not required the capture or handling of protected or endangered animals. All data about species' locations were collected by observation at distance using binoculars. The described field studies were carried out on privately-owned farms with the permission of farmers.

Study sites

The study was carried out in two localities of central Spain, Campo Real sited in Madrid province (40°19′N, 3°18′W. 1 145 ha) and Calatrava, in Ciudad Real province (38°54′N, 3°53′W. 9 016 ha). Both regions are under a Mediterranean climate with annual mean precipitations around 550 mm. These sites are flat to slightly undulated, encompassing mosaics of different agrarian substrates. Extensive dry cereal croplands and ploughed lands make up more than 50% of the surface, with a varying cover of fallows of different ages, leguminous crops and interspersed patches of olive groves, vineyards and fruit tree orchards. Pasturelands and scrublands are also present but in a low percentage.

Little and Great Bustard data

Little and Great Bustard data were collected between March - April 2008 and 2009 in Calatrava and April - May 2011 and 2012 in Campo Real, during the period of reproductive activity of both species (Cramp and Simmons, 1980). Surveys were made by car routes throughout the available roads and tracks that cover the entire study site, stopping at every 500 m to ensure the record of all individuals, which were geo-referenced. Each study site was surveyed simultaneously by two car-teams, each composed by two experienced observers and covering a half of the study area, in order to fully cover the study site in a single bustard daily activity period. Surveys were made within the first three hours after daybreak and the three hours before sunset since this is the moment of highest activity, and thus individuals are easier to detect (Cramp and Simmons, 1980). Only Little Bustard males were considered in this study since females are very difficult to observe due to their secretive behaviour. The detectability of Little Bustard males and Great Bustard males and females were almost complete since the vegetation height is relatively low at this time of the year. In addition, Little Bustard males were also detected acoustically. The Great Bustard presents a lek mating system in which individuals tend to aggregate around conspecifics (Morales and Martín, 2002; Alonso et al., 2004). Thus, Great Bustard individuals observed in the same flock were considered as a single occurrence record in subsequent analyses in order to avoid the potential effects that conspecific clustering could have in the modelling process.

Environmental predictors

We used as environmental predictors variables related to substrate types and topography according to existing ecological knowledge on the species (Lane et al., 2001; Suárez-Seoane et al., 2002; Morales et al., 2005*b*; López-Jamar et al., 2011). All the environmental variables were rasterized for model calibration, considering a cell size of 50 x 50 m. Land-use variables were extracted from land-use maps elaborated from field surveys in each study site and year. Fields on land-use maps were classified regarding their potential to affect the presence of Little and Great Bustards. Thus, agricultural habitat types were: 1) arable lands, including cereal crops and ploughed lands, 2) leguminous crops, which are important for both Little and Great Bustards (Martínez, 1994; Salamolard and Moreau, 1999; Lane et al., 2001), 3) young fallows (hereafter referred to as fallows), 4) fallows of more than two years and low height scrublands (hereafter called natural vegetation), 5) dry woody cultures which include olive groves and vineyards, 6) others, which comprises urban substrates, fruit tree orchards and forest (Fig. 4.1). Land-use rasters reflected the proportion of the corresponding land use inside each cell. Land-use proportion was calculated taking into account all land-use categories, so that the sum of all of them was 1 for each cell. As it is highly recommended to reduce the number of variables for model calibration (Elith et al., 2011), the variable Others was not considered for the analysis since both species avoid the agricultural substrates enclosed in this category (Cramp and Simmons, 1980; Salamolard and Moreau, 1999).

A topography position index (TPI) was also calculated from the digital elevation model, constructed from maps of five meter elevation contour lines. This index was calculated as the elevation value of each cell minus the mean elevation of the neighbouring cells within a particular radius. In this study, a radius of 250 m was selected according to the biological characteristics of the species, given their size and their lek mating system (Jiguet et al., 2000; Morales and Martín, 2002). Therefore, it classifies each cell regarding the elevation of the neighbour cells, reflecting how visible a particular location is. From a behavioural point of view, the selection of areas according to their visibility could result from a trade-off between being detected by conspecifics and concealment from potential predators (Aspbury and Gibson, 2004).

Habitat suitability models of Little and Great Bustards

MaxEnt was selected for modelling the spatial distribution of each study species since it is a presence-only approach. This is a machine-learning

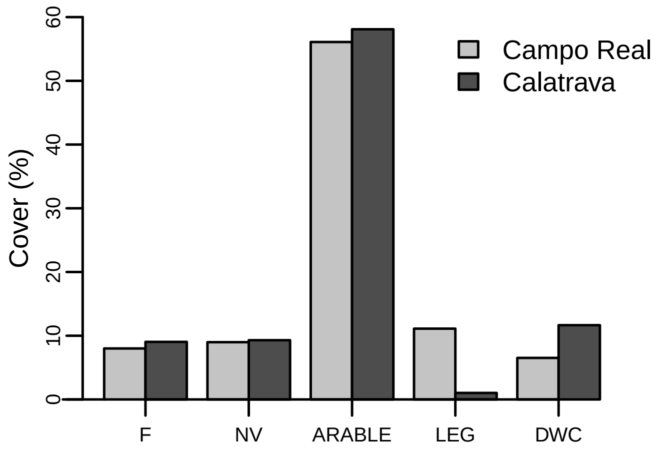

Figure 4.1: **Land use cover in the study sites**. Cover percentage of the land uses considered for MaxEnt modelling in 2011 in Campo Real and 2008 in Calatrava (F: short term fallows, NV: natural vegetation encompassing long term fallows and low height scrubs; Arable: cereal fields and ploughed lands; LEG: leguminous crops; DWC: dry woody cultures).

method based on the principle of maximum entropy (Jaynes, 1957) that has widely been employed in many ecological studies (for further details see Phillips et al., 2004; Elith et al., 2011). MaxEnt models have been proved to yield one of the highest quality predictions among several modelling methods and the best performance at low sample sizes (Hernandez et al., 2006; Pearson et al., 2007; Wisz et al., 2008).

The species distribution modelling required two independent set of observations, one for calibrating the model and the other for evaluating model predictions (Peterson et al., 2011). Models were built separately for each species and study site with datasets from years 2008 and 2011 for Calatrava and Campo Real respectively. The regularization parameters to reduce model over-fitting were selected automatically by the program (Elith et al., 2011). Predictive maps of probability of habitat suitability for each species and study site were built from calibration datasets and subsequently transformed to Boolean maps of presence/absence by selecting a threshold. We decided to use the average suitability approach (Cramer, 2003), which fixes the threshold at the mean of all predicted cell values from the calibration dataset. This approach was chosen because it does not require true absence data and because of its effectiveness and simplicity (Liu et al., 2005).

Models were evaluated using 2009 and 2012 datasets respectively for Calatrava and Campo Real. Model evaluation should deal with two aspects, the performance and the significance of the model (Peterson et al., 2011). First, model performance shows how well or poorly the model classifies presence and absence of the species. Omission error rate (the proportion of presence occurrence records of the evaluation dataset that fall in an area predicted as unsuitable for the species) was used as a measure of model performance, expecting low omission rates for good models (Peterson et al., 2011). This measure of model performance was selected because it does not need true absence records for its calculation (Peterson et al., 2011). Second, it is also necessary to assess model significance, ie. whether the model predicts presence occurrence records from the evaluation dataset better than expected under random prediction (Peterson et al., 2011). Thus, one-tailed binomial tests (one per model) were performed to evaluate whether the proportion of correctly classified occurrences differs from the proportion of area predicted as presence by the model.

Coexistence and exclusive use areas of Little and Great Bustards

Since we were mainly interested in the delimitation of areas in which both species might coexist, a coexistence map was built in each study site. Coexistence maps were generated by superimposing both the Little and the Great Bustard Boolean maps, generating a new one with four cell types: 1) cells predicting presence of both species, 2) cells predicting only Little Bustard presence, 3) cells predicting only Great Bustard presence and 4) cells predicting absence of both species. The surface and density of each species for coexistence, exclusive use and absence areas were calculated in each study site. In addition, means of each land use cover in coexistence and exclusive use areas were calculated in order to describe the land use composition of each area type. Finally, we evaluated habitat suitability differences between coexistence and each species exclusive use areas. In order to eliminate the spatial trends of the data we used a third order polynomial regression with the spatial coordinates (Legendre and Legendre, 1998). Residuals of the regression were analysed by a Student t test to determine whether probabilities of habitat suitability differed between these area types for both species.

Environmental predictors were generated using ArcGis v9.3 program (ESRI, 2007). TPI was built by the extension "Topographic Position Index (TPI) v 1.2" (Jennes, 2006) and MaxEnt modelling was performed by the package "dismo" (Hijmans et al., 2012) for the R software v2.14 (R Development Core Team, 2013).

4.3 Results

Campo Real presented densities of 4.02 Little Bustards and 5.6 Great Bustards/km^2 in 2011, higher than the 2.48 Little Bustards and 1.9 Great Bustards/km^2 found in Calatrava 2008.

Habitat suitability models of Little and Great Bustards predicted the distribution of evaluation points accurately and better than random for the two study sites (Table 4.1). Little Bustard models predicted a greater extension of presence area than Great Bustard models for both study sites. Little Bustard model in Campo Real showed the highest predicted presence area as well as the lowest omission error rate, predicting correctly almost all the evaluation data set (Table 4.1).

Table 4.1: Percentage of predicted presence area of Little and Great Bustards in Campo Real 2012 and Calatrava 2009 (corresponding with the evaluation datasets). Omission error rates (proportion of presence occurrence records of the evaluation dataset that fall in an area predicted as unsuitable for the species) and p-values of one-tailed binomial test for evaluating model performance and significance respectively are provided.

	Campo Real		Calatrava	
	Little bustard	Great bustard	Little bustard	Great bustard
Predicted area(%)	72.07	49.73	58.50	54.55
Omission error rate	0.09	0.33	0.21	0.11
P	0.003	0.0375	<0.001	<0.001

Models for Little Bustard were influenced mainly by the presence of dry woody cultures and fallows as shown by their contribution percentages (i.e. the relative contribution of each variable to the model. Table 4.2). The response was positively related to fallow cover while the cover of dry woody cultures was negatively related with the predicted probabilities of habitat suitability in both study sites (Fig. 4.2). The cover of leguminous crops was also an important variable, positively related with the Little Bustard predicted distribution in Campo Real (Fig. 4.2). TPI was one of the most relevant environmental predictors in Calatrava, with highest predictive power at values around 0, indicating a preference for flat zones (Fig. 4.2).

Differences between study sites were greater in Great Bustard models. Arable land appeared as one of most relevant predictors, especially in Calatrava's model (Table 4.2). Campo Real's model was highly influenced also by the presence of fallows and leguminous crops, both showing a positive relationship with the predicted probability of habitat suitability (Fig. 4.2).

In Campo Real, 45.33% of the surface corresponded to the coexistence area (Fig. 4.3a). The Little Bustard exclusive use area presented a cover value of 20.78%, whereas the Great Bustard exclusive area reached a lower cover of 12.62%. In Calatrava, the predicted coexistence area accounted for the 36.15% of the surface (Fig. 4.3b), lower than the value found in Campo Real. The area predicted as exclusively used by the Little Bustard in Calatrava reached 22.38% cover, while the predicted Great Bustard exclusive area was 20.80%.

In Campo Real, the density of Little Bustards in the predicted coexistence area was slightly higher than in the exclusive use area (Table 4.3). The same pattern was found for Great Bustards in Calatrava site. However, densities in coexistence area were lower than in exclusive use area in the case of Little Bustard in Calatrava and Great Bustard in Campo Real (Table 4.3). Regarding land use composition, Little Bustard exclusive use areas showed a higher cover of fallows and natural vegetation than Great Bustard exclusive use and coexistence areas in both study sites (Fig. 4.4). Little Bustard exclusive use area showed a lower value of arable surface in Calatrava than in Campo Real. In addition, this value was also lower

Table 4.2: Contribution percentages of each environmental predictor (percentage of each land use type, and Topographic position index at 250 m resolution) to each species and study site models yielded by MaxEnt. Models were built using Little and Great Bustard observations from 2011 for Campo Real and 2008 for Calatrava.

	Campo Real		Calatrava	
	Little bustard	Great bustard	Little bustard	Great bustard
Fallows	20.60	37.41	43.16	5.59
Natural Vegetation	0.56	5.98	4.49	1.331
Arable	11.39	16.32	2.10	77.82
Dry woody cultures	44.94	5.45	20.24	10.36
Leguminous crops	19.74	28.08	0.50	1.10
TPI250	2.77	6.78	29.49	3.81

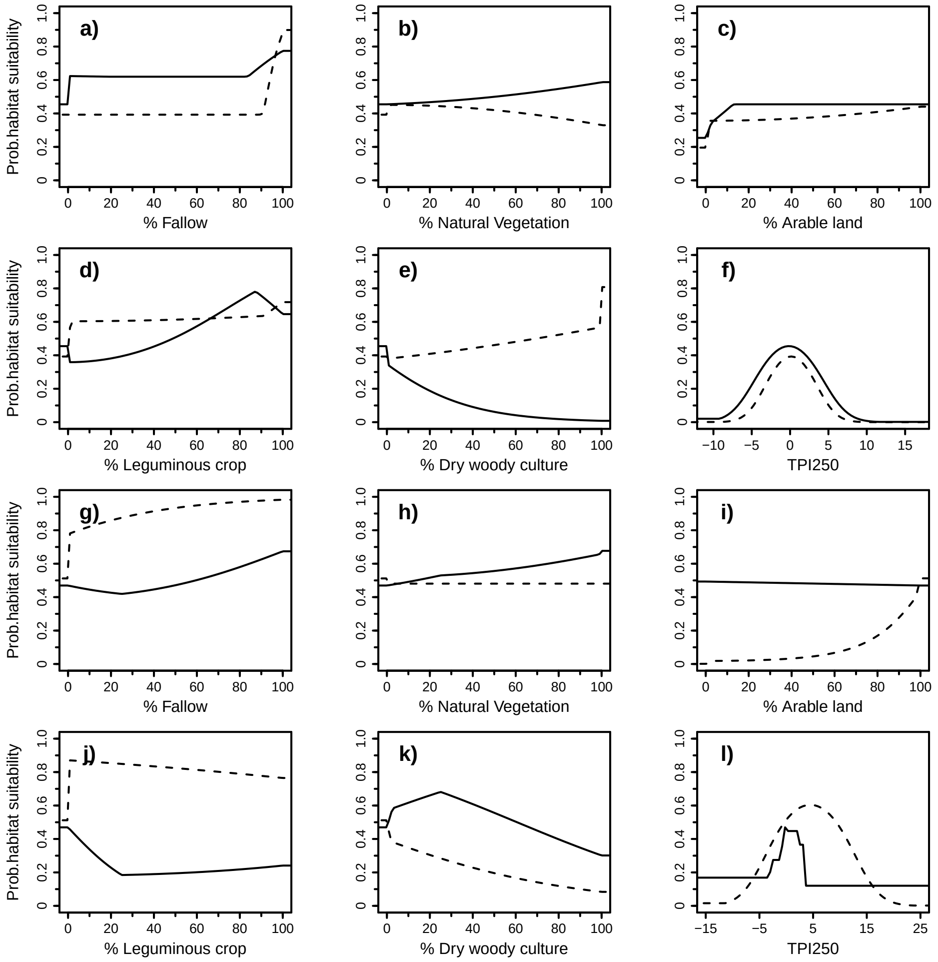

Figure 4.2: **Probabilities of habitat suitability for the environmental predictors.** Maxent response curves representing the probability of habitat suitability for each environmental predictor (percentage of land uses and Topographic position index at 250 m resolution, TPI250) for the study species in Campo Real (a-f) and Calatrava (g-l). Solid lines correspond to Little Bustard response curves while broken lines correspond to Great Bustard response curves.

than the cover of Great Bustard exclusive use and coexistence areas in both study sites (Fig. 4.4).

The residuals of the polynomial regression were significantly different between coexistence and exclusive use areas for both species in both study sites. The Little Bustard showed higher probabilities of habitat suitability in areas where only this species was predicted as present than in areas in which it might coexist with the Great Bustard (Campo Real: $t_{0.05;1868.391}$ =12.047, *P* <0.001; Calatrava: $t_{0.05;\,9703.717}$ =98.200, *P* <0.001, Fig. 4.5). The

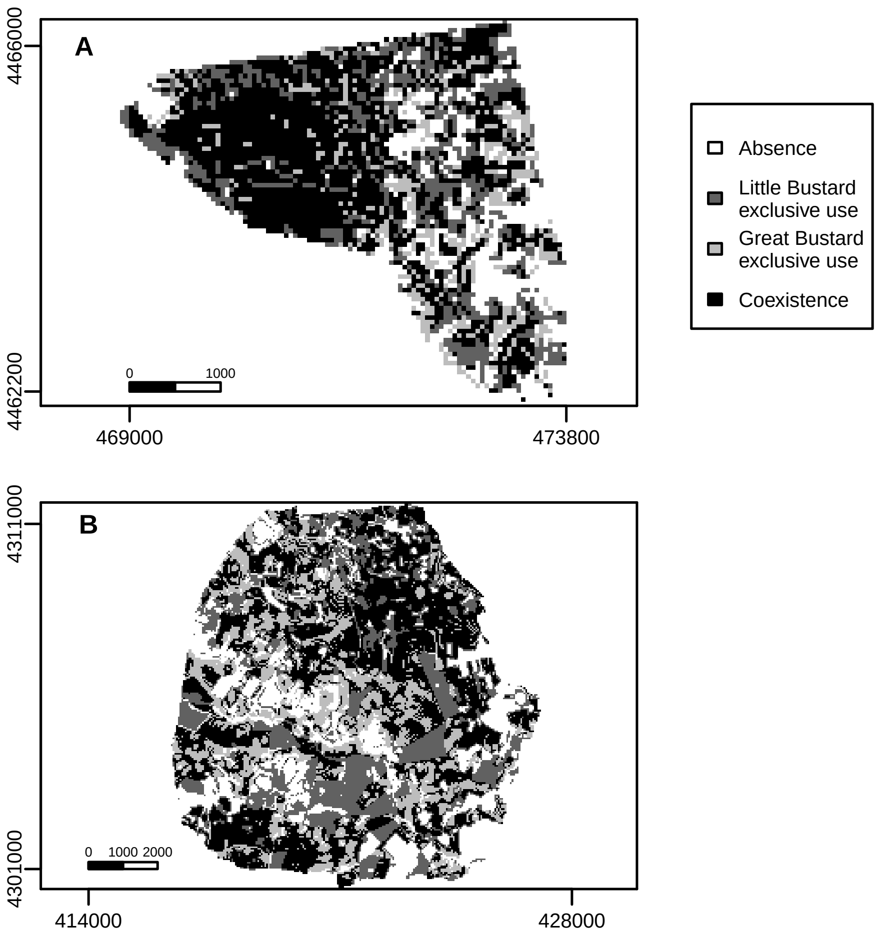

Figure 4.3: **Coexistence maps of little and great bustard.** Maps of Little Bustard and Great Bustard coexistence for 2011 in Campo Real (a) and 2008 in Calatrava (b), showing also areas of exclusive use and areas in which both species were predicted to be absent. The scale bar is given in meters.

same pattern was found for Great Bustards in Campo Real ($t_{0.05;\,1150.884}$ =21.817, *P* <0.001), although this species showed higher probabilities of habitat suitability in coexistence areas than in areas of exclusive use in Calatrava ($t_{0.05;\,13177.676}$ =-27.053, *P* <0.001, Fig. 4.5).

4.4 Discussion

The models yielded by MaxEnt for two endangered bird species linked to pseudo-steppe landscapes, the Little and the Great Bustards, were

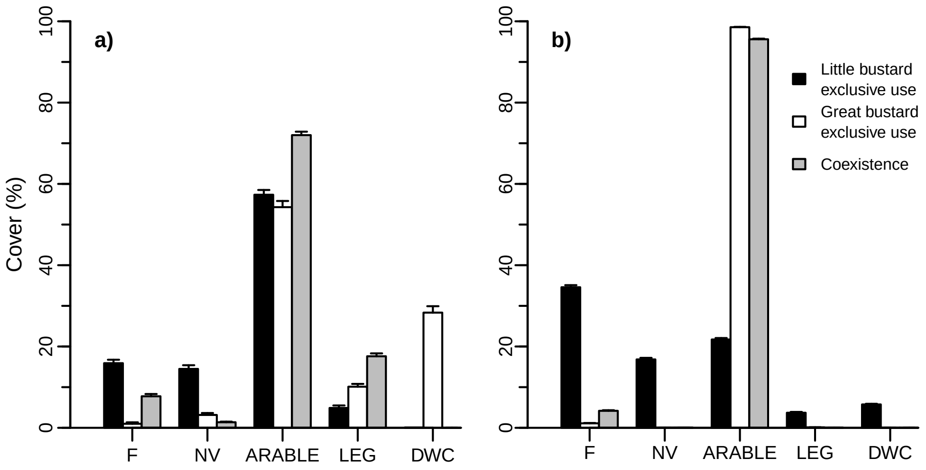

Figure 4.4: **Land use cover in each area type.** Mean and standard error of land use cover in the predicted Little and Great Bustard exclusive use and coexistence areas for 2011 in Campo Real (a) and 2008 in Calatrava (b) (F: short term fallows, NV: natural vegetation encompassing long term fallows and low height scrubs; Arable: cereal fields and ploughed lands; LEG: leguminous crops; DWC: dry woody cultures).

able to predict suitable areas accurately. It is important to note that Little Bustard results correspond only to males and conclusions may not apply to females which might show a different habitat selection pattern. Our results showed that models are not only species-specific but also context-dependent. Little Bustard presence areas seem to be the result of

Table 4.3: Densities of Little (males/km^2) and Great Bustards (individuals/km^2) in the different area types generated by superimposing the predicted presence maps of Little and Great Bustards for 2011 in Campo Real and 2008 in Calatrava.

	Campo Real		Calatrava	
	Little bustard	Great bustard	Little bustard	Great bustard
Absence area	2.46	0.41	0.81	0.05
Little bustard exclusive area	5.04	0.84	4.71	0
Great bustard exclusive area	0.69	5.54	1.23	1.01
Coexistence area	5.20	3.66	2.52	1.35

a more complex combination of different substrate types while the Great Bustard shows a higher dependence on arable fields. Coexistence areas are also context-dependent at local scale and tend to harbour less suitable habitat than areas of exclusive use. The results found in this study have implications for conservation and management strategies.

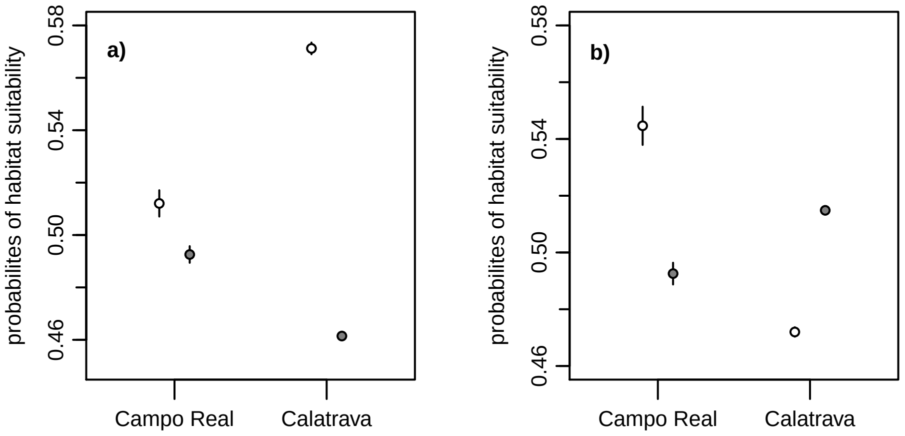

Figure 4.5: **Probabilities of habitat suitability of coexistence and exclusive use areas.** Mean and 95% confidence interval of probabilities of habitat suitability in coexistence and exclusive use areas for the Little (a) and Great Bustards (b) in Campo Real 2011 and Calatrava 2008. Student t tests were performed with the residuals of the polynomial regression although original probabilities are shown for the sake of interpretation. Probability means of coexistence areas are represented as gray dots and probability means of exclusive use areas are represented as white dots.

