Bird Conservation International (2021) 1–23. © The Author(s), 2021. Published by Cambridge University Press on behalf of BirdLife International
doi:10.1017/S0959270921000423

An update on the conservation status of the Little Bustard *Tetrax tetrax*: global and local population estimates, trends, and threats

MANUEL B. MORALES[1]* and VINCENT BRETAGNOLLE[2]

[1]*Terrestrial Ecology Group. Departamento de Ecología and Centro de Investigación en Biodiversidad y Cambio Global (CIBC). Universidad Autónoma de Madrid. c/ Darwin, 2. 28049. Madrid, Spain.*
[2]*CEBC-CNRS, UMR 7372, CNRS and La Rochelle Université, 79360 Beauvoir sur Niort, France.*

**Author for correspondence; e-mail: manuel.morales@uam.es*

(Received 18 March 2020; revision accepted 23 August 2021)

Summary

The Little Bustard *Tetrax tetrax* is an iconic species and an indicator of healthy grassland and farmland ecosystems. It formerly ranged almost continuously from north-western Africa and Iberia to central Asia, encompassing France, Italy, southern Russia, and the Middle East, occupying natural grass steppes, pastured grasslands, and extensive cereal farmland. Today, two main distribution sub-ranges persist: a western one comprising the Iberian Peninsula, France, and Sardinia, and an eastern one encompassing mainly southern Russia and Kazakhstan but reaching north-western China and isolated spots in Turkey. We describe the changes that occurred across the species' range and were documented during the last and current centuries and revise the status and trends of Little Bustard populations throughout that range. We provide the first global estimate of the world population, as well as those of the two sub-ranges, discussing the main threats and global conservation implications of these estimates. Historically abundant in Europe and northern Africa, the Little Bustard has strongly declined over the second half of the 20th century, becoming extinct in at least 15 countries. Such spectacular regression is mainly associated with land-use change and agricultural intensification. Other threats are legal hunting, poaching, and collision with power-lines. In the last two decades, the species has severely declined (c.6% yearly rate) in its traditional population stronghold, the Iberian Peninsula. Conversely, there is evidence of recent population growth in some areas of the Eastern range, but increases are unquantified and require further study. Many populations are probably small and scattered, with no reliable information on size and trends. Nevertheless, the Eastern range may now be considered the species' stronghold with more than half the world's population. The diverging dynamics and ecological differences between the two sub-ranges require a global conservation strategy that treats each as a different conservation unit to assure the species' recovery.

Keywords: conservation units, designatable units, disjoint distribution, Eastern Palearctic, grassland birds, steppe birds, Western Palearctic

Introduction

Steppe and farmland birds are currently experiencing significant declines throughout the world, mainly due to land-use change and agriculture intensification (Onrubia and Andrés 2005, Donald *et al.* 2006, Vorisek *et al.* 2010). Farmland birds are considered a group of high conservation concern (BirdLife International 2018), since agricultural habitats host a large proportion of birds with a threatened conservation status in Europe (BirdLife International 2004, Burfield 2005) and farmland birds have declined the most rapidly (Inger *et al.* 2015, Rosenberg *et al.* 2019). Birds relying on extensive agriculture are indeed threatened worldwide: bustards (Otididae) are a prime example, as a family of birds living in open, farmed, or grazed landscapes in Asia, Africa, Europe, and Australia. Bustards are well adapted to open lands, but the ecological traits that lend to this adaptation also make them highly susceptible to land-use changes (Collar 1996, Collar *et al.* 2017). Indeed, eight of the 26 recognized species (31%) are threatened, while seven (27%) more are 'Near Threatened', which is about three times higher than other bird rates (Collar *et al.* 2017, BirdLife International 2018). There are very few recent complete accounts of the global population status (size or trends) or distribution range changes for a bustard species (see, for example, Palacín and Alonso 2008 and Alonso and Palacín 2010 for the Great Bustard *Otis tarda*).

The Little Bustard *Tetrax tetrax* is a Palearctic bustard inhabiting natural grasslands and agricultural landscapes. It is an iconic species of Palearctic farmland and grassland ecosystems and is considered a good indicator of healthy grassland and farmland bird communities (Bretagnolle *et al.* 2018, Traba and Morales 2019). It disappeared from large areas of its original distribution during the 20th century (Cramp and Simmons 1980, Schulz 1985, Collar 1996), and has steeply declined in many others (Jolivet and Bretagnolle 2002, García de la Morena *et al.* 2018). The species' world distribution extends from Portugal to north-western China (BirdLife International 2020). Although Little Bustards' preferred habitats, i.e. steppes, grasslands, and cereal farmland, are widespread throughout this range, two markedly disjoint sub-ranges formed c.40 years ago: a western breeding range, whose core is located in the Iberian Peninsula, and the eastern breeding range, which harbours the populations of south Russia, Ukraine, Kazakhstan, Kyrgyzstan, north-west China, northern Iran, and Turkey. These two subpopulations are now separated by a gap of c.2,900 km, and indeed these two nuclei were assigned to different subspecies (*T. t. tetrax* and *T. t. orientalis*, respectively), although the species is now considered monotypic (Collar 1996). In both nuclei, migratory as well as resident populations occur, the latter encompassing breeding populations in the wintering areas used by its corresponding migratory populations (Cramp and Simmons 1980, Villers *et al.* 2010, Gauger 2007, Sehhatisabet *et al.* 2012).

Using available information, our aim here is to provide a thorough and up-to-date description of the changes that occurred across the species' distribution range during the previous and current centuries and review the population status and trends throughout that range. We provide the most accurate global estimate of the world population currently available, as well as estimates of the two nuclei, assessing the main threats affecting the species in different parts of its range. Finally, we discuss the implications of these estimates and trends in relation to the species' world conservation status. The Little Bustard has been classified as 'Vulnerable' in Europe in 1994, 2004 and 2015 (BirdLife International 2015), but may be upgraded in future reassessments. It is listed in Annex I of the EU's Birds Directive as well as in Annex II of the Bern Convention, and it has recently been included in Annexes I and II of the Bonn Convention on Migratory Species (https://www.cms.int/en/species/appendix-i-ii-cms). Its current global conservation status on the IUCN Red List is 'Near Threatened' (BirdLife International 2020). The Little Bustard is a challenging case study, in which two isolated and ecologically distinct populations of roughly equivalent size show opposite trends. Based on our review results, we draw attention on the fact that a common overall conservation status for these two nuclei may not be an efficient global conservation strategy, and thus advocate for their treatment as separate conservation units.

