

Positive interactions between vulnerable species in agrarian pseudo-steppes: habitat use by pin-tailed sandgrouse depends on its association with the little bustard

C. A. Martín¹, F. Casas¹, F. Mougeot², J. T. García¹ & J. Viñuela¹

¹ Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC-UCLM-JCCM), Ciudad Real, Spain

² Estacion Experimental de Zonas Áridas (EEZA, CSIC), Almería, Spain

Keywords

compositional analysis; farmland birds; habitat preferences; mixed-species flocks; *Pterocles alchata*; *Tetrax tetrax*.

Correspondence

Carlos A. Martín, Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC-UCLM-JCCM), Ronda de Toledo s/n, E-13071 Ciudad Real, Spain. Tel: +34 926 295 450; Fax: +34 926 295 451
Email: carlosalfonso.martin@uclm.es

Received 17 December 2009; accepted 14 January 2010

doi:10.1111/j.1469-1795.2010.00349.x

Abstract

Positive interactions between species can have important conservation implications, especially when the species associating are both vulnerable. We studied the habitat use of pin-tailed sandgrouse *Pterocles alchata* and their association with another vulnerable species, the little bustard *Tetrax tetrax* in agrarian pseudo-steppes of central Spain using radio-tracking. The occurrence of mixed-species flocks varied seasonally, being more frequent in winter (65% of pin-tailed sandgrouse flocks). In this season, pin-tailed sandgrouse preferred stubble fields and fallows. Moreover, we found that habitat selection of pin-tailed sandgrouse depended on the association with little bustards in mixed-species flocks. When in mixed-species groups, sandgrouse changed their agrarian substrate preferences, and used stubble fields significantly more often than when in sandgrouse-only flocks. We also provide evidence that pin-tailed sandgrouse benefited from the anti-predator vigilance of little bustards, allowing sandgrouse to exploit new feeding grounds (stubble fields) that would otherwise be too risky to exploit. Our results indicate a close positive association between these two species, which are both declining in Europe, and we discuss implications for their management and conservation. We also recommend taking into account inter-specific positive interactions when designing conservation strategies for threatened species.

Introduction

Several studies have shown that habitat selection patterns can be influenced by the presence of hetero-specifics, including predators (Wootton, 1992; Pitt, 1999; Forstmeier & Weiss, 2004; Bongí *et al.*, 2008; Morosinotto, Thomson & Korpimäki, 2010) and competitors (Svårdson, 1949; Cody, 1981; Robinson & Terborgh, 1995; Petit & Petit, 1996; Aunapuu & Oksanen, 2004; Boyer & Rivault, 2006). However, the effect of mutualistic or positive associations between species remains less explored (Slagsvold, 1980). In birds and mammals, inter-specific groups or associations can be composed by closely related species or by species belonging to different Orders. It is frequently assumed that these associations occur because they provide the participants some evolutionary benefit over those that do not mix, and functional advantages are thus attributed to such associations (Morse, 1977; Berner & Grubb, 1985; Terborgh, 1990; Stensland, Angerbjörn & Berggren, 2003; Sridhar, Beauchamp & Shanker, 2009). Functional explanations usually fall within two major, non-exclusive categories: foraging advantages (individuals benefit from the mixed-species association by summing up their capacities to locate patchy food resources; Krebs, 1973; Stensland *et al.*, 2003)

and anti-predator benefits (individuals benefit from the association by increasing their abilities to detect and deter predators; Terborgh, 1990; Sridhar *et al.*, 2009). Mixed-species groups can be larger than single-species ones, and could allow earlier detection, more efficient defences and increased safety in numbers (Jullien & Clobert, 2000; Arroyo, Mougeot & Bretagnolle, 2001; Stensland *et al.*, 2003). One species could also benefit from the better vigilance behaviour of the other, for instance when they differ in morphology, size or behaviour (Sridhar *et al.*, 2009).

The pin-tailed sandgrouse *Pterocles alchata* is a threatened species whose European population mainly concentrates in the agricultural pseudo-steppes and pasturelands of the Iberian peninsula (De Juana, 1997; BirdLife International, 2004; Suárez *et al.*, 2006). This medium-size steppe bird often joins up with little bustard *Tetrax tetrax*, another threatened species in Europe (De Juana, 1997; De Borbón, Barros & De Juana, 1999), forming mixed-species flocks that can include hundreds of birds of each species (De Borbón *et al.*, 1999).