The Little and the Great Bustards have been the object of many habitat selection studies due to their interest as lekking species and their worrying conservation status caused by changes in agricultural practices during the last decades. Our models showed that both species benefit from the presence of short term fallows in accordance with previous studies (Morales et al., 2005*b*; Delgado et al., 2010; López-Jamar et al., 2011). Little Bustard males' preference for short term fallows as habitats that ensure conspicuousness for sexual displaying and food supply (Morales et al., 2005*b*; Delgado et al., 2010), is reflected in our models by their high contribution percentages. In the case of Great Bustard, the importance of fallow cover in explaining the distribution pattern seems particularly context-dependent. In Campo Real, fallows appear as a relevant substrate type for Great Bustard while the effect on its distribution is minimal in Calatrava. Leguminous crops play also an important role for both species when they are present in the landscape. In the case of Little Bustard, leguminous crops reach a similar importance in the model as fallow lands in Campo Real, but remain as a minor variable in Calatrava, where the presence of this substrate is clearly marginal.

However, these species differ in their responses to other landscape variables, indicating some level of niche segregation at local scale. For instance, the relevance of arable lands is clearly different between species, being the cover of this land use more important for the Great Bustard. The presence of dry woody cultures plays a minor role in the distribution pattern of the Great Bustard but not for the Little Bustard, which avoids vineyards and olive groves in accordance with previous studies (Morales et al., 2005*b*; Lapiedra et al., 2011). Finally, the importance of topography varies between species and study sites. The Little Bustard shows in both study sites the same preference for flat zones where they are visible to other individuals during the sexual display season. However, the relevance of flat zones changes with the study site, being especially high in Calatrava, which might be due to its higher variability in topography. In the case of the Great Bustard, its distribution pattern is hardly affected by topography, while land use variables acquire a major role in determining the species' distribution in both study sites. The differences found between study sites might be indicating that habitat selection depends on the particular landscape composition. This is especially noteworthy for the Great Bustard, which may be explained by its greater niche width (Morales et al., 2006). Nevertheless, results might also be influenced by the SDMs' dependency on the environmental context, since the model calibration process depends on the particular combination of variables that occurs in each study site (Peterson et al., 2011). Although the spatial scale selected may influence observed response patterns, this seems to occur only at high cover values of some land uses (Fig. 4.2). In any case, results are consistent with the existing habitat selection knowledge for the species, as pointed out previously.

Our results show that concentrating conservation efforts on preserving the habitats most preferred by one species at local scale may be detrimental for the other given their different requirements, leaving habitats relevant to that species without protection. Therefore, a multi-species approach may help prioritize conservation efforts on coexistence areas. Our study shows that coexistence and exclusive use areas of Little and Great Bustards differ in their habitat features, which may also vary in relation to the local environmental context. The area predicted as suitable for the coexistence of these species is greater than the surface of each species exclusive use in both study sites. However, different situations emerge when looking at probabilities of habitat suitability and actual densities. In two cases, Little Bustard in Calatrava and Great Bustard in Campo Real, the corresponding exclusive use area harbours better habitat conditions for the target species and also higher density. Thus, the coexistence area might correspond to suboptimal zones for the species. However, we cannot disentangle whether the low probabilities of habitat suitability predicted for coexistence areas are due to poor habitat quality or to the avoidance of heterospecifics since both factors can affect distribution patterns (Morris, 2003*c*). The other two cases (Little Bustard in Campo Real and Great Bustard in Calatrava) present similar densities but different habitat suitability for each area type. The exclusive Little Bustard area in Campo Real shows higher habitat suitability than the coexistence area. It seems that Little Bustards might occupy less suitable areas in the absence of enough space or good quality habitats. However, the pattern for Great Bustards in Calatrava is the opposite, with higher probabilities of habitat suitability in coexistence areas. Therefore, the coexistence area in Calatrava seems to reflect Great Bustard habitat preferences whereas Little Bustards concentrate mainly in their exclusive use area. Low density might allow Little Bustards to occupy their most preferred habitat features without using areas suitable for the Great Bustard. It is noteworthy that each species presents lower densities in the absence and exclusive use areas of the other species, a fact that might support the hypothesis of segregation between these two steppe-birds. Consequently, by prioritizing the preservation of coexistence areas, we may be protecting low quality habitats that are being used by the two (or more) species because higher quality exclusive areas are scarce, thus preventing natural between-species avoidance.

Some interesting conservation consequences arise from this study. Both species seem to benefit from high percentage of short-term fallows and leguminous crops at landscape scale, so that promoting the application of agri-environmental schemes that favour the concentration of these habitats in small areas in the landscape is desirable. In this context, Concepción and Díaz (2010) emphasized that the effects of agri-environmental schemes are limited by their application at field level, and plans designed at landscape level are needed to maintain the mosaic structure of this extensive cereal croplands. For instance, the traditional two-year rotation system known as Iberian dry-farming would benefit species linked to extensive cereal croplands since it maintains a complex and dynamic structure of different and complementary land uses (Suárez et al., 1997). However, their different habitat preferences constrain the potential delimitation of coexistence areas encompassing high quality habitats at local scale. In order to meet species' spatial requirements, protected areas for these (and probably other) steppe birds should cover territories large enough to allow their coexistence by the selection of their preferred areas, or their tendency to segregate in space. Therefore, the role played by biotic interactions in a community should be considered when designing conservation strategies at least at local scale. Finally, the context-dependence of habitat selection in these species advices designing conservation measures for particular landscape situations.

Spatial distribution modelling is a useful tool for species conservation since it can integrate behavioural traits and landscape measurements and helps identifying general responses to environmental variables. In addition, it allows the extrapolation of results to other regions in order to preserve non-occupied areas of suitable habitat that could be potentially colonized at long term (Hanski, 1999). This is important even in the case of the Great Bustard whose strong breeding philopatry constrains the colonization of unoccupied areas (Martín, 2009).

4.5 Conclusions

The identification of coexistence areas of two farmland birds at local scale described in this study provides insightful results that might apply in other cases. Concentrating efforts on one umbrella species may be hazardous if that species does not adequately reflect the ecological requirements of sympatric heterospecifics. Hence, a multi-species approach may be more adequate, and the identification of coexistence areas may provide an idea of the spatial requirements of a particular assemblage. However, when coexistence areas correspond to suboptimal habitats for species that would be otherwise segregated due to their different ecological requirements, focusing efforts on these areas may be misleading at local scale. Moreover, the influence of the local environmental context in determining coexistence areas is not detected at broader scales, at which species sharing requirements overlap in their distribution ranges. Finally, integrating information of species distribution models built at local scale might lead to a better understanding of general patterns at broader scales (Araújo and Luoto, 2007).

4.6 Acknowledgements

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CHAPTER 5

Not only habitat but also sex: factors affecting spatial distribution of Little Bustard *Tetrax tetrax* families.

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Abstract

Species distribution patterns are determined not only by habitat preferences but also by biotic factors. Particularly, the presence of conspecifics may yield different types of benefits and costs for the individuals involved. This study analyses the spatial distribution of Little Bustard families during the breeding season in relation to the distribution of male core areas in three Spanish populations of the species. A compositional analysis was used to evaluate habitat selection and the habitat types most preferred by females with offspring. Spatial analyses were performed to evaluate the proximity of Little Bustard families to male core areas and male displaying sites. The habitat selection pattern was similar between regions, with semi-permanent vegetation and stubbles as most preferred habitats while others, such as ploughed land, were avoided. Families were located closer to male core areas than expected by chance and were spatially associated to male displaying sites. Little Bustard females may obtain different benefits from this spatial association such as access to more food resources and chances for second matings after a clutch loss. Also in stubbles, the capture of prey by chicks would be easier and semi-permanent habitats would serve as shelter. These results highlight the importance of intraspecific interactions in the definition of the habitat selection pattern of females and families. This study shows how spatial point pattern analysis may be a useful tool for integrating landscape and behavioural ecology.

5.1 Introduction

Habitat selection is one of the most important processes used to explain and predict the spatial distribution of species at different scales (Guisan and Zimmermann, 2000; Suárez-Seoane et al., 2002; Guisan and Thuiller, 2005), although biotic interactions may modify the distribution patterns based on pure habitat requirements (Rosenzweig, 1981; Pearson and Dawson, 2003; Araújo and Luoto, 2007). In some cases, aggregated spatial distribution of conspecifics can be explained as a result of resource clustering (Cornulier and Bretagnolle, 2006), but individuals can also obtain direct benefits from settling near conspecifics (Stamps, 1988; Reed and Dobson, 1993; Danchin et al., 1998). The presence of conspecifics can be a cue to habitat quality (Boulinier et al., 1996; Beauchamp et al., 1997; Danchin et al., 1998; Serrano et al., 2001; Ward and Schlossberg, 2004) facilitating its assessment, which is often a difficult and time-consuming process (Slagsvold, 1986). Furthermore, individuals may display a clumped distribution pattern as an antipredatory strategy (Perry and Andersen, 2003; Kullmann et al., 2008) or to gather valuable information about mates during the breeding season (Höglund and Alatalo, 1995; Melles et al., 2009). Thus, it seems necessary to take into account both the landscape configuration and the behavioural traits of the species to describe spatial distribution patterns. However, studies that integrate behavioural ecology with landscape ecology are scarce due to the difficulties to integrate the different spatial scales involved in these approaches (Lima and Zollner, 1996; Melles et al., 2009).

The Little Bustard, *Tetrax tetrax*, is a medium sized Paleartic steppe bird whose distribution ranges from Morocco and the Iberian Peninsula to Central Asia (Del Hoyo et al., 1996). The populations of this species have suffered a drastic decline throughout its range mainly due to agricultural intensification (Goriup, 1994). Nowadays, the Iberian Peninsula holds more than half of the world's population (García de la Morena et al., 2006). The species occupies areas of extensive grassland or cereal farmland, characterized by a varying degree of heterogeneity of land uses depending on the prevailing landscape type (Morales et al., 2005*b*; Silva et al., 2010*a*). Habitat selection patterns of Little Bustard males have been well studied (Martínez, 1994; Jiguet et al., 2000; Morales et al., 2005*b*; Delgado et al., 2010; Ponjoan et al., 2012), showing a marked preference for fallows and legume crops, which can ensure conspicuousness during the sexual display thanks to the low vegetation height, but also a high availability of food (Martínez, 1998; Morales et al., 2008). However, the knowledge of the biology and habitat selection patterns of females is scarce (but see Salamolard and Moreau, 1999; Morales et al., 2008; Lapiedra et al., 2011), largely because of their extremely secretive behaviour during the breeding season, which makes female observation difficult to obtain. Contrary to male preferences, females seem to select habitats with higher vegetation cover and greater amounts of litter and green weeds which may provide shelter and food for themselves and their offspring (Salamolard and Moreau, 1999; Morales et al., 2008). Understanding the ecology of females, particularly those aspects related with breeding success, is essential to ensure the viability of Little Bustard populations (Morales et al., 2005*a*; Delgado et al., 2009).

The Little Bustard shows sexual dimorphism and males provide no parental care to offspring (Cramp and Simmons, 1980). The mating system has been described as an exploded lek (Jiguet et al., 2000), in which resources may influence settlement of male loosely aggregated territories (Traba et al., 2008), to which females are attracted and in which they may nest (Jiguet et al., 2000; Morales et al., 2013). In nidifugous species, such as the Little Bustard, female decisions at the moment of nesting should be the result of a trade-off between finding mating and nesting areas but also suitable places for rearing fledglings (Blomqvist and Johansson, 1995). However, to our knowledge, there are no studies that analyze the spatial distribution of Little Bustard families in relation to male display sites.

The aims of this study are (1) to analyze the habitat selection pattern of Little Bustard families during the breeding season; (2) to explore the role played by intraspecific relationships, namely the presence of males, to determine their spatial distribution.

5.2 Methods

Study area

The study was conducted in three areas located in central and northeast Spain dominated by a cereal pseudo-steppe landscape. Two sites were located in the Ebro Valley in Catalonia: Bellmunt (41°47′N, 0°57′E) and Belianes (41°35′N, 0°59′E) and the other one in the Spanish southern plateau, in Ciudad Real province (38°57′N, 3°56′E) (Table 5.1). The regions are all under dry Mediterranean climate, with annual precipitation means around 400 mm. These three study sites are included within important areas for the conservation of steppe birds in Spain (Traba et al., 2007).

The three study areas present very little natural vegetation cover due to changes in land use for agriculture and are dominated by cereal crops (more than 50% of their surface). In summer, dry cereal and legume crops become stubble fields (ST) after harvesting. Ploughed areas (PL), dry woody cultures (DWC, including olive groves, vineyards and almond tree orchards), same-year fallows (hereafter called simply fallows, F) and fallows older than two years and low height scrublands (both classified as natural vegetation, NV) were present in every study site. Other minor substrates (OTHERS) were fruit tree orchards, pastures and urban areas. In order to determine the availability of the different habitat types, land-use maps were drawn by assigning to each field one of the previous habitat types for each study area.

Little Bustard surveys

Little Bustard male surveys were carried out between April and May 2008, corresponding with the period of maximum sexual display activity of males in Spain (Cramp and Simmons, 1980). Surveys consisted of car routes using the existing rural track and road network, which is dense in the three areas, completely covering each site, along which survey points separated by 500 m were established. Observation time at each point was 10 min, during which all Little Bustard males detected within spotting scope reach were recorded. Males detected acoustically were searched for by spotting scope in order to determine their actual position, so that virtually all active males present were finally detected visually. One survey was made in each study area with two car-teams surveying simultaneously. Each survey was made within the first three hours after daybreak and the three hours before sunset, these being the period when males are more active and thus, easier to detect (see, for example, Morales et al., 2008; Delgado et al., 2010, for the same survey methodology). All the individuals were mapped and finally, maps were revised to detect potential double counts. Family surveys were carried out 7-31 July 2008, following the same procedure described for males. In this case, the number of fledglings was recorded and those observations with at least one Little Bustard fledgling were designated as family. The detectability of families might differ among substrate types given the secretive behaviour of females and chicks. However, cereal and leguminous crops were already harvested when surveys were carried out, allowing a nearly complete detection of families on stubbles (the dominant habitat). Special survey effort was made in the case of fallows and other habitat types with higher vegetation, which were carefully scanned for families. Productivity was measured as the number of fledgling per female.

Analysis of habitat selection

Family habitat selection was assessed by means of a compositional analysis for each area (Aitchison, 1986; Aebischer et al., 1993). This analysis compares the log-ratios of the used and the available habitats, avoiding misinterpretations owing to the lack of independence among the proportions of different types of substrates found inside family home ranges. Using arbitrary study area boundaries to obtain the different substrates' availability may lead to biases due to the fact that individuals were only monitored in part of their distribution range, or to substrate composition dissimilarities between the predefined boundaries of the study area and the real distribution of the organisms (Aebischer et al., 1993). Thus, a Minimum Convex Polygon (MCP) was drawn using the geo-references of all male and family locations. Then, availability of each substrate type was determined by extracting the information on land use maps for the MCP.

In order to establish family home range, each family observation was assigned a circular buffer with a 600 m radius. This buffer provides an area approaching the average Little Bustard family home range during the rearing period as estimated from radio-tracking by Lapiedra et al. (2011). This analysis was repeated for buffers of 400 and 800 m radius in order to determine whether results were sensitive to radius choice. Since similar results were obtained, hereafter only results of 600 m radius buffer are presented. The proportions of habitat types used by families were obtained by superimposing the defined home range of the families on maps of land use. Since compositional analysis requires that home range areas contain all available habitats, those habitat types not included within the home range were assigned proportion values of 0.00003, this being one order of magnitude lower than the minimum value found different from zero inside the family buffers (Aebischer et al., 1993; Bingham and Brennan, 2004; Delgado et al., 2010). Compositional analysis was conducted in two stages. First, the existence of a selection pattern other than random was tested by using Wilks' lambda (λ) statistic (Aebischer et al., 1993). Then, if the habitat selection pattern differed from random, the order of preference of each habitat type was calculated by constructing a matrix of means of the differences in the log-ratios of the proportions of the used and available habitats for all the individuals. A positive value shows that the habitat is selected, whereas a negative one indicates habitat avoidance. For each habitat its t-value was calculated, indicating whether its use differed significantly from random. Finally, all habitats were ranked according to the number of positive values that they contributed to the matrix (Aebischer et al., 1993).

Spatial distribution pattern

The fixed kernel method with least-square cross-validation (Worton, 1989; Seaman and Powell, 1996) was used to define the distribution of Little Bustard males during the period of sexual display from individual observations in each study area. This method has been frequently employed for estimating home ranges since it describes a territory in terms of a probabilistic model and is free of parametric assumptions of the data (Worton, 1989). Core areas (areas intensively used by animals) of displaying males were delineated by the "change in gradient" technique (Harris et al., 1990), analysing the number of males accumulation curve between consecutives isopleths. The core area was defined by the surface enclosed within the isopleth in which a first decline in the slope of the number of males accumulation curve was observed. Finally, core areas of the Ciudad Real population enclosed the territory within the 40% isopleth and core areas of the Bellmunt and Belianes populations were defined by the territory enclosed within the 50%. The area enclosed by the isopleths does not need to be continuous in space (Harris et al., 1990).

To analyse the spatial distribution of Little Bustard families in relation to male core areas several variables were calculated for each family observation: 1) The distance from the family observation to the closest male core area centroid, 2) the probability of male presence in the point where the family was sighted (calculated by means of the kernel function), 3) the mean of male presence probability inside the predefined family home range, 4) the maximum of male presence probability inside the predefined family home range and 5) the coefficient of variation of male presence probability inside the predefined family home range. In order to determine whether the spatial distribution of Little Bustard families follows a random pattern, 100 series of n random points (being n the number of families detected in the corresponding study area) were generated within each study area. The same variables calculated for the families were also calculated for each random point. The mean of the overall random points represents the mean of a randomly distributed population. A Hotelling's t-test was used to test the hypothesis of different means between families and the theoretical reference value of a randomly distributed population for each study area (Carrascal et al., 2008).

A bivariate Ripley's K function analysis was conducted with data from each study area to assess whether a spatial association between the location of males and females exists and at what scales it occurs (Wiegand and Moloney, 2004). This function analyses the spatial association between two different types of points and detects scale dependent changes in the spatial pattern. The null hypothesis of independence between the male and female point patterns was evaluated. Ripley's L function, a transformation of K function into a linear one, was used since it stabilizes the variance and makes the results easier to interpret (Ripley, 1981). Since the spatial aggregation between males and females could arise from a coincidental habitat selection pattern, we used a bivariate Ripley's K function to analyze the degree of spatial aggregation between females and the field's centroids of their preferred habitats, identified in the previous compositional analysis.

Compositional analysis and kernel smoothing parameters were performed using the package "adehabitat" (Calenge, 2006) for the R software v.2.14 (R Development Core Team, 2010), while the ArcGis 9.3 program (ESRI, 2007) was employed to calculate kernels. Spatial variables were calculated in R software v.2.14, Hotelling t-tests were performed by the package "ICSNP" (Nordhausen et al., 2012) and Ripley's functions were performed by the package "ads" (Pelissier and Goreaud, 2010), both for the R software v.2.14.

5.3 Results

Different male, family and fledgling densities were found between study areas (Table 5.1). Bellmunt and Belianes showed similar values of male density although the highest family and fledgling density were found in Belianes. Ciudad Real was the locality with the lowest male, family and fledgling densities.

Table 5.1: Description of study area with corresponding densities of males, families and fledglings (in 2008). Productivity (measured as the number of fledglings per female) and the number of families are also given.

	Study area		
	Bellmunt	Belianes	Ciudad Real
Area (ha)	1794	1839	10698
Number of families	12	34	5
Number of males/100 ha	4.24	4.02	2.34
Number of families/100 ha	0.67	1.85	0.05
Number of fledglings/100 ha	1.23	2.39	0.09
Productivity	2.44	1.30	1.11

Habitat selection pattern

The availability of the different habitats differed between study areas, although stubbles remained as the most abundant habitat in all localities (Fig. 5.1). The compositional analysis showed that habitat selection by Little Bustard families differed significantly from random in all study areas (Bellmunt: $\lambda = 0.0596$, $P < 0.001$; Belianes: $\lambda = 0.3575$, $P < 0.001$; Ciudad Real: $\lambda = 0.1048$, $P = 0.046$). In the three study sites there was a positive selection of stubbles and semi-permanent vegetation habitats (being fallows in Ciudad Real and natural vegetation in Bellmunt and Belianes, Table 5.1). Ploughed lands and ”Others”tended to be avoided inside Little Bustard family home ranges (Fig. 5.1).

Table 5.2: Rank matrix of substrates based on the comparison between the proportion of available habitat within the total Minimum Convex Polygon (minimum area enclosing all the Little Bustard observations) and the proportion inside the home range of the families in three study areas. Each element in the matrix represents the mean differences between usage and availability replaced by its sign. Triple sign indicates significant deviation from random with p < 0.05. The rank reflects substrate preference based on the sum of positive values in each row, where high values indicate a greater preference for that substrate. Substrate abbreviations see Fig. 5.1.

Study site	Substrate type (usage/availability)	F	NV	ST	PL	DWC	OTHERS	Rank
Bellmunt	F		− − −	− − −	−	−	−	0
	NV	+++		+	+++	+	+++	5
	ST	+++	−		+++	+	+++	4
	PL	+	− − −	− − −		−	−	1
	DWC	+	−	−	+		−	2
	OTHERS	+	− − −	− − −	+	+		3
Belianes	F		−	− − −	+	+	+++	3
	NV	+		−	+++	+	+++	4
	ST	+++	+		+++	+++	+++	5
	PL	−	− − −	− − −		−	+	1
	DWC	−	−	− − −	+		+++	2
	OTHERS	− − −	− − −	− − −	-	− − −		0
Ciudad Real	F		+++	+	+	+	+++	5
	NV	− − −		− − −	−	−	−	0
	ST	−	+++		+	+	+++	4
	PL	−	+	−		+	+	3
	DWC	−	+	−	−		+	2
	OTHERS	− − −	+	− − −	−	−		1

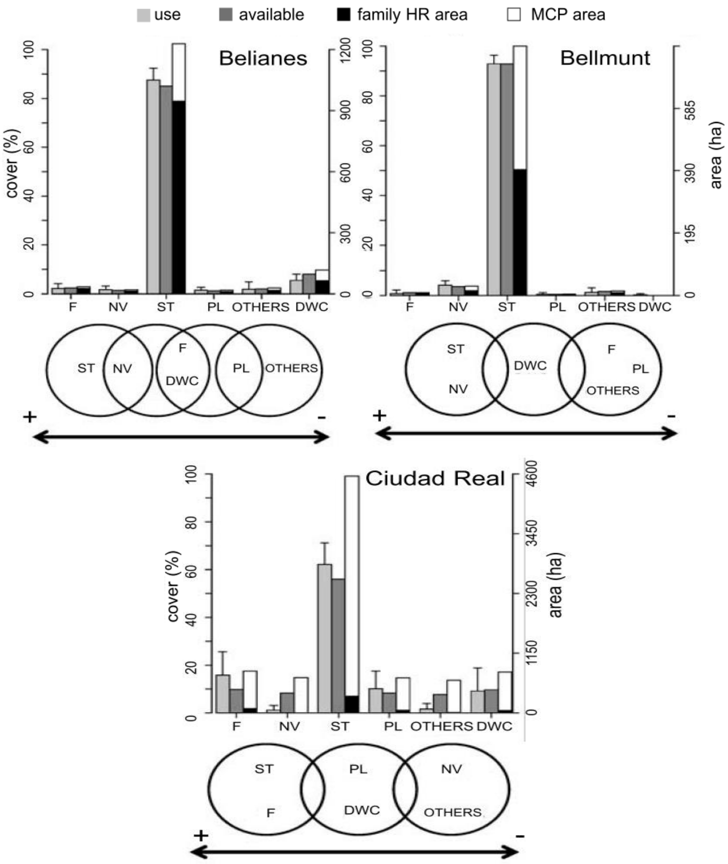

Figure 5.1: Proportion of available substrates within the total MCP and the mean proportion and standard deviation of the substrates within the assigned home range of the families in three study areas. F – fallows; NV natural vegetation; ST – stubbles; PL – ploughed areas; DWC – dry woody cultures; OTHERS – pastures, fruit tree growing and urban areas. Also the area of each habitat type inside the MCP and the area of the overall family home range surface are provided. Below each graphic a diagram with the interpretation of the Compositional Analysis is provided complementing results showed in Table 5.2. Habitats within the same circle do not differ significantly in their use by Little Bustard families. Arrows represent a gradient from most preferred (+) to less preferred (−) habitats.

