

MIGRATION PATTERNS OF IBERIAN LITTLE BUSTARDS *TETRAX TETRAX*

PATRONES DE MIGRACIÓN DE SISIONES COMUNES *TETRAX TETRAX* IBÉRICOS

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SUMMARY.—The term “migratory” refers to animals performing yearly round-trips between breeding grounds and post-breeding areas, whereas the term “sedentary” refers to those remaining the whole year in their breeding grounds. However, migration is a complex and varying phenomenon governed by genetic and environmental factors, particularly in species with wide distribution ranges. Here we describe and classify the seasonal movement patterns of 71 little bustards *Tetrax tetrax*, an endangered Palearctic steppe bird, radio- and satellite-tracked in the Iberian Peninsula. Four major movement patterns were identified, with 89% of little bustards behaving as migrants, among which 75% (summer migrants and summer-winter migrants) performed their first movement after breeding during the summer (mainly between May and July), whereas 14% (winter migrants) left their breeding sites in autumn (mainly between September and November). The remaining 11% were strictly sedentary.

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On average, summer migration started on June 14th, and winter migration on October 3rd, while pre-breeding migration started on March 23rd. Summer migration occurred in most Iberian regions, although it was mainly found in semiarid Mesomediterranean areas. Winter migration occurred only in the northern half of the Peninsula, being the only pattern found in Subatlantic and highland areas. All winter migrants wintered in Thermomediterranean localities of southern Iberia. The sedentary pattern was found only in the Semiarid Mesomediterranean and Thermomediterranean sectors. This is a good example of complex intraspecific variation in the migratory behaviour of a species that occupies a diverse range of environments. The variability of movement patterns of Iberian little bustards is much greater than previously thought and should be taken into account in conservation programmes for the species.

Key words: climate seasonality, Mediterranean climate, Portugal, satellite tracking, Spain.

RESUMEN.—El término ‘migratorio’ hace referencia a animales que realizan viajes de ida y vuelta entre sus áreas reproductivas y posreproductivas, mientras que el término ‘sedentario’ hace referencia a aquellos que permanecen el año completo en sus zonas de reproducción. No obstante, la migración es un fenómeno complejo y variable gobernado tanto por factores genéticos como ambientales, especialmente en especies con rangos de distribución amplios. En este trabajo describimos y clasificamos los patrones de movimiento estacional de 71 individuos de sison común *Tetrax tetrax*, un ave esteparia Paleártica amenazada, monitoreados mediante radioseguimiento terrestre y vía satélite en la península Ibérica. Se identificaron cuatro patrones principales de movimiento estacional. El 89% de los sisones marcados presentaron un comportamiento migrador, de los cuales el 75% (migradores estivales y migradores estivales-invernales) realizaron los primeros movimientos posreproductivos en verano (principalmente entre mayo y julio), mientras que el 14% (migradores invernales) abandonaron las áreas de cría en otoño (principalmente entre septiembre y noviembre). El 11% restante mostró un comportamiento estrictamente sedentario. En promedio, la migración estival comenzó el 14 de junio y la migración invernal tuvo lugar el 3 de octubre, mientras que la migración pre-reproductiva lo hizo el 23 de marzo. La migración estival estuvo presente prácticamente en todas las regiones ibéricas, aunque se encontró principalmente en áreas mesomediterráneas semiáridas. La migración invernal se encontró exclusivamente en la mitad norte de la Península, siendo el único patrón migratorio presente en las poblaciones subatlánticas y de paramera. Todos los migradores invernales invernaron en localidades termomediterráneas del sur peninsular. El patrón sedentario se encontró exclusivamente en poblaciones de los sectores mesomediterráneo semiárido y termomediterráneo de la Península. Estos resultados proporcionan un excelente ejemplo de variación interespecífica compleja en el comportamiento migratorio de una especie que ocupa un amplio rango de condiciones ambientales. La variabilidad de patrones de migración que muestran los sisones ibéricos es mucho mayor de lo que previamente se pensaba. Estos resultados deben ser tenidos en cuenta en los programas de conservación de la especie.

Palabras clave: clima mediterráneo, España, estacionalidad climática, Portugal, seguimiento por satélite.

INTRODUCTION

Animals performing an annual displacement between breeding and post-breeding areas are usually classified as migratory (Bernis, 1966; Sinclair, 1983; Terrill and Able, 1988). These movements are generally

associated with seasonal oscillations in the availability of food resources, so that animals moving between areas that provide complementary resources during the year would potentially obtain selective advantages (Harden Jones, 1968; Lack, 1968; Levey and Stiles, 1992; Carrascal, 2004). However, migration

is a complex and ever-evolving phenomenon showing enormous intra- and interspecific variation (see Newton, 2010, for a recent thorough review). This variation is mainly driven by genetic differences and populations can adapt very quickly to local environmental conditions, giving rise to considerable variation in migratory behaviour within populations, especially in those species with wide distribution ranges (Alerstam *et al.*, 2003; Pulido, 2007). Individuals from different populations, or even the same population, may perform migratory movements of different magnitude and timing. Considering such individual variability, Terrill and Able (1988) classified bird migration patterns as annual, partial or differential. They used the term *annual migrant* (also termed *total migrants*) for species or populations where all individuals migrate from breeding sites, *partial migrant* for populations where some individuals do and others do not migrate (Gauthreaux, 1982; Lundberg, 1988), and *differential migrant* for populations where some classes of individuals (age, sex or social status) differ in the timing of migration, distance travelled, or both (Gauthreaux, 1982; Ketterson and Nolan, 1983). Several studies have revealed that different species formerly defined as strictly *sedentary* exhibit significant inter-individual variation in movement patterns, a situation that occurs particularly among medium to large-sized non-passerines such as grouse and bustards, which often track resources seasonally due to their changing availability at regional or sub-regional scales (Cade and Hoffman, 1993; Schroeder and Braun, 1993; Alonso *et al.*, 2000; Morales *et al.*, 2000).

