Biased adult sex ratios in Western Europe populations of Little Bustard *Tetrax tetrax* as a potential warning signal of unbalanced mortalities

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Summary

Adult sex ratios (ASRs) have proved to correlate with population trends, which make them potential useful indicators of a species' population trajectory and conservation status. We analysed ASRs and proportion of juveniles in flocks of an endangered steppe bird, the Little Bustard *Tetrax tetrax*, using surveys made during the non-breeding period in seven areas within its Western European range (one in Portugal, four in Spain, and two in France). We found overall male-biased ASRs, as all the seven surveyed areas showed a male-biased ASR mean value. Five areas were below the threshold median value (female sex ratio = 0.4) considered to be consistent with an increased probability of extinction, according to earlier population viability analyses for the species. We also found a significant positive correlation between female ratio and the proportion of young individuals in the non-breeding flocks surveyed. Our results (strongly male-biased ASRs) support the hypothesis that the viability of Little Bustard populations in Western Europe is threatened by an excess of female mortality, something that should be quantified in the future, and emphasise the value of monitoring sex ratio as a population viability indicator in species where monitoring survival is difficult to achieve.

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Introduction

Biased adult sex ratios (ASRs) are a recognised problem for the conservation and management of vulnerable populations (Dale 2001, Clout *et al.* 2002). For example, in the case of birds, species listed by the IUCN as "Globally Threatened" or "Near-threatened" show significantly male-skewed ASRs when compared with non-threatened species (see Donald 2007 for a review). Extinction risk has been predicted to increase rapidly with extremely male-skewed ASRs, since female shortage may add further negative effects to low productivity (Morales *et al.* 2005a), as well as the likelihood of Allee effects (Engen *et al.* 2003).

Skewed ASRs may arise from a wide variety of factors, including sexual differences in adult survival rates related to cost of reproduction (Bennett and Owens 2002), cost of sexual displays (Székely *et al.* 2014), greater exposure of either sex to predation (Christe *et al.* 2006), and anthropogenic mortality (Grüebler *et al.* 2008). Additionally, they may arise from biased sex-ratio at birth (Komdeur 1996), sex-biased dispersal and immigration (Clarke *et al.* 1997), sexual differences in chick or juvenile mortality (Clutton-Brock 2007, Martín *et al.* 2007), or from

demographic stochasticity in small populations (Lande 1993). Regardless of the underlying mechanism, an overabundance of males in relation to available females can lead to low population growth rate and viability, due to the production of fewer offspring, higher competition between males (Dale 2001, Clout *et al.* 2002), or additional fitness costs on females due to aggressive behaviour such as mate harassment (Clutton-Brock 2007). Therefore, biased sex ratios can create feedbacks that reinforce the decline of female numbers thereby increasing the risk of population extinction (Le Galliard *et al.* 2005, Rankin *et al.* 2011).

Determining ASR variation, as well as the causes and implications, therefore provides important insights into population demography and conservation (e.g. Donald *et al.* 2007, Grayson *et al.* 2014). However, compared with other risks to small or declining populations, such as Allee effects (Courchamp *et al.* 1999) or inbreeding depression (Brook *et al.* 2002), research examining relationships between sex ratios and population viability is limited.