Spatial distribution pattern

Families showed distances to male core areas significantly lower than expected by chance in all study areas (Table 5.3). The probability of male presence in a point where a family was located was significantly higher than the theoretical value of a randomly distributed population in Bellmunt and Belianes but did not differ from random in Ciudad Real. However, the same trend was found in the three study sites, with values of male presence higher than expected by chance. The coefficient of variation of male presence probability inside family home range areas presented significant differences in all study areas, taking values lower than expected from random. Likewise, the mean and maximum of male presence probability inside the family home ranges were significantly different from random in Bellmunt and Belianes, with values higher than reference ones. Thus, family observations were found closer to areas which had higher probability of male presence during the mating period and this probability showed less variation inside family home ranges than expected by chance.

Family locations were spatially aggregated with displaying male locations in all study areas (Fig. 5.2). Regarding the spatial relationship between families and their preferred habitat types shown by the compositional analysis, stubble field centroids and Little Bustard broods were significantly aggregated (Fig. 5.2). Little Bustard families and natural vegetation centroids were independently distributed in Bellmunt and Belianes (Fig. 5.2), although almost the entire area of this habitat fell within the family home ranges (Fig. 5.1). However, in Ciudad Real families were aggregated with fallow field centroids (Fig. 5.2) but there were still large patches of unused fallows within the Minimum Convex Polygon (the minimum area enclosing all the Little Bustard observations, Fig. 5.1).

5.4 Discussion

Our study shows that in different Spanish Little Bustard populations, females do not establish their home ranges at random, preferring stubbles and habitats which offer higher vegetation density at low to medium heights, such as fallows and natural vegetation, which is consistent with results from previous studies (Jiguet et al., 2002; Morales et al., 2008; Lapiedra et al., 2011). In addition, Little Bustard broods were spatially aggregated with male display core areas which may bring benefits during the rearing period.

Table 5.3: Spatial distribution of Little Bustard families in relation to the male core areas for each study site (Mean, standard deviation and Hotelling t-test results, see methods for details). For each variable, the mean value of the families was compared with a reference value obtained from 100 series of n random points (being n the number of families detected in each study area. Bellmunt: 12 families; Belianes: 34 families; Ciudad Real: 5 families).

Study site		Mean	SD	Reference value	t	d.f.	P
Bellmunt	Distance to the closest male core area centroid (m)	658.76	222.05	1211.53	74.37	11	0.0000
	Probability of male presence at the family observation point	0.1130	0.1189	0.0283	6.08	11	0.0313
	Home range mean raster value	0.0672	0.0437	0.0264	10.45	11	0.0079
	Home range max raster value	0.1713	0.0903	0.0981	7.87	11	0.0171
	CV of the home range	0.6946	0.1828	1.3620	159.95	11	0.0000
Belianes	Distance to the closest male core area centroid (m)	875.33	412.91	1087.50	8.98	33	0.0052
	Probability of male presence at the family observation point	0.0327	0.0209	0.0174	18.11	33	0.0002
	Home range mean raster value	0.0281	0.0153	0.0169	18.19	33	0.0002
	Home range max raster value	0.0588	0.0218	0.0402	24.81	33	0.0000
	CV of the home range	0.5754	0.2506	1.0973	147.51	33	0.0000
Ciudad Real	Distance to the closest male core area centroid (m)	853.94	261.29	1297.23	14.39	4	0.0192
	Probability of male presence at the family observation point	0.0084	0.0042	0.0043	4.82	4	0.0931
	Home range mean raster value	0.0083	0.0051	0.0043	3.5	4	0.1558
	Home range max raster value	0.0213	0.0109	0.0112	4.34	4	0.1056
	CV of the home range	0.7014	0.2949	1.0942	8.87	4	0.0408

We found very low productivity values of Little Bustard in the three study areas, which is consistent with information obtained from radio tagging studies conducted on some of them (Lapiedra et al., 2011) and similar to that found in previous studies in other Spanish populations (Morales et al., 2007, own unpublished data). These low productivity values pose a serious threat to the subsistence of these populations since productivity has been highlighted as a key demographic parameter for the viability of Little Bustard populations (Morales et al., 2005*a*; Delgado et al., 2009). Moreover, the number of families found in these areas seems very low compared to male densities, as reported in other populations of central Spain and France (Inchausti and Bretagnolle, 2005; Delgado et al., 2009). If the sex ratio is biased towards males, the female shortage may add a further negative effect to the low productivity, increasing even more the extinction risk of the species in the study areas as shown by population viability analysis (Morales et al., 2005*a*).

Little Bustard families presented a similar habitat selection pattern in the three study populations. Semi-permanent vegetation was one of the most preferred habitat types. Families selected fallows in Ciudad Real and old fallows and low height scrublands in Bellmunt and Belianes. These substrates are characterized by greater vegetation cover and height than stubbles, so they could work as concealment places from predators or bad weather conditions (Silva et al., 2004). In addition, semi-permanent vegetation harbours a greater amount of green weed cover and insect availability (Lapiedra et al., 2011) facilitating the access of females with offspring to food resources. Stubble fields, resulting from the harvest of cereal and leguminous crops, were also a selected habitat and comprise more than half of the available surface within the Little Bustard distribution range in the study areas during summer. At this period, stubbles remain as habitat basically providing food resources (Silva et al., 2007; Lapiedra et al., 2011). However, other habitat types are clearly avoided, such as pastures which are daily grazed by sheeps, fruit tree orchards and wooded patches, which is in accordance with previous studies (Salamolard and Moreau, 1999; Wolff et al., 2001).

The spatial aggregation between Little Bustard families and the territories previously occupied by males may bring several benefits to females with offspring. If females remained and nested close to male territories as seen in previous studies (Jiguet et al., 2000; Morales et al., 2013), they would save energy by avoiding movements to distant places. During the rearing period, access to food resources could be crucial for determining female distribution. The diet of chicks consists of arthropods, mainly orthopterans and large beetles, at least until 3 weeks old (Cramp and

Simmons, 1980; Jiguet, 2002). The territories of Little Bustard males hold more abundance of large beetles than areas outside them (Traba et al., 2008), though it has been shown that abundance of food resources inside male territories does not influence male attractiveness (Jiguet et al., 2002). However, females would have access to larger amounts of food by settling near or within the male core areas and this could increase the probability of chick survival and therefore the reproductive success of females. Moreover, this would be also a good strategy to acquire new mating opportunities after a clutch loss, especially in a species like the Little Bustard with a high rate of first clutch failure (Lapiedra et al., 2011).

Our results show that the distribution of Little Bustard families is associated to male display locations even though some females with chicks move considerably far from the nesting site (Lapiedra et al., 2011). However, the spatial aggregation between families and Little Bustard male display locations could be due to a coincidental habitat selection pattern at landscape level. Although previous studies have shown that males and females have different microhabitat requirements, males requiring habitats that promote conspicuousness whilst females select habitats that guarantee concealment (Morales et al., 2008), at landscape level a variable degree of overlap in habitat selection may exist, especially in those regions affected by agricultural intensification. In Bellmunt and Belianes indeed, Little Bustard family home ranges harbour almost the entire available surface of semi-permanent vegetation areas (fallow and natural vegetation) (Fig. 5.1), which is also one of the habitat types most preferred by males for sexual displaying (Martínez, 1994; Morales et al., 2005*b*; Delgado et al., 2010; Ponjoan et al., 2012). Thus, when the overall suitable habitat is saturated owing to its scarceness in the landscape, we cannot disentangle whether the association between brood ranging areas and male display sites is produced by its use by males or by coincident habitat preferences of both sexes. In Ciudad Real, however, Little Bustard broods are aggregated with fallow fields but, despite the large available surface of this habitat inside the MCP (Fig. 5.1), females with offspring still stay closer to male core displaying areas. Therefore, these results suggest that display locations of males could influence the decisions of females regarding the establishment of their brooding range.

5.5 Conclusions

The spatial aggregation between Little Bustard families and male territories found in this study reflects processes that operate at the individual level, although they may have effects on the population's dynamic and, therefore, important implications for conservation. The management aiming to enhance the species' population conditions should bear in mind not only male requirements but also the suitable habitat for females during the chick rearing season. In both cases, it seems necessary to maintain an extensive farmland model that ensures a mosaic landscape of different agrarian substrates, but keeping a certain proportion of fallows and natural vegetation areas. Finally, the studies based on spatial point patterns may result a useful tool for integrating behaviour and landscape ecology given that they allow to evaluate the consequences of individual-level responses on population dynamics, such as habitat use or conspecific attraction, in this case mediated by mate choice, which could not be detected by exclusively a behavioural approach.

5.6 Acknowledgements

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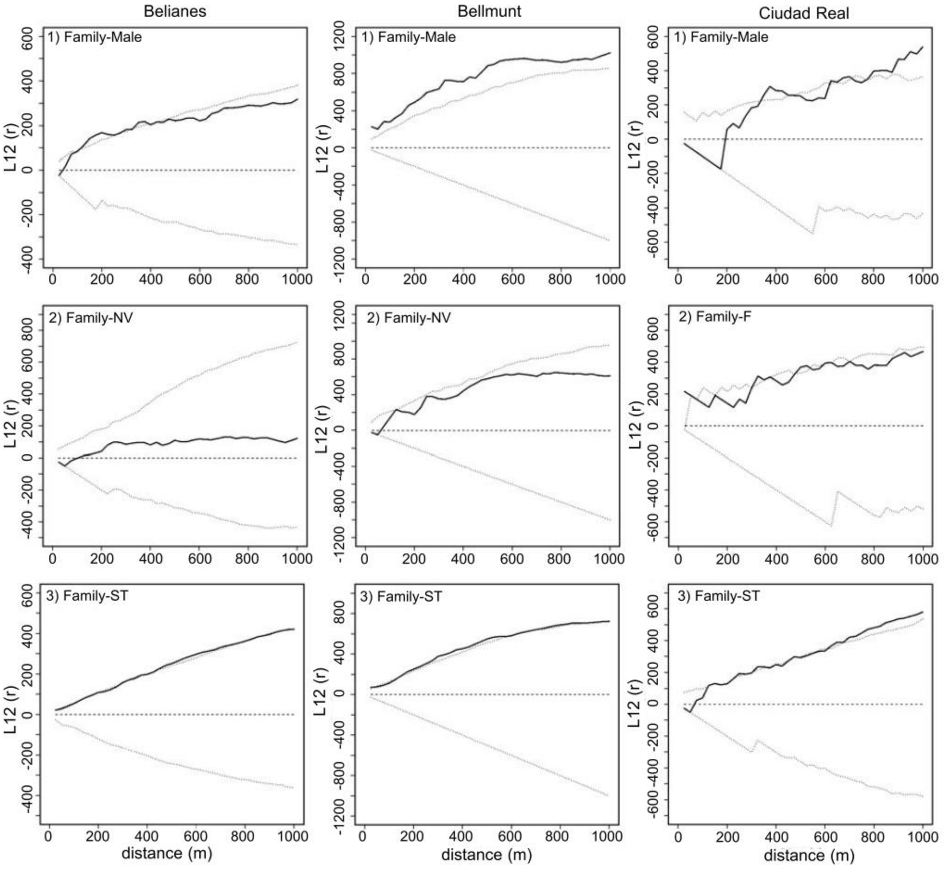

Figure 5.2: Analysis of Ripleys bivariate function L(r) for evaluating spatial correlation between 1) family observations and male observations for Belianes, Bellmunt and Ciudad Real; 2) family observations and centroids of natural vegetation fields (NV) for Belianes and Bellmunt and families and centroids of fallow fields (F) for Ciudad Real; 3) family and centroids of stubble fields (ST) for the three study areas. The solid line represents the observed function, the broken line represents the expected function under spatial complete randomness and dotted lines indicate 95% confidence limits resulting from the randomisation of the distribution pattern. The spatial pattern is random when the observed L(r) falls within the confidence limits, uniform if it occurs below them and clumped if it occurs above them.

Chapter 6

Effects of human activity on physiological and behavioral responses of an endangered steppe bird.

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Abstract

Animals may perceive humans as a form of predatory threat, a disturbance, triggering behavioral changes together with the activation of physiological stress responses. These adaptive responses may allow individuals to cope with stressful stimuli, but a repeated or long-term exposure to disturbances may have detrimental individual- and population- level effects. We studied the effects of human activities, particularly hunting, on the behavior and physiological status of a near-threatened nongame steppe bird, the little bustard. Using a semiexperimental approach, we compared before, during, and after weekends: 1) the type and intensity of human activities and 2) the behavior and 3) physiological stress (fecal corticosterone metabolites) of wintering birds. Higher rates of human activity, in particular those related to hunting, occurred during weekends and caused indirect disturbance effects on birds. Little bustards spent more time vigilant and flying during weekends, and more time foraging in the mornings after weekend, possibly to compensate for increased energy expenditure during weekends. We also found increased physiological stress levels during weekends, as shown by higher fecal glucocorticoid metabolite concentrations. Increased corticosterone metabolite levels were associated with the highest levels of hunting-related disturbances. Little bustard showed marked behavioral and physiological (stress hormones) responses to human activities that peaked during weekends, in particular hunting. The long-term effect of this particular activity carried out during weekends from autumn throughout winter might adversely impact wintering populations of this nongame endangered species, potentially counteracting conservation efforts conducted on local as well as foreign breeding populations.

6.1 Introduction

Wildlife may perceive humans as potential predators and elicit different antipredator responses (e.g. Beale and Monaghan, 2004). Exposure to human activities can modify behavior, physiological status, and ultimately affect the fitness of disturbed animals (Arlettaz et al., 2007; Barja et al., 2007; Ellenberg et al., 2007). In fact, the recently rising intensity and variety of human leisure activities could increase the encounter rate between humans and wild animals and, therefore, their potential negative impact on wildlife (Steven et al., 2011). Among these leisure activities, hunting has received particular attention not only due to its consumptive nature on game species but also due to indirect effects on their behavior and distribution (e.g. Fox and Madsen, 1997; Thiel et al., 2007). However, impacts of hunting on nongame species, including species of conservation concern, are still poorly known (Casas et al., 2009; Sastre et al., 2009).

The effect of human disturbances on animals may be addressed through their influence on spatial distribution, habitat use, or behavioral patterns (Watson and Moss, 2004; Sastre et al., 2009). Disturbed individuals may relocate to disturbance-free areas that may be of lower quality (Thiel et al., 2008) or spend more time vigilant to the detriment of foraging or resting (Casas et al., 2009; Wang et al., 2011). Human disturbances may also impoverish individual condition or physiological status (Strasser and Heath, 2013; Rehnus et al., 2014), reduce parental care or even prompt nest abandonment in birds (Arroyo and Razin, 2006; Strasser and Heath, 2013).

At the physiological level, organisms exposed to human disturbances may increase glucocorticoid production through the activation of stress responses (Axelrod and Reisine, 1984; Zhang et al., 2011; Strasser and Heath, 2013). The short-term release of glucocorticoids is an adaptive response that redirects energy from nonvital activities toward survival (Sapolsky et al., 2000). However, the prolonged exposure to stressors and the cumulative effects of maintaining elevated glucocorticoid levels may induce deleterious effects (Romero et al., 2009), such as the suppression of the immune or reproductive functions (Wingfield et al., 1997; Sapolsky et al., 2000). Glucocorticoid levels have been widely used as a physiological indicator of stress in wildlife (e.g. Navarro-Castilla et al., 2014). Fecal glucocorticoid metabolites reflect free glucocorticoids in plasma, yielding an accurate profile of the adrenocortical activity (Sheriff et al., 2010), and offer the advantage of being a non-invasive method for studying wild animal stress responses (Millspaugh and Washburn, 2004). In addition, disturbed organisms may also modify their diet or increase their use of energy stores, which may eventually affect their nutrient balance (e.g. altered nitrogen balance and fecal nitrogen contents in herbivores; Blanchard et al., 2003).

Farmland and steppe bird species are currently the most threatened bird group in Europe, with 83% of species having unfavorable status (Burfield, 2005). Agricultural habitats are increasingly humanized, both through the intensification of farming activities and through an increased recreational use of these areas. Human activities may thus have an important and increasing effect on these farmland birds (Onrubia and Andrés, 2005; Casas et al., 2009; Sastre et al., 2009), but studies of human disturbance in this context are still scarce. Among farmland birds, the little bustard (*Tetrax tetrax*) is a near-threatened medium-sized steppe bird (BirdLife International, 2012) whose populations have dramatically declined in most of its Palearctic range (Goriup, 1994). Nowadays, the Iberian Peninsula holds more than half of the world breeding population (García de la Morena et al., 2006). During winter, little bustards gather in large flocks formed by males, females, and juveniles from local and other breeding populations (migratory birds breeding in western France spend the winter in central Spain; Villers et al., 2010). Birds remain gregarious until the beginning of the breeding season, when birds return to reproductive areas and males settle on exploded leks (Jiguet et al., 2000). In winter, little bustards are basically herbivorous, feeding mainly on *Leguminosae* and *Cruciferae* (Cramp and Simmons, 1980) and show preferences for new fallows and stubbles (Leitão and Costa, 2001; Silva et al., 2004).

Wintering little bustards are confronted with various types of potential human disturbances in agricultural habitats, among which one of the most important is hunting. This is a very important socioeconomic activity in rural areas of the Iberian Peninsula, which takes place in autumn and throughout winter in more than 80% of the territory (Casinello, 2013). It is frequently concentrated on weekends, together with other leisure activities, like cycling or hiking. Only indirect effects of hunting disturbance on the species are expected because the little bustard (as occurs with most steppe birds) is not a game species, and therefore, it is not hunted, due to its unfavorable conservation status, but it shares habitat with game species, such as the red-legged partridge (*Alectoris rufa*) and the Iberian hare (*Lepus granatensis*).

We report here on little bustard's behavioral and physiological responses to varying human activity levels, which could be important sources of disturbance. We studied temporal variations in human activity rates as well as temporal changes in little bustard behavior (flocking behavior, time activity budgets), habitat use, and physiological status (stress levels, evaluated through fecal glucocorticoid metabolites). Finally, we evaluated whether the concentration of glucocorticoid metabolites in feces increased with higher intensities of specific human activities. We predicted that during weekends: 1) human disturbance rates would be greatest; 2) little bustard's flocks would be larger to potentially buffer deleterious effects associated with disturbances; 3) birds would spend more time being vigilant, to the detriment of foraging (although such behavior could be modulated by flock size); and 4) birds would show higher stress hormone levels.

6.2 Methods

Study area

This study was carried out in Campo de Calatrava (Ciudad Real, central Spain) within a Special Protection Area (SPA 157, ca. 38°54'N, 3°55'W). The area is flat to slightly undulated (590-685 m a.s.l) and is primarily used for cultivation of dry cereal and, to a lesser extent, olive groves (*Olea europaea*), leguminous crops (*Vicia spp.* and *Pisum sativum*) and vineyards (*Vitis vinifera*). Cereal is grown in a traditional way creating a mosaic of sown, ploughed, stubble and fallow fields of different ages (Table 6.1). The area has been highlighted as a hotspot for steppe birds (Traba et al., 2007) and holds a significant population of breeding (ca. 100) little bustards, which increases during autumn/winter (ca. 1500-2000) with the arrival of wintering birds (Casas and Mougeot, unpublished data). Hunting modalities are driven and walked-up shooting for red-legged partridges and walked-up hunting with greyhounds for Iberian hares.

Sampling design

Since hunting is only allowed over weekends in the study area, we followed a semi-experimental approach that consisted in comparing data before, during, and after weekends. Hereafter, we refer to data collected before, during, and after a given weekend as belonging to a given "Trial" (or replicate). In winter 2010-2011, trials included data collections over 3 days: Friday, Sunday, and Monday. In winter 2011-2012, we conducted additional surveys on Thursday, Saturday, and Tuesday. For analyses, each survey day was assigned to 1 of 3 categories (hereafter "Week Period"): before weekend (Thursday and Friday), during weekend (Saturday and Sunday), or after weekend (Monday and Tuesday).

Human activity rate and little bustard flock surveys

Quantification of human activities and surveys of little bustard flocks were carried out for 11 trials: 9 during winter 2010-2011 (October 2010 and January 2011) and 2 during winter 2011-2012 (December 2011 and January 2012).

We conducted car surveys within the study area using predefined road transects (Fig. 6.1). In winter 2010-2011 transects were longer (32.3 km of tracks or small roads) than in winter 2011-2012 (10.6 km. Fig. 6.1). The density of roads and tracks allowed a full coverage of the places most used by little bustards inside the study area, the covered area being more extensive during the first winter than during the second one. During surveys, we drove at low speed (<20 km/h) and stopped every 500 m at suitable viewpoints to scan for human activity and little bustard flocks, which were geo-referenced. We also located human activity and bird observations occurring between stops if they were not detected during stops for scans. We mapped all observations and flock movements, making particular efforts to avoid double counting during surveys (we kept for analysis only observations for which we were confident that they were not sampled twice). Transects were conducted not only in the morning (08:00-14:00 h; n=36), but also in the afternoon for some trials (14:00-18:00 h; n=12). We recorded all little bustard flocks (n=113), including those flying, and noted flock size (number of little bustards; 1-1100) and the habitat used (as one of the following categories: stubbles, ploughed fields, old fallows, cereal crops, vineyards, olive groves, pastures, or urban areas) when birds were not in flight. We considered also mixed flocks with the pin-tailed sandgrouse (*Pterocles alchata*), which are frequently observed

Table 6.1: Habitat availability in the study area during winter (adapted from Martín et al., 2010).

Habitat type	Description	Proportion (%)
Cereal	Crops of barley, oats or wheat	58.62
Stubble	Recently harvested cereal or legume crops	7.86
Fallow	Fallows of one or more years	7.14
Ploughed land	Ploughed fields without vegetation	9.77
Legume	Crops of *Vicia spp.* or *Pisum sativum*	1.36
Pasture	Fields of short scrubland or pasturelands	7.36
Olive grove	Olive tree plantation	3.53
Vineyards	Vine plantation	3.08
Others	Urban fields, stream vegetation, fruit tree orchards, and maize	1.29

during winter (Martín et al., 2010). For human disturbances, we recorded in each transect the number of people, dogs, cars, tractors, and cyclists. We estimated disturbance rates by type as the total number of people, vehicles, or dogs observed divided by transect length (disturbances/km). Additionally, we recorded the number of hunting shots heard during 5 min at 6 fixed hunting shot sampling points established along transects (Fig. 6.1), and estimated shooting rate (shots/min) for each given transect.