Little bustards *Tetrax tetrax* are medium-sized, mainly herbivorous, Palearctic steppe birds. Many little bustard populations are experiencing severe declines following increasing agriculture intensification (Jolivet and Bretagnolle, 2002; Morales *et al.*, 2008a; de Juana, 2009). As a consequence,

the species is considered “Near threatened” globally (BirdLife International, 2012), and “Vulnerable” in Europe (BirdLife International, 2004). During the breeding season (March-July), little bustards tend to spend most of their time in their breeding areas (Schulz, 1985; Jiguet and Bretagnolle, 2001; Delgado *et al.*, 2010; Ponjoan *et al.*, 2012), but, from late summer through autumn and winter, they gather in flocks and may disperse to areas not used for breeding (Cramp and Simmons, 1980), a widespread behaviour among Iberian steppe birds (Suárez *et al.*, 1997). Northern populations of little bustards (from west-central France to northern Kazakhstan) have been described as totally or partially migratory (Cramp and Simmons, 1980; del Hoyo *et al.*, 1996). Within western Europe, populations in northern and central France are clearly migratory (Villers *et al.*, 2010) and spend the winter in the Iberian Peninsula, which is the stronghold of the western Palearctic breeding population (54,000-108,000 males, García de la Morena *et al.*, 2006). However, the migratory status of the little bustard populations in Iberia is not so clear and this species has been variously described as sedentary, dispersive, transhumant or partially migrant (Bernis, 1966; Cramp and Simmons, 1980; Díaz *et al.*, 1996; Villers *et al.*, 2010; Martínez, 2011). In some regions, birds have been reported to leave their breeding areas, concentrating at certain wintering sites, but in other regions they are said to stay in the same area all year round (García de la Morena *et al.*, 2006, 2007). Previous studies have shown that some Iberian little bustards may repeat regular round-trips between spatially separated breeding and summering or wintering areas, to which they show inter-annual fidelity and that may be just a few kilometres to several hundred kilometres apart (García de la Morena *et al.*, 2004; Ponjoan *et al.*, 2004; Sampietro *et al.*, 2008). In spite of all of this information, no clear quantitative and quali-

tative description of the different seasonal movement patterns observed in the species within the Iberian Peninsula exists, nor has there been an analysis of why such variation occurs. Our aim was thus to describe and classify the seasonal movement patterns of radio- and satellite-tagged little bustards captured at both breeding and wintering areas in the Iberian Peninsula. We describe variations in the timing and range of the movements conducted by the birds, and hypothesise that the observed variation may have a regional basis, associated with differences in resource availability, related to bioclimatic variations, at a peninsular scale. We finally discuss such results within the framework of the ecology of bird migration in Mediterranean ecosystems.

MATERIAL AND METHODS

Study area

Little bustards were captured throughout most of their range in the Iberian Peninsula (fig. 1). The latitude of captures ranged from 37.682° N at Castro Verde (Baixo Alentejo, southern Portugal) to 43.235° N at Terra Chá (Galicia, northwestern Spain), whereas longitude varied from 8.151° W at Castro Verde to 1.194° E at Plana de Lleida (Catalonia, northeastern Spain). Altitude ranged from 124 m.a.s.l. at Castro Verde to 1,385 m.a.s.l. at the highlands of Teruel (Aragón, eastern Spain).

The relatively large geographical extent of the Iberian Peninsula (583,254 km²), together with its complex orography (two central plateaus and a series of transverse mountain ranges generating a south-eastward decline of the oceanic influence on climate), and centuries of human-induced landscape modifications, have produced high environmental variability and a mosaic-like habitat configuration at regional and local scales,

particularly in the Mediterranean climate area (Alcaraz *et al.*, 2006). To summarise such variation, we used the bioclimatic classification of the Iberian Peninsula elaborated by Benito (2002), which takes into account different climatic variables (Sánchez Palomares *et al.*, 1999) and has already been used to explain the distribution patterns of Iberian birds (Sainz, 2003) (table 1 and fig. 1).

Bird tagging and tracking

From 2001 to 2006, we captured birds either during the breeding season (May-June) on display sites or in wintering areas (November-March) using leg nooses or cannon nets (Ponjoan *et al.*, 2010). Sex and age were determined using plumage characteristics (Cramp and Simmons, 1980; Otero, 1985; Jiguet and Wolff, 2000). We captured and tagged 71 adult little bustards (54 males, 15 females and two birds of unknown sex). Thirty birds were captured in the Ebro Valley (29 on Lleida Plains, one in the nearby highlands of Teruel), 27 were captured on the Southern Plateau, eight in Baixo Alentejo (Portugal) and Extremadura, four on the Northern Plateau, and two in Galicia (fig. 1).