Methods

We systematically reviewed all recent published results of Little Bustard censuses, surveys, trends, and distribution assessments throughout the species' entire range. We focused mainly on the breeding season, although information on winter numbers and distribution was also used to complete our assessments. We used a variety of data sources, including papers published in scientific journals and books (including field guides), as well technical reports, bird atlases and other documents supported by local or international conservation authorities and/or organizations (e.g. BirdLife International, EBCC, local BirdLife partners, and public administrations). Our search was not limited to per-country figures, and we also compiled data from different regions within countries when available. The different types of data and data sources used are summarized in Table 1. We assessed the quality of estimates under three categories: "High quality" estimates are based on standardized and repeatable survey methods; "Medium quality" estimates are based on repeatable survey methods available only for a part of the territory considered, and expert guesses for the remaining part; while "Low quality" estimates are based only on expert guesses. In addition, when available in the literature, we compiled error measures as either ranges or 95% confidence intervals. In some cases. we estimated the range of population estimates from values obtained from different literature sources. To avoid overestimation of accuracy, medium and low-quality estimates were rounded to the thousands and given as approximate (see Table 3).

Population estimates for the western range are based on breeding surveys, and thus provided as number of males, while those from the eastern range are mainly based on post-breeding surveys and given as total number of individuals. In order to derive an estimate of total individuals from males in western countries, we used a sex ratio value provided in a recent study of adult sex ratio in Little Bustard populations across most of Western Europe (France, Spain, and Portugal). This value, the median proportion of adult females plus female-like individuals in the populations studied across those countries, was estimated at 0.47 (Serrano-Davies *et al*. in review). The world estimate was calculated as the sum of total individuals in the western range and the winter estimate of total individuals in the eastern range. Percentages in relation to the total world population were obtained for countries and regions with high quality estimates. Finally, a qualitative trend assessment was made for each country/region based on the sources reviewed.

Results

Historical (pre-1980) changes in distribution range, population status and trends

Until the early 20th century, the Little Bustard was probably distributed throughout a Palearctic longitudinal belt between 30°N and 50°N, breeding in most countries of southern and central Europe, northern Africa, the Middle East, and central Asia (Cramp and Simmons 1980). In the Western Palearctic, until 1940, the species still bred in large areas of the Iberian Peninsula, France, the Pannonian region and the Danube valley, Ukraine, and southern Russia. It was also present, though more patchily, in north-eastern Germany, Italy (on both the continent and the two large islands of Sicily and Sardinia) and northern Greece, as well in north-western Morocco, northern Algeria, Tunisia, western Anatolia, Syria, and the Caucasus (Schulz 1985). However, by mid-century, the Little Bustard breeding range had dramatically shrunk. Apart from the Iberian and Russian strongholds, the Little Bustard had disappeared from most of its former European range (see Table 2 for extinction dates across a range of countries). By 1980, two relict nuclei remained in Hungary and Crimea, but the small breeding range of northern Greece had already disappeared, and the French population was scattered over the central-western plains and the Mediterranean arch (Schulz 1985), while Italian birds were restricted to a relict population with a few tens of individuals in Apulia (south-eastern Italy), and a larger one in Sardinia (Schulz 1985, Petretti 2006). This was basically the European distribution reported in the first European Atlas of Breeding Birds, which compiled data from the early 1970s to the mid-1990s (Hagemeyer and Blair 1997).

Table 1. Different types of data used in this revision. The general method used to produce the data and the type of source providing them are also presented.

Type of data	Method	Type of Source
Breeding male numbers	Direct counts	Scientific journals
		National/regional census reports
	Extrapolated census results	Scientific journals
		National/regional census reports
	Miscellaneous	NGO compilations (e.g BirdLife International)
Breeding male densities	Direct counts	Scientific journals
		National/regional census reports
Total individuals	Direct winter counts	Scientific journals
	Expert assessment	Scientific Journals
		NGO compilations (e.g BirdLife International)
Historical records and trends	Miscellaneous	Ornithological books
		Scientific Journals
		NGO compilations (e.g BirdLife International)
UTM squares or other distribution units	National/regional censuses and atlases	National/regional census reports
		National/regional atlas reports
		Ornithological books
Distribution maps	Miscellaneous	Ornithological books
		NGO compilations (e.g BirdLife International)

Table 2. Estimated year or decade of extinction of the Little Bustard as a breeder over the 20th and early 21st centuries in different countries and regions of the western Palearctic. Based on Schulz (1985), Snow and Perrins (1998), and G. Palumbo (pers. comm.), Cherkaoui *et al*. (2020) and Patrikeev (2004) for continental Italy, Morocco, and Azerbaijan, respectively.

Country	Year
Germany	1907
Poland	1909
Austria	1921
Former Czechoslovakia	1945
Hungary	1970s
Moldova	1930
Sicily	1950s
Continental Italy	2000s
Greece	1950s
Serbia	1948
Romania	Before 1900
Bulgaria	1950
Tunisia	1930
Algeria	Before 1990
Morocco	2010s
Azerbaijan	1940s

Table 3. Synthesis of national and regional Little Bustard populations for the Western and Eastern distribution ranges. Western range: the total number of individuals is derived from the number of males using the regional sex ratio estimated in Serrano-Davies *et al.* (in review; see Methods). Eastern range: only the total number of individuals is available in the literature. Error measures are provided when available in literature, either as range, or as 95% confidence intervals (CI). The quality of estimates is assessed as follows: High= based on standardized and repeatable survey methods; medium= repeatable method-based surveys available only for a part of the territory and based on expert guesses for the remaining; low= based only on expert guesses. To avoid optimistic bias in accuracy, medium and low-quality estimates are rounded to the thousands and given as approximate (*circa*, c.). The world estimate is the sum of the Western range (extrapolated to individuals) and the winter Eastern range figures (rounded to the hundreds), while percentages in relation to the total world population are given only for high quality estimates. A qualitative trend assessment is provided for each country/region.