In this study, we assessed ASR in Little Bustard (*Tetrax tetrax* Linnaeus, 1758) post-breeding and wintering flocks in seven different study areas distributed across the species non-breeding range in Western Europe (from West France to South Portugal) (Figure 1) in order to infer potential demographic implications for breeding populations. This species is experiencing a dramatic decline in range and numbers in its main European population stronghold, the Iberian Peninsula. Therein it has decreased by 50% in the last 10 years (Silva 2010, Silva *et al.* 2014, García de la Morena et al. 2018), as well as in the migratory population of France, which has collapsed in the last 30 years; 95% between 1986 and 2000 (Bretagnolle *et al.* 2011, 2018). The Little Bustard is a lekking species (Schulz 1985, Jiguet and Wolff 2000); males provide no parental care, so breeding success and population growth are particularly limited by female rather than by male numbers (Partridge and Endler 1987). According to a previous population viability analysis conducted on Little Bustard (Morales *et al.* 2005a), the proportion of males relative to the total adult population should not exceed 50% to maintain population viability. Observations in an area of high Little Bustard density in Portugal in the 1980s (prior to current population decline) indicated that around two thirds of the population consisted of females and fledglings (Schulz 1985), suggesting a ratio of adult females well above 50% (estimated to be 1 male: 1.1–1.3 females). At the beginning of 2000s, a sex ratio of c.1:1 was also found in Portugal in a well-conserved high breeding density population (Silva *et al.* 2014). Here we aimed to test whether the ASR at a time of large-scale population decline was male biased. We also explored the relationship between ASR and the proportion of young individuals observed in non-breeding flocks (as an indirect indicator of Little Bustard population productivity). Finally, we discuss potential causes and consequences of sex ratio skewness in this species, highlighting the need for extensive monitoring of ASRs during the non-breeding season in this declining species.

Methods

Study species and study areas

The Little Bustard is a medium-sized Palearctic, polygynous steppe bird (Collar *et al.* 2017) with an "exploded-lek" mating system, in which only females (Jiguet and Wolff 2000, Morales *et al.* 2001) provide parental care. It occurs in natural steppes as well as in agricultural landscapes (Cramp and Simmons 1980). In Western Europe, the species inhabits mainly dry farmland with varying degrees of agricultural intensification, from very extensive landscapes, dominated by long-term fallows and pastures, to highly
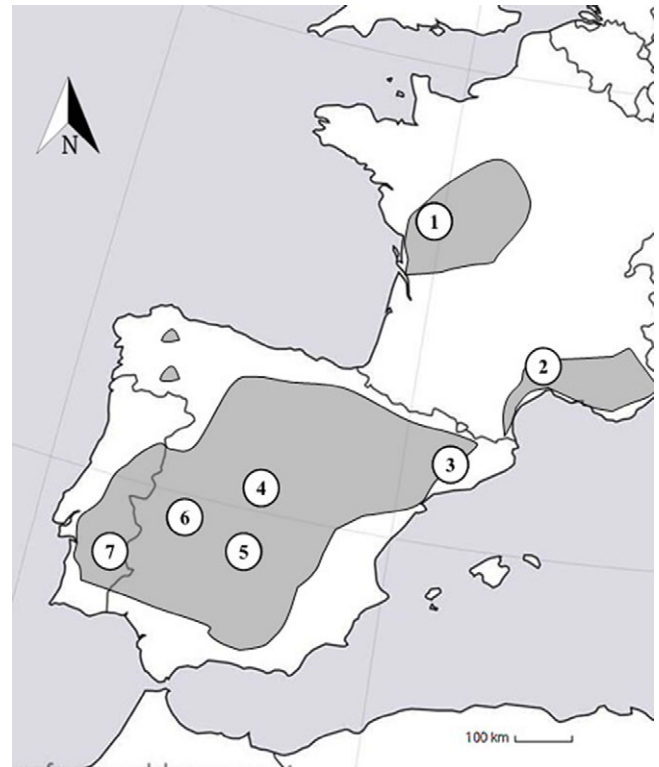

Figure 1. Map showing the distribution of the Little Bustard in continental Western Europe and locations of the study sites: (1) West France (Poitou–Charentes region); (2) South France (Costières Nîmoises region); (3) Catalonia (Northeast Spain); (4) Central Spain (Madrid–Toledo provinces); (5) La Mancha (Ciudad Real province); (6) Extremadura (Cáceres province), and (7) Portugal (Alentejo province).