Of the finally monitored birds, 18 carried satellite transmitters (Platform Transmitter Terminals, PTTs), either battery or solar-powered, and 53 carried VHF transmitters (Biotrack Ltd., United Kingdom), both attached by means of a breakaway backpack Teflon-ribbon harness (Kenward, 2001). Three types of PTTs were used: one 35 g battery-powered (North Star Science and Technology, LLC, Baltimore, MD), two 18 g solar-powered Argos PTTs (Microwave Telemetry Inc., Columbia, MD), and six 30 g solar-powered Argos/GPS PTTs (Microwave Telemetry Inc., Columbia, MD). VHF transmitters lasted between one month and 4.4 years (mean = 1.7 years) and satellite transmitters lasted between one month to 3.3 years

(mean = 1.0 year), all depending on the fate of each bird or battery life. In all cases, the tag weight was below the 4-5% relative weight of the bird suggested to minimise the effects of an additional mass on bird movements (Caccamise and Hedin, 1985;

Kenward, 2001). Argos PTTs were programmed on an 8 hour on/48 hour off duty-cycle (*ca.* 3 days). Argos/GPS PTTs were set to collect fixes at 2-hour intervals from the GPS satellite network. Both Argos and Argos/GPS PTTs used the Argos-Tiros

TABLE 1

Climatic, ecological and geographical description of bioclimatic sectors defined by Benito (2002) for the Iberian Peninsula.

[*Descripción climática, ecológica y geográfica de los sectores bioclimáticos definidos por Benito (2002) para la península Ibérica.*]

Bioclimatic sector¹	Climatic and ecological characteristics	Geographical zone²
<i>Humid temperate Atlantic</i>	Rainy, mild winters. Peak productivity in summer	Northern and north-western fringe
<i>Subatlantic-Oromediterranean</i>	Rainy, short or absent summer drought, cold winters. Peak productivity in summer	Northern mountain areas, including Pyrenees, Cantabrian, Iberian and Central Range
<i>Humid Submediterranean</i>	Moderately rainy, relatively short summer drought, warm summers, cold winters. High spring productivity, very low winter productivity	Central Portugal, areas of Central Range, areas of Mediterranean coast (Catalonia) and southern mountain ranges
<i>Subhumid Supramediterranean</i>	Moderately dry, variable summer drought, warm summers, cold winters. High spring productivity, very low winter productivity	Northern Plateau, Pre-Pyrenean and Iberian highlands
<i>Semiarid Mesomediterranean</i>	Dry, marked summer drought, hot summers, fresh winters. Productivity peaks in spring and autumn	Most of Southern Plateau, Ebro valley, south-eastern highlands and parts of eastern Portugal.
<i>Thermomediterranean</i>	Dry, marked summer drought, hot summers, mild winters. Productivity peaks in spring and autumn, but moderate winter productivity	Southern Portugal, Extremadura, Guadalquivir valley and most of Mediterranean coast