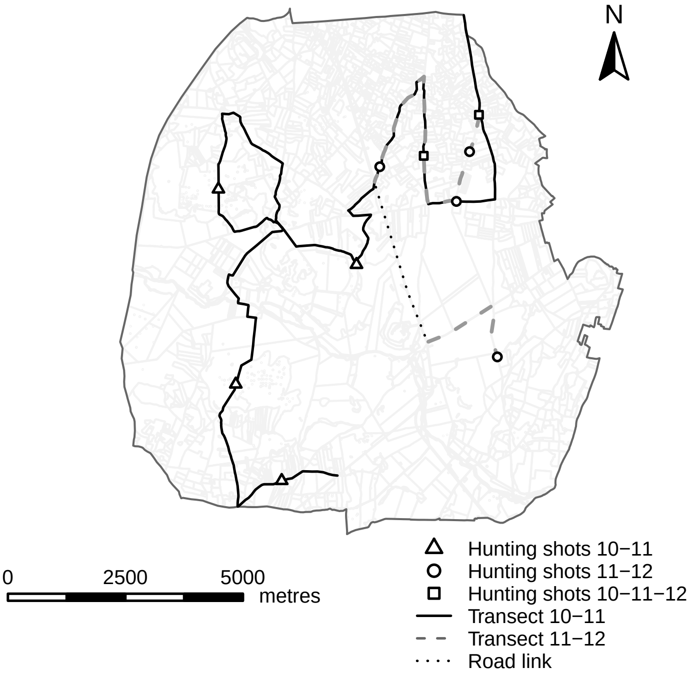

Figure 6.1: Map of the study area showing the road transects used for surveys during the winters 2010 - 2011 and 2011 - 2012. The location of hunting shots sampling points is indicated by triangles (winter 2010 - 2011), circles (winter 2011 - 2012), and squares (used both winters).

Little bustard behavior

We measured little bustard behavior through behavioral scans during the 2 trials conducted in winter 2011-2012, during morning and afternoon observations. We recorded the proportion of observed individuals being vigilant (i.e. with the neck extended in a typical upward posture), foraging, resting, or walking following the instantaneous scan sampling method (Martin and Bateson, 1993). We also recorded date, time, and overall flock size for each scan. The car was used as a hide at a minimum distance of 300 m from the flock, and we used binoculars or a spotting scope for behavioral scanning. When flock size was less than 20 birds (n=4), we recorded the behavior of all individuals in 1 scan. For large flocks (sometimes up to several hundreds of individuals; n=23), several scan samplings (1-7 scans) were conducted on different groups of individuals within the flock, with a 2-min interval between consecutive scans; in each scan, we sampled the behavior of at least 18 individuals (18-50 individuals). We performed a total of 77 scans (18 in the morning and 59 in the afternoon) in 27 flocks, with an average of 31 ± 9 individuals sampled per scan.

Fecal samples collection

Little bustards in the study area usually gather at night in a single large communal mixed-species roost (of up to 1500 individuals with ca. 1000 pin-tailed sandgrouse) in the same large stubble field or nearby. During the 2 trials conducted in winter 2011-2012, we collected little bustard fecal samples from that large roost at 3 periods: before, during, and after the weekend, to estimate fecal glucocorticoid metabolite concentrations.

Fecal sampling was carried out at dawn after the birds had left the roost (between 08:00 and 09:00). Each morning, we randomly collected 20-30 fresh individual little bustard feces (feces were at least 10 m apart, in order to minimize the possibility of sampling twice the same individual — little bustards move very little when roosting except if disturbed during the night). Fresh feces were characterized by a layer of mucus and the absence of dehydration signals. Each fecal sample was individually stored in a labeled plastic bag and kept refrigerated until taken to the lab (less than 1 h after collection) where it remained frozen at $-20\,^{\circ}\mathrm{C}$ until assayed. We sampled little bustard feces on 4 different days during each trial, with a total of 8 collections and 229 samples. The temperatures at night during fecal sampling were low ($2.3\,^{\circ}\mathrm{C} \pm 1.7\,^{\circ}\mathrm{C}$), which should reduce the potential loss of glucocorticoids with increasing time after defecation, which is temperature dependent (Thiel et al., 2005). We also measured the effects of environmental exposure on corticosterone metabolite concentrations in feces, and observed that a loss of fecal corticosterone metabolite concentration occurred only at 12 h after first sampling, and was proportional to initial concentration levels (See Appendix A).

Glucocorticoid metabolites in feces: extraction and enzyme immunoassay

Fecal glucocorticoid metabolites were extracted from fecal samples according to the modified method of Young et al. (2004). Frozen fecal samples were dried at 90 °C until constant weight, and then 0.08 g of dry samples were placed in assay tubes with 2 mL of phosphate buffer and 2 mL of pure methanol. Tubes were shaken for 16 h and the supernatants were centrifuged at 4000 rpm for 30 min. Pellets were discarded and the fecal extracts were stored at −20 °C until analyzed. A commercial corticosterone enzyme immunoassay (EIA, DRG Instruments GmbH, Marbug, Germany) was used for the quantification. The cross-reactivity of the antibodies with other substances according to the manufacturer was 2.4% for 11-deoxycorticosterone, while the cross-reactivity of corticosterone was insignificant (less than 1%) with any other substance (aldosterone, cortisol, and progesterone).

Three tests were done to validate the EIA: parallelism, accuracy, and precision. A parallelism test of serial dilutions of extracts was performed with dilution ratios of 1:32, 1:16, 1:8, 1:4, 1:2, and 1:1, and a curve parallel to those of the standard was obtained. Recovery (accuracy) was 147.4 ± 36.9% (n=6). Intra- and interassay coefficients of variation (precision) were calculated with extracts and the obtained values were 5.3 ± 1.6% (n = 6) and 8.2 ± 2.8% (n=3), respectively. In each assay, we used a control (185 ng/mL corticosterone) included in the DRG kit. When standard corticosterone metabolite concentrations deviated more than 10% from the expected value, the assay was rejected and the samples were reanalyzed. The assay sensitivity for corticosterone was found to be > 4.1 ng/mL.

Statistical analysis

We analyzed temporal variations in human activity rates using generalized linear mixed models (GLMMs). Six dependent variables (the number of people, dogs, cars, tractors, cyclist, or shots, counted during a given transect) were fitted to models using a negative binomial error distribution and log link function, with the (log-transformed) transect length (km) included as an offset. For the response variable “number of shots” we did not include an offset because the number of hunting shot detection points and the time spent there (5 min) were equal for all transects. Variation in little bustard flock size was also analyzed using GLMM with negative binomial error distribution (log link function), considering the (log-transformed) transect length (km) as an offset. Initial models included the following explanatory variables: Winter (to test for possible differences between the winters 2010-2011 and 2011-2012), Week Period (3 levels: before, during, and after weekend), Daytime Period (2 levels: AM vs. PM) and the interaction Week Period × Daytime Period. Because hunting only occurred during the weekend, GLMMs for the number of shots were built only with the weekend data in order to evaluate differences on shooting rate between winters and daytime periods. The variable "Trial" was included as a random effect (in order to account for the nonindependence of data collected around a given weekend). Non-significant ($P > 0.05$) terms were sequentially removed from the initial models, starting with interactions.

For little bustard behavior, we first analyzed factors influencing the probability of whether observed little bustards were in flight or on the ground, using GLMM with binomial error distribution (logit link function). The response variable was a 2-vector function: number of individuals on flight / number of individuals on the ground. Models included Trial as random factor and the same explanatory variables as for flock size models. We analyzed variations in the proportion of individuals foraging or vigilant during scans using generalized linear models (GLMs) with binomial error distribution adjusted for overdispersion and a logit link function. The dependent variables were 2-vector functions (number of individuals vigilant or foraging / number of individuals sampled during scan performing a different behavior). We used GLM since data were available only for 2 replicates (winter 2011-2012), including Trial as a fixed effect. We also included Week Period, Daytime Period, and Flock size (log-transformed) as well as all possible 2-way interactions between these variables as explanatory variables. We log-transformed flock size because preliminary analyses indicated that the best relationship between behavioral rates and flock size was log-linear rather than linear (with saturated changes for the largest flock sizes). Flock size is known to affect individual behavior, in particular vigilance, which may decrease with increasing group size (Manor and Saltz, 2003; Casas et al., 2009). Non-significant variables were sequentially removed from the initial full model, starting with interactions.

We performed GLMMs with binomial error distribution for each substrate type to evaluate whether habitat use frequency varied before, during, and after the weekend, using data from both winters (2010-2011 and 2011-2012; n=39). We considered the following substrate types: stubble, cereal, ploughed lands, and old fallows (the other habitats being infrequently and only marginally used). Models included Trial as random factor and Week Period and Daytime Period as explanatory variables.

We did not include the interaction Week Period × Daytime Period due to the sample size.

We analyzed variation in fecal corticosterone metabolites (log-transformed to normalize the variable) using GLM with Gaussian error distribution. We included Trial (2 levels: December 2011 and January 2012) and Week Period (3 levels: before, during, and after weekend) as explanatory variables. Secondly, we explored the associations between little bustard fecal corticosterone metabolite levels and specific human activity rates using also GLMs with Gaussian error distribution. Fecal glucocorticoid concentrations measured in the samples collected at dawn on a day t were indicative of physiological stress levels the previous day (t_{-1}) due to the delay between the stressing events and the increase of corticosterone metabolites in the feces (Nakagawa et al., 2003; Staley et al., 2007). Thus, we used the human activity frequencies observed in the day previous to the feces collection for this analysis. Frequencies of each activity type were categorized into low, medium and high (See Fig. 6.5 for interval values).

All analyses were conducted using R version 3.1.1 (R Development Core Team, 2014).

6.3 Results

Temporal variations in human activity rates

Human activity rates did not differ between winters (2010-2011, 2011-2012), but strongly differed between week periods (Table 6.2). More people were observed during weekend mornings (Table 6.2; Fig. 6.2). Dogs were more frequently observed during weekends and more abundant in the mornings than in the afternoons (Table 6.2; Fig. 6.2). More cars and cyclists were observed during the weekend than before the weekend, although no differences were found after weekends (Table 6.2; Fig. 6.2). Hunting shots were only reported during weekends and were more frequent during mornings (Table 6.2. Fig. 6.2). In contrast, tractors tended to be less frequent during weekend afternoons (marginally significant estimate; Table 6.2; Fig. 6.2). Regarding people and dogs observed during weekends, 95% and 99% were hunters and hunting dogs, respectively, whereas on weekdays, observed people were mainly farmers (68% and 77% before and after, respectively), but never hunters. The number of cars during weekends correlated positively with the number of hunters ($\rho = 0.53$).

Table 6.2: Results of the GLMMs testing for temporal variations in human activity rates, little bustard flock sizes and flying probability. Overall effects of explanatory variables as well as estimates of each factor level (± SE) and their significance are given.

Response variables*	Explanatory variables				Variable level estimates ****			
		χ^2	df	P		Estimate	z-value	P
People/Km **					Intercept (a)	-0.410 ± 0.299	-1.37	0.170
	Week Period	39.80	2	<0.001	Weekend (b)	2.334 ± 0.372	6.27	<0.001
					After (a)	0.470 ± 0.403	1.17	0.244
	DTP	1.09	1	0.296	Pm (a)	0.588 ± 0.562	1.04	0.296
	Week Period × DTP	13.43	2	0.001	Pm × Weekend (a)	-2.906 ± 0.800	-3.63	<0.001
					Pm × After (a)	-0.319 ± 0.778	-0.41	0.682
Dogs/Km **					Intercept (a)	-0.858 ± 0.464	-1.85	0.065
	Week Period	19.06	2	<0.001	Weekend (b)	2.437 ± 0.605	4.03	<0.001
					After (a)	-1.125 ± 0.734	-1.53	0.125
	DTP	7.91	1	0.005	Pm	-2.013 ± 0.716	-2.81	0.005
Cars/Km **					Intercept (a)	-0.195 ± 0.253	-0.77	0.441
	Week Period	14.13	2	<0.001	Weekend (b)	1.197 ± 0.325	3.68	<0.001
					After (ab)	0.371 ± 0.343	1.08	0.280
Cyclists/Km **					Intercept (a)	-2.285 ± 0.695	-3.29	0.001
	Week Period	5.97	2	0.05	Weekend (b)	2.095 ± 0.864	2.43	0.015
					After (ab)	0.012 ± 0.972	0.01	0.990
Tractor/Km **					Intercept (a)	-0.214 ± 0.295	-0.72	0.469
	Week Period	1.64	2	0.441	Weekend (a)	-0.226 ± 0.229	-0.99	0.323
					After (a)	0.264 ± 0.236	1.12	0.264
	DTP	0.38	1	0.538	Pm (a)	-0.281 ± 0.457	-0.62	0.538
	Week Period × DTP	7.534	2	0.023	Pm × Weekend (a)	-1.854 ± 1.097	-1.69	0.091
					Pm × After (a)	-0.578 ± 0.641	-0.90	0.367
Shots/min**					Intercept (a)	3.594 ± 0.441	8.16	<0.001
	DTP	5.83	1	0.016	Pm (b)	-2.272 ± 0.941	-2.42	0.016
Flock size **					Intercept (a)	3.048 ± 0.334	9.14	<0.001
	Week Period	7.30	2	0.026	Weekend (ab)	-0.073 ± 0.326	-0.22	0.823
					After (b)	-0.902 ± 0.335	-2.69	0.007
Flying probability ***					Intercept (a)	-5.477 ± 1.141	-4.80	<0.001
	Week Period	465.22	2	<0.001	Weekend (b)	2.030 ± 0.102	19.97	<0.001
					After (a)	-0.127 ± 0.191	-0.67	0.505

* All models included "Trial"as a random effect. Initial models (see Supplementary Table B.1) included the following explanatory variables: Winter (2010-2011 vs. 2011-2012), Week Period (before, during, and after weekend), Daytime Period (DTP = AM vs. PM) and the interaction between Week Period and DTP. GLMMs for number of shots/min used only data from weekend (no shots were recorded before or after weekend).

** Human activity variables and flock size were fitted using negative binomial error distribution, with transect length (log-transformed) included as an offset (except for number of shots; see Methods).

*** For flying probability (i.e. whether an observed flock was in flight or on the ground), we used binomial error distribution and a logit link.

**** Different letters indicate significant differences ($P < 0.05$, Tukey's HSD) between levels. The intercept corresponds with before weekend and AM levels of the variables Week Period and Daytime Period, respectively.

Temporal variations in little bustard behavior

Little bustard flock size did not differ significantly between winters or daytime periods but was significantly influenced by week period, with smaller flocks found after weekends (Fig. 6.3; Table 6.2). The proportion of little bustards in flight when first detected was also significantly affected by week period: more birds were observed flying during weekends than before or after weekends (Fig. 6.3; Table 6.2).

The proportion of little bustards being vigilant within scanned groups depended on flock size and week period, with a significant interaction between these variables (Table 6.3). Before weekends, the proportion of vigilant birds increased with flock size (slope ± SE: 0.604 ± 0.245. Fig. 6.3). In contrast, during and after weekends, the proportion of vigilant birds decreased with flock size (slopes ± SE: -0.529 ± 0.261 and -1.359 ± 0.282, during and after weekends, respectively. Fig. 6.3).

The proportion of little bustards foraging also varied with flock size and week periods, depending on daytime period (Table 6.3). More birds were foraging in the mornings after weekends and during afternoons before weekends (Table 6.3. Fig. 6.3). Moreover, the proportion of birds foraging increased with flock size, this relationship being stronger during mornings (slope ± SE: 0.228 ± 0.153) than afternoons (slope ± SE: 0.173 ± 0.103).

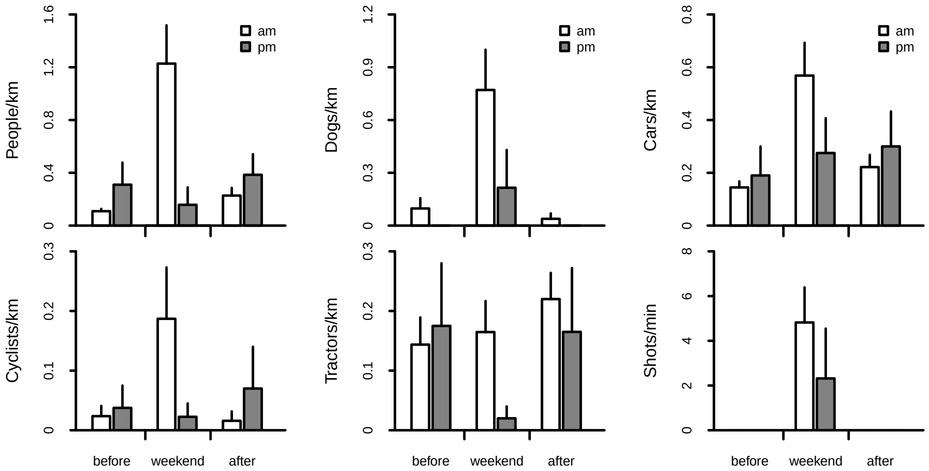

Figure 6.2: Mean (± SE) human activity frequencies according to week and daytime periods.

Temporal variations in habitat use

During winter, little bustards used mostly stubbles (57.2% of the total birds observed), followed by ploughed fields (16.7%), cereal crops (16.2%), and, to a lesser extent, old fallows (9.2%) and pastures or field margins (0.7%). The proportion of little bustards observed in different habitat types differed between week periods and daytime periods (Table 6.4). Little bustards used stubbles more frequently during the weekend and on the afternoons and tended to use old fallows more often after the weekend (Table 6.4). The use of cereals was at its highest before the weekend but reduced after the weekend (Table 6.4). Ploughed fields were used more often after the weekend and on the afternoons (Table 6.4).

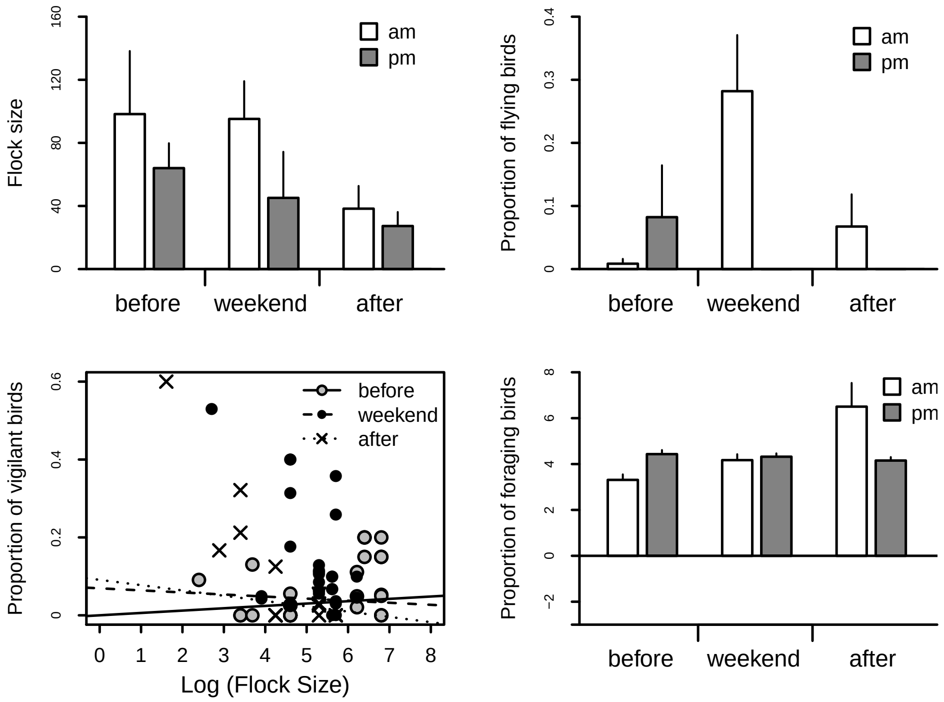

Figure 6.3: Proportion (mean ± SE) of little bustards that were flying when first detected, flock sizes (mean ± SE), and proportion (least square means ± SE) of little bustards foraging within flocks according to week and daytime periods. The proportion of vigilant birds varied with (log-transformed) flock size, with different slopes for each level of week period (see text).

Table 6.3: Results of the GLMs analyzing temporal variation in the proportion of little bustards being vigilant or foraging within flocks (n=77 scans). Overall effects of explanatory variables as well as estimates of each factor level or covariate (± SE) and their significance are given.

Response variables*	Explanatory variables				Variable level estimates			
		χ^2	df	P		Estimate	z-value	P
Vigilance					Intercept	-6.248 ± 1.629	-3.84	<0.001
	Log (FS)	5.89	1	0.015	Log (FS)	0.604 ± 0.271	2.23	0.029
	Week Period	25.31	2	<0.001	Weekend	6.929 ± 1.964	3.53	<0.001
					After	9.108 ± 2.150	4.24	<0.001
	Log(FS) × Week Period	25.77	2	<0.001	Weekend ± log(FS)	-1.133 ± 0.347	-3.26	0.002
					After × log(FS)	-1.963 ± 0.440	-4.46	<0.001
Foraging					Intercept	-3.684 ± 1.173	-3.14	0.003
	Log(FS)	10.92	1	0.001	Log (FS)	0.595 ± 0.196	3.04	0.003
	DTP	8.71	1	0.003	Pm	3.546 ± 1.287	2.76	0.008
	Week Period	12.31	2	0.002	Weekend	0.862 ± 0.366	2.36	0.021
					After	3.193 ± 1.094	2.92	0.005
	Week Period × DTP	13.12	2	0.001	Pm × Weekend	-0.976 ± 0.426	-2.29	0.025
					Pm × After	-3.473 ± 1.115	-3.11	0.003
	Log (FS) × DTP	4.25	1	0.039	Log (FS) × pm	-0.436 ± 0.220	-1.98	0.052

*Initial models included Log(FS) (flock size, log-transformed), Trial (December vs. January), Week Period (before, weekend, an after weekend) and Daytime Period (DTP = AM vs. PM), an all possible 2-way interactions as explanatory variables (see Supplementary Table B.2).

Table 6.4: Results of the GLMMs (with binomial error distribution) analyzing temporal variation in the proportion of little bustards using a given habitat type (n=39 transects). Overall effects of explanatory variables as well as estimates of each factor level (± SE) and their significance are given.

Response variables*	Explanatory variables				Variable level estimates **			
		χ^2	df	P		Estimate	z-value	P
Ploughed Field					Intercept (a)	-4.393 ± 1.221	-3.60	<0.001
	Week Period	666.08	2	<0.001	Weekend (b)	1.643 ± 0.106	15.51	<0.001
					After (c)	3.168 ± 0.125	25.42	<0.001
	DTP	44.70	1	<0.001	Pm	-1.685 ± 0.252	-6.69	<0.001
Cereal					Intercept (a)	-3.390 ± 2.275	-1.49	0.136
	Week Period	536.26	2	<0.001	Weekend (b)	-5.041 ± 0.218	-23.11	<0.001
					After (ab)	-75.038 ± 48.380	-1.55	0.121
	DTP	125.28	1	<0.001	Pm	2.044 ± 0.183	11.19	<0.001
Stubble					Intercept (a)	-0.469 ± 0.893	-0.53	0.599
	Week Period	353.68	2	<0.001	Weekend (b)	0.874 ± 0.091	9.57	<0.001
					After (c)	-1.135 ± 0.092	-12.36	<0.001
	DTP	83.36	1	< 0.001	Pm	1.010 ± 0.111	9.13	<0.001
Old fallow					Intercept (a)	-5.415 ± 1.438	-3.77	<0.001
	Week Period	182.09	2	<0.001	Weekend (a)	0.208 ± 0.133	1.57	0.117
					After (b)	1.553 ± 0.128	12.10	<0.001

* All models included"Trial" as a random effect. Models included Week Period (before, weekend, and after weekend) and Daytime Period (DTP = AM vs. PM) as explanatory variables. The model for "Old fallow"did not include the variable DTP (only one observation was recorded during afternoon).

** Different letters indicate significant differences (P <0.05, Tukey's HSD) between levels. The intercept corresponds with before weekend and AM levels of the variables Week Period and Daytime Period respectively.

Human disturbances and fecal corticosterone metabolite levels

Fecal corticosterone metabolite levels varied between week periods depending on trial (Trial: $\chi^2 = 4.19$, P=0.041; Week period: $\chi^2 = 18.61$, $P < 0.001$; Trial × Week period: $\chi^2 = 14.38$, $P < 0.001$). Fecal corticosterone metabolite levels were greater during weekends than before weekends for both Trials and greater during weekends than after weekends, but only for the January Trial (Fig. 6.4).