intensive farmland, dominated by cereal and irrigated crops (Wolff *et al.* 2001, Morales *et al.* 2005b, 2006, Silva 2010, Traba *et al.* 2022). The species' range has greatly reduced over the last century, becoming extinct in at least 10 European countries (Morales and Bretagnolle 2022). Western European populations are nowadays restricted to France, Spain, Portugal, and Sardinia (Morales and Bretagnolle 2021). At present, the Little Bustard is considered "Near-Threatened" worldwide and "Vulnerable" in Europe (BirdLife International 2018), but it is red-listed as "Endangered" in France (IUCN France *et al.* 2016) and Spain (López-Jiménez et al. 2021), and as "Vulnerable" in Portugal (Cabral *et al.* 2005). The Little Bustard is a relatively long-lived species (see Mañosa et al. 2018, Bretagnolle *et al.* 2022). Females reach sexual maturity in their first year whereas males reach sexual maturity in their second year (Inchausti and Bretagnolle 2005). Breeding occurs from April to July; after breeding, Little Bustards gather in flocks formed by birds of both sexes and different ages that include individuals from nearby populations distant up to a few 10s of kilometres (García de la Morena *et al.* 2015, Morales *et al.* 2022), which stay together until migration (if those populations are migratory) or may join other flocks during winter (Morales *et al.* 2022). During the breeding season, Little Bustard males are easily detectable, unlike females, which are much more difficult to detect due to their cryptic plumage, elusive behaviour (Jiguet and Wolff 2000), and habitat selection (Morales *et al.* 2008b). Thus, calculating accurate and reliable ASR values for Little Bustard populations based on surveys during the breeding season is, in practice, impossible. In this species, ASR may be better assessed from counts of sexed individuals in post-breeding flocks where individuals of both sexes and all ages are together under similar detectability conditions (female behaviour in winter

does not make them less conspicuous). As stated, and contrary to other lekking species (see Catry *et al.* 2006 and references therein), sexual segregation during the non-breeding period does not occur in the Little Bustard, and no differential migration by sex has been observed (authors' unpublished data; see Morales *et al.* 2022 for a thorough review of the species' non-breeding behaviour and movements). Sexual size dimorphism is modest (males are only slightly larger than females: 800–1000 g, versus 700–900 g, respectively) (Cramp and Simmons 1980), but differences in plumage coloration are still present in winter (see description below, and Supplementary Material Appendix 1), which allows their differentiation under good visibility.

Our study was conducted during the 2013–2014 non-breeding period (September–March) in seven study areas historically known to harbour non-breeding flocks in France, Spain, and Portugal (Figure 1). Study areas in Spain included one in the Lleida plains in Northeast Spain (hereafter "Catalonia"; nine different sites); one between Madrid and Toledo provinces (hereafter "Central Spain"; four different sites); one in Ciudad Real province (hereafter "La Mancha"; two different sites), and one in Cáceres province (hereafter "Extremadura"; two different sites). One area was located in Southwest Portugal (Évora, Alentejo province, hereafter "Portugal") and included one site. Two study areas were located in France, one in Western France (Poitou–Charentes region, hereafter West France; 11 sites), and the other in Southern France (Costières Nîmoises, hereafter South France; one site).

In the Iberian Peninsula, the Little Bustard is mainly resident or partially migratory, exhibiting dispersive movements during the post-breeding period (i.e. between summer and winter) (Silva *et al.* 2017, García de la Morena *et al.* 2015). Catalonia and Central Spain gather up only individuals from their respective regions (García de la Morena *et al.* 2015). La Mancha, Extremadura, and Portugal do receive wintering migrants from areas in Northern Spain, but breeding numbers in those areas are comparatively small (García de la Morena et al. 2018) and their impact on winter ASR estimates in those study areas can be considered as negligible. In France, the Western population is mainly migratory (Villers *et al.* 2010), in sharp contrast to the sedentary population inhabiting the Mediterranean area (Wolff 2001). Again, given the small size of the French migratory population (c.115–300 males (Gendre *et al.* 2018), and the much larger size of Iberian populations (c.39,000 males in Spain and c.9,000 males in Portugal, García de la Morena et al. 2018, Silva et al. 2018), the overall effect of wintering French birds in ASR estimates from Iberian flocks can be considered negligible. On the other hand, the sedentary Mediterranean French population does not receive migrants from Central France (V. Bretagnolle unpublished data), so ASRs from wintering flocks there reflect the situation from South France breeding populations. We therefore assume ASRs in wintering flocks in our study areas to be representative of ASRs in breeding populations in their corresponding regions.