In this study, our objectives were two fold: firstly, to study association patterns between pin-tailed sandgrouse and little bustards, in order to evaluate the influence of these mixed-

species associations on habitat use by sandgrouses and secondly, to analyse the conditions under which sandgrouses associated with little bustards to better understand the biological significance of these mixed-species associations and the potential benefits derived from these associations. Finally, we discuss the management and conservation implications of our findings on these two species, which are both currently declining and are of conservation concern in Europe.

Material and methods

Study species

The pin-tailed sandgrouse is a *Pteroclididae* typical of steppes and extensive agricultural habitats. It occurs in the Iberian Peninsula and south-east France, north of Africa, south-east Turkey and the Middle East through Iraq and Iran to Uzbekistan and the south of Kazakhstan (De Juana, 1997). Pin-tailed sandgrouses are highly gregarious, with seasonal differences in flock size. Flocking behaviour reaches a maximum during the winter, when groups of several hundreds of birds have been reported, while flocks are much smaller during the breeding season (De Borbón *et al.*, 1999).

The little bustard is a medium-sized *Otididae* that has suffered major population declines in most of its Palaearctic range, mainly due to agricultural intensification (Collar, 1996). More than half of the world's population is concentrated in the Iberian Peninsula (De Juana & Martínez, 2001).

While the pin-tailed sandgrouse is currently classified as a 'Least Concern Species' worldwide, the little bustard is categorized as 'Near Threatened' (BirdLife International, 2008*a,b*). Both species hold an 'Unfavourable Conservation Status' in Europe (BirdLife International, 2004), and a 'Vulnerable Status' in Spain (García de la Morena *et al.*, 2004; Suárez & Herranz, 2004).

Study area

This study was carried out in the agricultural pseudo-steppes of Campo de Calatrava, Spain, within a special protection area (SPA 157, *c.* 38°54'N, 3°55'W, Ciudad Real province, 8978 ha; Fig. 1). The area is flat to slightly undulated (590–685 m a.s.l.) and is primarily used for the cultivation of dry cereal (barley *Hordeum vulgare*, oats

Avena spp. and wheat *Triticum* spp.) and, to a lesser extent, *Vicia* spp. and *Pisum sativum*. The area also includes few olive groves *Olea europaea* and vineyards *Vitis vinifera*. The field size averages 3.26 ha (SD = 11.16 ha; *n* = 1849). Most cereals are grown in a traditional way that creates a landscape mosaic of sown, ploughed, stubble and fallow fields of