Country/region		Present estimate		Source	Estimate reliability	Percentage of world total (range)	Trend assessment
		Males	Individuals				
Western Range	Spain	38,856 (range = 27,037-59,136)	57,118 (range = 39,744-86,930)	García de la Morena *et al.* (2018)	High	22 (13-39)	Crash (48% in 11 years)
	Portugal	8,900 (CI = 5,008-12,836)	13,083 (CI = 7,362-18,869)	Silva *et al.* (2018)	High	5 (2-8)	Crash (49% in 13 years)
	France	2,455 (range = 2,429-2,478)	3609 (range = 3,571-3,643)	Gendre *et al.* (2018)	High	1.4 (1.1-1.6)	Negative in last 16 years (stable in last 8 years)
	Italy (Sardinia)	352	517	Nissardi and Zucca (2011)	High	0.2	Negative
	Western Europe	**50,563 (range = 34,474-74,450)**	**74,328 (range = 51,194-109,959)**		**High**	**28 (16-49)**	**Negative**
	North Africa	0	0	Palacín and Alonso (2009)	High	0	Extinct?
	Total	**50,563 (range = 34,474-74,450)**	**74,328 (range = 51,194-109,959)**		**High**	**28 (16-49)**	**Negative**
Eastern Range	Russia		c.17,000–121,000	Fedosov *et al.* (2016), Kornev and Gavlyuk (2017), Oparin (2018)	Low		Positive, but likely to reverse due to land-use changes
	Ukraine		c.100	Andryushenko and Stadnichenko (1999) BirdLife Int. (2020)	Low		Unknown

Table 3. (Continued)

Country/region	Present estimate		Source	Estimate reliability	Percentage of world total (range)	Trend assessment
	Males	Individuals				
Kazakhstan and Kyrgyzstan		c.20,000	Collar *et al.* (2017), BirdLife Int. (2020)	Low		Positive, but likely to reverse due to land-use changes
China		<1,000	Gao *et al.* (2008) Collar *et al.* (2017)	Low		Unknown
Other Asian countries		c.100	BirdLife Int. (2020)	Low		Unknown
Total (breeding)		**c.38,000–142,200**		**Low**		**Positive, but likely to reverse due to land-use changes**
Total (wintering)		**189,347 (171,693-207,000)**	**Gauger (2007) Heiss (2013) Yousefi *et al.* (2017)**	**High**	**72 (54-93)**	**Positive, but likely to reverse due to land-use changes**
World		**c.263,700 (c.222,900-317,000)**				

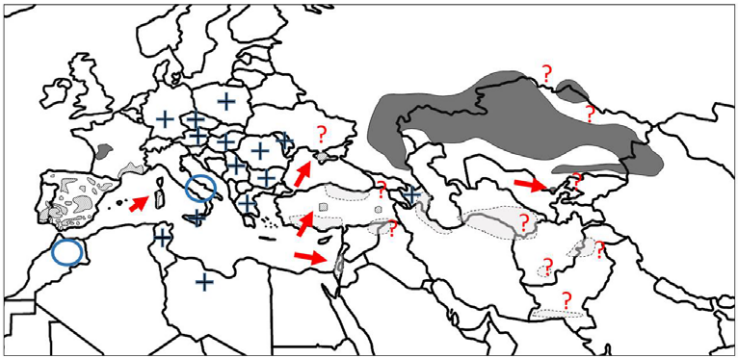

Figure 1. Updated world distribution of the Little Bustard. Pointed patches represent areas where the species is mainly resident or partial migrant and grey ones correspond to areas where it is basically a breeding visitor. Light grey patches with dashed limits indicate wintering areas. Based on Birdlife International (2020) and updated with results from different sources used in this revision. Spain: Spanish national census (García de la Morena *et al*. 2018); Portugal: Silva and Pinto (2006) and 2nd European Atlas of Breeding Birds (Keller *et al*. 2020); France: French national count (Gendre *et al*. 2018) and 2nd European Atlas of Breeding Birds (Keller *et al*. 2020); Sardinia: 2nd European Atlas of Breeding Birds (Keller *et al*. 2020); eastern Europe: 2nd European Atlas of Breeding Birds (Keller *et al*. 2020); Turkey: 2nd European Atlas of Breeding Birds (Keller *et al*. 2020) and Kirwan *et al*. (2008); Kazakhstan: Wassink and Orel (2007), Ayé *et al*. (2014) and Wassink (2016). Circles: recent extinctions reported in this revision; crosses: documented historical extinctions; question marks: doubtful reports. Arrows highlight small relict populations, either breeding or wintering.

Likewise, by 1980 only three relict African populations remained in northern Morocco (Palacín and Alonso 2009), while the presence of the species in Syria and Turkey was already in doubt (Schulz 1985). Thus, in less than 100 years, the geographical range of the Little Bustard experienced dramatic fragmentation and contraction, which led to the markedly disjunct distribution formed by the current eastern and western breeding sub-ranges. In the process of range fragmentation, the species has gone extinct in at least nine countries or regions of the western Palearctic (Table 2). Figure 1 summarizes the 2020 distribution range of the Little Bustard. Above we review trends since 1980 in those countries or regions where data were sufficient to assess population size and trends. Population size estimates are compiled in Table 3, which also presents an estimate of the world population size.

Western range

At present, Little Bustard populations are found in Spain, Portugal, France, and Italy. The former populations of northern Africa can be considered on the very brink of extinction (see below).

Spain: Schulz (1985) tentatively estimated the Spanish Little Bustard population at 50,000–70,000 individuals and considered the species widespread in the country's main agricultural plains, i.e. the Northern and Southern Plateaus, Extremadura, the Ebro and Guadalquivir valleys. Based on censuses carried out in 1993–1994 in known Little Bustard sites, De Juana and Martínez (1996) provided a much higher estimate of 100,000–200,000 males and extended the species' range to the south and east, which was confirmed by the Spanish Atlas of Breeding Birds (García de la Morena *et al*. 2003). Although no trend estimate was available at the time, De Juana and Martínez (1996) detected a pattern of population fragmentation as well as isolation in peripheral areas traditionally

regarded as important for the species (e.g. Northern Plateau, Andalucía, and the Ebro Valley). García de la Morena *et al.* (2004) reviewed regional population sizes and trends available for the 1990s and early 2000s, confirming fragmentation and negative trends in most Spanish populations, both central and peripheral. For example, in the traditional stronghold of Extremadura, the species declined by 40% in nine years, while in the peripheral populations of Navarra and Catalonia the decrease was 27% in four years and 25–54% in six years, respectively. However, no reliable trend was available for the entire country, partly due to the lack of data from the Southern Plateau, which harboured the bulk of the Spanish population. In 2005, a first Spanish national breeding survey was carried out, resulting in a new but still broad estimate of 43,000–71,700 individuals (García de la Morena *et al.* 2006). Although this figure cannot be directly compared to that provided by De Juana and Martínez (1996) due to methodological differences, its much lower values clearly suggested an overall decline in the species in Spain between the mid-1990s and the mid-2000s, consistent with the regional decreases reported in that period (García de la Morena *et al.* 2006). This national census confirmed the fragmentation and isolation of populations in peripheral areas and suggested an increasing rarity in traditional core regions (García de la Morena *et al.* 2006).