Non-breeding flock data

Data were collected between 1 September 2013 and 6 March 2014. All observations were made by specialists on the species with long experience in counting, sexing, and ageing Little Bustards in flocks. We used a visual counting and mapping method (Bibby *et al.* 2000) adapted for a large area to locate the flocks (García de la Morena *et al.* 2007). Surveys consisted of car routes using the existing rural track and road network; stops were made every 500–1,000 m, usually at high-visibility points, to scan visually the area looking for Little Bustard flocks. Each site was surveyed by a team of one to five observers provided with 8–10 × 40 binoculars and 20–40 × 80 telescopes (see Garcia de la Morena *et al.* 2007 for more survey details). Flocks were examined *ad libitum* (i.e. as much time as needed) under good visibility conditions until the individuals flew, or observation conditions became unsuitable for individual sex or age assignment. Only flocks detected the same day at least 100 m apart were considered an independent sample unit (Faria and Silva 2010). During that time, the highest possible number of individuals in the flock were examined and assigned to a sex and age category. When flock size was >100 individuals (five flocks in Catalonia, five flocks in La Mancha), it was not always possible to examine the whole flock. In this case, a random subsample of non-repeated birds of the flock was examined. Finally, one flock from Central Spain was examined on a digital video recording on a computer screen. Each individual examined within a flock was categorised according to its plumage characteristics (Jiguet and Wolff 2000) as follows: adult males (which have a characteristic thicker neck with a clear delimitation between the white belly and the brown neck, and sometimes traces of black and white on the neck or breast, typical of male breeding plumage); females (adults or one-year-old female birds, where the delimitation between the brown in the neck and the belly is gradual and less clear-cut); female-like individuals (individuals that did not have male plumage, but could be either females or young); young (individuals clearly identified as having fledged the previous breeding season, that displayed a series of bars on their greater and lesser wing covers, typical of young; young cannot be identified after November); undetermined (individuals that the observer was not able to safely assign to any category (Jiguet and Wolff 2000). (See Supplementary Material Appendix 1 for more details on identification and plumage traits).

Data treatment and analyses

A total of 86 flock observations from the seven study areas was obtained, from which we calculated three ASR estimates. A first estimate of ASR for each flock was calculated as the proportion of adult individuals that were identified as females (Minimum female ratio, MinFR = females / [males + females]). We also estimated a non-conservative proportion including individuals likely to be adult females in each flock as [females + female-like individuals] / [females + female-like individuals + males]. This estimate can be contemplated as a Maximum adult female ratio (MaxFR) because it considers all female-like individuals to be adult females (something unlikely, as some of those must be juvenile males). Neither of those two calculations include unidentified individuals, the proportion of which varied among areas (see Table 1) in relation to visibility (average distance at which flocks were assessed, topography, or vegetation) or time of counting (from December onwards discrimination between young birds and adult females is not possible). To address this problem, we also performed a bootstrap analysis. We used a binomial distribution (function 'rbinom', $P = 0.5$; 10,000 iterations) to randomly assign sex to the individuals within the "unknown" and "female-like" categories from each flock, on the basis that both sexes are evenly distributed (50% females, 50% males), and added those assigned-sex individuals to observed individuals of each sex. This bootstrap procedure provided a frequency distribution of estimated sex ratio for each area, with its mean and 95% confidence interval (CI), allowing us to assess whether these overlapped or not with 0.5 (equal adult sex ratio).

We also investigated the relationship between productivity and ASR estimates. For this purpose, we fitted a zero-inflated negative binomial model using the glmmTMB package (Brooks *et al.* 2017).

We used counts of young (with flock size as an offset), a proxy of overall population productivity (albeit a minimum estimate, as some young could be included in the "female-like" category), as response variable, and tested if it varied with adult sex ratio (F/M, i.e. number of adult females per adult male), included as a fixed effect in the model. We also added Julian date as fixed effect to account for phenological variations in juvenile survival or flocking behaviour during winter, and study area as a random intercept. This analysis was performed with data from four of the study populations (La Mancha, Central Spain, West France, and Portugal), as young individuals could not be clearly identified in the other three (Table 1).