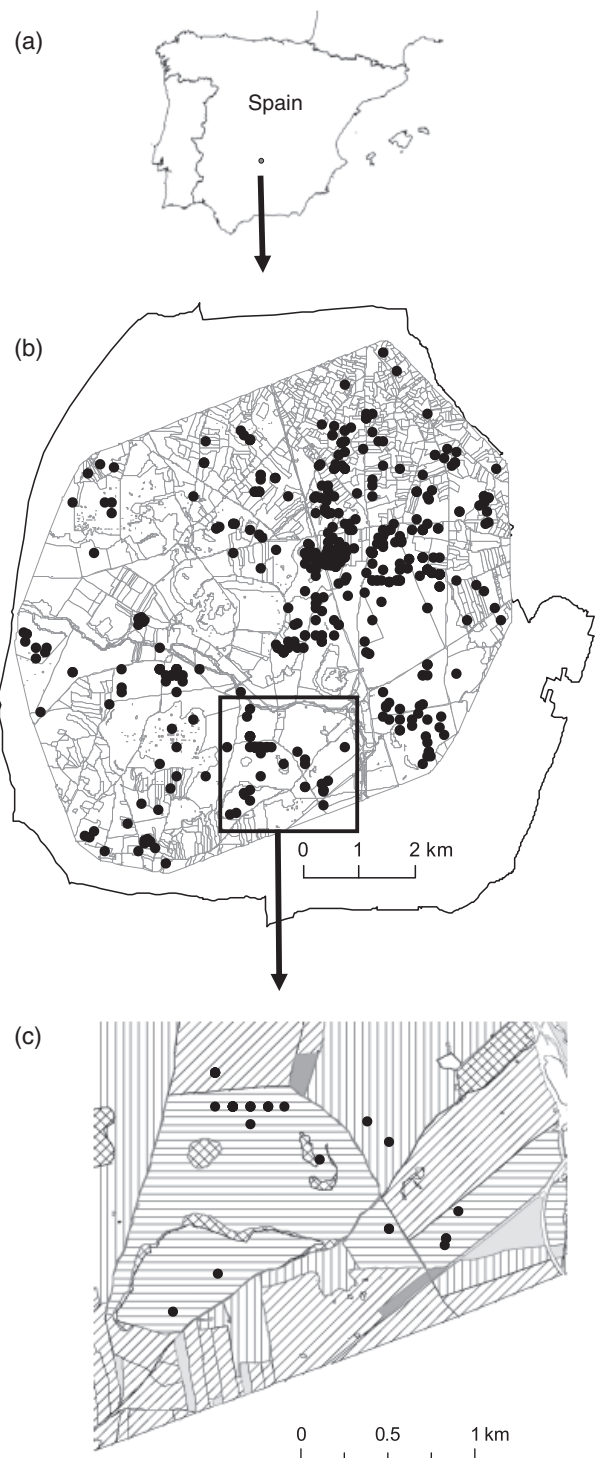


Figure 1 (a) Location of the study area. (b) Map of the study area showing the limits of the special protection area of Campo de Calatrava (SPA 157), the fixes of radio-tagged pin-tailed sandgrouses *Pterocles alchata* (black circles) and the minimum convex polygon containing them (area showing farmland fields). (c) Example of fixes distribution and agrarian substrate composition in part of the study area in the winter season. Vertical lines, fallows; horizontal lines, stubbles; diagonal lines, cereal; crosshatch, pastureland; light grey, ploughed fields; dark grey, vineyards and olive groves; white, other land uses.

Table 1 Main substrates in the study area and their relative surface in winter

Substrate	Description	Proportion (%)
Crops		
Cereal	Crops of barley, oats or wheat	58.62
Stubble	Recently harvested cereal or legume fields	7.86
Fallow	Unploughed cereal fallows with one or more years and dense herbaceous coverage	7.14
Plough	Ploughed fields, mostly without vegetation (<20% weed vegetation cover). When they had developed a significant herbaceous vegetation cover (>20%) they were classified as fallow land	9.77
Legume	Crops of <i>Vicia</i> spp. or <i>Pisum sativum</i>	1.36
Pastureland	Fields of short scrubland and pastureland	7.36
Olive groves	Olive tree plantation	3.53
Vineyard	Vine plantation	3.08
Others	Vegetation of rivers and streams, piles of stones, maize and fruit trees plantation	1.29

different ages. Cereals are harvested between June and early July. This farming system is complemented with extensive sheep grazing in stubbles, fallows and small areas of short scrubland and pastureland. The study area holds a population of *c.* 200 breeding and *c.* 1000 wintering pin-tailed sandgrouses and >200 breeding males and *c.* 1400 wintering little bustards (Martínez, 2005; authors unpubl. data).

Field procedures

Between 2007 and 2008, we caught 15 pin-tailed sandgrouses at night using a thermal camera (Panatec, Madrid, Spain) to locate roosting birds, and large hand-held nets and spotlights to catch them. Sandgrouses were tagged with 11 g TW3 backpack-mounted radio transmitters (Biotrack, Wareham, UK) and released at the capture site shortly (*c.* 20 min) after capture. The total weight of the transmitter plus harness did not exceed the recommended limit of 3–5% of the bird's weight (Kenward, 2001).

Marked birds were subsequently located by radio-tracking, using Biotrack Sika telemetry receivers and a three-element directional YAGI antenna. We located birds weekly using visual observation after triangulation, until the transmitter battery was exhausted (battery life \sim 1.1 years) or until the bird died ($n = 3$). For each observation of a tagged bird, we recorded the following: (1) the geographical location (with a Garmin eTrex Vista Cx GPS, nearest 3–4 m); (2) the type of agrarian substrate (see Table 1); (3) the number of sandgrouses in the flock; (4) the number of little bustards in the flock; (5) the flight initiation distance (that is the distance between the observer and the flock when the birds took off; Blumstein, 2003). The latter was measured using the GPS, by recording the distance walked between the location where the observer flushed the birds and the location of the flock. In some occasions (*c.* 13% of the locations), no visual contact could be established with the birds (for instance, when located in fenced fields); we then determined the location through triangulation, using two or more bearings taken from the edge of the farmland plot (White & Garrot, 1990). Radio-tracking surveys were carried out from dawn until dusk in order to include the whole day-time activity period of the species.

Habitat use analysis

Because sandgrouses are highly gregarious and individual home ranges of radio tagged birds overlapped to a great extent, we pooled all fixes from the tagged birds and created a minimum convex polygon of 61.3 km² that included all locations (Fig. 1). We assumed that the habitats within this polygon and their proportions represented the habitat available to birds, whether used or not (Johnson, 1980). The agrarian substrate types within this area (see Table 1) were mapped using ArcMap 9.1 (ESRI 1999–2005) at different times during the life cycle of sandgrouse: (1) pre-breeding (March–May); (2) breeding (June–August); (3) post-breeding (September–November); (4) winter (December–February). The seasonal area of each substrate was calculated using the ArcMap extension V-LATE.