¹ See their distribution in fig. 1

² See their location in fig. 1

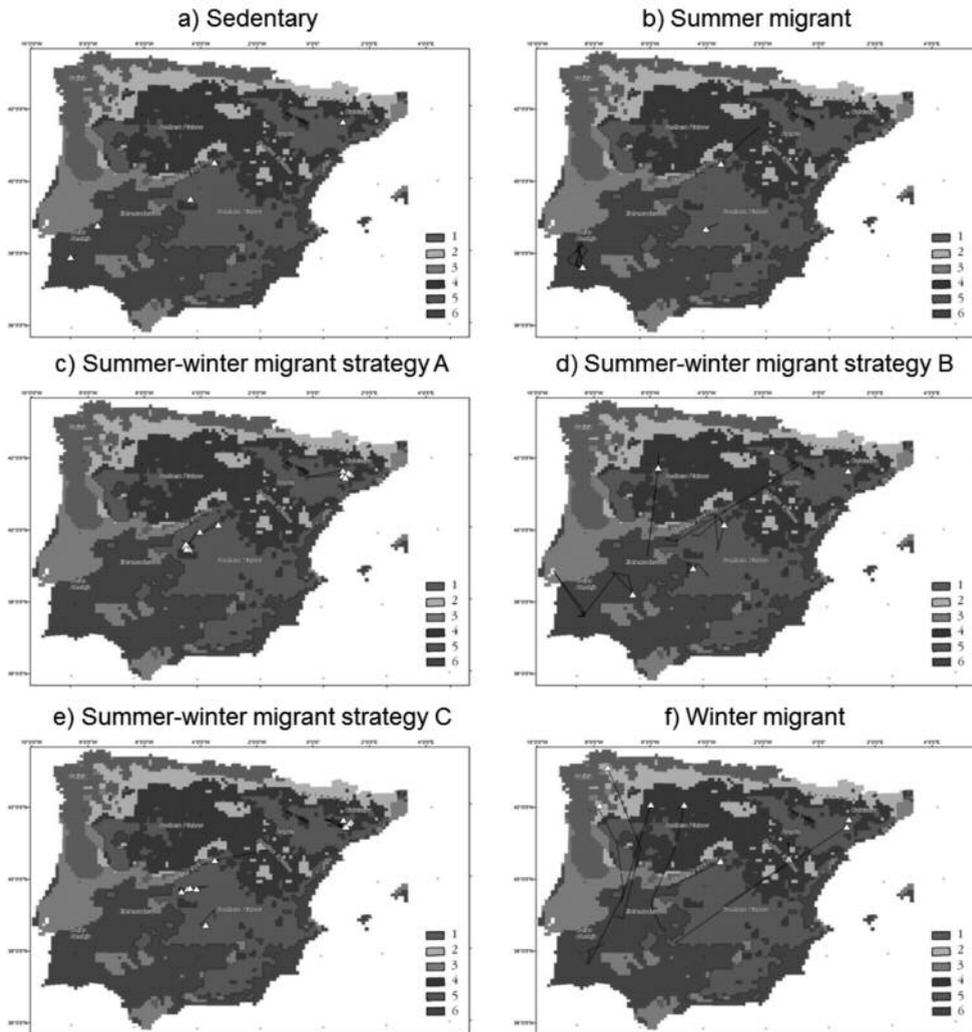


FIG. 1.—Geographical occurrence of little bustard migration patterns in the Iberian Peninsula: Sedentary, summer migrant, summer-winter migrant (including 3 different strategies: A, B, C; see text) and winter migrant. White triangles: origin breeding area of tagged little bustards; solid lines: main registered movements. Climatic sectors of the Iberian Peninsula by 10×10 km UTM squares corresponding to (1) Humid Temperate Atlantic, (2) Subatlantic- Oromediterranean, (3) Humid Submediterranean, (4) Subhumid Supramediterranean Continental, (5) Semiarid Mesomediterranean and (6) Thermomediterranean (Benito, 2002).

[Distribución geográfica de los patrones de migración del sisón común en la península Ibérica: sedentarios, migrantes estivales, migrantes estivales-invernales (incluyendo 3 estrategias diferentes: A, B, C; véase el texto) y migrante invernal. Triángulos blancos: origen (área de cría) de los sisones marcados; líneas continuas: principales movimientos registrados. Sectores climáticos de la península Ibérica por cuadrículas UTM de 10×10 kilómetros correspondientes a (1) Húmedo Atlántico Templado, (2) Subatlántico-Oromediterráneo, (3) Húmedo Submediterráneo, (4) Subhúmedo Supramediterráneo Continental, (5) Semiárido Mesomediterráneo y (6) Termomediterráneo (Benito, 2002).]

satellite system to obtain estimates of PTT locations using the Argos Multi-satellite Service (Service Argos, 2001). Data were received every 3-7 days via e-mail from the Argos Service Automated Distribution System. Estimated locations and GPS fixes were reported as latitude and longitude pairs based on the World Geodesic System 1984 (WGS84), with measurement times recorded as calendar days and Coordinated Universal Time (UTC) hours/minutes. For each Argos-estimated location, a quality index (location class, LC) was assigned, based on the location accuracy. Location classes assigned by Argos (3, 2, 1, 0, A, B, and Z) predict relative accuracy of the location estimates in decreasing order. GPS fix accuracy is about ± 15 m (Microwave Telemetry Inc.), better than all Argos locations (Service Argos, 2001). For birds provided with PTT, we used preferentially LCs 3, 2 and 1. We only included locations of lower quality (LCs 0, A and B) when they were consistent with little bustard movements in terms of distance covered and time elapsed between locations (considering a maximum flight speed of 90 km/h), following the indications of Minimum Redundant Distance (MRD) and Distance, Angle, and Rate (DAR) provided by Douglas (2006). For birds with Argos/GPS, only GPS fixes were considered, except when battery charge did not allow GPS locations to be obtained. In such cases, we used ARGOS system fixes based on the criteria mentioned above.

Little bustards fitted with VHF transmitters were tracked from the ground every 7 to 30 days. When a bird could not be found from ground (basically, outside the breeding season), we searched from aircraft (CESSNA 172 and 182 aircraft or ultralight models) equipped with Yagui directional antennas and a multiband receptor (AOR-AR8200, ATS R4000). From 2001 to 2007 we performed 59 flights and *c.* 224 h of aerial surveys.

Data treatment and analysis

Movements of tagged little bustards were analysed based on variation in both the absolute distance to breeding sites during the annual cycle, and the relative distance between breeding sites and post-breeding summering and wintering areas, following a combination of the approaches used by Morales *et al.* (2000) and Palacín (2007) to study the seasonal movements of the closely related great bustard *Otis tarda* (fig. 2). When considering whether and when individuals moved from their breeding grounds, birds were classified as *sedentary* if they remained in the *breeding area* all year round. Birds that left their breeding range for some continuous period in the year (longer than 30 days) were classified as *summer migrants* if they departed only in summer (see below for monthly definition of seasons); *winter migrants*, if they left it only during the autumn-winter period; or *summer-winter migrants*, if they left the breeding area both during the summer and autumn-winter periods. In this last category, some birds used a single area outside the breeding season or different areas in summer and winter. For all migrant birds, we defined as the *summering area* the area where they spent the summer period, and the *wintering area* as the area where they spent the autumn-winter period. If both were the same area, i.e. where the summer and wintering ranges overlapped, it was termed the *non-breeding area*.

We established each individual's breeding site as the "origin point" of its movements. For birds captured during the breeding season (i.e. *breeding site*), the capture location was set as the origin. For those captured during the post-breeding period, we used as "origin" the arithmetic mean of locations obtained during their first monitored breeding season. To homogenise the information available from all the different individuals, locations were filtered to select a single location per

bird and day. For cases where > 1 location per day was available, the mean arithmetic daily location was calculated.

In order to assess whether a little bustard had made a significant movement to a different area, both within the same period or between different seasons, we evaluated its daily movement state and identified displacements above a threshold travel speed of 8 km/day (from locations separated by at least 24 hours; García de la Morena *et al.*, in prep., following Shimazaki *et al.*, 2004). For each individual, we calculated the monthly distance from the origin as the mean value of all linear distances to origin obtained in the corresponding month. The monthly variation of distance to origin was analysed by means of one-way ANOVA after logarithmic transformation of the data. To analyse the movement phenology of each individual we calculated the mean value of its last Julian date presence at the breeding site and either the first Julian date of absence from it or the first Julian date of presence in a post-breeding area, and vice-versa. Differences in mean post-breeding, autumn and pre-breeding departure dates were analysed between regions and years by means of non-parametric Kruskal-Wallis tests.