Since 2005, evidence for decline has been confirmed in male counts: 65% decline in key Little Bustard areas of Extremadura over 1993–2008 (De Juana 2009, Figure 3a), an average 61% decline (range 30–100%) in eight populations of the Madrid region over 2000–2007 (Morales *et al.* 2007), 56% and 55% declines in male and female densities respectively in a SPA of the Southern Plateau over 2002–2014 (Casas *et al.* 2019, Figure 3), and 50% and 75% declines in the number of males and females respectively over the same period in Catalonia (Mañosa *et al.* 2015). In addition, the analysis of the data from the Spanish Common Breeding Bird Monitoring Program (SACRE)

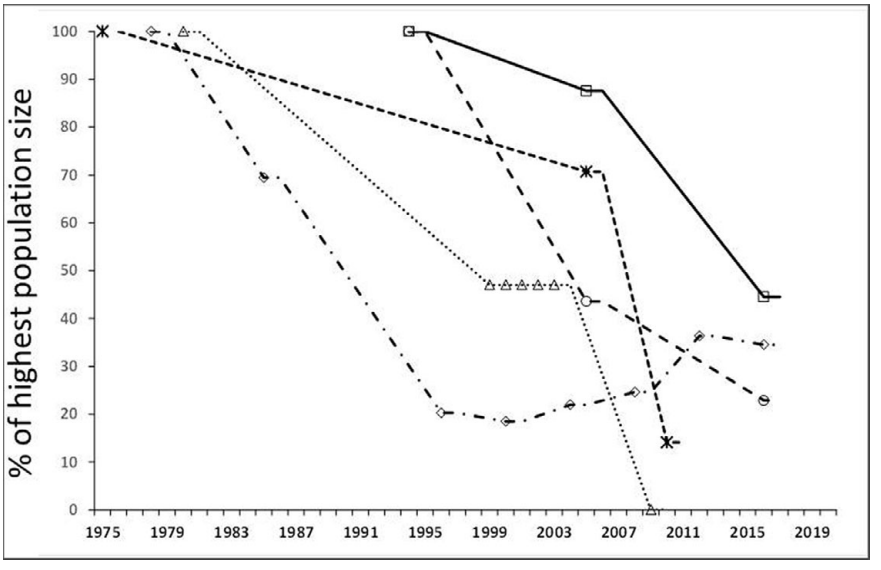

Figure 2. Trends of Little Bustard populations in different countries of the Western Palearctic. Data are presented as a percentage of highest population size (symbols) to allow easy comparison between countries. Although for some countries (Spain, Portugal) the comparison between early and recent estimates must be made with caution (see text), the trajectories (shown as mobile-mean trend lines) illustrate the different times in which significant population declines occurred. Solid line and open squares: Portugal; long-dashed line and open circle: Spain; short-dashed line and asterisks: Italy; dotted line and open triangles: Morocco; dashed-and-dotted line and open diamonds: France.

yielded an overall population trend of -76.19%, and a mean yearly population trend of -5.4 (CI: -6.3 to -4.5) over 1998–2018 (SEO/BirdLife 2018), indicating an alarming population decrease. Winter surveys fully confirm these trends: Morales *et al.* (2015) reported an overall reduction of 76% of total numbers wintering in some key areas of central Spain between the winters of 2003–2004 and 2013–2014. Finally, a second national breeding survey carried out in 2016 using the same methodology as the first, yielded a new estimate of 38,856 breeding males (range 27,037–59,136), which would imply a total population of 51,808 individuals (see Garcia de la Morena *et al.* 2018 for calculations based on sex-ratio estimates). Eighty-seven percent of the population was concentrated in the southern half of the country, with the Southern Plateau harbouring c.65% of the total. The population of the northern half is considerably smaller, with most of the birds concentrated in the Ebro valley and some areas in the Northern Plateau. The estimated reduction of the total number of breeding males in Spain is 48% in just 11 years (Table 3), which corresponds to an average yearly decrease of 5.7%. On average, male densities (number of birds/km² per 10 x 10 UTM cell) decreased by 38% (range 25–67%). National winter surveys carried out in the same years (2005–2006 and 2016–2017), though yielding much smaller total estimates since counts are incomplete, suggest exactly the same trend: from 16,429–35,929 to 6,668–29,848 individuals, i.e. a 38-50% decline despite substantial methodological differences (García de la Morena *et al.* 2006, 2018). The Spanish population of Little Bustard, although probably still the largest population worldwide, is currently crashing at a 5-6% annual decline rate.

Portugal: Portugal holds the second largest Little Bustard population in the species' western range, largely connected with the Spanish population of Extremadura (Silva 2010). The first published population size estimates were 10,000–20,000 individuals (Goriup 1994). A national census conducted in spring 2005 yielded 17,515 males, i.e. c.35,030 individuals under a 1:1 adult sex ratio (Silva and Pinto 2006), a figure to be treated with caution given the biased sex ratios detected in other Iberian populations (Silva 2010, García de la Morena *et al.* 2018). Between 90% and 95% of this population occurs in the Alentejo region, south of the Tagus River. The result of this first Portuguese national census cannot be directly compared with previous estimates due to methodological differences, and thus population trends could not be well assessed (Silva 2010). A second national census conducted in 2016 yielded an estimate of 8,900 breeding males (95% CI: 5,008–12,836), i.e. a 49% reduction between 2003 and 2016 (Silva *et al.* 2018). The Portuguese population of Little Bustard is therefore currently declining at the same overall rate as the Spanish one. Figure 3 illustrates this trend in two localities of Alentejo.

France: The Little Bustard trends in France have been most continuously monitored, with censuses carried out in 1980, 1995, 2000, 2004, 2008, 2012 and 2016, and distribution updates published in the French Bird Atlas in 1976, 1994 and 2015. Published records even date back to the late 19th century (Ternier 1892): the species was common, although irregularly distributed and fluctuating until the 1930s–1950s (Yeatman 1976). At that time, the Little Bustard was still distributed over all the main agricultural plains, including Poitou-Charentes, Beauce and Champagne (respectively, western, and northern regions of the country), the pastures of Limagne and les Causses (close to the Massif Central), and the lower valleys of Rhône and Durance, in the Mediterranean arch ranging from Narbonne to Camargue (Yeatman 1976, Issa and Muller 2015). A national census carried out in spring 1978–1979 provided the first quantitative estimate of the Little Bustard population in France: 7,200 males (André 1985), with a clear split in the distribution between the two main nuclei, whose populations differed in ecology and migration behaviour. The migratory population (6,800 males) inhabited intensive cereal farmland from central-western to eastern France (hereafter, the 'western population'), while the southern sedentary one (400 males) was located from the Languedoc to the Provence regions and occupied dry Mediterranean grasslands (hereafter, the 'Mediterranean population'). In 1985, the national population was estimated at 5,000 males (with 400 in the Mediterranean population: Jolivet and Bretagnolle 2002), but only at 1,460 males in 1995–1996 (Jolivet and Bretagnolle 2002, revised in Gendre *et al.* 2018), of which 648 belonged to the western