Winter habitat selection was studied using compositional analysis as described by Aebischer, Robertson & Kenward (1993), and habitats were ranked according to relative use. The basis for analysis is the proportional habitat use by individual animals. Compositional Analysis uses MANOVA to analyse two sets of data (habitat availability and use) in which variables are represented as proportions. Cereals were chosen as the denominator in the log ratios. For all statistical tests, probability values of ≤ 0.05 were considered significant. Habitat categories that were available but seldom used by sandgrouses were grouped as follows: olive groves and vineyards were regrouped in the same land use category and legume crops (<2% in the study area) were included in the 'other' land use category (see Table 1). In some analyses, it was also necessary to regroup ploughs, pasturelands, olive groves, vineyards, legumes and 'other' land uses in a single category. Zero values of use were assigned values of 0.01 (a value lower than any other proportion of habitat use) as suggested by Aebischer *et al.* (1993). For compositional analysis, we only used data of individuals with at least five locations.

Results

During the study, we gathered 419 fixes of radio-tagged birds (*c.* 28 fixes per bird) that corresponded to 227 diurnal

Table 2 Number of individuals radio-tracked (*n*) and mean (\pm SE) number of locations per radio-tracked pin-tailed sandgrouse *Pterocles alchata* in each season. Associated number of flocks, mean (\pm SE) flock size and accumulated number of sandgrouses in those flocks are also shown

Season	<i>n</i>	Locations	Flocks	Flock size ^a	Number of birds ^a
Post-breeding	10	14.3 \pm 8.3	76	74.0 \pm 9.0	4960
Winter	14	11.4 \pm 6.0	62	97.7 \pm 15.7	5567
Pre-breeding	10	5.3 \pm 3.1	42	31.4 \pm 5.7	1069
breeding	10	6.3 \pm 4.6	47	6.9 \pm 2.7	247

^aFlock size was determined in 194 cases.

observations of sandgrouse flocks (because sometimes more than one radio-tagged bird were in the same flock). Flock size was determined in 194 of the cases. Average flock size differed between the four seasons (ANOVA, $F_{3,190} = 11.76$, $P < 0.0001$, Table 2, see also Fig. 2). We could accurately determine the species composition for 201 sandgrouse flocks. In these, 65% were single-species flocks (only pin-tailed sandgrouse) and 35% were mixed-species flocks (with little bustards). The occurrence of mixed-species flocks varied seasonally (post-breeding: 29%, $n = 20$ flocks; winter: 65%, $n = 40$; pre-breeding: 26%, $n = 9$ and breeding: 3%, $n = 1$; $\chi^2 = 42.5$, d.f. = 3, $P < 0.0001$), being higher in winter (all comparisons with winter: $P < 0.001$). The mean number of little bustards associated to sandgrouse flocks also differed between the four seasons (ANOVA, $F_{3,190} = 13.39$, $P < 0.0001$), with averages of 31, 143, 18 and zero little bustards in the post-breeding, winter, pre-breeding and breeding seasons, respectively (see also Fig. 2).

The association of sandgrouses with little bustards allowed the formation of larger flocks: in winter, mixed-species groups were significantly larger than sandgrouse-only groups (sandgrouse-only flocks: mean size of 40 individuals, $n = 21$; mixed-species flocks: mean size of 340 individuals, $n = 37$; $t = -4.183$, d.f. = 56, $P = 0.0001$). The mean number of sandgrouses per flock was also higher in mixed-species flocks than in sandgrouse-only flocks (sandgrouse-only flocks: mean size of 40 individuals, $n = 21$; mixed-species flocks: mean size of 118 individuals, $n = 37$; $t = -2.645$, d.f. = 56, $P = 0.011$).

Compositional analysis of habitat selection showed that during the winter (i.e. the season when mixed-species flocks were more frequent) habitat selection of radio-tracked pin-tailed sandgrouses differed significantly from random ($\chi^2 = 45.90$, d.f. = 6, $P < 0.0001$; 11 radio-tracked individuals, 126 locations). Stubble fields were significantly more used than any other habitat. Fallows were the second preferred habitat and were significantly more used than the rest of the habitats except for cereals. Cereals were preferred to pastureland and the habitat category regrouping olive groves and vineyards. There was no detectable difference in the use of the bottom four categories (ploughs, pasturelands, olives groves plus vineyards and others), implying that the order of their assigned ranks meant little. Moreover the use of agrarian substrates in winter differed between sandgrouse-only flocks and those mixed with little bustards (MANOVA, $F_{3,18} = 3.42$, $P = 0.039$). Mixed-species flocks showed a clear preference for stubble fields ($\chi^2 = 28.22$,