For analysis and definition of migration patterns, we used a subsample of 47 individuals with data available for at least one complete annual cycle, i.e., with locations during the breeding (April-June), summer (July-September), and winter (November-February) periods. March and October are travelling months during which most pre-breeding and post-breeding movements, respectively, occur (see Cramp and Simmons [1980] for species annual phenology). The remaining 24 cases were subsequently assigned to one of the migratory patterns defined from the previous subsample after replacing the information missing for some of these periods (mainly due to movement out of an individual's known home range)

with a minimum distance to the breeding site, estimated from the cover of re-location flights. These individuals were included in the calculations of the overall proportion of birds following each migratory pattern in each population, but excluded from the statistical analyses describing movement patterns (see below).

Individual migration patterns were evaluated in relation to the bioclimatic sectors (Benito, 2002) within which their breeding areas were located: Subatlantic-Oromediterranean, Subhumid Supramediterranean or Semiarid Mesomediterranean and Thermo-mediterranean.

RESULTS

Migration patterns

We were able to assign a particular migratory pattern to 63 of the 71 birds that were tracked. Of these, 8 (13%) were considered as *sedentary*, 5 (8%) as *summer migrants*, 10 (16%) as *winter migrants* and 40 (63%) as *summer-winter migrants* (table 2). The remaining 8 birds left breeding areas in summer but their tracking was not detailed enough to assign them to one of the migratory categories considered (*summer* or *summer-winter migrants*). Therefore, within the entire sample (N = 71), 11% of birds did not migrate, 75% performed their first movement after breeding during the summer (including the 8 birds with unassigned migratory pattern) and 14% left their breeding sites in autumn-winter.

Sedentary birds (N = 8) stayed all year round in the neighbourhood of their breeding sites (fig. 2a). *Summer migrants* (N = 5) performed movements of up to 162 km (mean \pm SD 77 \pm 56 km, fig. 2b) and there were significant differences in distances moved from breeding-wintering sites during summer months ($F = 7.1$, d.f. = 7, $P < 0.001$).

TABLE 2

Number of tagged little bustards assigned to different movement patterns and migration strategies in relation to the bioclimatic sector of their corresponding breeding area (SAOM: Subatlantic and Oromediterranean, SHSM: Sub-humid Supramediterranean, SMM: Semiarid Mesomediterranean, TM: Thermomediterranean, NA: non-assigned). * Birds leaving their breeding areas in summer but with insufficient information to assign them to the summer or summer-wintering pattern.

[Número de siones comunes marcados asignados a los diferentes patrones de movimiento en función del sector bioclimático de sus correspondientes áreas de cría (SAOM: Subatlántico-Oromediterráneo; SHSM: Subhúmedo Supramediterráneo; SMM: Semiárido Mesomediterráneo; y TM: Termomediterráneo. * Aves que abandonaron las áreas de cría pero para las que se carecía de información suficiente para clasificarlas como migradoras estivales o migradoras estivales-invernales.]

Pattern	Total	SAOM	SHSM	SMM	TM	
Sedentary	8			6	2	
Summer migrant	5			2	3	
Summer-winter migrant	Strategy A	18		1	17	1
	Strategy B	7			5	1
	Strategy C	15		1	15	
	Total	40		1	37	2
Non-assigned*	8		1	4	3	
Winter migrant	10	3	2	5		
General total	71	3	4	54	10	

Among *summer-winter migrants* different strategies were observed regarding the extent of movements and use of postbreeding areas. Some birds ($N = 18$; 45%) used the same postbreeding areas from summer to winter, performing movements up to 53 km (mean \pm SD = 20 ± 14 km), during the winter (Strategy A, fig. 2c). Postbreeding areas were significantly distant from breeding sites ($F = 12.4$, d.f. = 11, $P < 0.001$, $N = 18$). The remaining *summer-winter migrants* used different post-breeding areas during summer and winter. Among these birds, 7 (17.5 %) moved to summering areas located closer than wintering areas (Strategy B). In these

cases, summer movements were up to 92 km long (mean \pm SD = 26 ± 26 km), whereas they reached up to 410 km (mean \pm SD = 108 ± 134 km) during autumn (mainly during October; see Migration phenology section below and fig. 2d; $F = 3.1$, d.f. = 11, $P < 0.01$, $N = 7$). On the other hand, 15 birds (37.5 %) moved up to 57 km (mean \pm SD = 16 ± 1 km) to wintering areas closer to their breeding sites than summering ones ($F = 8.64$, d.f. = 11, $P < 0.001$, $N = 15$), that could be as far as 161 km (mean \pm SD = 36 ± 39 km) (Strategy C; fig. 2e).