We used R, version 3.5.1 (R Core Team 2018) for all analyses, and the residuals from the generalised linear model were tested for normality via qqplot function (package MASS) (Venables and Ripley 2002).

Results

Altogether, 4,774 birds belonging to 86 flocks were assessed, of which 3,756 were assigned to an age/sex category during our fall/winter surveys in the seven study areas (Table 1). Most of those birds were in Spanish regions; 3,689 birds, representing around 16.4% of the estimated Spanish wintering population (Garcia de la Morena *et al.* 2018). Overall, both estimates of ASR were indicative of a male bias in all study populations, with the exception of MaxFR for South France (Table 2). These biases were confirmed by our bootstrapping analyses that took into account unidentified birds

and still showed little overlap with a 0.5 sex ratio value in all populations (Figure 2).

Bootstrapped mean ASR values were below 0.5 for all study areas, and only in three of them was the 95% CI above 0.5: La Mancha, Portugal and Extremadura (the latter having a very large CI, from 0 to 1, but a very low mean (Table 2). Lowest values were found for West France and Central Spain, and highest values in Portugal and La Mancha (Table 2). MinFR and MaxFR estimates fell within the CIs of the bootstrapped values for four out of seven study areas, the exceptions being Catalonia, South France, and West France (Table 2).

There was a positive relationship between the proportion of young individuals (a proxy of productivity) and ASR in the flock, as well as a significant negative relationship with observation date: F/M ratio: -1.366 ± 3.095, $\chi^2_1 = 7.054$, $P = <0.01$, $\hat{\sigma} = 0.55$; Julian date: 0.079 ± 0.104, $\chi^2_1 = 6.741$, $P = <0.01$, $\hat{\sigma} = -0.73$) (Figure 3).

Discussion

Our results show that non-breeding flocks had male-skewed ASRs in all of the study areas and suggest that, on average, only 19–44% of adult birds from the studied populations were females. Our bootstrapped ASR estimations, as well as MaxFR, can be considered optimistic, which means that the real skew in populations could be even stronger. Previous population viability analyses had shown that female ratio values below 0.40 were associated with a population extinction probability over 0.8 at a 30-year horizon time (see Morales *et al.* 2005a) (Figure 3). Our results indicate that five out of

Table 1. Descriptive statistics showing sample sizes (N = number of surveyed flocks), number of identified individuals per sex and age, and number of undetermined individuals in each study population during the 2013–2014 winter surveys.

	Study area							
	Catalonia	Central Spain	Extremadura	La Mancha	Portugal	South France	West France	Total
N of flocks	10	5	3	5	5	39	19	86
Males	176	79	54	713	38	589	154	1803
Females	26	15	3	560	26	0	11	641
Female-like	87	2	11	49	0	992	68	1209
Young	2	0	13	74	3	0	11	103
Undetermined	240	0	20	122	20	614	2	1018

Table 2. Summary statistics showing mean ± SD minimum (MinFR) and maximum (MaxFR) estimates (non-bootstrapped data) and mean and 95% CI for bootstrapped estimates of adult female ratio for each study population during the 2013–2014 winter surveys.