and 812 to the Mediterranean population. A third national census performed in 1999–2000 yielded a total of 1,300 males (460 in western and 840 in Mediterranean populations: Jolivet and Bretagnolle 2002). In summary, the Little Bustard population of western France had experienced a 94% decline in 22 years, while at the national scale the decrease was 82%, the steepest ever documented for a bird species in France (Jolivet and Bretagnolle 2002). Conversely, the Mediterranean population remained stable over that period and even slightly increased. After 2000, the western population seems to have stabilized at around 300–340 males (thanks to a combination of conservation measures, including agri-environmental contracts and population reinforcement, Bretagnolle *et al.* 2011, Bretagnolle *et al.* 2018), as shown by the national censuses carried out in 2004, 2008 and 2012 (Gendre *et al.* 2018; see Figure 3c for trends in two areas of Poitou-Charentes). The Mediterranean population has steadily increased from 1,114–1,283 males in 2004 to 1,329–1,483 and 2,021–2,331 males estimated in 2008 and 2012, respectively, due to crop abandonment over the last decade favoured by EU's agricultural policy, as well as to land expropriation for construction of a high-speed railway (Devoucoux 2014). The latest national spring census, carried out in 2016, yielded a total of 2,455 males (range: 2,429–2,478), 313 of which belong to the western population and 2,142 to the Mediterranean one (Gendre *et al.* 2018), thus supporting the previous trends but showing a slight decrease in both the Mediterranean and western populations. The species is now strictly confined to small areas of France (detailed map in Gendre *et al.* 2018; Fig. 1).

Italy: Historically, Little Bustards were locally common in flat areas of central and southern continental Italy, as well as in Sardinia and Sicily. On the mainland, the bulk of the population was found in Apulia, as well as in Abruzzo and Molise, where it nested locally until the end of the 1960s. It was also irregularly reported further north, in the eastern Padanian plains (Petretti 2007). The species occupied c.50,000 ha in 1950, but only 1,200 ha by the 1980s (Petretti 1985). The Apulian population was estimated at 10,000–100,000 individuals in the early 20th century, although it began to decline when extensive livestock management was replaced by arable crops in the 1940s (Petretti 2006). By the 1960s, the population had fallen to around 1,000 individuals distributed over the plateau area known as Tavoliere of Gargano (in Gargano National Park). That was the last population on the mainland, which continued to decrease to 500–1,000 birds during the 1970s, and late 20th century to 15–20 birds in 2005 (Petretti 2006). This relict population is completely isolated from the rest of the species' range and can be considered today as functionally extinct, with no sightings of birds since 2010 (G. Palumbo pers. comm.). The Little Bustard became extinct in Sicily in the late 1960s (Snow and Perrins 1998, Massa and La Mantia 2007). Thus, Sardinia hosts the only remaining Little Bustard population in Italy, estimated at 1,500–2,000 individuals in the mid-1980s (Schenk and Aresu 1985), over coastal lowlands and inner plateaus of central and western Sardinia dominated by extensive pastoral and arable landscapes (Santangeli and Dolman 2011). It has declined severely during the last decades, to only 352 males in 2010–2011 (Nissardi and Zucca 2011).

North Africa: Historical reports indicate that the Little Bustard was a common breeder until the 20th century in cultivated plains from Tunisia to north-western Morocco (Cramp and Simmons 1980, Schulz 1985). However, during the 20th century, it sharply declined in the region (Schulz 1985). It was also a common winter visitor throughout the same range, at least until the 1970s (Cramp and Simmons 1980, Palacín and Alonso 2009) and Thévenot *et al.* (2003) noted the presence of 1,000 wintering birds near Larache (Morocco) in 1964. However, during the last three decades of the 20th century Little Bustards became rapidly scarce, both as breeders and winter visitors, presumably due to land use transformations (agricultural intensification, irrigation, and infrastructure) and hunting pressure (Palacín and Alonso 2009, Cherkaoui *et al.* 2020). The Little Bustard's historical range in Morocco encompassed two disjunct areas, one in the north-west between Tangier and El Jadida, and another in the north-east close to the Algerian border (Palacín and Alonso 2009). There are no recent records of the species in the latter area, suggesting it is probably extinct there. However, Little Bustards were still present until 2005 in five localities of

the north-west (in the Hachef and Loukos river valleys) for which Palacín and Alonso (2009) reported a total of 47 birds observed in the pre-breeding season (early March–early April) in four consecutive years (1999–2003). Later records are extremely scarce, and no observations have been reported after 2009. A tiny nucleus rediscovered in 2017, the southernmost African population of Little Bustard, was extinct by 2020 (Cherkaoui *et al.* 2020). The current entire Moroccan population is restricted to the area of Tangier, where only two birds were seen in the last few years (Cherkaoui *et al.* 2020). The population in Morocco may thus be considered functionally extinct. Wintering birds near Larache over the last 60 years dropped from 1,000 (1960s) to 100 (1980s), remained at c.100 until the 1990s and finally went extinct in the 2000s. The species vanished from Algeria during the 1990s, both as a breeder and wintering visitor (Isenmann and Moali 2000), and it can be currently considered extinct in Tunisia as well (Isenmann *et al.* 2005). In summary, the Little Bustard is probably extinct in North Africa (and thus from the entire African continent), but further fieldwork may be required to confirm this assertion.

Eastern range

Information on Little Bustard numbers and trends in its oriental range is scarce and available only for a few regions: southern Russia, Ukraine, central Asian countries, and Turkey. Breeding and wintering estimates differ, with winter estimates relying on counts of birds migrating across the main flyway or staying at winter quarters, while breeding estimates are local or incomplete.