Finally, *winter migrants* ($N = 10$) stayed at their breeding sites through the summer,

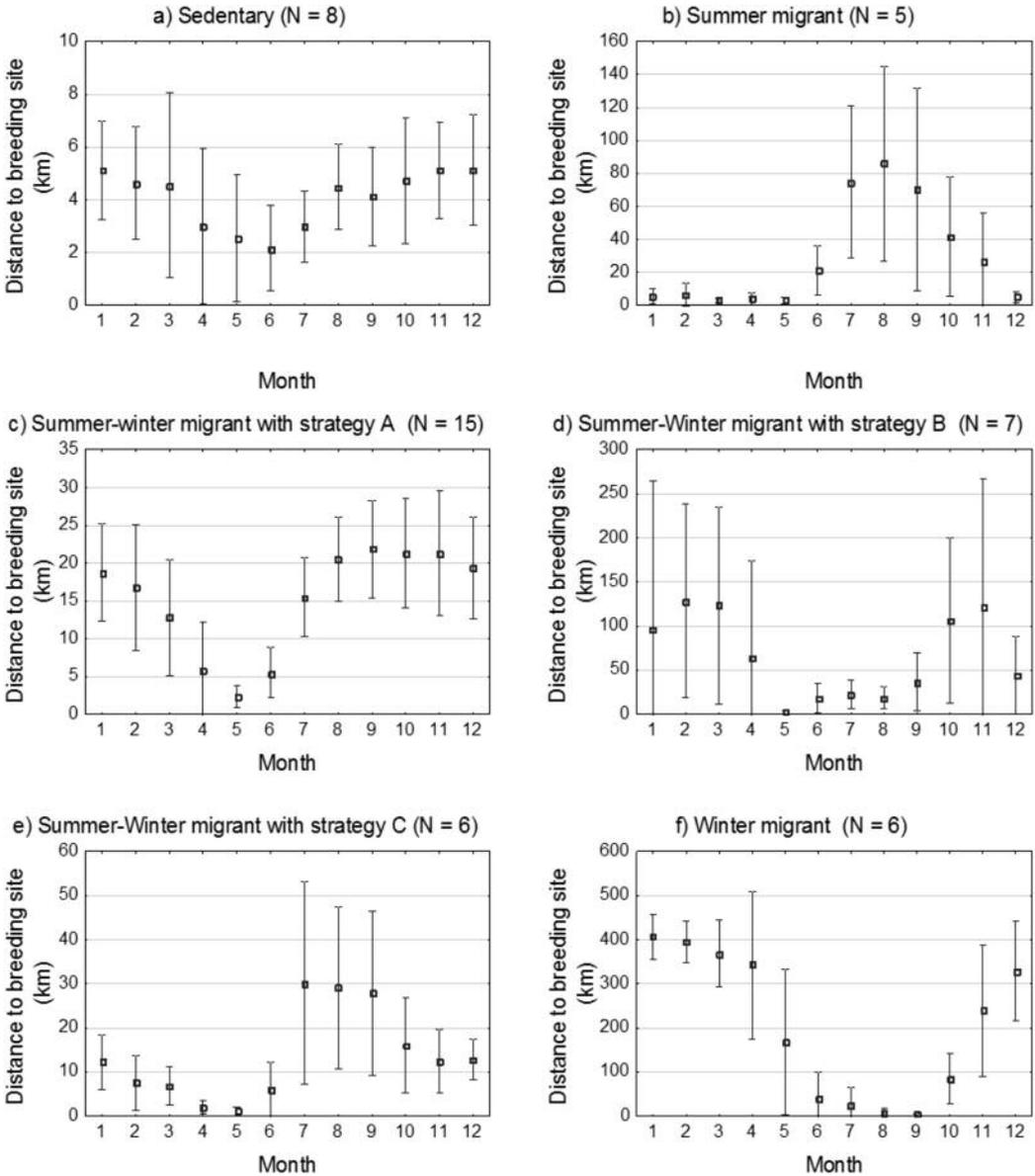


FIG. 2.—Mean distance (\pm 95% confidence limits) to origin (breeding site) of little bustards with contacts over a complete annual cycle, classified in 6 migration patterns: sedentary, summer migrant, summer-winter migrant (including 3 different strategies: A, B, C; see text) and winter migrant. All patterns were statistically significant in monthly distance to breeding site.

[Distancia media (\pm 95% de intervalo de confianza) al origen (área de cría) de los sisones con registros a lo largo de un ciclo anual completo, clasificados en 6 patrones de migración: sedentarios, migrantes estivales, migrantes estivales-invernales (incluyendo 3 estrategias diferentes: A, B, C; véase el texto) y migrante invernal. Todos los patrones fueron estadísticamente significativos respecto a la distancia mensual al área de cría.]

performing long distance movements of up to 464 km (mean \pm SD = 319 \pm 148 km) in autumn (fig. 2f; $F = 5.2$, d.f. = 11, $P < 0.001$).

Migration phenology

Summer migrants and *summer-winter migrants* left their breeding areas, on average, on June 14th, although the earliest and latest dates observed for this type of movement were April 16th and August 23rd, respectively. Most, movements occurred in May (34%), June (28%) and July (26%). The average start of summer migration also varied between years 2000 and 2006 (Kruskal-Wallis test: $H = 18.297$, d.f. = 6, $N = 54$, $P < 0.01$).

Winter migrants moved to their wintering grounds on average on October 3rd. Most movements were recorded in that month (61%), followed by September (21%) and November (9%), although the total migration period extended from May to December. No interannual differences were detected (Kruskal-Wallis tests: $H = 5.43$, d.f. = 3, $N = 35$, $P = 0.14$ and $H = 5.13$, d.f. = 6, $N = 35$, $P = 0.53$, respectively). The return of the little bustards from wintering sites to their breeding areas (pre-breeding migration) occurred on average on March 23rd. March saw the majority of these movements (37%), followed by April (27%) and February (22%). There were some earlier records of movements, in December and January. No significant differences in the date of return to the breeding area were observed between years (Kruskal-Wallis test: $H = 8.928$, d.f. = 7, $N = 49$, $P = 0.26$).