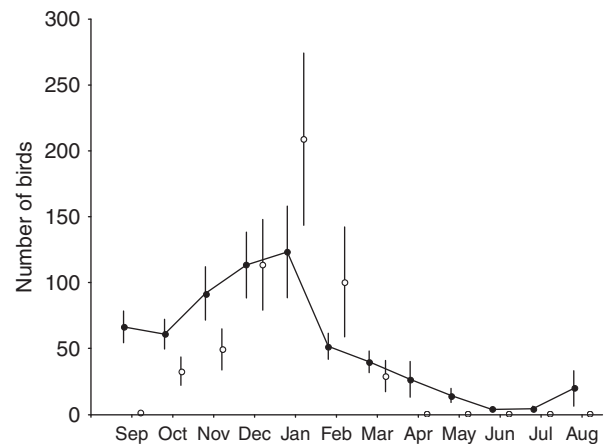


Figure 2 Monthly average (\pm SE) size of pin-tailed sandgrouse *Pterocles alchata* flocks (black dots) and the associated number of little bustards (white dots) in Campo de Calatrava, central Spain. March–May, pre-breeding; June–August, breeding; September–November, post-breeding; and December–February, winter.

d.f. = 3, $P < 0.0001$; 11 radio-tracked individuals, 97 locations) whereas sandgrouse-only flocks did not ($\chi^2 = 2.61$, d.f. = 3, $P = 0.456$; 11 radio-tracked individuals, 25 locations). These results were not biased towards habitat selection of any individual because during winter all tagged sandgrouses were observed both in mixed-species flocks (mean = 77.5%; minimum = 50.0%; maximum = 92.9%; 11 radio-tracked individuals, 122 locations), and in sandgrouse-only flocks (mean = 22.5%; minimum = 7.1%; maximum = 50.0%).

Flight initiation distance positively correlated with the total flock size ($n = 157$, $r = 0.41$, $P < 0.0001$) and was significantly greater in mixed-species flocks than in sandgrouse-only flocks (sandgrouse-only flocks mean: 95 m, $n = 98$; mixed-species flocks mean: 151 m, $n = 60$; $t = -5.054$, d.f. = 156, $P < 0.0001$), the difference being significant even when controlling for total flock size (ANCOVA, $F_{2,154} = 19.19$, $P < 0.001$; flock size: $t = 3.595$, $P < 0.001$; flock type: $t = 2.386$, $P = 0.018$).

Discussion

To our knowledge, this is the first study that provides detailed information on the patterns of association between pin-tailed sandgrouses and little bustards. These

inter-specific associations, or mixed-species flocks, resulted from an attraction between the two species themselves and not merely a forced aggregation at clumped resources. Indeed, pin-tailed sandgrouse and little bustards in mixed-species flocks behaved as members of the same group (i.e. feeding, moving or flying at the same time and direction). The relative proportion of sightings of mixed-species flocks varied seasonally and appeared to be mostly influenced by the occurrence of breeding activities (nesting and brood-rearing) of each species. Mixed-species associations occurred between October and March, being much more frequent in the winter season (December–February). During the breeding season (April–July for bustards and June–August for sandgrouse), only one mixed-species flock was observed (11 sandgrouse and 15 little bustards), possibly consisting of non-breeding birds.

Mixed-species flocks, which were larger than sandgrouse-only flocks, might procure both anti-predator and foraging benefits. Animals in larger groups benefit from the safety in numbers effect (Terborgh, 1990; Jullien & Clobert, 2000), the confusion effect (Morse, 1980) and/or the selfish herd effect (Hamilton, 1971). Furthermore, larger groups also promote earlier detection of predators and allow each individual to spend less time being vigilant or to take fewer risks than if they foraged alone (Pulliam, 1973; Sridhar *et al.*, 2009), thereby increasing their rate of food intake. Other studies have also proved that the decreased-vigilance effect can operate across bird species (Sullivan, 1984; Goodale & Kotagamab, 2008) and that mixed-species groups could be more efficient to detect predators if the participant species are somewhat different when they scan for predators (Heymann & Buchanan-Smith, 2000; Sridhar *et al.*, 2009). All these anti-predator advantages might occur in mixed-species flocks of sandgrouse and bustards given that they involve more individuals than those formed by just one species. Additionally, vigilance skills might differ between both species due to their differences in body size and height (little bustards are taller and have a longer neck than sandgrouse; Collar, 1996; De Juana, 1997), which might increase the efficiency to detect predators in mixed-species flocks.