| Study area	MinFR	MaxFR	Bootstrapped mean	CI 2.5%	CI 97.5%
Catalonia	0.133 ± 0.167	0.439 ± 0.090	0.357	0.290	0.421
Central Spain	0.232 ± 0.183	0.246 ± 0.162	0.171	0.071	0.274
Extremadura	0.333 ± 0.577	0.448 ± 0.508	0.233	0.000	1.000
La Mancha	0.362 ± 0.140	0.400 ± 0.102	0.437	0.306	0.512
Portugal	0.456 ± 0.207	0.456 ± 0.207	0.416	0.230	0.583
South France	0.0 ± 0.0	0.511 ± 0.300	0.364	0.320	0.406
West France	0.062 ± 0.129	0.304 ± 0.174	0.195	0.141	0.253
Total	0.107 ± 0.199	0.430 ± 0.257			
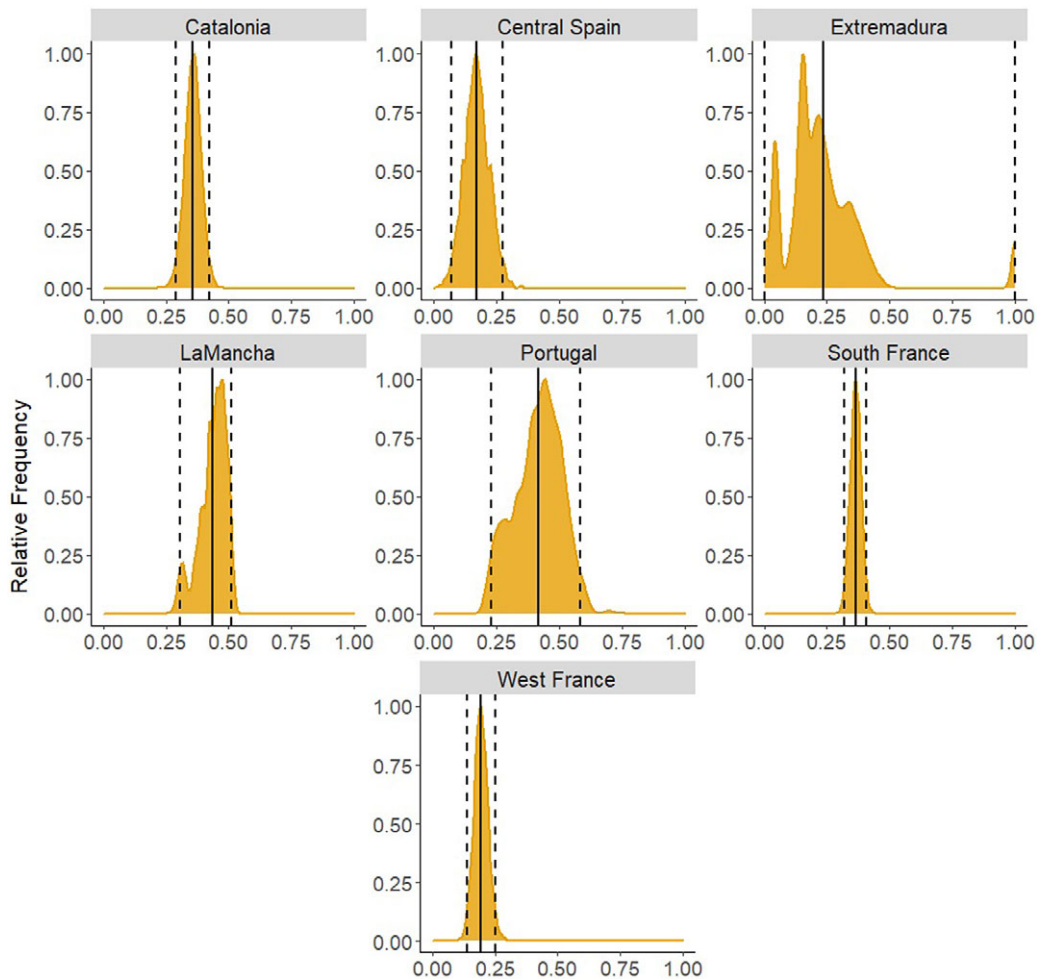
Figure 2. Frequency distribution of the bootstrapped estimate of female ratio distribution in each study area. The black continuous line indicates the mean value and the dashed lines indicate 95% CI.

the seven populations had a mean ASR value under that threshold. According to bootstrapped estimates, two of the study areas (Central Spain and West France) were extremely male biased and only La Mancha and Portugal had mean ASR values within a range that would allow population viability. Given our sampling protocols, the lack of sexual segregation in winter or of different migratory strategies by sex, we have no reasons to believe that our sample is not a random representation of all Little Bustards wintering in the Iberian Peninsula, suggesting that our ASR is representative for the whole Iberian population. Overall, therefore, the percentages of females described in this study are considerably low, and our results thus raise serious concerns about the viability of Little Bustard populations in Western Europe. Indeed, all study populations have moderately or strongly decreased in the last 10 years (García de la Morena et al. 2018, Bretagnolle *et al.* 2018, Morales and Bretagnolle 2021), except for South France (see Devoucoux *et al.* 2018). The West France migratory population has in fact undergone one of the steepest declines documented for any bird species in Europe, with 94% loss of displaying males in 30 years (Inchausti and Bretagnolle 2005).