Geographic and climatic variation of migratory patterns

The prevalence of these migratory patterns apparently varied between bioclimatic sectors where breeding areas are located. The most

geographically extended movement was summer migration (74.6% of birds, including *summer*, *summer-winter migrants* and unassigned migratory birds that also moved during summer), which occurred in all bioclimatic sectors except among the Subatlantic and Oromediterranean breeding populations, although it was mainly found in Semiarid Mesomediterranean populations of the Southern Plateau and the Ebro Valley.

Summer migrants usually moved to sites with more productive agriculture (Silva *et al.*, 2007), including some irrigated areas relatively far from the breeding grounds, as found on the Southern Plateau and Alentejo, or to cool upland areas (with a lower mean temperature in summer but unsuitable in winter also due to low mean temperature), as exemplified by little bustards travelling from their breeding grounds on the Southern Plateau to the slopes of the Central System or the highlands of the Iberian System, moving to the Subhumid Supramediterranean bioclimatic sector (fig. 1).

Summer-winter migrants that used only a single post-breeding area (i.e. having overlapping summering and wintering ranges) also tended to move to irrigated areas, closer and at lower altitude than breeding areas, but suitable for the non-breeding period within the same bioclimatic sector because of temperate temperatures.

Summer-winter migrants with summer areas closer than wintering areas breed mostly in those Semiarid Mesomediterranean areas where both summer and winter are harsh due to continentality. These little bustards usually spend the summer in close-by but higher altitude areas (Subhumid Supramediterranean) but need to move to distant and lower altitude wintering grounds located in Thermomediterranean areas (in the Southern Plateau and Extremadura). Finally, the *summer-winter migrant* pattern, with distant summering areas but closer wintering grounds, was found in birds that

bred exclusively in Semiarid Mesomediterranean zones of the Southern Plateau and the Ebro Valley, where summer drought reduces the suitability of breeding grounds by affecting the availability of the green vegetation that the birds consume.

The winter migration pattern was represented only by 14.1% of birds, all of them breeding in the northern half of the Iberian Peninsula, and was in fact the only movement pattern found in the Subatlantic populations of Galicia and the highlands of the Iberian System. Within the northern half of the Peninsula, this pattern was detected also in populations breeding in Subhumid Supramediterranean areas of the Northern Plateau, as well as in 50% of birds breeding in Semiarid Mesomediterranean areas of the Ebro Valley and Southern Plateau. All *winter migrants* wintered in Thermomediterranean localities of the southern half of the Iberian Peninsula. In contrast, the strictly *sedentary* pattern was found only in 11.3% of our birds, which bred in the semiarid Mesomediterranean (Southern Plateau and Ebro Valley) and Thermomediterranean sectors (Extremadura and Alentejo).

DISCUSSION

Our results provide a good example of complex intraspecific variation within the migratory behaviour of a particular species, especially when it occupies a large diversity of physiographical, climatic and human land-use conditions, as is the case with the Iberian little bustards. In fact, the variability of migration patterns found in Iberian little bustard populations is much greater than previously thought, both between and within different regions and bioclimatic sectors.

This variability encompasses strictly *sedentary* individuals and birds that perform regular movements (in terms of timing and spatial range), alternating breeding areas

with distinct summering and/or wintering grounds. These latter can therefore be considered as truly migratory (Bernis, 1966; Sinclair, 1983) when they change bioclimatic sectors and move at least some tens of kilometres between seasons. It is worth noticing that the strictly *sedentary* pattern, traditionally considered as characteristic of Iberian little bustard populations (Bernis, 1966; Cramp and Simmons, 1980; Díaz *et al.*, 1996; Villers *et al.*, 2010) only applied to a minority of birds in our sample and it is probably the less frequent one in the Iberian Peninsula. In fact none of the studied populations can be considered as completely sedentary, since in all of them there were birds leaving the breeding grounds at some point of the annual cycle. Consequently, these populations should be classified as partially migratory (Terrill and Able, 1988). Moreover, partial migration seemed to be the most frequent pattern, mainly involving summer movements, particularly in Thermo and Mesomediterranean areas. Our radio and satellite tracking results highlight the important role of summer migration in the annual cycle of many Iberian little bustard populations. However, the majority of our tagged birds were males, and further tracking effort is needed to determine whether females generally follow similar patterns and strategies, or whether they differ from males in extent and phenology of their movements (i.e. differential migration, see Terrill and Able, 1988), as described for other polygynous birds, including other bustard species such as the great bustard (Schroeder, 1985; Cade and Hoffmann, 1993; Morales and Martín, 2002).

Moreover, there are little bustard populations located further north or at higher altitudes, in the Subatlantic Oromediterranean and Subhumid Supramediterranean bioclimatic sectors of Iberia, that are completely migratory and whose individuals leave their breeding sites every year to winter at medium

to long distances, up to several hundred kilometres away according to our own tracking data. These movements are consistent with the virtual disappearance of little bustards from the Spanish northern breeding areas in winter (García de la Morena *et al.*, 2006). Fidelity both to breeding and summering and/or wintering sites has been observed (own unpublished data) and involves a change of bioclimatic sector, and such movements could thus be considered true migrations, at least when birds regularly move several tens of kilometres.