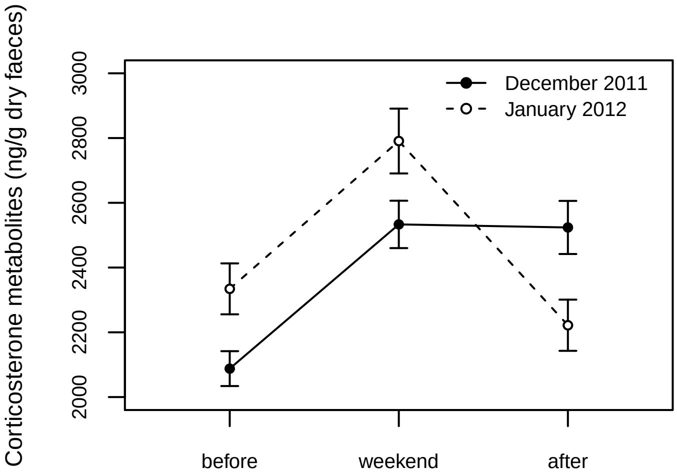

Figure 6.4: Mean (±SE) fecal corticosterone metabolite levels according to week period and trial.

We further investigated fecal corticosterone metabolite variations according to specific human activity levels. Corticosterone metabolite levels were significantly affected by the number of people/km ($F_{2,196}$ = 8.13, P <0.001), dogs/km ($F_{2,196}$ = 7.73, P <0.001), cars/km ($F_{2,196}$ = 8.77, P <0.001), and shots/min ($F_{2,196}$ = 6.41, P=0.002), whereas no differences were found for tractors/km ($F_{2,196}$ =2.64, P=0.074) or cyclists/km ($F_{2,196}$ =2.25, P=0.108). Post hoc Tukey's Honestly Significant Difference (HSD) tests showed that corticosterone metabolite levels were significantly greatest at both intermediate and high levels of cars/km and shots/min, and they were greatest only for the highest levels of people/km and dogs/km (Fig. 6.5).

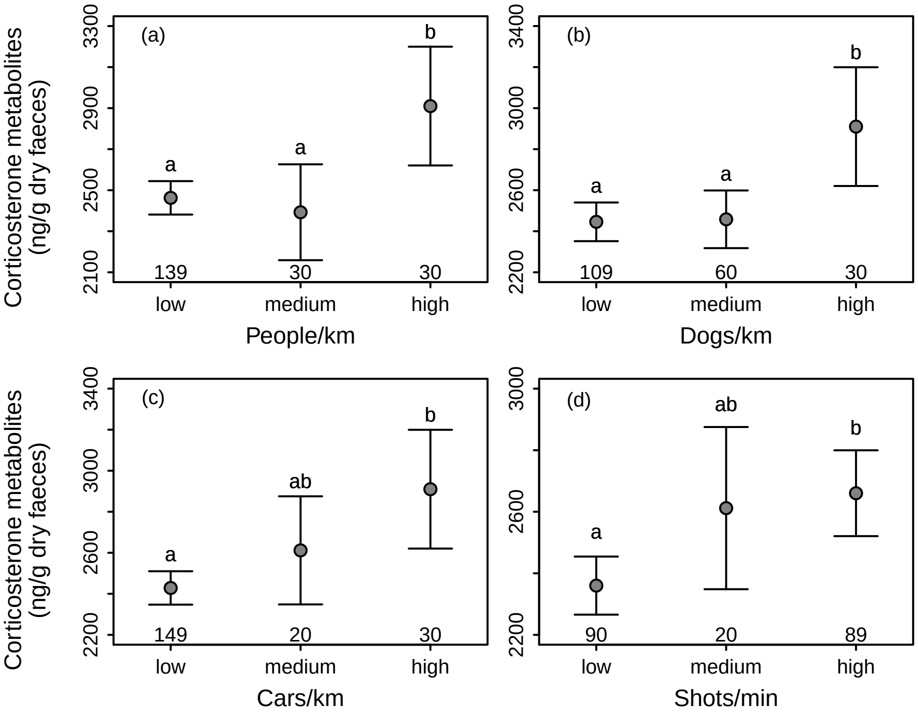

Figure 6.5: Mean (±95% confidence intervals) fecal corticosterone metabolite levels according to human disturbance: a) people/km, b) dogs/km, c) cars/km, and d) shots/min. Disturbance frequencies were classified into 3 levels (low, medium, and high). The particular intervals for each disturbance type were 1)people/km: low (0, 1.01), medium (1.01, 2.01), and high (2.01, 3.02); 2)dogs/km: low (0), medium (0, 1.00), and high (1.00, 2.83); 3)cars/km: low (0.09, 0.35), medium (0.35, 0.60), and high (0.60, 0.85); 4)shots/min: low (0), medium (0, 0.50), and high (0.50, 5.20). Sample sizes for each frequency category are given in the bottom of the graphs. Different letters indicate significant differences (*P* <0.05, Tukey's HSD) between categories.

6.4 Discussion

Our results showed that disturbances due to human activities affected the behavior and physiological stress of wintering little bustards (but see Appendix C for nutritional status results). Human presence in our study area during weekdays was overall low and mainly related to farming activities but was much higher during weekends, mainly because of hunting activities. Other leisure activities, such as cycling or hiking, were also more common in the weekends than during weekdays, but with lower absolute frequency than hunting activities.

Disturbances and behavior

Little bustards reacted to human disturbances by modifying their behavior. The probability of detecting birds in flight was higher during weekends, indicating that little bustards spend more time flying in response to higher levels of human disturbance. Escape is a crucial response performed by organisms (Ydenberg and Dill, 1986), and may be adjusted to perceive risk, increasing the flight initiation distance with risk probability (Frid and Dill, 2002; Thiel et al., 2007). The escape movements caused by disturbance could also lead to the redistribution of individuals toward disturbance-free areas (Casas et al., 2009). Additionally, we found that the relationship between vigilance rate and flock size was influenced by week period. During and after weekends, a lower proportion of birds were vigilant in larger flocks, where more individuals are scanning the surroundings (e.g. Lima, 1995) or because individual predation risk decreases with group size (Hamilton, 1971). In our case, the negative relationship between vigilance rate and group size was weaker during weekends than after weekends, suggesting that little bustards exposed to high levels of disturbance exhibit maximum vigilance rates regardless of flock size (Manor and Saltz, 2003). Indeed, increased vigilance is an antipredatory response, which allows individuals to flee from potential predators before an attack occurs (Caro, 2005). Our results are in accordance with Casas et al. (2009) who reported higher vigilance rates in little bustards in France during hunting days. In addition, the use of stubbles increased during the weekend, possibly indicating that birds look for safer places, with higher vegetation cover, to spend the night after disturbances.

The different behavioral pattern found between weekends and after weekends might reflect an energy-allocation trade-off between vigilance and foraging activity. The increase in the safety-related responses to disturbance described above could be associated with higher energetic expenditure. The higher energy expenditure and the longer time spent in vigilance during weekends reduced both the energy and time available to other behaviors like foraging. This may also explain the behavioral pattern found in the mornings after weekends, when vigilance rate decreased but when foraging was at its highest, and when little bustards also used old fallows more often, a habitat with potentially greater availability of food resources (Morales and Traba, unpublished data). After disturbance events, organisms may need to compensate for the energy losses resorting to increase food intake (Blanc et al., 2006), as observed here. Moreover, little bustard flocks spread in smaller ones after being exposed to higher human pressure, a behavioral response that may improve resource exploitation by avoiding foraging competition (Sansom et al., 2008). Although it has been questioned that reduced vigilance time implies a greater food intake by increasing feeding rate (e.g. Powolny et al., 2012), the change in little bustard foraging patterns after weekends points out to a strategy for recovering energy stores.

Physiological responses to disturbances

Increased human disturbances during weekends were associated with greater glucocorticoid metabolite concentrations in feces. Although physiological stress is an adaptive response to cope with adverse impacts of risky environments and situations, the long-term exposure to elevated glucocorticoids may lead to noxious effects such as physiological damage or immune inhibition, which may in turn affect population growth (Sapolsky et al., 2000; Ellenberg et al., 2007). Importantly, corticosterone metabolites in little bustards remained high after weekends, at least in the December Trial (when shot rate was more intense than in January), suggesting a persistent negative effect that may last at least 1 day after the disturbance events. Fecal glucocorticoid metabolite levels appeared directly associated with certain types and intensities of disturbances, indicating that observed patterns are not merely a temporal association. Little bustard glucocorticoid metabolite levels were particularly affected by hunting shot rates and cars, even at intermediate frequencies, and by high rates of disturbance by people and dogs, which mainly occurred in our study area due to hunting: partridge shooting involves large numbers of hunters walking in fields and hare hunting with greyhound dogs involves smaller groups of hunters and dogs covering large areas. For hare hunting, the predatory behavior of greyhounds (running at high speed through fields) could likely mean a higher perceived threat to birds (Lafferty, 2001; Martinetto and Cugnasse, 2001). The physiological responses of little bustards to this hunting activity could be strengthened by its non-predictable and intense nature (Beale and Monaghan, 2004; Blanc et al., 2006).

By contrast, low or intermediate frequencies of human presence (in our area, associated with individual farmers in fields, or small groups of walkers on tracks), cyclist and tractors working in fields, did not seem to affect little bustard fecal glucocorticoid metabolites. The rather low intensity of cycling in our area, together with the fact that bikers stay on tracks, might explain this lack of effect. Farmers, tractors, and walkers are more constantly distributed over the week and are present all year round, so they may potentially represent nonlethal predictable events, which may facilitate habituation (Conomy et al., 1998).

In addition to measuring glucocorticoid metabolite concentrations in feces, we also measured the carbon and nitrogen contents in a sample of little bustard feces collected before and during weekend (see Appendix C). These preliminary data indicate a significant qualitative difference, with carbon content ca. 10% greater during weekends than prior to weekends, and nitrogen content about 1% greater during weekends than prior to weekends (Appendix C). These qualitative differences may reflect differences in diet or metabolism (e.g. a greater mobilization of energy stores resulting in increased fecal C content during weekends). The lack of detailed information on the winter diet of little bustards and on the chemical composition of the consumed plant species complicates the interpretation of these data. Future studies could look into more detail at possible changes in diet before, during, and after weekends in order to better link disturbance effects on habitat use, diet quality, and nutritional status.

6.5 Conclusions

Hunting and recreation pressures are increasing worldwide over all areas that are accessible for humans. These areas may still support high-value biodiversity, and understanding the different levels of subtle and direct impacts of such increasing disturbance will be a key to set targeted management strategies for particularly high biodiversity areas (e.g. using time and spatial access restrictions). Our results showed that high levels of human activities during weekends exert a negative effect on little bustards (behavioral and physiological responses consistent with anti-predatory strategies; Beale and Monaghan, 2004). Hunting appears as a particularly important source of disturbance for this declining species (see also Casas et al., 2009), prompting changes on its behavior and inducing physiological stress, which may even persist after the disturbance has disappeared. Human-induced changes in the behavior and physiology may have consequences on individual fitness (Strasser and Heath, 2013), and ultimately on population dynamics (Ellenberg et al., 2007), which could be particularly worrying for this threatened species. The impact of high stress levels associated with hunting activity during winter might have also consequences on the following breeding season. If adults arrive to breeding areas with depleted body condition (induced by maintained high corticosterone levels), they may require longer time to regain the adequate condition to start reproduction. During winter, central Spain hosts not only local populations but also populations breeding in France, which have severely declined and are subject to intense conservation management (Bretagnolle and Inchausti, 2005; Villers et al., 2010). Thus, an inadequate management of areas with wintering little bustards may counteract the benefits obtained through conservation efforts focused on breeding populations elsewhere. The creation of hunting-free areas harboring good quality foraging habitats for the species, may aid to reduce the impact of hunting activity (Casas et al., 2009).

Further studies should link species physiological, behavioral, and distribution changes to population declines. Because the impacts of disturbances on free-living animals may be detected earlier on individuals than on populations (Ellis et al., 2012), improving the knowledge about the physiology of threatened species may help their conservation. The use of noninvasive techniques to quantify the physiological stress of wildlife has received great support, particularly when involving endangered species (Millspaugh and Washburn, 2004). This could be a promising tool for our target species given the high mortality rate of handled little bustards (Ponjoan et al., 2008). Determining the physiological response of little bustards using fecal glucocorticoid metabolites may give new insights on whether changing agricultural practices cause physiological stress and how organisms adapt to new environments with increasing human pressure. Because human pressure in agricultural areas may likely continue to increase, its effects on steppe birds of conservation concern should be carefully monitored to avoid potential negative impacts on their declining populations.

6.6 Acknowledgements

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6.7 Appendix A. Environmental exposure of little bustard feces

Levels of glucocorticoid metabolites in feces might be affected by bacterial activity and environmental conditions, and may decrease with increasing exposure time after defecation (Thiel et al., 2005). In order to evaluate a potential temporal loss of glucocorticoid metabolites in feces, we investigated the effects of exposure time of feces under the natural conditions in the study area (i.e. at the temperature and humidity conditions they were when we collected them). For this experiment, we collected 12 individual fecal samples at dawn on the 18^{th} of December 2011, and divided each individual sample in four equal parts (subsamples), each stored in an individual labeled bag. The first subsample was kept refrigerated, and frozen at -20°C within 1 h after detection, as for the usual fecal sample collections (exposure time T0). The three other subsamples were left inside the unclosed bags in the field, thus under the natural temperature / humidity conditions of the collection site, and were sequentially collected and frozen 3 h later, 6 h later and 12 h after T0 collection (exposure times T1, T2 and T3, respectively). Subsequently, we assayed glucocorticoid metabolites in all fecal subsamples in the laboratory.

Effects of exposure time on (log-transformed) corticosterone metabolite levels in feces were tested using GLMM with restricted maximum likelihood that included Sample Identity as a random effect (to account for repeated measures of same samples at different times). Explanatory variables included the categorical variable Exposure Time (T1-T2-T3), the initial corticosterone metabolite level (measured at T0) as a covariate, as well as the interaction Exposure Time × initial corticosterone metabolite level. We performed analyses with all data or removing one outlier value (from one sample at T2), and obtained similar results in terms of statistical significance. The data reported in results exclude the outlier.

Exposure time affected corticosterone metabolite levels, depending on initial level in feces (Exposure time: $\chi^2 = 11.13$; df = 3; $P = 0.011$; Initial corticosterone metabolites: $\chi^2 = 9.16$; df = 1; $P = 0.003$. Exposure time × Initial corticosterone metabolites interaction: $\chi^2 = 14.42$; df = 3; $P = 0.002$). Post-hoc test (Tukey's HSD) indicated that corticosterone metabolite levels measured at T1 (mean ± SE= 3267 ± 269 ng/g dry faeces) or T2 (3268 ± 221 ng/g) did not differ from those measured at T0 (3809 ± 213 ng/g). However, corticosterone metabolite levels at T3 (3040 ± 168 ng/g) were significantly lower than initial ones. Changes in corticosterone metabolite levels between T0 and T1 or between T0 and T2 were unrelated to initial corticosterone metabolite levels (slope ± SE of 0.002 ± 0.006 and 0.011 ±

0.007 respectively; Fig. A1), but changes in corticosterone metabolite levels between T0 and T3 were greater when initial corticosterone metabolite levels were higher (slope: 0.021 ± 0.005; Fig. A1). We thus only had evidence for loss of fecal corticosterone metabolite concentration at 12 hours (T3) after initial sampling (T0), and this loss appeared greater for samples which initially had higher fecal corticosterone metabolite levels.

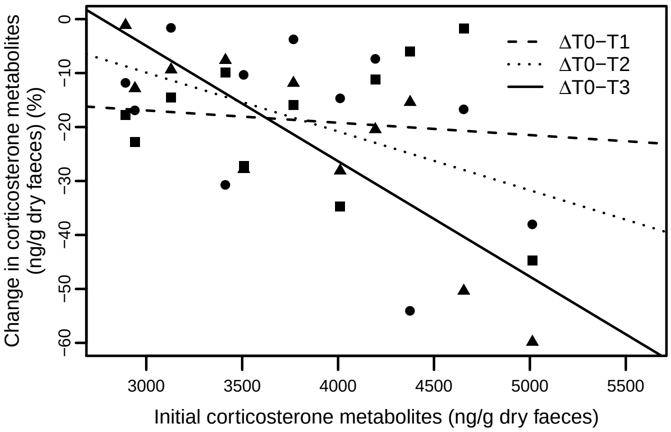

Figure 6.6: **Figure A1.** Relationship between changes on corticosterone metabolite levels with increased exposure time to natural environmental conditions and corticosterone metabolite concentration from initial collection (T0). Fecal samples were collected at 3 h (T1), 6 h (T2) and 12 h (T3) after the initial collection.

6.8 Appendix B

Table 6.5: **Table B1.** Full models of the GLMMs testing for temporal variations in human activity rates, little bustard flock sizes and flying probability. Human activity variables and flock size were fitted using negative binomial error distribution and a log link, with transect length (log-transformed) included as an offset (except for number of shot). For number of shots, models were fitted only with weekend data, since no hunting occurred during week days. For flying probability (i.e. whether an observed flock was in flight or on the ground), we used binomial error distribution with logit link. All models included "Trial" as a random effect, and Winter (2010-2011 vs. 2011-2012), Week Period (before, during, and after weekend), Daytime Period (DTP = AM vs. PM) and the interaction between Week Period and DTP as explanatory variables.

Response variable	Explanatory variables	Full model		
		χ^2	df	P
People/km	Winter	0.00	1	0.999
	Week Period	40.06	2	<0.001
	DTP	0.98	1	0.322
	Week Period×DTP	12.86	2	0.002
Dogs/km	Winter	0.36	1	0.550
	Week Period	24.04	2	<0.001
	DTP	0.00	1	0.999
	Week Period × DTP	0.00	2	1.000
Cars/km	Winter	0.00	1	0.969
	Week Period	14.59	2	0.001
	DTP	0.05	1	0.824
	Week Period × DTP	1.41	2	0.494
Cyclists/km	Winter	1.21	1	0.272
	Week Period	8.32	2	0.016
	DTP	0.01	1	0.938
	Week Period × DTP	2.40	2	0.302
Tractors/km	Winter	0.07	1	0.793
	Week Period	1.64	2	0.441
	DTP	0.37	1	0.544
	Week Period × DTP	7.54	2	0.023
Shots/min	Winter	0.23	1	0.631
	DTP	6.08	1	0.014
Flock size	Winter	0.76	1	0.384
	Week Period	4.76	2	0.093
	DTP	0.08	1	0.773
	Week Period × DTP	0.25	2	0.882
Flying probability	Winter	0.99	1	0.319
	Week Period	514.00	2	<0.001
	DTP	36.28	1	<0.001
	Week Period × DTP	0.00	2	1.000

Table 6.6: **Table B2.** Full models of the GLMs analyzing temporal variation in the proportion of little bustards being vigilant or foraging within flocks (n=77 scans). Initial models included as explanatory variables LogFS (flock size, log-transformed), Trial (December vs January), Week Period (before, during, and after weekend) and Daytime Period (DTP = AM vs. PM), an all possible two-way interactions.

Response variable	Explanatory variables	Full model		
		χ^2	df	P
Vigilance	Trial	0.05	1	0.817
	DTP	5.58	1	0.018
	LogFS	0.08	1	0.778
	Week Period	3.00	1	0.083
	LogFS DTP	3.96	1	0.047
	LogFS Week Period	9.26	2	0.010
	Week Period × DTP	2.69	1	0.101
	Trial × LogFS	0.25	1	0.619
	Trial × DTP	1.46	1	0.227
	Trial × Week Period	0.60	1	0.437
Foraging	Trial	0.01	1	0.931
	DTP	4.84	1	0.028
	LogFS	6.95	1	0.008
	Week Period	0.01	1	0.919
	LogFS DTP	2.10	1	0.147
	LogFS Week Period	0.14	2	0.932
	Week Period × DTP	2.05	1	0.152
	Trial × LogFS	0.04	1	0.836
	Trial × DTP	0.37	1	0.543
	Trial × Week Period	0.01	1	0.946

6.9 Appendix C. Carbon and Nitrogen contents of little bustard fecal samples before and during weekends

In addition to measuring stress hormone levels in little bustard feces, we also investigated variation in their Carbon and Nitrogen contents, comparing these before and during weekends.

Methods

During the two trials conducted in winter 2011-2012, for which we collected little bustard fecal samples from that large roost, we used a subset of the samples collected before weekend (n=60) and during the weekend (n=58) to estimate fecal C-N content.

Frozen fecal samples were dried at 90°C for 24 h in a forced air oven and then powdered with liquid nitrogen. N and C were quantified in 2.5 mg of each homogenized sample by elemental analyses using the dynamic flash combustion method at 1050°C in a LECO CHNS-932 microanalyzer (Leco, Michigan USA). Final results were obtained by multiplying exact weight by the percentage obtained in the combustion analysis. Analyses were conducted by a certified laboratory Microanálisis Elemental (Málaga, Spain). We analyzed variation C and N content (% of fecal sample dried weight) separately, using GLMs with Beta error distribution (appropriate for proportion data). We included as explanatory variables Trial (2 levels: December 2011 and January 2012), Week Period (2 levels for C and N analysis: before and during weekend) and the interaction between these two variables.

Results and discussion

The proportion of N in feces differed between Trials ($\chi^2 = 14.93$, $P < 0.001$; December 2011: 3.38 % ± 0.13, n=59; January 2012: 3.87% ± 0.13, n=59), and between week periods ($\chi^2 = 99.44$, $P < 0.001$), being higher during weekends (before weekend: 2.98% ± 0.12, n=60; weekend: 4.29% ± 0.10, n= 58). The interaction Trial × Week period was not significant ($\chi^2 = 0.00$, $P = 0.991$).

Similarly, the proportion of C in feces differed between Trials ($\chi^2 = 33.57$, $P < 0.001$; December 2011: 26.92% ± 0.85; January 2012: 31.43% ± 0.90), and between week periods ($\chi^2 = 167.07$, $P < 0.001$), being also higher during weekends (before weekend: 24.11% ± 0.57; weekend: 34.41%

± 0.69), with no significant interaction Trial × Week period (χ^2 = 0.16, P =0.691).

The C and N contents of feces (which represent on average 33% of dry feces weight) of little bustards appeared qualitatively different before and during weekend diet. Feces reflecting weekend ingestion presented a C content 10% greater than prior to weekends, while the increase in N content was around 1%. Such qualitative differences may reflect differences in diet quality. A non-mutually-exclusive explanation could be a greater mobilization of energy stores resulting in increased fecal C content during weekends, which may be facilitated by the increase in glucocorticoid levels, which are involved in catabolism and energy balance (Clinchy et al., 2013). However, detailed studies about the diet of this species in winter, the chemical composition of the plant species consumed by little bustards and the species metabolism are currently lacking, preventing us from understanding the reasons behind the observed qualitative differences. Further research is therefore needed to better link disturbance effects on habitat use, diet quality and nutritional status.

Chapter 7

General discussion

There is little doubt about the fundamental role played by biotic interactions in regulating populations, shaping community structure, and even promoting evolutionary change (Morin, 2011). Novel empirical studies add increasing evidence of their key influence across many different patterns observed in nature, perhaps in a more relevant manner than previously thought, affecting species distribution even at broad geographic scale (Grant and Grant, 2006; Heikkinen et al., 2007; Ripple et al., 2014; Duckworth et al., 2015). But the rapid and massive impacts of current global change are most likely to alter the network of species interactions in ecological communities worldwide because of the invasion of alien species or habitat modification among other processes (Fukami et al., 2006; Auer and Martin, 2013; Boström-Einarsson et al., 2014; Stenseth et al., 2015). Variation in species interactions may in turn affect species' population size and community formation (e.g. Stenseth et al., 2015). This is particularly relevant in the case of species at risk for which changes in the outcome of biotic interactions can exacerbate the negative impacts of variation in other environmental features. Therefore, the implementation of conservation strategies should move from classical views in which management measures obey solely to the reestablishment of suitable physical or habitat features, toward those which wisely incorporate the effects of biotic interaction in population dynamics.