As for the foraging advantages, an animal in a mixed-species assemblage could learn about the location of irregularly distributed food patches by watching the foraging activities of nearby hetero-specifics or by following them (Krebs, 1973; Giraldeau & Beauchamp, 1999). In the seasonally changing agricultural mosaic of sown, ploughed, stubble and fallow fields, flock associations of sandgrouse and bustards could enhance the success in locating patchily distributed food resources, at least outside the breeding season. Nevertheless, the existence of such hetero-specific groups requires some degree of resource partitioning between the participant species in order to avoid or minimize competition (Pianka, 1974; Roughgarden, 1976; Walter, 1991), which could be achieved through different food preferences. Indeed, the diets of pin-tailed sandgrouse and little bustards overlap slightly: the former feeds mainly on seeds (De Juana, 1997; Suárez *et al.*, 1999), while the

latter feeds mostly on green plants (Martínez, 1994; Jiguet, 2002).

The use of cereal fields after harvest (i.e. stubbles) by pin-tailed sandgrouse was intensive in the winter, when sandgrouse form large flocks and often associate with little bustards to feed on fallen grain and sometimes on green shoots. Other studies have also indicated that stubble fields are important feeding grounds for other steppe birds, suggesting that their maintenance could be of key importance for the conservation of steppe birds in general (Suárez, Naveso & de Juana, 1997; Tella & Forero, 2000; Lane, Alonso & Martín, 2001; Moorcroft *et al.*, 2002; Silva, Pinto & Palmeirim, 2004). We showed that pin-tailed sandgrouse changed their land-use preferences when associating with little bustards. In the winter, pin-tailed sandgrouse did not select stubble fields, unless they associated with little bustards (mixed-species flocks were found in stubbles more often than expected but not sandgrouse-only flocks). Sandgrouse might thus take advantage of the presence of the little bustard to use these habitats. They might benefit from the greater height of the bustards allowing them an effective vigilance in a substrate where the height of the vegetation would normally prevent access to sandgrouse. The association with little bustards would provide sandgrouse access to important benefits in terms of food, such as cereal grains fallen during harvesting. Our results on flight initiation distance support this hypothesis and suggest that sandgrouse rely on the vigilance of little bustards in these habitats.

The benefits of forming mixed-species flocks are less clear for little bustards, but benefits and costs for associating do not have to be equally distributed between the two participating species (Stensland *et al.*, 2003; Sridhar *et al.*, 2009). Pin-tailed sandgrouse might initiate and benefit from the mixed-species flocks at little or no cost for little bustards, which have a different diet. Little bustards could nevertheless benefit from the association (the extra number of individuals could help for detecting or deterring predators). Although our results suggest anti-predator benefits are a likely explanation for these mixed-species associations, the alternative hypothesis (foraging advantages) could not be rejected and would require further investigation. In fact, other studies have highlighted that protection from predators is not always a sufficient cause for mixed-species flocking, and support the view that either increased feeding efficiency alone or feeding efficiency and predation protection in combination encourage animals to forage in mixed-species groups (Berner & Grubb, 1985).

Conservation and management implications

Our results suggest that the conservation of these two species, which are both declining and of conservation concern in Europe, is intimately linked, not simply because they share the same agro-steppe habitat but also because they usually join together to obtain anti-predator and foraging advantages. Pin-tailed sandgrouse and little bustards have a very similar winter distribution and mixed-species flocks

have been observed in many Iberian regions (e.g. Extremadura, Madrid and Castilla-La Mancha) and in south-east France (La Crau), indicating that this association is widespread. Therefore, global conservation strategies should aim to preserve both species together, and local conservation efforts intended to preserve pin-tailed sandgrouses should include the conservation of the little bustard wintering populations. More generally, when similar positive interactions occur, they should be taken into account when designing conservation strategies for other threatened species.

Acknowledgements

We thank all farmers, hunting managers and gamekeepers of Campo de Calatrava for allowing us to work on their properties. Nuria Sumozas, María Calero, Israel Hervás and Ana Benítez collaborated during some stages of the work and two anonymous referees provided helpful comments on this paper. The study was financed by the Dirección General de Investigación (projects CGL2007-66322/BOS and CGL2008-04282/BOS), and the Consejería de Educación y Ciencia of Castilla-La Mancha (projects PAI08-0171-9582 and PAC06-137). The Consejería de Medio Ambiente y Desarrollo Rural of the Junta of Castilla-La Mancha allowed us to capture and radio-tag the birds. C.A. Martín holds a postdoctoral contract (13P Programme, CSIC), and F. Casas was supported by a postdoctoral grant of the Junta de Comunidades de Castilla-La Mancha (JCCM).