The wide range of environmental conditions (orographic, climatic and land-use related) encompassed by the little bustard distribution area in Iberia may help to understand why there is such variability in its migratory behaviour. Moreover, observed inter-annual variations in phenology could reflect interannual variations in meteorological conditions, in the present case probably due to the particularly hot and dry conditions of 2005. The little bustard is basically herbivorous, although arthropods are an important food resource during the breeding season (Jiguet *et al.*, 2002; Traba *et al.*, 2008), and the structure and composition of vegetation has proved to be a determinant factor in its habitat selection and spatial distribution (Morales *et al.*, 2008b; Faria *et al.*, 2012). All but the Galician populations of Iberian little bustards occur in Mediterranean climatic regions, in which a more or less severe summer drought imposes strong restrictions on ecosystem productivity (Silva *et al.*, 2007; Lapidra *et al.*, 2011), both at the primary and the secondary levels (Blondel and Aronson, 1999). Other bird species inhabiting Iberian Mediterranean ecosystems also perform summer movements to more northern or higher altitude localities, tracking peak productivity: examples include the great bustard (Morales *et al.*, 2000; Alonso *et al.*, 2001; Palacín, 2007; Palacín *et al.*, 2009; Alonso *et al.*, 2009), the lesser kestrel *Falco naumanni*

(Olea *et al.*, 2004; Catry *et al.*, 2011), Montagu's harrier *Circus pygargus* (Limiñana *et al.*, 2008) and the common quail *Coturnix coturnix* (Sardà-Palomera *et al.*, 2012).

Little bustard summer movements are more common in bioclimatic sectors where the summer drought is more severe. In populations of more northern, oceanic or upland areas, where peak productivity occurs in summer (Costa *et al.*, 1998; Alcaraz *et al.*, 2006) birds do not need to leave breeding areas, although productivity decreases significantly in winter, forcing these little bustards to perform at least a winter migration. Moreover, in summer these areas receive little bustards from other populations (own tracking data; Villarino *et al.*, 2002 for Galicia region) probably because primary productivity in their breeding areas, located mainly in the Thermo and Mesomediterranean sectors, decreases during this season, a movement pattern described for the common quail by Sardà-Palomera *et al.* (2012). Also, large areas of the Iberian Northern Plateau or the highlands of the Iberian System are subject to relatively harsh winters due to their high altitude and continentality, showing highly seasonal productivity patterns with minima both in winter and summer (Tellería *et al.*, 1988), and here little bustards usually perform both summer and winter movements. Therefore, little bustard movements seem to be adapted to exploiting seasonal peaks of resource abundance and avoiding resource depression (Alerstam *et al.*, 2003).

In addition to natural variation in productivity, human land-use may probably be playing a role in modulating the current migratory behaviour of Iberian little bustards. The ecological niche of the little bustard changes between the breeding and non-breeding seasons (Suárez-Seoane *et al.*, 2008) and migration is in a large degree an adaptation to exploiting different habitats for survival or reproduction, in a complementary

way across the annual cycle. The presence of highly summer-productive cultivation in or close to the breeding grounds, including irrigated crops such as alfalfa (e.g. García de la Morena *et al.*, 2006; Silva *et al.*, 2007; Ponjoan, 2012), may be attenuating the expected summer and winter migratory behaviour associated with productivity fall in a particular area.

The described variability in the migration behaviour of Iberian little bustards is consistent with what is known about movements in other Palearctic and closely related bustard species, namely the great bustard and the houbara bustard *Chlamydotis undulata*, for which partial migration has been described (Morales *et al.*, 2000; Alonso *et al.*, 2001; Palacín, 2007; Combreau *et al.*, 2011). In the case of the great bustard, movement patterns are very similar to those described here for the little bustard (Morales *et al.*, 2000; Alonso *et al.*, 2001; Palacín, 2007), which is unsurprising since these two species are sympatric over large extents of their distribution ranges (del Hoyo *et al.*, 1996) and are therefore subjected to similar environmental constraints (e.g. Delgado *et al.*, 2011).

From an evolutionary perspective, there is evidence that migratory behaviour can have a genetic basis in the little bustard. For example, little bustards hatched from eggs collected in the Spanish Southern Plateau (from sedentary or short-distance migrant populations, as shown in this study) and used to reinforce the migratory populations of central-western France did not migrate and overwintered on their French breeding grounds (Villers *et al.*, 2010). A recent study has revealed very low genetic diversity and differentiation among eight little bustard populations in Spain and France (García *et al.*, 2011). However, the observed migratory patterns of both Spanish and French little bustard populations, some of which share migration routes and wintering grounds in

central and southern Spain (Delgado *et al.*, 2010; Villers *et al.*, 2010), where a great proportion of the overall western Palearctic population concentrates (García de la Morena *et al.*, 2006), may explain the existence of some gene flow between populations (García *et al.*, 2011). Indeed, the existence of individually different migration phenotypes within a population, as also pointed by Villers *et al.*, (2010), seems to reflect significant genetic differentiation starting at the individual level, although other non-genetic factors, such as variation in environmental conditions, or the experience and body condition of individuals could play an important role (Pulido, 2007), as described also in the great bustard (Palacín *et al.*, 2011).

Finally, our results have significant conservation implications and highlight the importance of protecting both the summer and winter post-breeding areas that harbour little bustard populations for most of the annual cycle. The variation in the migratory behaviour of the Iberian populations described in this paper should be also taken into account in conservation programmes for the species, at least within the western Palearctic context. In this respect, our results and those of García *et al.* (2011) on genetic structure suggest that little bustard conservation measures should be framed in metapopulation theory and follow a coherent strategy to preserve genetic diversity and migration routes (Esler, 2000; Driscoll and Lindenmayer, 2011; Riou *et al.*, 2012).

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