Farmland birds in Europe have suffered overall declines mainly due to the multifactorial impacts of agricultural intensification and nowadays represent the most endangered group among European birds (Chamberlain et al., 2000; Donald et al., 2001, 2006; Inger et al., 2015). The little bustard is one of these species linked to agricultural landscapes, whose world population size and distribution range have undergone severe reductions since the 19th century (Cramp and Simmons, 1980; Goriup, 1994; Tucker and Heath, 1994). Unfortunately, the species still shows an alarming negative trend, and hence, urgent measures are required in order to revert its regression (de Juana, 2009; BirdLife International, 2012; SEO/Birdlife, 2012). The species' habitat preferences are well-established at different scales, particularly for breeding males (Martínez, 1994; Suárez-Seoane et al., 2002; Morales et al., 2005*b*; Suárez-Seoane et al., 2008; Delgado et al., 2010; Silva et al., 2010*a*), a necessary step for designing successful conservation policies. Indeed, the application of agri-environmental schemes in a French region under intensive agriculture effectively increased the population of breeding males (Bretagnolle et al., 2011).

However, the role of biotic interactions in the little bustard ecology is a less explored topic. Most studies dealing with the effects of biotic interactions have been focused on issues regarding sexual selection and mating system (Jiguet and Bretagnolle, 2001, 2006, 2014). This species has received great attention because of its exploded lek mating system (Jiguet et al., 2000), in which resource availability within male territories may play an important role in female attendance (Traba et al., 2008; Morales et al., 2013). Thus, the effects of intraspecific interactions, involving both males and females, in the formation and evolution of leks have been well investigated. However, few studies address how conspecifics influence habitat use and territory establishment (Delgado et al., 2010; Devoucoux, 2014; Morales et al., 2014), and only one considers interspecific interactions, specifically the formation of mixed flocks with the pin-tailed sandgrouse during winter (Martín et al., 2010). Nevertheless, this study does not evaluate the potential effects of this positive association for the little bustard. Because of the current changes in the availability of most suitable habitats for the little bustard due to the intensification of rotational fallows, which generates increased surface of bare ground, as well as the disappearance of long-term ones, ecologists should delve into the effects of biotic interaction in order to fully comprehend the species' population dynamics and aid in its conservation (Morris, 2003*a*,*c*). In this sense, the present thesis has contributed to improve the knowledge about the effects of conspecifics and to shed light in the role played by interspecific interactions in the habitat use, spatial distribution and behavior of little bustards, generating far-reaching implications for the conservation of this species.

As mentioned above, the little bustard population declines have been mainly related to processes of agricultural intensification through changes on landscape configuration, decreased availability of good quality habitats and food shortage for chicks (Wolff et al., 2001, 2002; Inchausti and Bretagnolle, 2005; Morales et al., 2005*b*; Bretagnolle et al., 2011). The reduction of shared resources may intensify competition between co-occurring species when these resources become limiting (e.g. Strubbe and Matthysen, 2009). Interspecific competition constitutes a pervasive ongoing force governing population and community dynamics through its effects on resource use, reproductive success or individual survival (Ziv et al., 1993; Martin and Martin, 2001; Berger and Gese, 2007; Dhondt, 2010). Furthermore, it is a driver of evolutionary divergence which can be even observed in ecological time (Adams, 2004; Grant and Grant, 2006; Stuart et al., 2014). But despite the loss of good quality habitats for the little bustard, which may reinforce competitive interactions, no attention has been paid to the potential negative effects of interspecific competition with other coexisting steppe birds. Results presented in *CHAPTER 2* and *CHAPTER 3* are the first to provide support for the existence of competition between the little and great bustards, two ecologically and phylogenetically close species (Cramp and Simmons, 1980; Del Hoyo et al., 1996; Del Hoyo and Collar, 2014).

The study of interspecific competition can be addressed from a wide variety of approaches: fitness measures (Martin and Martin, 2001), population size correlations (Cooper et al., 2007, *CHAPTER 3*), behavioral observations (Human and Gordon, 1996; Peck et al., 2014), resource partitioning (Ziv et al., 1993; Martin and Martin, 2001), ecological niche variations (Pianka, 1974; Peers et al., 2013, *CHAPTER 2*) or, habitat distributions (Morris, 1989; Rodríguez, 1995, *CHAPTER 3*). Based on the ecological niche theoretical framework, the novel methodology applied in *CHAPTER 2* enabled to build multidimensional niche hyperspaces in accordance with the *Hutchinsonian* niche concept (1957) to evaluate whether the little and great bustards interact when coexisting. The data used in this chapter were collected in different regions across Spain with different population sizes of the target species. This allowed for comparisons between the little bustard ecological niche in allopatry and sympatry and exploring potential density-dependent variations. The results of this study suggested that the little and the great bustard competitively interact when coexisting, which was supported by results of *CHAPTER 3*. The little bustard shifted its ecological niche, built with habitat variables, depending on great bustard presence. In sympatry, the little bustard expanded its niche breadth. Although theory predicts that ecological release from a putative competitor should expand niche breadth due to the incorporation of resources previously restricted by the dominant competitor ("Ecological release hypothesis" Schoener, 1989; Bolnick et al., 2010), niche expansion may also arise when the presence of a competitor forces individuals of the subordinate species to use less suitable resources. This may be likely the case for the two species considered, if the occupation of shared habitats by the great bustard induces an increased use of unsuitable habitats like ploughed lands in the little bustard. In addition, the little bustard displaced its niche position toward a higher proportional use of natural vegetation, one of its most preferred habitats, when in sympatry. The increased use of a preferred habitat by little bustards in the presence of a putative competitor is in accordance with habitat selection theory, which predicts that competing species segregate in their preferred habitats when co-occurring (Rosenzweig, 1981; Morris, 1988). But contrary to competition theory, which predicts low niche overlap because competing species should segregate their ecological niches in order to attain a stable coexistence (Pianka, 1974; Chesson, 1991; Leibold, 1995), little and great bustards highly overlapped in their habitat niche hyperspace. Most surprisingly, niche overlap increased with density of great bustard, the presumed dominant competitor due to its greater size (Cramp and Simmons, 1980, *CHAPTER 3*), until reaching a saturation value. This apparently contradicts the prevailing idea that niche overlap decreases as competition intensifies (Pianka, 1974). However, increased niche overlap in sympatry may arise because interspecific competition is currently operating between the species. For instance, Young (2004) found that niche overlap between competing salmonids increased with competitor density because the species' habitat distribution converged at high densities. The positive relationship between niche overlap and great bustard density may indicate that competition has intensified due to habitat change and that these species have not yet resolved their competition by segregating their niches or by competitive exclusion.

Niche analysis failed to detect density-dependent effects of interspecific competition on niche variation. This fact could be related with the type of variables employed as niche dimensions, which summarized information from several habitat variables. If competition occurs in particular habitats (e.g Abramsky et al., 1991), the method used here to create niche hyperspace may have generated confounding results. Thus, *CHAPTER 3* attempted to overcome these shortcomings by analyzing the habitat distribution of the two species. However, the species may also compete for other resources like food, especially during the highly demanding rearing period when chicks of both species feed mainly on arthropods (Jiguet, 2002; Bravo et al., 2012). Therefore, future studies evaluating interspecific competition between these species should also search for effects on their diet composition.

Because, as stated before, interspecific competition may operate only in particular habitats within the landscape, *CHAPTER 3* used habitat selection theory to further elucidate the effects of interspecific competition between these bustard species. By using data from different years and different extensive cereal farmlands areas, this chapter analyzed the set of joint densities in pairs of habitats. Results presented in this chapter strongly supported the existence of interspecific competition between the little and great bustards, reinforcing the first evidences provided by findings of *CHAPTER 2*. The study of density-dependent habitat selection illustrated the different strategies followed by these bustard species, in accordance with previous knowledge of their habitat selection (Lane et al., 2001; Wolff et al., 2001; Morales et al., 2005*b*, 2006; Delgado et al., 2010; López-Jamar et al., 2011). Habitat selection by the great bustard was that of a generalist species, with no clear habitat preferences, whereas the little bustard behaved like a specialist, choosing preferentially some particular habitats (fallows of different ages and legume crops) over others (see also Morales et al., 2006). Results of *CHAPTER 3* highlighted several important issues. First, these bustard species seemed to compete asymmetrically for resources because the great bustard modulated little bustard's habitat choice whereas great bustard's habitat distribution was not affected by the little bustard. Second, interspecific competition was not widespread and seemed to occur only in cereal habitat, involving interference interactions. As many great bustards occupied cereals, the attractiveness of this agrarian habitat decreased for the little bustard which progressively moved toward fallows and legume crops, their most preferred habitats. This study also supported the idea that competing species do not need to completely segregate in different habitats for stable coexistence, as generally assumed by habitat selection theory (Rosenzweig, 1981; Morris, 1988). Instead, individuals' habitat choice seems to trade-off the cost of intra- and interspecific competition.

Cereal crops have been considered as an unsuitable habitat for the little bustard due to their vegetation structure (e.g. Morales et al., 2008). This fact may be also linked to interspecific competitive processes not explored before (*CHAPTER 3*). In accordance with the ideal free distribution hypothesis (Fretwell and Lucas, 1969), the use of cereal as a secondary habitat by little bustards might mitigate intraspecific competition owing to increased density in the preferred habitat. In this line of evidence, analyses in *CHAPTER 2* found a density-dependent variation in the little bustard niche position toward a higher proportional use of cereals as conspecific density increased. Overall, findings of *CHAPTER 2* and *CHAPTER 3* may help to understand the disproportioned decline in some little bustard populations not explained merely by changes due to agricultural intensification (de Juana, 2009). Furthermore, they may be a harbinger of future negative population trends. Fallow surface seems inexorably prone to decrease because the modification of the European Common Agricultural Policy in 2009 abolished the requirement for farmers to leave 10% of their land as fallow. This means that intraspecific competition will likely intensify in little bustard populations where critical habitats are limited. The recovery of Iberian great bustard populations over the last decades (Fig. 7.1; BirdLife International, 2012; Alonso and Palacín, 2010; SEO/Birdlife, 2012) may be limiting the viability of little bustard populations in those regions with high great bustard density because intraspecific competition would not be mitigated by the use of cereal as an alternative habitat. Therefore, the effects of species interactions should be integrated within conservation schemes. Although *CHAPTER 3* did not find an inverse correlation between the population numbers of these bustard species, opposite trends have been detected by the long-term national breeding censuses (Fig. 7.1). This pattern has also been observed at local scale in different long-term monitored sites (F. Mougeot comm. pers. and personal observations). This highlights the need of future studies evaluating population sizes of great and little bustards in different regions where both species co-occurr in order to determine whether interspecific competition is actually a mechanism causing population declines.

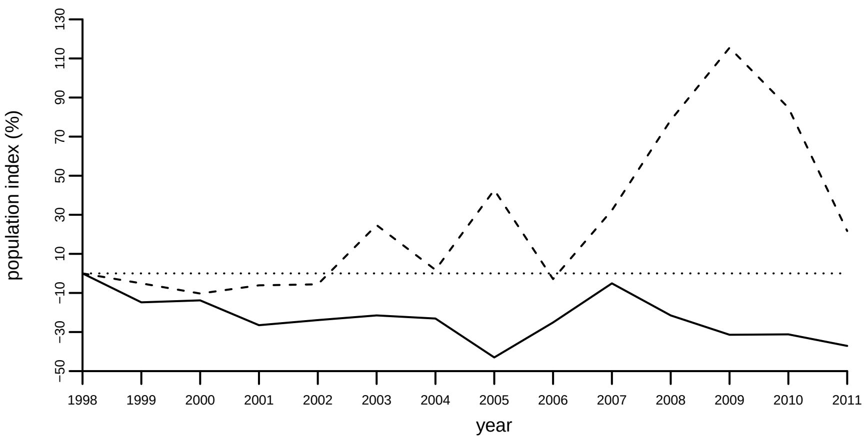

Figure 7.1: Temporal variation in population index (%) for the little (solid line) and great bustard (dashed line) calculated from national population surveys during the breeding season. Dotted line indicates no variation in population numbers from the first year of surveys in 1998 (After SEO/Birdlife, 2012).

In the light of results presented in *CHAPTER 2* and *CHAPTER 3*, conservation policies should take into account the differences in the little and great bustards' habitat requirements and the effects of interspecific competition in their habitat distribution in order to favor balanced population trends in both species. Thus, *CHAPTER 4* provided some guidelines directed at the conservation of both species by modelling spatially their distribution in two extensive cereal farmland study sites. This study revealed that both species benefited from the availability of short-term fallows and legume crops (Lane et al., 2001; Wolff et al., 2001; Morales et al., 2005*b*), habitats where the species did not compete (*CHAPTER 3*). Therefore, the application of agri-environmental schemes promoting a greater availability of these agrarian habitats is desired. Although the model predicted a larger surface of areas potentially occupied by both species, which may facilitate *a priori* the delimitation of protected areas, overall these zones were not the most suitable ones for each species. Areas predicted to be exclusively used by one species harbored the most suitable conditions of habitat and topography for each species. Therefore, conservation policies should not be guided by the apparent facility of protecting areas that are suitable for both little and great bustards because that could leave the best environmental conditions for each species without protection as well as ignoring the relevant effects of biotic interactions (*CHAPTER 2* and *CHAPTER 3*). It is thus worth favoring the tendency of these species to segregate in space and to use different preferred habitats. Finally, this study also highlighted that conservation policies should be designed at local scales in order to incorporate the particular landscape configuration, especially in these dynamic farmland systems, because species habitat use may vary depending upon the relative proportion of habitats (Morris, 2003*c*).

However, competition is not the only biotic force operating in ecological communities and facilitation is receiving increasing support as a relevant mechanism influencing population and community dynamics (e.g. Bruno et al., 2003). For instance, heterospecific attraction has been demonstrated in different species (Thomson et al., 2003; Fletcher, 2007; Forsman et al., 2008), although the mechanisms underlying attraction to other individuals have been mostly studied in the basis of conspecific attraction (Danchin et al., 2004). Individuals belonging to the same species may obtain different benefits from settling close to others, for instance, reduced predation risk or cues of good quality habitats (Pulliam, 1973; Thomson et al., 2003; Sebastián-González et al., 2010), even when territoriality should prevent aggregation (e.g Lack, 1948; Alonso et al., 2004). In the little bustard, males defend territories displaying agonistic behaviors but their territories are loosely aggregated (Jiguet et al., 2000). Likewise, females may obtain different benefits by settling close to males despite other cost associated with proximity. *CHAPTER 5* evaluated whether females with offspring are attracted to male conspecifics by analyzing their spatial distribution in relation to the areas most used by displaying males during the mating period. This study demonstrated that indeed females with offspring moved closer to areas previously used by breeding males. After nest abandonment, females rearing chicks perform movements searching for resources to feed their offspring and to ensure their safety (Lapiedra et al., 2011). Females selected preferentially semi-permanent vegetation in the form of short- and long-term fallows as well as natural vegetation of low shrubs (*CHAPTER5* Lapiedra et al., 2011). These are also the agrarian habitats most preferred by breeding males (e.g. Morales et al., 2005*b*; Delgado et al., 2010), and therefore, the observed spatially aggregated distribution could be due simply to a coincidental pattern of habitat selection between both sexes. However, this was not the case. Results presented on *CHAPTER 5* clearly showed that when enough preferred habitat was available in the landscape, females with offspring still moved closer to core areas of breeding males. Although territory quality does not seem to influence female mate choice (Jiguet et al., 2002), females may easily access important food resources for chicks by keeping closer to male territory (Traba et al., 2008; Morales et al., 2013). Recommendations for conservation also arise after this results. The protection of best quality sites for males to establish their breeding territories are likely to enhance also female productivity, a critical demographic parameter for population viability (Morales et al., 2005*a*). The presence of enough fallows may fulfill requirements of food and shelter for females with offspring and may reduce mortality due to early harvesting of cereals (Bretagnolle et al., 2011; Lapiedra et al., 2011; Morales et al., 2013). Because female ranging patterns are associated with differential reproductive success (Lapiedra et al., 2011), future studies should explore in greater detail whether the two ranging patterns performed by females also differ in their distribution relative to previous male breeding territories.

Because the little bustard inhabits human-generated landscapes, the species lives in permanent contact with humans and their associated activity, mainly related with agricultural work but also with outdoor activities, which may have effects on the species other than the modification of agrarian habitats. Thus, results presented in *CHAPTER 6* represent the first attempt to link human impacts of leisure and agricultural activities with variation in physiological stress and behavioral responses of wintering little bustards. Winter is a critical period for most organisms in temperate regions because they confront harsher environmental conditions, like low temperatures or food deprivation, which may compromise their survival or future reproduction (Watson, 1985; Duriez et al., 2012). Human presence and activity during this period may likely intensify the adverse impacts caused by severe climatic conditions. This study showed that during winter, human presence in cereal farmlands was low during weekdays and mainly associated to farming practices. This clearly contrasted with the significant increase of human activity during weekends, owing essentially to hunting but also to other outdoor activities like cycling and hiking, which are becoming commoner in these landscapes. Based on the measurement of corticosterone metabolites in feces, a method specially recommended for endangered species due to its non-invasive nature (Millspaugh and Washburn, 2004), *CHAPTER 6* revealed that the high rates of human presence observed during weekends induced physiological stress in little bustards. Most interestingly, the increase on fecal corticosterone metabolite levels was directly tied to hunting disturbance. Hunting is a very important socio-economic activity in these agricultural regions and occurs during autumn and winter (Casinello, 2013). It is well-known that hunting exerts important direct and indirect effects on game species (Fox and Madsen, 1997; Thiel et al., 2007), but its effects on non-game species is a less explored issue (e.g. Casas et al., 2009; Sastre et al., 2009). Although the short-term release of glucocorticoids is an adaptive response directed at ensuring individual survival (Sapolsky et al., 2000), little bustards persistently exposed to hunting disturbance may suffer the deleterious effects associated with maintaining high glucocorticoids levels (Wingfield et al., 1997; Sapolsky et al., 2000; Romero et al., 2009). However, physiological data here presented did not allow to determine whether corticosterone levels reached during weekends caused physiological damage. Therefore, future research analyzing glucocorticoids concentration in populations under different human disturbance pressures is required to gain new insights into the effects of elevated glucocorticoids on individual condition and their potential translation into impacts at population level. Monitoring variation in physiological parameters at individual level may aid to develop preliminary and efficient solutions that mitigate the subsequent consequences at higher organization levels.

CHAPTER 6 added also novel behavioral information to a previous study of Casas et al. (2009) on how behavioral patterns are affected by human activity. In particular, Casas et al. (2009) found that hunting induces higher vigilance rates and the relocation of little bustards into free-hunting areas. Behavioral data of *CHAPTER 6* showed that little bustards adjusted their responses in order to cope with increased levels of human disturbance by prioritizing safety during and immediately after disturbances (weekend) and then resorting to energy recovery after disturbance events (after weekend). The increased human activity during weekends forced little bustards to spend more time in escape movements and in vigilance. Human disturbances appeared to decouple the negative relationship between group size and the proportion of birds being vigilant found very often in many species (Manor and Saltz, 2003; Sansom et al., 2008; Powolny et al., 2012), so that little bustards tended to exhibit maximum vigilance rate even in large groups. Likewise, little bustards used mostly stubbles because this habitat may offer concealment due to their greater vegetation cover in this time of the year. After weekends, little bustards changed their strategy clearly toward a recovery of the energy lost during disturbance events. Birds increased the time allocated to foraging activities in smaller groups, thus reducing foraging competition (Sansom et al., 2008), and occupied preferentially old fallows which may harbor greater food availability (own unpublished data). Despite the relevant contribution of this study to improve the knowledge about wintering little bustards, it does not enable to precisely disentangle the effects of a given human activity in the observed behavioral responses. Thus, experimental studies controlling the type and intensity of human activity may help clarify how different agricultural practices or human leisure activities affect little bustard behavior.

Conclusiones

A partir de los resultados obtenidos a lo largo de los trabajos que conforman la presente tesis doctoral se extraen las siguientes conclusiones:

1. La intensificación de la competencia intraespecífica debida al aumento de la densidad de sisones provoca un desplazamiento en el nicho ecológico del sisón hacia un mayor uso de los cereales. Por lo tanto, la ocupación de este hábitat secundario para el sisón mitiga los efectos negativos de un incremento en la densidad dentro de los hábitats preferentes, es decir, barbechos, eriales y cultivos de leguminosas.

2. Tanto los análisis relativos al nicho ecológico como los de distribución de hábitat mostraron que el sisón y la avutarda son dos especies que mantienen relaciones de competencia. La competencia parece producirse de manera asimétrica, siendo la avutarda el competidor dominante ya que modifica el uso del hábitat del sisón, lo que no ocurre en el caso contrario. La competencia entre ambas acontece en el cereal, de manera que este hábitat pasa a ser progresivamente menos atractivo para el establecimiento de los territorios de machos de sisón a medida que aumenta la densidad de avutarda en el cereal. Así, los sisones hacen un uso cada vez mayor de sus hábitats preferentes. Este proceso de competencia entre ambas especies parece que no sólo se debería a la pura explotación de los recursos sino que habría involucrados también procesos de interferencia.

3. La coexistencia de estas especies no implica su completa segregación en distintos hábitat, tal y como asumen las teorías de selección de hábitat.

4. La competencia interespecífica parece obligar al sisón a utilizar en mayor proporción hábitats menos favorables, como puede ser el labrado, debido a que la presencia de avutarda restringe el uso del

cereal como hábitat secundario para el sisón, lo que produciría una expansión de su nicho ecológico en situaciones de simpatría.

5. Ambas especies se benefician de la presencia de barbechos jóvenes y cultivos de leguminosas por lo que el aumento en la superficie de estos sustratos sería una eficaz medida de conservación tanto para el sisón como para la avutarda. Sin embargo, las distintas preferencias de hábitat y los procesos de competencia entre estas dos especies pueden dar lugar a que las zonas donde coexisten a escala local no sean óptimas para el mantenimiento de poblaciones estables de ambas especies. Por tanto, desde una perspectiva de conservación, se requiere que en aquellas regiones donde ambas especies coexisten, la superficie agraria bajo protección y sometida a medidas agroambientales sea lo suficientemente extensa como para garantizar la segregación espacial entre ambas, ya que los procesos de competencia pueden imposibilitar la recuperación del sisón en aquellas zonas con escasez de barbechos y altas densidades de avutarda.

6. Las hembras de sisón con crías se localizaron más próximas a las zonas que previamente congregaron un mayor número de machos reproductores. La agregación espacial detectada entre hembras y machos no parece justificarse exclusivamente por un uso coincidente del hábitat sino que la presencia de los machos puede ser utilizada por las hembras como un indicador de calidad de hábitat o de abundancia de recursos.

7. La selección por parte de las hembras de zonas con vegetación semipermanente, en concreto barbechos jóvenes y eriales con matorral de bajo porte, indica que es necesario incentivar el mantenimiento de una fracción del territorio destinado a estos sustratos, lo que ofrecería, por ejemplo, zonas de nidificación donde no se produjese mortalidad debido a la siega prematura del cereal. Esto podría ayudar a aumentar la preocupantemente baja productividad de las hembras.

8. La actividad cinegética tuvo un efecto importante tanto en la respuesta comportamental como fisiológica de los sisones invernantes. Así, la caza provocó que los sisones sufrieran un aumento en los niveles de estrés fisiológico. Además, los sisones optaron por una estrategia comportamental dirigida a garantizar su seguridad durante el desarrollo de la actividad cinegética mientras que, una vez finalizado el evento estresante, su comportamiento se dirigió hacia

la recuperación energética. Los efectos que la caza ejerce sobre los sisones durante el periodo invernal han de ser tenidos en cuenta para la conservación de la especie, ya que no sólo pueden afectar a sisones de poblaciones peninsulares sino además a individuos migradores procedentes del oeste de Francia, que pasan los inviernos en estas regiones y cuyas poblaciones están siendo objeto de medidas de conservación.

9. En resumen, las interacciones bióticas tanto con individuos de la misma especie como con heterospecíficos, incluyendo al hombre, juegan un papel fundamental en el uso del hábitat y la distribución del sisón, lo cual tiene relevantes implicaciones para la conservación de la especie.

Bibliography

Abramsky, Z., O. Ovadia, and M. L. Rosenzweig. 1994. The shape of a *Gerbillus pyramidum* (Rodentia: Gerbillinae) isocline: an experimental field study. Oikos 69:318–326.