Breeding populations: The Little Bustard in Russia was historically distributed throughout the country's steppe belt, even penetrating the forest-steppe biome (Spangenberg 1951). However, over the 20th century, it has disappeared from many regions, and the current range is limited to the Volga–Don interfluve, the Volga–Ural interfluve and eastern Cis-Caucasia (review in Oparin *et al.* 2018). The current size of the Russian population is difficult to assess due to the marked disparity of estimates in the different regions. According to BirdLife International (2018), the Russian population may comprise 14,000–17,000 individuals. The main population is within Orenburg oblast, at the south-eastern limit of European Russia (Antonchikov 2011), which, with the Saratov oblast situated further west in the Volga Valley (5,900 birds; Shlyakhtin *et al.* 2004), holds the bulk of the population in Russia. Shlyakhtin *et al.* (2004) also provided ranges of breeding densities in the Saratov oblast, from 0.01 ± 1.1 individuals/km² in cereal fields, perennial grass prairies and northern steppe to 0.8 ± 0.3 individuals/km² in southern steppes. There are however other estimates for the Russian population. For instance, Fedosov *et al.* (2016) suggested that 75,000 individuals were possibly present in the eastern part of the Orenburg oblast in 2016, although this figure is an extrapolation of local densities to the total area of habitat, and thus should be viewed cautiously. Conversely, the Orenburg Red Data Book suggests that 2,000–3,000 individuals are present (Kornev and Gavlyuk 2017). The Orenburg oblast population seems to have increased since the early 1980s, which is consistent with reports from elsewhere in Russia over the same period, leading to the recolonisation of large areas (Collar *et al.* 2017). Korovin (2014) also refers to significant increases in breeding male densities from 0 to 5 individuals/km² between 1990 and 2010 further east, in the trans-Ural region of Chelyabinsk. The abandonment of intensive agriculture after the fall of the Soviet Union may have contributed to bustard recovery (Kamp *et al.* 2011). A recent survey conducted in fall (October) in Saratov oblast, reported about 30,000 birds (95% CI: 15,015–46 225; Oparin *et al.* 2018). Counts were repeated (although irregularly) between 1997 and 2016 and maximum numbers at the level of the the entire region peaked at c.50,000 individuals in 2014 (Oparin *et al.* 2018). Therefore, a significant population increase seems to have occurred there in the first decade of the current century, which Oparin *et al.* (2018) attributed to a 20% increase in the area of habitat suitable for nesting (secondary virgin steppe) in the 1990s–2000s, as well as to a significant decrease in grazing pressure. As a provisional and conservative assessment of the Little Bustard population size in the core of the Russian species' range, we have summed Saratov's and Orenburg's minimum and maximum values to obtain a population size range c.17,000–121,000 individuals (see Table 3).

The situation in Ukraine is also unclear. Andryushenko and Stadnichenko (1999) estimated only 100–110 individuals restricted to Crimea (BirdLife International 2020). This estimate is most probably outdated, and no trend figure is currently available for the country. For Kazakhstan and Kyrgyzstan, BirdLife International (2020) provided an educated guess (and as such it must be taken cautiously) of 20,000 individuals, mainly in Kazakhstan, where the species is distributed across the country's steppe belt and breeds in most provinces (Wassink and Oreel 2007, Wassink 2016; see revision in Collar *et al.* 2017). There seems to be consensus among authors about the overall recovery of the Little Bustard in this vast region (Collar *et al.* 2017).

In Turkey, the Little Bustard was breeding in Inner Anatolia near Tuz Lake during the late 20th and early 21st centuries (Goriup and Parr 1985, Eken and Magnin 2000, Kirwan *et al.* 2008), with a few males and some females reported (Kirwan *et al.* 2008). Some individuals have been recorded in the post-breeding period in eastern Anatolia, but breeding there was not confirmed, and a few isolated and sporadic observations have been reported in the early 2000s along the Black Sea coast and in the Mediterranean district, all in the non-breeding season (Kirwan *et al.* 2008). Overall, only 5–50 males may remain in Turkey. In Iran, there was historically a small breeding population, spread across the lowlands south-east of the Caspian Sea (Evans 1994, Scott 1995). Although the presence of breeding Little Bustards in Iran has not been confirmed in recent times, a careful investigation is required before their extinction can be ascertained (Sehhatisabet *et al.* 2012). Finally, in north-west China, Collar *et al.* (2017) reviewed recent reports (Gao *et al.* 2008) and concluded that probably fewer than 1,000 birds remained, confined to Xinjiang province and Ningxia Hui autonomous region in the north-west and north of the country, respectively.

Wintering populations: The most reliable information for the eastern population probably comes from winter censuses. Azerbaijan hosts the bulk of the wintering population of the eastern range. Some historical records prior to 1930 reported a total wintering population of 200,000–300,000 individuals, as well as some breeding birds persisting up to the early 20th century (Patrikeev 2004). More recently, 150,000 birds were wintering in natural steppes and fallows, from the Caspian coastal plains to the Greater Caucasus foothills (Gauger 2007). Little Bustard densities in these areas can be very high, averaging 55 birds/km^2, but increasing to 100 birds/km^2 in smaller flocking sites, and flock size may range from <100 birds (most frequently) to several tens of thousands of individuals (Gauger 2007). The latter study reported an increase in the number of Little Bustards wintering in Azerbaijan during the early 2000s, which could reflect the population increase documented in breeding areas after the abandonment of intensive agriculture following the Soviet Union's breakdown. The area of Besh Barmag Mountain, close to the Caspian coast, is a main bottleneck for migratory eastern Little Bustards. Heiss (2013, 2016) estimated that 105,895–123,491 Little Bustards crossed this bottleneck in the autumn migration in the winter of 2011–2012, i.e. 41–48% of the species' world population and 71–82% of the eastern contingent is using this flyway, though only a few thousand Little Bustards cross this bottleneck on the spring migration (Heiss 2013). Other winter quarters occur in northern Iran, along the Caspian coast, but also in the north-west, near the Azerbaijani border and the north-east, bordering Turkmenistan and Afghanistan (Yousefi *et al.* 2017), although there are historical observations from more central parts of the country (Sehhatisabet *et al.* 2012). The wintering population in Iran appears to reach c.57,000 individuals (Yousefi *et al.* 2017), and occupies a variety of habitats, including farmland, pastures, and halophytic shrub-steppes (Sehhatisabet *et al.* 2012). As in Azerbaijan, this wintering population seems to have increased steadily in numbers and geographical range in recent times (Yousefi *et al.* 2017), in part presumably due to a hunting ban enforced in 2006–2009 to prevent an avian influenza outbreak (Sehhatisabet *et al.* 2012), although the habitat changes that occurred in Russian and central Asian breeding grounds may have also contributed. Nevertheless, the area surveyed has increased in Iran (Yousefi *et al.* 2017) and shifts of wintering areas might have occurred due to habitat modification. Therefore, we recommend caution when treating these figures. Considering estimates by Gauger (2007), Heiss (2013) and Yousefi (2017), the Iranian and Azerbaijani contingents add up to 171,693–207,000 Little Bustards over-wintering south of the Caspian Sea, which provides a minimum estimated size of the eastern Little

Bustard population. Therefore, either the Russian or Kazakh breeding populations (or both) are currently underestimated. The Little Bustard has been reported in winter in other sites beyond the core areas described above, from Lebanon to Afghanistan and Pakistan (Figure 1), but either in very small numbers or as erratic visitor (Grimmet *et al.* 2009, Morales *et al.* 2021). Adequate research based on telemetry is required to assess and validate these reports.