References

- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–1325.
- Arroyo, B., Mougeot, F. & Bretagnolle, V. (2001). Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). *Behav. Ecol. Sociobiol.* **50**, 109–115.
- Aunapu, M. & Oksanen, T. (2004). Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. *Evol. Ecol.* **17**, 371–392.
- Berner, T.O. & Grubb, T.C.J. (1985). An experimental analysis of mixed-species flocking in birds of deciduous woodland. *Ecology* **66**, 1229–1236.
- BirdLife International. (2004). *Birds in the European Union: a status assessment*. Wageningen: BirdLife International.
- BirdLife International (2008a). *Pterocles alchata*. In *IUCN 2008. 2008 IUCN Red List of Threatened Species*. Available at <http://www.iucnredlist.org> (accessed 4 February 2009).
- BirdLife International. (2008b). *Tetrax tetrax*. In *IUCN 2008. 2008 IUCN Red List of Threatened Species*. Available at <http://www.iucnredlist.org> (accessed 4 February 2009).
- Blumstein, D.T. (2003). Flight initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Mgmt.* **67**, 852–857.
- Bongi, P., Ciuti, S., Grignolio, S., Del Frate, M., Simi, S., Gandelli, D. & Apollonio, M. (2008). Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. *J. Zool. (Lond.)* **276**, 242–251.
- Boyer, S. & Rivault, C. (2006). Habitat selection and coexistence of invasive cockroach species (Dictyoptera) in sugar-cane fields on Réunion island. *Acta Oecol.* **29**, 16–26.
- Cody, M.L. (1981). Habitat selection in birds: the roles of vegetation structure, competitors and productivity. *Bioscience* **31**, 107–113.
- Collar, N. (1996). Family *Otididae*. In *Handbook of the birds of the world*. 240–273. Del Hoyo, J., Elliot, A. & Sargatal, J. (Eds). Barcelona: Lynx Editons.
- De Borbón, M.N., Barros, C. & De Juana, E. (1999). El gregarismo en las gangas ibérica y ortega. In *La Ganga Ibérica (Pterocles alchata) y la Ganga Ortega (Pterocles orientalis) en España: Distribución, abundancia, biología y conservación*: 195–214. Herranz, J. & Suárez, F. (Eds). Ministerio de Medio Ambiente: Organismo Autónomo Parques Nacionales.
- De Juana, E. (1997). Family *Pteroclididae* (Sandgrouse). In *Handbook of the birds of the world*: 30–57. Del Hoyo, J., Elliot, A. & Sargatal, J. (Eds). Barcelona: Lynx Editons.
- De Juana, E. & Martínez, C. (2001). Little bustard (*Tetrax tetrax*). In *European Union Action Plans for Eight Priority Bird Species*: 1–17. Schaffer, N. & Gallo-Orsi, U. (Eds). Luxembourg: European Commission.
- Forstmeier, W. & Weiss, I. (2004). Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* **104**, 487–499.
- García De La Morena, E.L., De Juana, E., Martínez, C., Morales, M.B. & Suárez, F. (2004). Sisón Común *Tetrax tetrax*. In *Libro Rojo de las Aves de España*. Madroño, A., González, C. & Atienza, J.C. (Eds). Madrid: SEO/Bird-Life-Dirección General de Conservación de la Naturaleza. Ministerio de Medio Ambiente.
- Giraldeau, L.A. & Beauchamp, G. (1999). Food exploitation: searching for the optimal joining policy. *Trends Ecol. Evol.* **14**, 102–106.
- Goodale, E. & Kotagamab, S.W. (2008). Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behav. Ecol.* **19**, 887–894.
- Hamilton, W.D. (1971). Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311.
- Heymann, E.W. & Buchanan-Smith, H.M. (2000). The behavioural ecology of mixed-species troops of callitrichine primates. *Biol. Rev.* **75**, 169–190.
- Jiguet, F. (2002). Arthropods in diet of little bustards *Tetrax tetrax* during the breeding season in western France. *Bird Study* **49**, 105–109.
- Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.