We observed a positive relationship between frequency of young individuals in the flocks and F/M ratio. Even if some young could have been included in the "female-like" category, the same applies for adult females, so this productivity index is a minimum estimate and does not necessarily invalidate the positive relationship observed, which is consistent with the idea of reduced population viability in populations with male-skewed ASRs. Population growth would therefore increase with every additional offspring that is a female instead of a male (Wedekind 2002), an especially important aspect for threatened species with male-skewed ASRs. We observed a negative relationship between sampling date and the frequency of young counts in flocks, which may reflect juvenile mortality or may be explained by an increasing difficulty in discerning young from adult individuals as the winter moult period advances (Cramp and Simmons 1980) (see Supplementary Material Appendix 1 photo-guide). Nevertheless, the small number of young individuals recorded in non-breeding flocks is consistent with the low productivity (i.e. number of fledglings per female) reported in some of our study areas (Lapiedra *et al.* 2011, Morales *et al.* 2008a, Tarjuelo *et al.* 2013, Bretagnolle *et al.* 2018, Cuscó *et al.* 2020, Faria and Morales 2018).

In lekking species such as Little Bustard (Jiguet and Wolff 2000), there is no male parental care. The number of breeding events is mostly constrained by the minimum number of breeding females present each year in each population (Inchausti and Bretagnolle 2005). Therefore, population viability is highly sensitive to female shortages, but only to extreme male deficit (Partridge and Endler 1987). Operational sex ratio is a far more critical demographic
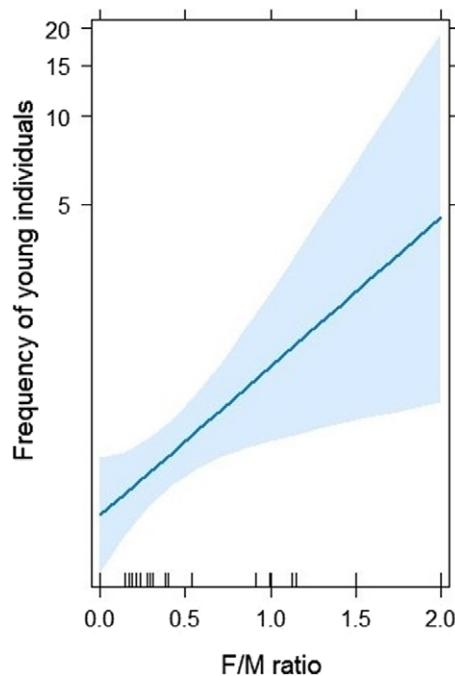
Figure 3. Model-effect plot showing the association between mean (solid line) and 95% CI (shaded area) frequency of young individuals (number of young observed in relation to size of flock) and adult female ratio (F/M) in Little Bustard non-breeding flocks (data from four of the study populations: Central Spain, La Mancha, Western France, and Portugal).

parameter than ASR (Bessa-Gomes *et al.* 2004), but is ultimately very difficult to measure in the Little Bustard. Therefore, a relationship between ASR and a key demographic parameter such as offspring production suggests that ASR in wintering flocks might be used as a proxy of population dynamics in this secretive and difficult-to-study vulnerable species. As specified above, some wintering populations consist of a mix of birds from various breeding populations originating from quite different sites, while others (such as South France) are resident. Therefore, the dynamics of resident, partially or fully migratory populations may not be equally reflected in ASR values assessed in winter flocks. Nevertheless, our results support the idea that ASRs in wintering flocks provide important information about the current status of Little Bustard populations at a regional scale and are relevant in order to foresee population viability of this threatened species. Further, overall they highlight the importance and value of monitoring a declining species like the Little Bustard outside the breeding season as an alternative strategy to obtain relevant demographic parameters difficult to estimate during the breeding period. The measurement of ASR in non-breeding flocks is particularly important in terms of population monitoring programmes, considering that Little Bustard females are very difficult to detect during the breeding season, when censuses and monitoring programmes are necessarily limited to counting displaying males. In this context, and to increase reliability of obtained estimates, it would be advisable to minimise the number of unassigned individuals in non-breeding flocks between areas. Therefore, the surveys should be performed during a time window that is adjusted to the regional phenology, usually September and October for our study sites, when vegetation is usually low (improving visibility) and juveniles are still easy to distinguish from females. Moreover, a minimum effort in terms