Discussion

Distribution range and population trends

The present markedly disjunct global distribution range of the Little Bustard is largely the result of the historical extinction process that occurred in Central and Eastern Europe as well as North Africa over the 20th century. Both the western (20th and early 21st centuries) and the eastern ranges (20th century) have contracted, with regressions in core areas and extinctions of more peripheral populations (North Africa, continental Italy, Middle East, Turkey, and trans-Caucasian regions). Our review highlights the concerning, if not alarming, distribution patterns and population trends exhibited by the Little Bustard's western population during the late 20th century and the first two decades of the 21st. Conversely, estimates in the eastern branch population would suggest an overall increase over the last 20-30 years in that region, although their low quality advises caution when interpreting, and much information is lacking at local scale.

The results compiled from the latest Little Bustard local estimates for the western range plus the winter numbers for the eastern range yield a grand total for the world population of c. 222,900–317,000 individuals (Table 3). This figure must be viewed with caution since the accuracy of the data used to calculate the global sum is highly variable. Moreover, the calculation of total individuals in west European countries is derived from an estimated proportion of females (Serrano-Davies *et al.* in review). Nevertheless, these partial population and sex ratio estimates are based on standardized and repeatable survey and calculation methods, and thus can be considered reliable (Table 3). Despite limitations, this updated evaluation of the species' world population size clearly reduces the broad range of 100,000–500,000 individuals tentatively considered by BirdLife International (2020). At the European Union level, the total number of males breeding in the entire western range (50,563; Table 3) now falls below the interval provided by BirdLife for the IUCN European Bird Red List (56,800–111,000 males; BirdLife International 2015). This result indicates that the species' population status in the western range is worse than believed until recently.

Our results emphasize the divergent recent histories and present situations of western and eastern ranges. South-western Europe still harboured 60% of the world population in 2010 (Íñigo and Barov 2010), mostly concentrated in the Iberian Peninsula. While the Iberian population was thought to be in decline (Íñigo and Barov 2010), our review indicates it is actually collapsing: the Iberian population has lost c.50% of its effectives in just a single decade, with a current yearly decline of c.5–6%, and it is now under 50% of the world total (Table 3). In contrast, the eastern population seems to enjoy a better conservation status than previously thought, based on increasing winter counts in Azerbaijan and Iran, which are more reliable than breeding data, and it now outnumbers the western one, both for winter counts and breeding censuses, if we rely on the last estimates provided for Russia by Oparin *et al.* (2018) (Table 3). Nevertheless, more precise breeding population estimates based on standard and comparable census methods are critically required for eastern countries, particularly Russia and Kazakhstan.

Ongoing threats for the Little Bustard worldwide

Intensification of farmland management: The Little Bustard's optimal habitat is pseudo-steppe and extensive farmland (Brotons *et al.* 2004, Morales *et al.* 2013, Bretagnolle *et al.* 2018).

Therefore, modern agriculture and land-use transformation are the main threat Little Bustards have faced in recent decades (Bretagnolle *et al.* 2018, Traba and Morales 2019). Indeed, the transformation of traditional extensively, managed grasslands (either grazed or hayed) and cereal farmland into intensive agrarian landscapes has occurred in most of Europe over the second half of the 20th century (Collar *et al.* 2016). This transformation has not occurred simultaneously everywhere; for instance, it occurred in France in the 1980s and 90s, earlier in Italy, and over a decade later in Spain and Portugal, which produced different population collapse times over the western range as depicted in Figure 2. In addition, agriculture intensification and land-use transformation have altered Little Bustard population dynamics through different pathways. Agriculture and livestock management intensification have reduced habitat diversity at the landscape scale (loss of natural grasslands and fallows, spread of irrigation and woody crops) and field scale (homogenization of vegetation structure, disappearance of wild plants and arthropods through increased herbicide and pesticide application), decreasing the availability of key resources such as insect food and adequate nesting sites, and thus habitat suitability (Brotons *et al.* 2004, Faria *et al.* 2012, Faria 2015, Morales *et al.* 2013, Bretagnolle *et al.* 2018, Traba and Morales 2019). Food reduction, particularly of insects, has a direct negative impact on juvenile survival and thus population recruitment, which is a key parameter for population growth in this species (Morales *et al.* 2005, Inchausti and Bretagnolle 2005). Another pathway is the use of modern harvesting machinery, a potentially important though overlooked source of female and juvenile mortality, as well as nest failure (Inchausti and Bretagnolle 2005, Faria *et al.* 2016, Bretagnolle *et al.* 2018). This could account for, at least partially, the markedly male-biased sex ratios found in many populations (Serrano-Davies *et al.* in review), another important limitation to Little Bustard population viability (Morales *et al.* 2005).

The agricultural management factors that negatively affect Little Bustards, however, can positively influence their population dynamics. This is clearly what has occurred in the eastern range, where land abandonment after the Soviet Union collapsed allowed a spectacular population growth (Kamp *et al.* 2011). Such exponential increases have also occurred locally in the western range. For instance, the transformation to extensive farming of the grazed steppe of La Crau, known as *coussoul*, along with the abandonment of traditional vineyards and other cultivated areas in Costière Nimoise (Department of Gard), seem to have boosted the Little Bustard population growth in southern France (Wolff *et al.* 2001, Devoucoux 2014). In Gard, Devoucoux (2014) documented a process of exponential growth from a marginal population of less than 100 males to over 700 males in just 14 years in a 120 km area.

