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Maximum entropy niche-based modelling of seasonal changes in little bustard (*Tetrax tetrax*) distribution

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ABSTRACT

The effects of habitat fragmentation on species may change seasonally mainly due to variations in resource availability and biotic interactions. In critical periods, such as winter, when the importance of intraspecific competition diminish, species may relax their environmental requirements widening their ecological niche to exploit the scarcer trophic resources more efficiently in comparison with spring. Those variations in niche width may implicate seasonal expansions/retractions in species distribution. In this sense, an integrated knowledge on the spatial arrangement of breeding and wintering suitable patches is essential to infer seasonal movements (migratory connectivity). This paper shows that little bustard environmental preferences were more predictable and complex (controlled by a larger number of environmental factors) in spring than in winter, when potential distribution and ecological niche width were slightly larger. In spring, habitat variables (i.e. percentage of dry crops and pasturelands and altitude) ruled species' distribution; while, winter pattern was driven by mixed criteria, based on both habitat and climate (i.e. percentage of dry crops and wastelands and winter rainfall). Suitable patches were more connected across spatial scales in winter than in spring, i.e. landscape was perceived as less fragmented. The overlap between potential breeding and wintering distribution areas was high. In fact, most of the predicted wintering areas coincided or showed high connectedness with predicted breeding patches. Conversely, there were significant breeding patches that were predicted with low suitability, showing little connectedness with potential winter areas. Spring habitat was a better predictor of little bustard's wintering range than vice versa, which has clear management implications (preserving breeding sites closer to wintering areas ensures the conservation of a larger proportion of the total distribution range). This is an example of how predictive large-scale modeling procedures can contribute to the optimization of land management aimed at species conservation.

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1. Introduction

The fragmentation of a habitat into discontinuous patches negatively affects population recruitment (Robinson et al., 1995; Smith and Hellmann, 2002), survival (Harris, 1984) and movement (Shirley, 2006) of terrestrial animal species. In poorly connected landscapes, where individuals have to move across the matrix to reach adequate pieces of habitat for different purposes (i.e. foraging, reproduction, dispersion and predator avoidance), the fitness cost of movement (Brooker et al., 1999) becomes higher than in continuous landscapes. This fact consequently influences the dynamics, spatial structure and persistence of populations (Turchin, 1991). Nevertheless, the importance of fragmentation for species may change through time, mainly seasonally, individual movements reflecting variations in resource availability (Blake and Loiselle, 1991) and biotic interactions. In this context, linking breeding and non-breeding populations (i.e. migratory connectivity) to infer movement patterns between seasons is one of the ultimate goals of animal movement studies in ecology (Rubenstein and Hobson, 2004).

As a result of the European Common Agricultural Policy, traditional agri-systems in southern Europe are particularly vulnerable to fragmentation due to management intensification in productive areas and land abandonment in marginal ones (Pain and Pienkowski, 1997). These systems are known to host a considerable diversity of birds and other taxa, most of which are currently experiencing marked population declines (Robinson and Sutherland, 2002; Sanderson et al., 2005). Among the valuable avian species (Suárez et al., 1997) held by these systems, the little bustard *Tetrax tetrax* is one of most seriously threatened by land use changes (Wolff, 2001; Wolff et al., 2002; García et al., 2007), disappearing from many European countries during recent decades (Schulz, 1985; Goriup, 1994; Del Hoyo et al., 1996). This Palaearctic, medium-sized steppe bird, from the *Otididae* family, is currently classified as 'Near Threatened' (Collar et al., 1994) in the world and 'Vulnerable' in Europe (BirdLife International, 2004), including Spain (García de la Morena et al., 2004b). Although Iberian little bustard populations have been regarded as sedentary or dispersive (Cramp and Simmons, 1980), many of them can actually be considered as migratory or partially migratory since they completely, or partly, disappear from their breeding grounds, performing regular medium or long distance movements and congregating in certain wintering sites (García de la Morena et al., 2004a, 2006). In Madrid region (the study area), it is considered a resident species (Díaz et al., 1994; García de la Morena, 2002), although it exhibits a partial migratory behaviour, as suggested by recent radiotracking data (with some birds leaving the region during the non-breeding season; own unpubl. data). During the spring (breeding season), birds do not move much, spending most of time in their territories (Schulz, 1985; Jiguet, 2001) but, from late summer through the autumn and winter, they gather in flocks and disperse from spring areas to exploit food resources in different zones, a common behaviour in most Iberian steppe birds (Suárez et al., 1997). As found in some of these species (Morales et al., 2000; Alonso et al., 2001), little bustards display interannual fidelity to certain wintering sites, where they stay for a variable period of time before returning to their breeding territories (García de la Morena et al., 2004b; own unpubl. data).

Habitat preferences and distribution of little bustards in spring have been extensively explored at both local (Martínez, 1994, 1998; Salamolard and Moreau, 1999; Wolff et al., 2001; Morales et al., 2005, 2008; Traba et al., 2008) and regional scale (Suárez-Seoane et al., 2002, 2004; Osborne and Suárez-Seoane, 2002; García et al., 2007). However, few authors have focused on winter season (Leitão and Costa, 2001; Silva et al., 2004; García de la Morena et al., 2006, 2007), even if this knowledge is essential for understanding the species' biological cycle, as well as in the design of adequate conservation strategies (Rappole and McDonald, 1994; Sherry and Holmes, 1996). In the Mediterranean region, as in other temperate and seasonally regulated areas, winter is a critical period for birds (Tellería et al., 1988), both at individual and population levels (Wiens, 1989; Newton, 1998), since availability in food and other resources decrease and may vary considerably in space and time. As a result, the distribution and abundance of wintering little bustards is closely dependent on the local variation of those resources (mainly provided by extensive cereal farmlands), which they must track actively (Wolff, 2001). During this limiting period, birds may therefore respond by relaxing the requirements associated to certain dimensions of their ecological niche to exploit more efficiently a larger amount of trophic resources, thus allowing the species' survival (Hutchinson, 1957) in a wider potential distribution range. As a consequence of this niche expansion, wintering populations are expected to become more heterogeneous in their environmental preferences, according to the niche variation hypothesis (Van Valen, 1965; Bolnick et al., 2007), which predicts that each individual might continue to use a narrow range of resources but diverge from its conspecific competitors to minimize resource use overlap and competition. At the same time, intraspecific interactions would become less intense than interspecific relationships (Morin and Chuine, 2006), such as competition or predation (birds have to aggregate in flocks as a defense strategy against predators), in comparison with spring, when the relevance of territorialism and sexual behavior is higher. As a consequence of this shift in the importance of inter/intraspecific interactions, the relevance of certain niche dimensions (e.g. climate conditions) would be relatively higher in winter than in spring.

To approach seasonal variations in species' niche dimensions and their influence in spatial distribution, we took advantage of using the Maximum Entropy Modelling (MaxEnt; Phillips, 2005; Phillips et al., 2006). This novel technique provides a general-purpose machine learning method whose performance has been evaluated as one of the best when compared to other modelling distribution methods, particularly at small sample sizes (Elith et al., 2006; Hernández et al., 2006; Pearce and Boyce, 2006; Pearson et al., 2007). The following are among the main reasons to use it in this study: (1) it is an envelope-method specifically applied on presence-only data (the link between absences and habitat suitability may be confusing); (2) it has a good ability to fit complex functions between response and predictor variables; and (3) model selection and fitted models are not too complex, being similar in expressiveness to a GLM or GAM. As other niche-based models, MaxEnt describes suitability in ecological space, which is