- Jullien, M. & Clobert, J. (2000). The survival value of flocking in neotropical birds: reality or fiction? *Ecology* **81**, 3416–3430.
- Kenward, R.E. (2001). *A manual for wildlife radio tagging*. San Diego: Academic Press.
- Krebs, J.R. (1973). Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp.). *Can. J. Zool.* **51**, 1275–1278.
- Lane, S.J., Alonso, J.C. & Martín, C.A. (2001). Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? *J. Appl. Ecol.* **38**, 193–203.
- Martínez, C. (1994). Habitat selection by the Little Bustard *Tetrax tetrax* in cultivated areas of central Spain. *Biol. Conserv.* **67**, 125–128.
- Martínez, C. (2005). *Distribución, abundancia, requerimientos de hábitat y conservación de aves esteparias de interés especial en Castilla-La Mancha*. Madrid: Consejo Superior de Investigaciones Científicas.
- Moorcroft, D., Whittingham, M.J., Bradbury, R.B. & Wilson, J.D. (2002). The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *J. Appl. Ecol.* **39**, 535–547.
- Morosinotto, C., Thomson, R.L. & Korpimäki, E. (2010). Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. *J. Anim. Ecol.* **79**, 327–333.
- Morse, D.H. (1977). Feeding behavior and predator avoidance in heterospecific groups. *Bioscience* **27**, 332–339.
- Morse, D.H. (1980). *Behavioral mechanisms in ecology*. Cambridge: Harvard University Press.
- Petit, L.J. & Petit, D.R. (1996). Factors governing habitat selection by Prothonotary Warblers: field tests of the Fretwell–Lucas models. *Ecol. Monogr.* **66**, 367–387.
- Pianka, E.R. (1974). Niche overlap and diffuse competition. *PNAS* **71**, 2141–2145.
- Pitt, W.C. (1999). Effects of multiple vertebrate predators on grasshopper habitat selection: trade-offs due to predation risk, foraging, and thermoregulation. *Evol. Ecol.* **13**, 499–515.
- Pulliam, H.R. (1973). On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422.
- Robinson, S.K. & Terborgh, J. (1995). Interspecific aggression and habitat selection by Amazonian birds. *J. Anim. Ecol.* **64**, 1–11.
- Roughgarden, J. (1976). Resource partitioning among competing species: a coevolutionary approach. *Theor. Popul. Biol.* **9**, 388–424.
- Silva, J.P., Pinto, M. & Palmeirim, J.M. (2004). Managing landscapes for the little bustard *Tetrax tetrax*. Lessons from the study of winter habitat selection. *Biol. Conserv.* **117**, 521–528.
- Slagsvold, T. (1980). Habitat selection in birds: on the presence of other bird species with special regard to *Turdus pilaris*. *J. Anim. Ecol.* **49**, 523–536.
- Sridhar, H., Beauchamp, G. & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* **78**, 337–347.
- Stensland, E., Angerbjörn, A. & Berggren, P. (2003). Mixed species groups in mammals. *Mammal. Rev.* **33**, 205–223.
- Suárez, F. & Herranz, J. (2004). Ganga Ibérica *Pterocles alchata*. In: *Libro Rojo de las Aves de España*: 269–271. Madroño, A., González, C. & Atienza, J.C. (Eds). Madrid: SEO/BirdLife-Dirección General de Conservación de la Naturaleza, Ministerio de Medio Ambiente.
- Suárez, F., Hervás, I., Herranz, J. & Del Moral, J.C. (2006). *La ganga ibérica y la ganga ortega en España: población en 2005 y método de censo*. Madrid: SEO/BirdLife.
- Suárez, F., Hervás, I., Levassor, C. & Casado, M.A. (1999). La alimentación de la Ganga Ibérica y la Ganga Ortega. In: *La Ganga Ibérica (Pterocles alchata) y la Ganga Ortega (Pterocles orientalis) en España: Distribución, abundancia, biología y conservación*: 215–229. Herranz, J. & Suárez, F. (Eds). Ministerio de Medio Ambiente: Organismo Autónomo Parques Nacionales.
- Suárez, F., Naveso, M.A. & De Juana, E. (1997). Farming in the drylands of Spain: birds of the pseudosteppes. In: *Farming and Birds in Europe*: 297–330. Pain, D. & Pienkowski, M.W. (Ed.). London: Academic Press.
- Sullivan, K.A. (1984). The advantages of social foraging in Downy Woodpeckers. *Anim. Behav.* **32**, 16–22.
- Svårdson, G. (1949). Competition and habitat selection in birds. *Oikos* **1**, 157–174.
- Tella, J.L. & Forero, M.G. (2000). Farmland habitat selection of wintering lesser kestrels in a Spanish pseudosteppe: implications for conservation strategies. *Biodivers. Conserv.* **9**, 433–441.
- Terborgh, J. (1990). Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *Am. J. Primatol.* **21**, 87–100.
- Walter, G.H. (1991). What is resource partitioning? *J. Theor. Biol.* **150**, 137–43.
- White, G.C. & Garrot, R.A. (1990). *Analysis of wildlife radio-tracking data*. New York: Academic Press.
- Wootton, J.T. (1992). Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and Algae. *Ecology* **73**, 981–991.