Abramsky, Z., M. L. Rosenzweig, and B. Pinshow. 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. Ecology 72:329–340.

Adams, D. C. 2004. Character displacement via aggressive interference in Appalachian salamanders. Ecology 85:2664–2670.

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Aitchison, J. 1986. The statistical analysis of compositional data. Chapman and Hall, London, UK.

Aitken, K. E., and K. Martin. 2012. Experimental test of nest-site limitation in mature mixed forests of central British Columbia, Canada. The Journal of Wildlife Management 76:557–565.

Alonso, J. C., and J. A. Alonso. 1996. The great bustard *Otis tarda* in Spain: present status, recent trends and an evaluation of earlier censuses. Biological Conservation 77:79–86.

Alonso, J. C., C. A. Martín, J. A. Alonso, C. Palacín, M. Magaña, and S. J. Lane. 2004. Distribution dynamics of a great bustard metapopulation throughout a decade: influence of conspecific attraction and recruitment. Biodiversity and Conservation 13:1659–1674.

Alonso, J. C., and C. Palacín. 2010. The world status and population trends of the great bustard (*Otis Tarda*): 2010 update. Chinese Birds 1:141–147.

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences of the United States of America 97:5954–5959.

Araújo, M. B., M. Cabeza, W. Thuiller, L. Hannah, and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10:1618–1626.

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33:1677–1688.

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16:743–753.

Arlettaz, R., P. Patthey, M. Baltic, T. Leu, M. Schaub, R. Palme, and S. Jenni-Eiermann. 2007. Spreading free-riding snow sports represent a novel serious threat for wildlife. Proceedings of the Royal Society of London B: Biological Sciences 274:1219–1224.

Arroyo, B., and M. Razin. 2006. Effect of human activities on bearded vulture behaviour and breeding success in the French Pyrenees. Biological Conservation 128:276–284.

Aspbury, A. S., and R. M. Gibson. 2004. Long-range visibility of greater sage grouse leks: a GIS-based analysis. Animal Behaviour 67:1127–1132.

Auer, S. K., and T. E. Martin. 2013. Climate change has indirect effects on resource use and overlap among coexisting bird species with negative consequences for their reproductive success. Global Change Biology 19:411–419.

Axelrod, J., and T. D. Reisine. 1984. Stress hormones: their interaction and regulation. Science 224:452–459.

Barja, I., G. Silván, S. Rosellini, A. Piñeiro, A. González-Gil, L. Camacho, and J. C. Illera. 2007. Stress physiological responses to tourist pressure in a wild population of European pine marten. The Journal of Steroid Biochemistry and Molecular Biology 104:136–142.

Barnagaud, J.-Y., V. Devictor, F. Jiguet, M. Barbet-Massin, I. Le Viol, and F. Archaux. 2012. Relating habitat and climatic niches in birds. PLoS ONE 7(3):: e32819.

Beale, C. M., and P. Monaghan. 2004. Human disturbance: people as predation-free predators? Journal of Applied Ecology 41:335–343.

Beauchamp, G., M. Belisle, and L. A. Giraldeau. 1997. Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. Journal of Animal Ecology 66:671–682.

Begon, M., J. L. Harper, and C. R. Townsend. 1999. Ecología. Omega, Barcelona, Spain.

Benítez-López, A., J. Viñuela, F. Suárez, I. Hervás, and J. T. García. 2014. Niche-habitat mechanisms and biotic interactions explain the coexistence and abundance of congeneric sandgrouse species. Oecologia 176:193–206.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76:1075–1085.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology & Evolution 9:191–193.

Bingham, R. L., and L. A. Brennan. 2004. Comparison of type I error rates for statistical analyses of resource selection. The Journal of Wildlife Management 68:206–212.

BirdLife International. 2004. Birds in Europe II: population estimates, trends and conservation status. Birdlife International, Cambridge, UK.

———. 2012. *Tetrax tetrax*. *In* The IUCN Red List of Threatened Species. Version 2013.2 Available from: http://www.iucnredlist.org/.

Blanc, R., M. Guillemain, J.-B. Mouronval, D. Desmonts, and H. Fritz. 2006. Effects of non-consumptive leisure disturbance to wildlife. Revue d'écologie-la Terre et la Vie 61:117–133.

Blanchard, P., M. Festa-Bianchet, J.-M. Gaillard, and J. T. Jorgenson. 2003. A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. The Journal of Wildlife Management 67:477–484.

Blomqvist, D., and O. C. Johansson. 1995. Trade-offs in nest site selection in coastal populations of lapwings *Vanellus vanellus*. Ibis 137:550–558.

Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. The n-dimensional hypervolume. Global Ecology and Biogeography 23:595–609.

Bloom, D. E. 2011. 7 billion and counting. Science 333:562–569.

Bolger, D. T., M. A. Patten, and D. C. Bostock. 2005. Avian reproductive failure in response to an extreme climatic event. Oecologia 142:398–406.

Bolnick, D. I. 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. Nature 410:463–466.

Bolnick, D. I., T. Ingram, W. E. Stutz, L. K. Snowberg, O. L. Lau, and J. S. Paull. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proceedings of the Royal Society of London B: Biological Sciences 277:1789–1797.

Bonesi, L., P. Chanin, and D. W. Macdonald. 2004. Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. Oikos 106:19–26.

Boström-Einarsson, L., M. C. Bonin, P. L. Munday, and G. P. Jones. 2014. Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. Ecology 95:3056–3067.

Boulinier, T., E. Danchin, J.-Y. Monnat, C. Doutrelant, and B. Cadiou. 1996. Timing of prospecting and the value of information in a colonial breeding bird. Journal of Avian Biology 27:252–256.

Braunisch, V., P. Patthey, and R. Arlettaz. 2011. Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. Ecological Applications 21:955–967.

Bravo, C., C. Ponce, C. Palacín, and J. C. Alonso. 2012. Diet of young great bustards *Otis tarda* in Spain: sexual and seasonal differences. Bird Study 59:243–251.

Bretagnolle, V., and P. Inchausti. 2005. Modelling population reinforcement at a large spatial scale as a conservation strategy for the declining little bustard (*Tetrax tetrax*) in agricultural habitats. Animal Conservation 8:59–68.

Bretagnolle, V., A. Villers, L. Denonfoux, T. Cornulier, P. Inchausti, and I. Badenhausser. 2011. Rapid recovery of a depleted population of little bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme. Ibis 153:4–13.

Brittingham, M. C., and S. A. Temple. 1988. Impacts of supplemental feeding on survival rates of black-capped chickadees. Ecology 69:581–589.

Brown, W. L., and E. O. Wilson. 1956. Character displacement. Systematic Zoology 5:49–64.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18:119–125.

Burfield, I. 2005. The conservation status of steppic birds in europe. Pages 119–139 *in* G. Bota, M. B. Morales, S. Mañosa, and J. Camprodon, eds. Ecology and Conservation of Steppe-land Birds. Lynx Ed. & Centre Tecnològic Forestal de Catalunya, Barcelona, Spain.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Calsbeek, R., and R. M. Cox. 2010. Experimentally assessing the relative importance of predation and competition as agents of selection. Nature 465:613–616.

Caro, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, USA.

Caro, T., A. Engilis, E. Fitzherbert, and T. Gardner. 2004. Preliminary assessment of the flagship species concept at a small scale. Animal Conservation 7:63–70.

Carrascal, L. M., D. Palomino, J. Seoane, and C. L. Alonso. 2008. Habitat use and population density of the houbara bustard *Chlamydotis undulata* in Fuerteventura (Canary Islands). African Journal of Ecology 46:291–302.

Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain Region. Ecological Applications 11:961–980.

Casas, F., F. Mougeot, J. Viñuela, and V. Bretagnolle. 2009. Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. Animal Conservation 12:346–354.

Casinello, J. 2013. La caza como recurso renovable y la conservación de la naturaleza. CSIC, Madrid, Spain.

Cavieres, L. A., and E. I. Badano. 2009. Do facilitative interactions increase species richness at the entire community level? Journal of Ecology 97:1181–1191.

Chamberlain, D. E., R. J. Fuller, R. G. H. Bunce, J. C. Duckworth, and M. Shrubb. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37:771–788.

Chase, J. M., and M. A. Leibold. 2003. Ecological Niches: linking classical and contemporary approaches. The University of Chicago Press, Chicago, USA.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Chesson, P. 1991. A need for niches? Trends in Ecology & Evolution 6:26–28.

———. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Cimino, L., and S. Lovari. 2003. The effects of food or cover removal on spacing patterns and habitat use in roe deer (*Capreolus capreolus*). Journal of Zoology 261:299–305.

Clinchy, M., M. J. Sheriff, and L. Y. Zanette. 2013. Predator-induced stress and the ecology of fear. Functional Ecology 27:56–65.

Concepción, E. D., and M. Díaz. 2010. Relative effects of field- and landscape-scale intensification on farmland bird diversity in Mediterranean dry cereal croplands. Aspects of Applied Biology 100:245–252.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131–138.

———. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist 122:661–696.

Conomy, J. T., J. A. Dubovsky, J. A. Collazo, and W. J. Fleming. 1998. Do black ducks and wood ducks habituate to aircraft disturbance? The Journal of Wildlife Management 62:1135–1142.

Cooper, C. B., W. M. Hochachka, and A. A. Dhondt. 2007. Contrasting natural experiments confirm competition between house finches and house sparrows. Ecology 88:864–870.

Cornulier, T., and V. Bretagnolle. 2006. Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors. Ecography 29:240–250.

Cramer, J. S. 2003. Logit models: from economics and other fields. Cambridge University Press, Cambridge, UK.

Cramp, S., and K. E. L. Simmons. 1980. The Birds of the Western Paleartic. Vol II. Oxford University Press, Oxford, UK.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415–2428.

Danchin, E., L.-A. Giraldeau, T. J. Valone, and R. H. Wagner. 2004. Public information: from nosy neighbors to cultural evolution. Science 305:487–491.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life, 1st ed. John Murray, London, UK.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292:673–679.

Davis, S. E., R. G. Nager, and R. W. Furness. 2005. Food availability affects adult survival as well as breeding success of parasitic jaegers. Ecology 86:1047–1056.

de Candolle, A. P. 1855. Géographie botanique raisonnée. Victor Masson, Paris, France.

de Juana, E. 2009. The dramatic decline of the little bustard *Tetrax tetrax* in Extremadura (Spain). Ardeola 56:119–125.

Del Hoyo, J., and N. J. Collar. 2014. HBW and BirdLife International illustrated checklist of the birds of the world. Volume 1: non-passerines. Lynx Edicions & Birdlife International, Barcelona, Spain.

Del Hoyo, J., A. Elliott, and J. Sargatal. 1996. Handbook of the birds of the World, Vol. 3, Hoatzin to Auks. Lynx Edicions, Barcelona, Spain.

Delgado, A., and F. Moreira. 2010. Between-year variations in little bustard *Tetrax tetrax* population densities are influenced by agricultural intensification and rainfall. Ibis 152:633–642.

Delgado, M. P., M. B. Morales, J. Traba, and E. L. García de la Morena. 2009. Determining the effects of habitat management and climate on the population trends of a declining steppe bird. Ibis 151:440–451.

Delgado, M. P., M. A. Sanza, M. B. Morales, J. Traba, and D. Rivera. 2013. Habitat selection and coexistence in wintering passerine steppe birds. Journal of Ornithology 154:469–479.

Delgado, M. P., J. Traba, E. L. García de la Morena, and M. B. Morales. 2010. Habitat selection and density-dependent relationships in spatial occupancy by male little bustards *Tetrax tetrax*. Ardea 98:185–194.

Derbyshire, R., D. Strickland, and D. R. Norris. 2015. Experimental evidence and 43 years of monitoring data show that food limits reproduction in a food-caching passerine. Ecology :http://dx.doi.org/10.1890/15–0191.1.

Devoucoux, P. 2014. Conséquences et impacts prévisibles d'une perte d'habitat majeure sur une espèce menacée aux exigences écologiques complexes: effets de la mise en place du contournement ferroviaire à grande vitesse Nîmes-Montpellier dur la dynamique de la population d'Outarde canepetière des Costières de Nîmes. Ph.D. thesis. Faculté des Science Fondamentales et Appliquées. L'Universite de Poitiers, Poitiers, France.

Dhondt, A. A. 2010. Effects of competition on great and blue tit reproduction: intensity and importance in relation to habitat quality. Journal of Animal Ecology 79:257–265.

———. 2012. Interspecific competition in birds. Oxford University Press, New York (USA).

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition: Why did field biologists so long overlook the widespread evidence for interspecific competition that had already impressed Darwin? American Scientist 66:322–331.

———. 1989. Quaternary megafaunal extinctions: variations on a theme by paganini. Journal of Archaeological Science 16:167–175.

Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168–1170.

Donald, P. F., R. E. Green, and M. F. Heath. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London Series B-Biological Science 268:25–29.

Donald, P. F., F. J. Sanderson, I. J. Burfield, and F. P. J. van Bommel. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. Agriculture, Ecosystems and Environment 116:189–196.

Doncaster, C. P. 2000. Extension of ideal free resource use to breeding populations and metapopulations. Oikos 89:24–36.

Duckworth, R. A., V. Belloni, and S. R. Anderson. 2015. Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. Science 347:875–877.

Duong, T. 2014. ks: Kernel smoothing. R package version 1.9.3. http://CRAN.R-project.org/package=ks.

Duriez, O., B. J. Ens, R. Choquet, R. Pradel, and M. Klaassen. 2012. Comparing the seasonal survival of resident and migratory oystercatchers: carry-over effects of habitat quality and weather conditions. Oikos 121:862–873.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57.

Ellenberg, U., A. N. Setiawan, A. Cree, D. M. Houston, and P. J. Seddon. 2007. Elevated hormonal stress response and reduced reproductive output in YEllow-eyed penguins exposed to unregulated tourism. General and Comparative Endocrinology 152:54–63.

Ellis, R. D., T. J. McWhorter, and M. Maron. 2012. Integrating landscape ecology and conservation physiology. Landscape Ecology 27:1–12.

Elton, C. 1927. Animal ecology. Sidgwick and Jackson, London.

ESRI. 2007. GIS and mapping software. http://www.esri.com/.

Faria, N., J. E. Raba¸ca, and M. B. Morales. 2012. The importance of grazing regime in the provision of breeding habitat for grassland birds: the case of the endangered little bustard (*Tetrax tetrax*). Journal for Nature Conservation 20:211–218.

Fletcher, R. J. 2007. Species interactions and population density mediate the use of social cues for habitat selection. Journal of Animal Ecology 76:598–606.

Forsman, J. T., M. B. Hjernquist, J. Taipale, and L. Gustafsson. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. Behavioral Ecology 19:539–545.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Fox, A. D., and J. Madsen. 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. Journal of Applied Ecology 34:1–13.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Fukami, T., D. A. Wardle, P. J. Bellingham, C. P. H. Mulder, D. R. Towns, G. W. Yeates, K. I. Bonner, M. S. Durrett, M. N. Grant-Hoffman, and W. M. Williamson. 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. Ecology Letters 9:1299–1307.

García de la Morena, E. L., G. Bota, A. Ponjoan, and M. B. Morales. 2006. El Sisón Común en España. I Censo Nacional (2005). SEO/BirdLife, Madrid, Spain.

García de la Morena, E. L., M. B. Morales, G. Bota, J. P. Silva, A. Ponjoan, F. Suárez, S. Mañosa, and E. de Juana. 2015. Migration patterns of Iberian little bustards *Tetrax tetrax*. Ardeola 62:95–112.

Gaston, K. J. 2003. The structure and dynamics of geographical ranges. Oxford University Press, Oxford, UK.

Gause, G. 1934. The struggle for existence. Williams & Wilkins, Baltimore, USA.

Geange, S. W., S. Pledger, K. C. Burns, and J. S. Shima. 2011. A unified analysis of niche overlap incorporating data of different types. Methods in Ecology and Evolution 2:175–184.

Goriup, P. 1994. Little bustard *Tetrax tetrax*. Pages 236–237 *in* G. M. Tucker and M. F. Heath, eds. Birds in Europe: their conservation status. Birdlife International, Cambridge, UK.

Grant, P. R., and B. R. Grant. 2006. Evolution of character displacement in Darwin's finches. Science 313:224–226.

Grinnell, J. 1917. The niche-relationships of the California thrasher. Auk 34:427–433.

Grosholz, E. D., G. M. Ruiz, C. A. Dean, K. A. Shirley, J. L. Maron, and P. G. Connors. 2000. The impacts of a nonindigenous marine predator in California bay. Ecology 81:1206–1224.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Hakkarainen, H., E. Korpimäki, T. Laaksonen, A. Nikula, and P. Suorsa. 2008. Survival of male Tengmalm's owls increases with cover of old forest in their territory. Oecologia 155:479–486.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. Global Ecology and Biogeograhy 13:469–476.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Hardin, G. 1960. The competitive exclusion principle. Science 131:1292–1297.

Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data-a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20:97–123.

Heikkinen, R. K., M. Luoto, R. Virkkala, R. G. Pearson, and J.-H. Körber. 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecology and Biogeograhy 16:754–763.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29:773–785.

Higgs, P., and B. J. Fox. 1993. Interspecific competition: a mechanism for rodent succession after fire in wet heathland. Australian Journal of Ecology 18:193–201.

Hijmans, R. J., S. J. Phillips, J. Leathwick, and J. Elith. 2012. dismo: Species distribution modeling. R package version 0.7-17.

Höglund, J., and R. V. Alatalo. 1995. Leks. Princeton University Press, Princeton, New Jersey, USA.

Horreo, J. L., J. C. Alonso, and B. Milá. 2014. Dna sequences from the little brown bustard *Eupodotis humilis* suggest its close phylogenetic relationship to the little bustard *Tetrax tetrax*. Ostrich 85:97–101.

Hortal, J., J. A. Diniz-Filho, L. M. Bini, M. A. Rodríguez, A. Baselga, D. Nogués-Bravo, T. F. Rangel, B. A. Hawkins, and J. M. Lobo. 2011. Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. Ecology Letters 14:741–748.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution 15:56–61.

Human, K. G., and D. M. Gordon. 1996. Exploitation and interference competition between the invasive argentine ant, *Linepithema humile*, and native ant species. Oecologia 105:405–412.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Iñigo, A., and B. Barov. 2010. Action plan for the little bustard *Tetrax tetrax* in the European Union. SEO Birdlife and Birdlife International for the European Commission.

Inchausti, P., and V. Bretagnolle. 2005. Predicting short-term extinction risk for the declining little bustard (*Tetrax tetrax*) in intensive agricultural habitats. Biological Conservation 122:375–384.

Inger, R., R. Gregory, J. P. Duffy, I. Stott, P. Voříšek, and K. J. Gaston. 2015. Common European birds are declining rapidly while less abundant species' numbers are rising. Ecology Letters 18:28–36.

IUCN. 2012. Red List of Threatened Species. www.iucnredlist.org. 02-10-2013.

Jaynes, E. T. 1957. Information theory and statistical mechanics. Physical Review 106:620–630.

Jennes, J. 2006. Topographic Position Index (tpi jen.avx) extension for ArcView 3.x, v. 1.2. Jenness Enterprises. Available at: http://www.jennessent.com/arcview/tpi.htm.

Jiguet, F. 2002. Arthropods in diet of little bustard *Tetrax tetrax* during the breeding season in western france. Bird Study 49:105–109.

Jiguet, F., B. Arroyo, and V. Bretagnolle. 2000. Lek mating systems: a case study in the little bustard *Tetrax tetrax*. Behavioural Processes 51:63–82.

Jiguet, F., and V. Bretagnolle. 2001. Courtship behaviour in a lekking species: individual variations and settlement tactics in male little bustard. Behavioural Processes 55:107–118.

———. 2006. Manipulating lek size and composition using decoys: an experimental investigation of lek evolution models. The American Naturalist 168:758–768.

———. 2014. Sexy males and choosy females on exploded leks: correlates of male attractiveness in the little bustard. Behavioural Processes 103:246–255.

Jiguet, F., S. Jaulin, and B. Arroyo. 2002. Resource defence on exploded leks: do male little bustards, *T. tetrax*, control resources for females? Animal Behavior 63:899–905.

Jiménez-Valverde, A., N. Barve, A. Lira-Noriega, S. P. Maher, Y. Nakazawa, M. Pa¸pes, J. Soberón, J. Sukumaran, and A. T. Peterson. 2011. Dominant climate influences on North American bird distributions. Global Ecology and Biogeography 20:114–118.

Jolivet, C., and V. Bretagnolle. 2002. L'outarde canepetière en France: évolution récente des populations, bilan des mesures de sauvegarde et perspectives d'avenir. Alauda 70:93–96.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Keddy, P. A. 1989. Competition. Chapman and Hall, London, New York, USA.

Kimura, K., and S. Chiba. 2010. Interspecific interference competition alters habitat use patterns in two species of land snails. Evolutionary Ecology 24:815–825.

Kotler, B. P., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics 19:281–307.

Kremen, C., A. Cameron, A. Moilanen, S. J. Phillips, C. D. Thomas, H. Beentje, J. Dransfield, B. L. Fisher, F. Glaw, T. C. Good, G. J. Harper, R. J. Hijmans, D. C. Lees, E. Louis, R. A. Nussbaum, C. J. Raxworthy, A. Razafimpahanana, G. E. Schatz, M. Vences, D. R. Vieites, P. C. Wright, and M. L. Zjhra. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. Science 320:222–226.

Kullmann, H., T. Thünken, S. A. Baldauf, T. C. M. Bakker, and J. G. Frommen. 2008. Fish odour triggers conspecific attraction behaviour in an aquatic invertebrate. Biology Letters 4:458–460.

Lack, D. 1944. Ecological aspects of species-formation in passerine birds. Ibis 86:260–286.

———. 1948. Notes on the ecology of the robin. Ibis 90:252–279.

Lafferty, K. D. 2001. Disturbance to wintering western snowy plovers. Biological Conservation 101:315–325.

Laiolo, P. 2013. From inter-specific behavioural interactions to species distribution patterns along gradients of habitat heterogeneity. Oecologia 171:207–215.

Lane, S. J., J. C. Alonso, and C. A. Martín. 2001. Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? Journal of Applied Ecology 38:193–203.

Lapiedra, O., A. Ponjoan, A. Gamero, G. Bota, and S. Mañosa. 2011. Brood ranging behaviour and breeding success of the threatened little bustard in an intensified cereal farmland area. Biological Conservation 144:2882–2890.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Second English Edition. Elsevier Publishers, Amsterdam, Netherlands.

Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76:1371–1382.

Leitão, D., and L. Costa. 2001. First approach to the study of the non-breeding abundance and habitat use by the little bustard *Tetrax tetrax* in the lower Tejo grasslands (South Portugal). Airo 11:37–43.

Lima, S. L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Animal Behaviour 49:11–20.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology & Evolution 11:131–135.

Lin, Y.-T. K., and G. O. Batzli. 2002. The cost of habitat selection in prairie voles: an empirical assessment using isodar analysis. Evolutionary Ecology 16:387–397.

Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

López-Jamar, J., F. Casas, M. Díaz, and M. B. Morales. 2011. Local differences in habitat selection by great bustard *Otis tarda* in changing agricultural landscapes: implications for farmland bird conservation. Bird Conservation International 21:328–341.

MacArthur, R. H. 1984. Geographical ecology: patterns in the distribution of species. Princeton University Press, Oxford, UK.

Magaña, M., J. C. Alonso, C. A. Martín, L. M. Bautista, and B. Martín. 2010. Nest-site selection by great bustards otis tarda suggests a trade-off between concealment and visibility. Ibis 152:77–89.

Manor, R., and D. Saltz. 2003. Impact of human nuisance disturbance on vigilance and group size of a social ungulate. Ecological Applications 13:1830–1834.

Martín, B. 2009. Dinámica de población y viabilidad de la avutarda común en la Comunidad de Madrid. Ph.D. thesis. Universidad Complutense de Madrid, Madrid, Spain.