of number of flocks assessed would be required to obtain reliable sex ratio estimates at the regional scale, as there is considerable variation with the proportion of females among flocks. All these considerations will reduce potential biases and improve overall ASR and population productivity estimates.

Several factors may explain biased ASRs. On the one hand, Little Bustard females could be suffering higher mortality rates than males, at least in some populations (Bretagnolle *et al.* 2018). Moreover, as only females incubate the eggs, predation during incubation could result in a higher risk of female mortality. This has been shown for the Northern Wheatear (*Oenanthe oenanthe* L.), a ground-nesting species in which a large proportion (>20%) of adult females was estimated to be predated at the nest (Low *et al.* 2010). Male-biased sex ratios in adults have also been found in other farmland bird species, such as Winchat *Saxicola rubetra* (Grüebler *et al.* 2008). The reasons are unclear, but biased primary or secondary sex ratios might be linked to farming practices, including the use of pesticides (Bouvier *et al.* 2016). Additionally, in our study species, low productivity has been documented to be associated with a loss of suitable habitats (Morales *et al.* 2013, Bretagnolle *et al.* 2018, Lapiedra *et al.* 2011, Cuscó *et al.* 2020). Habitat loss and/or degradation has been linked to agricultural intensification (Silva *et al.* 2017, García de la Morena et al. 2018, Bretagnolle *et al.* 2018, Traba and Morales, 2019), including increasing application of agro-chemicals, which reduce food availability for declining steppe birds (Jiguet 2002, Cabodevilla *et al.* 2021). Agricultural abandonment and urbanisation have also probably contributed to the species' decline (Suárez 2004, Oñate 2005, Arroyo *et al.* 2022). More locally, anthropogenic mortality through collision with power lines and poaching could also be relevant decline factors (Marcelino *et al.* 2018). Other mechanisms such as genetic inbreeding (Briton *et al.* 1994, Eldridge *et al.* 1999), confinement to small and isolated populations (Dale 2001), or increased breeding costs for females in harsher conditions due to food depletion (e.g. Woolfenden 2001) may have skewed the Little Bustard ASRs in many populations. For example, in the study population of Catalonia, breeding females showed a high frequency of nesting failure due to agricultural works, predation, and desertion, which results in high frequency of replacement clutches (second and third) and probably deteriorates female physiological condition and thus survival, particularly in food-depleted habitats (Cuscó *et al.* 2020). All these factors could lead to the observed ASR skew. Without a swift and efficient management of factors reducing mortality of females and young, these populations will probably become functionally extinct in the very near future (Morales *et al.* 2005a, Bretagnolle and Inchausti 2005, Traba *et al.* unpublished report), as found in other species (Ewen *et al.* 2001, Grayson *et al.* 2014, Dutta *et al.* 2011).

Conclusions

The ASR values observed in a representative sample of the Western Europe wintering populations of the Little Bustard are male biased, and female shortage is probably strong enough to represent an important risk for the species' population functionality. The positive association between female ratio and the proportion of young individuals in the flocks surveyed suggests that future trends of Little Bustard populations could remain negative, with further increases in the skewness of ASRs. In addition, we observed similar patterns in distant populations throughout its Western distribution range, suggesting that environmental factors affecting Little

Bustard ASRs might be common and widespread. On general grounds, we conclude that extensive assessment of species' ASRs may prove useful to identify potential demographic problems: in the case of the Little Bustard, an improved demographic monitoring is needed to better understand the causes and consequences of the skew and to promote more efficient conservation measures.

Supplementary Materials. To view supplementary material for this article, please visit http://doi.org/10.1017/S0959270922000430.

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