Martín, C. A., F. Casas, F. Mougeot, J. T. García, and J. Viñuela. 2010. Positive interactions between vulnerable species in agrarian pseudo-steppes: habitat use by pin-tailed sandgrouse depends on its association with the little bustard. Animal Conservation 13:383–389.

Martin, P., and P. Bateson. 1993. Measuring behaviour: an introductory guide. Cambridge University Press, Cambridge, UK.

Martin, P. R., and T. E. Martin. 2001. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology 82:189–206.

Martin, T. E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? Ecology 82:175–188.

Martinetto, K., and J. M. Cugnasse. 2001. Reaction distance in Mediterranean Mouflon (*Ovis gmelini musimon x Ovis sp.*) in the presence of hikers with a dog on the CAROUX plateau (Herault, France). Revue d'écologie-la Terre et la Vie 56:231–242.

Martínez, C. 1994. Habitat selection by the little bustard *Tetrax tetrax* in cultivated areas of central Spain. Biological Conservation 67:125–128.

———. 1998. Microhabitat selection by the little bustard *Tetrax tetrax* during the breeding season. Ardeola 45:73–76.

Martínez-Meyer, E., A. T. Peterson, J. I. Servín, and L. F. Kiff. 2006. Ecological niche modelling and prioritizing areas for species reintroductions. Oryx 40:411–418.

May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Sciences of the United States of America 69:1109–1113.

Melles, S. J., D. Badzinski, M. J. Fortin, F. Csillag, and K. Lindsay. 2009. Disentangling habitat and social drivers of nesting patterns in songbirds. Landscape Ecology 24:519–531.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Wellbeing: Biodiversity Synthesis. World Resources Institute, Washington, DC, USA.

Millspaugh, J. J., and B. E. Washburn. 2004. Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. General and Comparative Endocrinology 138:189–199.

Mönkkönen, M., P. Helle, and K. Soppela. 1990. Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus spp.*): heterospecific attraction in northern breeding bird communites? Oecologia 85:218–225.

Morales, M. B., V. Bretagnolle, and B. Arroyo. 2005*a*. Viability of the endangered little bustard *Tetrax tetrax* population of western France. Biodiversity and Conservation 14:3135–3150.

Morales, M. B., F. Casas, E. García de la Morena, A. Ponjoan, G. Calabuig, J. Martínez-Padilla, J. T. García, S. Mañosa, J. Viñuela, and G. Bota. 2014. Density dependence and habitat quality modulate the intensity of display territory defence in an exploded lekking species. Behavioral Ecology and Sociobiology 68:1493–1504.

Morales, M. B., J. T. García, and B. Arroyo. 2005*b*. Can landscape composition changes predict spatial and annual variation of little bustard male abundance? Animal Conservation 8:167–174.

Morales, M. B., E. L. García de la Morena, M. P. Delgado, and J. Traba. 2007. Tendencia reciente y viabilidad futura de las poblaciones de sisón común (*Tetrax tetrax*) en la Comunidad de Madrid. Pages 40–55 *in* J. de la Puente, J. Pérez-Tris, M. Juan, and A. Bermejo, eds. Anuario ornitológico de Madrid 2006. SEO-Monticola, Madrid, Spain.

Morales, M. B., and C. A. Martín. 2002. The great bustard *Otis tarda*. The Journal of Birds of the Western Paleartic 4:217–232.

Morales, M. B., F. Suárez, and E. L. García de la Morena. 2006. Résponses des oiseaux de steppe aux différents niveaux de mise en culture et d'intensification du paysage agricole: analyse comparative de leurs effets sur la densité de population et la sélection de l'habitat chez l'Outarde Canepetière *Tetrax tetrax* et l'Outarde Barbue *Otis tarda*. Revue décologie - la Terre et la Vie 61:261–269.

Morales, M. B., J. Traba, and B. Arroyo. 2015. El sisón, una especie realmente amenazada. Quercus In press.

Morales, M. B., J. Traba, E. Carriles, M. P. Delgado, and E. L. García de la Morena. 2008. Sexual differences in microhabitat selection of breeding little bustards *Tetrax tetrax*: Ecological segregation based on vegetation structure. Acta Oecologica 34:345–353.

Morales, M. B., J. Traba, M. P. Delgado, and E. L. García de la Morena. 2013. The use of fallows by nesting little bustard *Tetrax tetrax* females: implications for conservation in mosaic cereal farmland. Ardeola 60:85–97.

Moreno, J. M. 2005. Evaluación preliminar de los impactos en España por efecto del cambio climático. Project ECCE Final Report. Secretaría General Técnica, Ministerio de Medio Ambiente, Madrid, Spain.

Morin, P. J. 2011. Community Ecology. Wiley-Blackwell, Chichester, UK.

Morris, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. Evolutionary Ecology 1:379–388.

———. 1988. Habitat dependent population regulation and community structure. Evolutionary Ecology 2:253–269.

———. 1989. Habitat-dependent estimates of competitive interaction. Oikos 55:111–120.

———. 1992. Scales and costs of habitat selection in heterogeneous landscapes. Evolutionary Ecology 6:412–432.

———. 1999. Has the ghost of competition passed? Evolutionary Ecology Research 1:3–20.

———. 2003*a*. How can we apply theories of habitat selection to wildlife conservation and management? Wildlife Research 30:303–319.

———. 2003*b*. Shadows of predation: habitat-selecting consumers eclipse competition between coexisting prey. Evolutionary Ecology 17:393–422.

———. 2003*c*. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.

———. 2004. Some crucial consequences of adaptive habitat selection by predators and prey: apparent mutualisms, competitive ghosts, habitat abandonment, and spatial structure. Israel Journal of Zoology 50:207–232.

———. 2009. Apparent predation risk: tests of habitat selection theory reveal unexpected effects of competition. Evolutionary Ecology Research 11:209–225.

Morris, D. W., D. L. Davidson, and C. J. Krebs. 2000*a*. Measuring the ghost of competition: insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. Evolutionary Ecology Research 2:41–67.

Morris, D. W., B. J. Fox, J. Luo, and V. Monamy. 2000*b*. Habitat-dependent competition and the coexistence of Australian heathland rodents. Oikos 91:294–306.

Mouillot, D., W. Stubbs, M. Faure, O. Dumay, J. A. Tomasini, J. B. Wilson, and T. Chi. 2005. Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. Oecologia 145:345–353.

Munday, P. L., G. P. Jones, and M. J. Caley. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology 82:2177–2189.

Nakagawa, S., E. Möstl, and J. R. Waas. 2003. Validation of an enzyme immunoassay to measure faecal glucocorticoid metabolites from Adélie penguins (*Pygoscelis adeliae*): a non-invasive tool for estimating stress? Polar Biology 26:491–493.

Navarro-Castilla, A., I. Barja, P. P. Olea, A. Piñeiro, P. Mateo-Tomás, G. Silván, and J. C. Illera. 2014. Are degraded habitats from agricultural crops associated with elevated faecal glucocorticoids in a wild population of common vole (*Microtus arvalis*)? Mammalian Biology - Zeitschrift für Säugetierkunde 79:36–43.

Nordhausen, K., S. Sirkia, H. Oja, and D. E. Tyler. 2012. ICSNP: Tools for Multivariate Nonparametrics. R package version1.0-9, http://CRAN.R-project.org/package=ICSNP.

Oñate, J. J. 2005. A reformed CAP? opportunities and threats for the conservation of steppe-birds and the agri-environment. Pages 253–282 *in* G. Bota, M. B. Morales, S. Mañosa, and J. Camprodon, eds. Ecology and Conservation of Steppe-land Birds. Lynx Ed. & Centre Tecnològic Forestal de Catalunya, Barcelona, Spain.

Onrubia, A., and T. Andrés. 2005. Impact of human activities on steppic-land birds: a review in the context of the Western Paleartic. Pages 185–209 *in* G. Bota, M. B. Morales, S. Mañosa, and J. Camprodon, eds. Ecology and conservation of steppe-land birds. Lynx Ed. & Centre Tecnològic Forestal de Catalunya, Barcelona, Spain.

Ovadia, O., and Z. Abramsky. 1995. Density-dependent habitat selection: evaluation of the isodar method. Oikos 73:86–94.

Palacín, C., and J. C. Alonso. 2008. An updated estimate of the world status and population trends of the great bustard *Otis Tarda*. Ardeola 55:13–25.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Pearson, R. G., T. P. Dawson, and C. Liu. 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27:285–298.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102–117.

Peck, H. L., H. E. Pringle, H. H. Marshall, I. P. Owens, and A. M. Lord. 2014. Experimental evidence of impacts of an invasive parakeet on foraging behavior of native birds. Behavioral Ecology 25:582–590.

Peers, M. J. L., D. H. Thornton, and D. L. Murray. 2013. Evidence for large-scale effects of competition: niche displacement in Canada lynx and bobcat. Proceedings of the Royal Society of London B: Biological Sciences 280:20132495.

Pelissier, R., and F. Goreaud. 2010. ads: Spatial point patterns analysis. R package version 1.2-10., http://CRAN.R-project.org/ package=ads.

Perry, E. F., and D. E. Andersen. 2003. Advantages of clustered nesting for least flycatchers in north-central Minnesota. The Condor 105:756–770.

Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2011. Ecological niches and geographic distributions. Oxford University Press, Oxford, UK.

Phillips, S. J., M. Dudík, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. *In* Proceedings of the twenty-first international conference on Machine learning. Banff, Alberta, Canada.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences of the United States of America 71:2141–2145.

———. 2000. Evolutionary Ecology. Benjamin Cummings, San Francisco, USA.

Ponjoan, A., G. Bota, and S. Mañosa. 2012. Ranging behaviour of little bustard males, *Tetrax tetrax*, in the lekking grounds. Behavioural Processes 91:35–40.

Ponjoan, A., B. Gerard, E. García de la Morena, M. B. Morales, A. Wolff, I. Marco, and S. Mañosa. 2008. Adverse effects of capture and handling little bustard. The Journal of Wildlife Management 72:315–319.

Powolny, T., C. Eraud, and V. Bretagnolle. 2012. Group size modulates time budget and foraging efficiency in captive skylarks, *Alauda arvensis*. Journal of Ornithology 153:485–490.

Prescott, G. W., D. R. Williams, A. Balmford, R. E. Green, and A. Manica. 2012. Quantitative global analysis of the role of climate and people in explaining late Quaternary megafaunal extinctions. Proceedings of the National Academy of Sciences of the United States of America 109:4527–4531.

Primack, R. B. 2012. A primer of Conservation Biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Pulliam, H. R. 1973. On the advantages of flocking. Journal of Theoretical Biology 38:419–422.

———. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. Vienna, Austria.

———. 2013. R: A Language and Environment for Statistical Computing. Vienna, Austria.

———. 2014. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Reed, J. M., and A. P. Dobson. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. Trends in Ecology & Evolution 8:253–256.

Rehnus, M., M. Wehrle, and R. Palme. 2014. Mountain hares *Lepus timidus* and tourism: stress events and reactions. Journal of Applied Ecology 51:6–12.

Ricklefs, R. 2007. History and diversity: explorations at the intersection of ecology and evolution. The American Naturalist 170:S56–S70.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science 235:167–171.

Ripley, B. D. 1981. Spatial Statistics. Wiley-Interscience, New York, USA.

Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biological Conservation 145:205–213.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. Science 343:151–162.

Robb, G. N., R. A. McDonald, D. E. Chamberlain, S. J. Reynolds, T. J. Harrison, and S. Bearhop. 2008. Winter feeding of birds increases productivity in the subsequent breeding season. Biology Letters 4:220–223.

Robinson, B. W., D. S. Wilson, and A. S. Margosian. 2000. A pluralistic analysis of character release in pumpkinseed sunfish (*Lepomis gibbosus*). Ecology 81:2799–2812.

Rodríguez, M. A. 1995. Habitat-specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. Evolutionary Ecology 9:169–184.

Romero, L. M., M. J. Dickens, and N. E. Cyr. 2009. The reactive scope model - a new model integrating homeostasis, allostasis, and stress. Hormones and Behavior 55:375–389.

Rosenzweig, M. L. 1974. On the evolution of habitat selection. Pages 401–404 *in* Proceedings of the First International Congress of Ecology. Centre for Agricultural Publishing and Documentation, The Hague.

———. 1981. A theory of habitat selection. Ecology 62:327–335.

Salamolard, M., and C. Moreau. 1999. Habitat selection by little bustard *Tetrax tetrax* in a cultivated area of France. Bird Study 46:25–33.

Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences of the United States of America 100:2474–2477.

Sansom, A., W. Cresswell, J. Minderman, and J. Lind. 2008. Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? Animal Behaviour 75:1869–1875.

Sapolsky, R. M., L. M. Romero, and A. U. Munck. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocrine Reviews 21:55–89.

Sastre, P., C. Ponce, C. Palacín, C. A. Martín, and J. C. Alonso. 2009. Disturbances to great bustards (*Otis tarda*) in central Spain: human activities, bird responses and management implications. European Journal of Wildlife Research 55:425–432.

Schmidt, K. A., J. Johansson, N. Kristensen, F. Massol, and N. Jonzén. 2015. Consequences of information use in breeding habitat selection on the evolution of settlement time. Oikos 124:68–80.

Schoener, T. W. 1983. Field experiments on interspecific competition. The American Naturalist 122:240–285.

———. 1989. The ecological niche. Pages 79–113 *in* J. M. Cherret, ed. Ecological concepts. Blackwell, Oxford, UK.

Seaman, E. D., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Sebastián-González, E., J. A. Sánchez-Zapata, F. Botella, and O. Ovaskainen. 2010. Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. Proceedings of the Royal Society of London Series B-Biological Science 277:2983–2990.

SEO/Birdlife. 2012. Resultados del programa de seguimiento de aves comunes en primavera SEO/Birdlife. SEO/Birdlife-Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, Spain.

Seppänen, J.-T., J. T. Forsman, M. Mönkkönen, and R. L. Thomson. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88:1622–1633.

Serrano, D., J. L. Tella, M. G. Forero, and J. A. Donazar. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. Journal of Animal Ecology 70:568–578.

Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2010. Assessing stress in animal populations: do fecal and plasma glucocorticoids tell the same story? General and Comparative Endocrinology 166:614–619.

Silva, J. P., B. Estanque, F. Moreira, and J. M. Palmeirim. 2014. Population density and use of grasslands by female little bustards during lek attendance, nesting and brood-rearing. Journal of Ornithology 155:53–63.

Silva, J. P., N. Faria, and T. Catry. 2007. Summer habitat selection and abundance of the threatened little bustard in Iberian agricultural landscapes. Biological Conservation 139:186–194.

Silva, J. P., J. M. Palmeirim, and F. Moreira. 2010*a*. Higher breeding densities of the threatened little bustard *Tetrax tetrax* occur in larger grassland fields: implications for conservation. Biological Conservation 143:2553–2558.

Silva, J. P., M. Pinto, and J. M. Palmeirim. 2004. Managing landscapes for the little bustard *Tetrax tetrax*: lessons from the study of winter habitat selection. Biological Conservation 117:521–528.

Silva, J. P., M. Santos, L. Queirós, D. Leitão, F. Moreira, M. Pinto, M. Leqoc, and J. A. Cabral. 2010*b*. Estimating the influence of overhead transmission power lines and landscape context on the density of little bustard *Tetrax tetrax* breeding populations. Ecological Modelling 221:1954–1963.

Simons, L. S., and T. E. Martin. 1990. Food limitation of avian reproduction: an experiment with the cactus wren. Ecology 71:869–876.

Slagsvold, T. 1986. Nest site settlement by the pied flycatcher: does the female choose her mate for the quality of his house or himself? Ornis Scandinavica 17:210–220.

Smith, J. N. M., P. R. Grant, B. R. Grant, I. J. Abbott, and L. K. Abbott. 1978. Seasonal variation in feeding habits of Darwin's ground finches. Ecology 59:1137–1150.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10:1115–1123.

Soulé, M. E., J. A. Estes, B. Miller, and D. L. Honnold. 2005. Strongly interacting species: conservation policy, management, and ethics. BioScience 55:168–176.

Staley, A. M., J. M. Blanco, A. M. Dufty, D. E. Wildt, and S. L. Monfort. 2007. Fecal steroid monitoring for assessing gonadal and adrenal activity in the golden eagle and peregrine falcon. Journal of Comparative Physiology B 177:609–622.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. The American Naturalist 131:329–347.

Steffen, W., A. Persson, L. Deutsch, J. Zalasiewicz, M. Williams, K. Richardson, C. Crumley, P. Crutzen, C. Folke, L. Gordon, M. Molina, V. Ramanathan, J. Rockström, M. Scheffer, H. J. Schellnhuber, and U. Svedin. 2011. The Anthropocene: from global change to planetary stewardship. Ambio 40:739–761.

Stenseth, N. C., J. M. Durant, M. S. Fowler, E. Matthysen, F. Adriaensen, N. Jonzén, K.-S. Chan, H. Liu, J. De Laet, B. C. Sheldon, M. E. Visser, and A. A. Dhondt. 2015. Testing for effects of climate change on competitive relationships and coexistence between two bird species. Proceedings of the Royal Society of London Series B-Biological Sciences 282:20141958.

Steven, R., C. Pickering, and J. G. Castley. 2011. A review of the impacts of nature based recreation on birds. Journal of Environmental Management 92:2287–2294.

Strasser, E. H., and J. A. Heath. 2013. Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. Journal of Applied Ecology 50:912–919.

Strubbe, D., and E. Matthysen. 2009. Experimental evidence for nest-site competition between invasive ring-necked parakeets (*Psittacula krameri*) and native nuthatches (*Sitta europaea*). Biological Conservation 142:1588–1594.

Stuart, Y. E., T. S. Campbell, P. A. Hohenlohe, R. G. Reynolds, L. J. Revell, and J. B. Losos. 2014. Rapid evolution of a native species following invasion by a congener. Science 346:463–466.

Suárez, F., M. A. Naveso, and E. de Juana. 1997. Farming in the drylands of spain: birds in the pseudosteppes. Pages 297–330 *in* D. J. Pain and M. W. Pienkowski, eds. Farming and Birds in Europe. Academic Press, Cambridge, UK.

Suárez-Seoane, S., E. L. García de la Morena, M. B. Morales, P. E. Osborne, and E. de Juana. 2008. Maximum entropy niche-based modelling of seasonal changes in little bustard (*Tetrax tetrax*) distribution. Ecological Modelling 219:17–29.

Suárez-Seoane, S., P. E. Osborne, and J. C. Alonso. 2002. Large-scale habitat selection by agricultural steppe birds in Spain: identifying species habitat responses using generalized additive models. Journal of Applied Ecology 39:755–771.

Svanbäck, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society of London Series B-Biological Sciences 274:839–844.

Svenning, J.-C., and F. Skov. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters 10:453–460.

Tarjuelo, R., M. B. Morales, J. Traba, and M. P. Delgado. 2014. Are species coexistence areas a good option for conservation management? applications from fine scale modelling in two steppe birds. PLoS ONE 9:e87847.

Thiel, D., S. Jenni-Eiermann, V. Braunisch, R. Palme, and L. Jenni. 2008. Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. Journal of Applied Ecology 45:845–853.

Thiel, D., S. Jenni-Eiermann, and R. Palme. 2005. Measuring corticosterone metabolites in droppings of capercaillies (*Tetrao urogallus*). Annals of the New York Academy of Sciences 1046:96–108.

Thiel, D., E. Ménoni, J.-F. Brenot, and L. Jenni. 2007. Effects of recreation and hunting on flushing distance of capercaillie. The Journal of Wildlife Management 71:1784–1792.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427:145–148.

Thomson, R. L., J. T. Forsman, and M. Mönkkönen. 2003. Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis. Oecologia 134:431–438.

Titeux, N., M. Dufrene, J. Radoux, A. H. Hirzel, and P. Defourny. 2007. Fitness-related parameters improve presence-only distribution modelling for conservation practice: the case of the red-backed shrike. Biological Conservation 138:207–223.

Traba, J., E. L. García de la Morena, M. B. Morales, and F. Suárez. 2007. Determining high value areas for steppe birds in Spain: hot spots, complementarity and the efficiency of protected areas. Biodiversity and Conservation 16:3255–3275.

Traba, J., M. B. Morales, C. P. Carmona, and M. P. Delgado. 2015. Resource partitioning and niche segregation in a steppe bird assemblage. Community Ecology In press.

Traba, J., M. B. Morales, E. L. García de la Morena, M. P. Delgado, and A. Krištín. 2008. Selection of breeding territory by little bustard (*Tetrax tetrax*) males in central Spain: the role of arthropod availability. Ecological Research 23:615–622.

Tucker, G., and M. Heath. 1994. Birds in Europe. Their conservation status. Birdlife International, Cambridge, UK.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:2025–2034.

Villers, A., A. Millon, F. Jiguet, J.-M. Lett, C. Attie, M. B. Morales, and V. Bretagnolle. 2010. Migration of wild and captive-bred little bustards *Tetrax tetrax*: releasing birds from Spain threatens attempts to conserve declining French populations. Ibis 152:254–261.

von Humboldt, A., and A. Bonpland. 1807. Essai sur la géographie des plantes. Chez Levrault, Schoell and Compagnie, Paris, France.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Wang, Z., Z. Li, G. Beauchamp, and Z. Jiang. 2011. Flock size and human disturbance affect vigilance of endangered red-crowned cranes (*Grus japonensis*). Biological Conservation 144:101–105.

Ward, M. P., and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18:519–525.

Watson, A. 1985. Social class, socially-induced loss, recruitment and breeding of red grouse. Oecologia 67:493–498.

Watson, A., and R. Moss. 2004. Impacts of ski-development on ptarmigan (*Lagopus mutus*) at Cairn Gorm, Scotland. Biological Conservation 116:267–275.

Wiegand, T., and K. A. Moloney. 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104:209–229.

Wiens, J. A. 1977. On competition and variable environments. American Scientist 65:590–597.

———. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. Trends in Ecology & Evolution 19:639–644.

Williams, P. H., M. B. Araújo, and P. Rasmont. 2007. Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? Biological Conservation 138:493–505.

Wilson, C. D., and D. Roberts. 2011. Modelling distributional trends to inform conservation strategies for an endangered species. Diversity and Distributions 17:182–189.

Wilson, E. O. 1992. The diversity of life. Penguin Books, London, UK.

Wingfield, J. C., K. Hunt, C. Breuner, K. Dunlap, G. S. Fowler, L. Freed, and J. Lepson. 1997. Environmental stress, field endocrinology, and conservation biology. Pages 95–131 *in* J. R. Clemmons and R. Buchholz, eds. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, UK.

Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, and N. P. S. D. W. Group. 2008. Effects of sample size on the performance of species distribution models. Diversity and Distributions 14:763–773.

Wolff, A., T. Dieuleveut, J.-L. Martin, and V. Bretagnolle. 2002. Landscape context and little bustard abundance in a fragmented steppe: implications for reserve management in mosaic landscapes. Biological Conservation 107:211–220.

Wolff, A., J.-P. Paul, J.-L. Martin, and V. Bretagnolle. 2001. The benefits of extensive agriculture to birds: the case of the little bustard. Journal of Applied Ecology 38:963–975.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the study of behavior 16:229–249.

Young, K. A. 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. Ecology 85:134–149.

Young, K. M., S. L. Walker, C. Lanthier, W. T. Waddell, S. L. Monfort, and J. L. Brown. 2004. Noninvasive monitoring of adrenocortical activity in carnivores by fecal glucocorticoid analyses. General and Comparative Endocrinology 137:148–165.

Zhang, S., F. Lei, S. Liu, D. Li, C. Chen, and P. Wang. 2011. Variation in baseline corticosterone levels of tree sparrow (*Passer montanus*) populations along an urban gradient in Beijing, China. Journal of Ornithology 152:801–806.

Zipkin, E. F., J. A. Royle, D. K. Dawson, and S. Bates. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. Biological Conservation 143:479–484.

Ziv, Y., Z. Abramsky, B. P. Kotler, and A. Subach. 1993. Interference competition and temporal and habitat partitioning in two gerbil species. Oikos 66:237–246.