Agriculture abandonment can however be reversed, and land-use changes may now again threaten the species in central Asia, as well as in southern France. After a period of agricultural abandonment following the fall of the Soviet Union, which has probably benefited many steppe birds in Russia and Kazakhstan (Shlyakhtin *et al.* 2004, Kamp *et al.* 2011), the return to intensive agriculture in recent years may negatively affect eastern populations of Little Bustard (Kamp *et al.* 2011, Collar *et al.* 2017). Ploughing was the main threat to the maintenance of steppe habitats in Russia and central Asia before the fall of the Soviet Union. Almost one million km^2 of Russian steppe were converted to arable land, in 1990 alone (Smelansky and Tishkov 2012). However, the breakdown of socialist economies halted land conversion and favoured the abandonment of agriculture in natural steppe regions in the former Soviet republics (Kamp *et al.* 2011), particularly in the less productive areas, so that between 1991 and 2007 more than 26 million hectares of cultivated steppe were abandoned in Russia (Smelansky and Tishkov 2012). After 2007 that tendency reversed again and nearly one million hectares were put back into cultivation, at least until 2012, affecting some regions considered key for the Little Bustard, such as Orenburg province (Smelansky and Tishkov 2012). Kamp *et al.* (2011) projected the proportion of land affected by different land-use changes and their direction (increase or decrease) up to 2020 in Kazakhstan. They forecast a 74% decrease in abandoned agricultural land (former cereal and fodder grass cultures), and these predicted changes are expected to affect the Little Bustard negatively. Other forecasted changes may potentially be beneficial for the

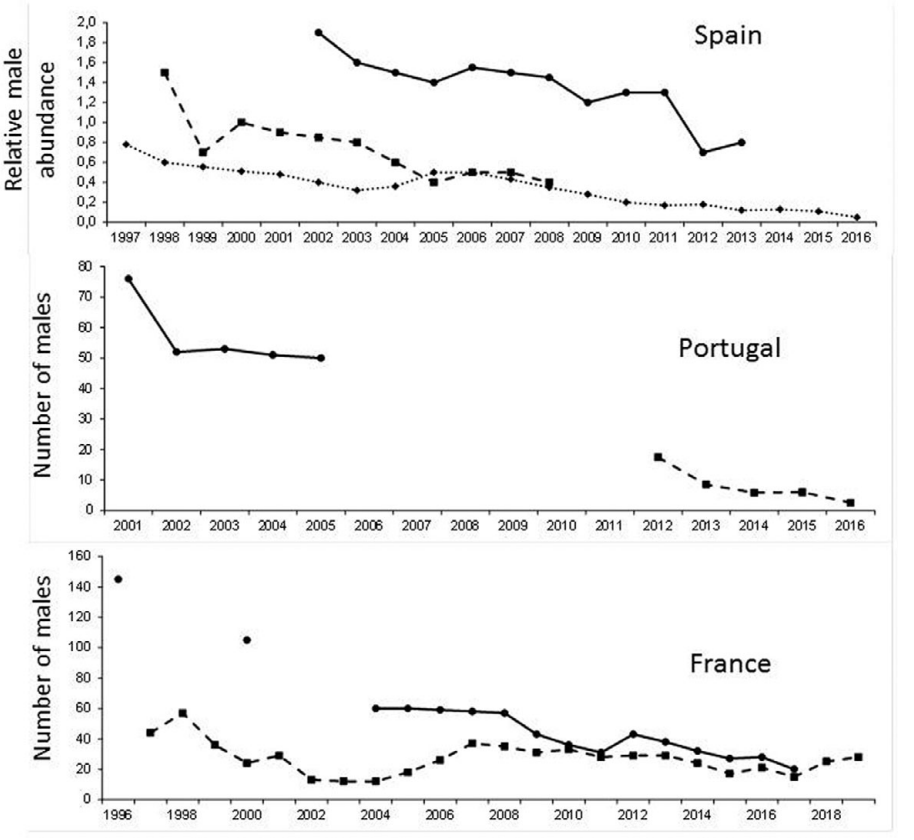

Figure 3. Examples of long-term local population trends in the three countries hosting the largest Little Bustard populations of the species' western range. Black dots indicate annual values. Spain, 3 localities. Solid line and black dots: mean relative abundance of 91–118 point-counts in Campo de Calatrava (central Spain, based on Casas *et al.* 2019); dashed line and black squares: mean relative abundance of 6 survey sites in Extremadura (south-western Spain, based on De Juana 2009); dotted line and black diamonds: mean number of males/km² in Navarra (northern Spain, based on García de la Morena and Morales unpubl. report). Portugal, 2 localities. Solid line and black dots: total number of males in Cabrela (Alentejo, N. Faria unpublished data); dashed line and black squares: mean number of males in 28 survey stations in Evora (Alentejo, N. Faria unpubl. data). France, 2 localities. Solid line and black dots: total number of males in Charentes (western France, NGO Charente Nature, unpublished data); dashed line and black squares: total number of males in ZA Deux Sèvres (western France, V. Bretagnolle, unpubl. data).

species, like a 33% decrease in overgrazed steppe or a 2.7% increase in low to moderately grazed steppe. Even the potentially negative impact of the enormous increase in cereal and fodder grass culture projected (53% and 66% respectively; Kamp *et al.* 2011) could be moderated by means of adequate agricultural management.

Such rapid, iterative, and reversed changes, occurring both in the west and the east, suggests the possibility that preferred breeding habitats in agricultural landscapes act as ecological traps for Little Bustards because of agricultural practices. Ecological traps are expected to occur in rapidly changing habitats under strong anthropogenic influence (Suvorov and Svobodová 2012), such as farmland, as shown for several bird species (Donald *et al.* 2002, Gruebler *et al.* 2012). Breeding female Little

Bustards in agricultural landscapes are attracted to temporary grasslands. When this habitat becomes scarce (as in western France, where they represent less than 15% of the surface area; Bretagnolle *et al.* 2018), females select them regardless of other traits that may influence breeding success such as vegetation height (which predicts mowing date) or distance to border (a proxy of predation risk). In western France, half of the nests in such grasslands, despite being in preferred habitat, are destroyed during mowing. Additionally, since the females do not show any other preference, the application of agri-environmental schemes (AESs) on temporary grasslands does not improve nest fate because, although nest destruction is reduced by AES (no mowing), the proportion of grasslands in AES remains low (Bretagnolle *et al.* 2018). The quantity and quality of those scarce but selected habitats is further decreasing in the western range (Morales *et al.* 2013, Silva *et al.* 2018, Traba and Morales 2019), and thus the risk of them becoming ecological traps increases. Therefore, the western range would require a conservation strategy in which extensively managed agricultural landscapes with a large enough proportion (>15%) of good quality grasslands are spared from more intensively managed ones. This would require a stronger stakeholder commitment with the conservation of farmland biodiversity (Gaba and Bretagnolle 2020), as well more conservation-focused and easier to apply agri-environmental schemes (i.e. those encompassed in EU's CAP; Díaz *et al.* 2021). Similar habitat change dynamics may be currently occurring in steppe and agricultural habitats of the eastern range, which urges for more geographically widespread, intensive, and standardized monitoring of eastern Little Bustard populations and their habitats.

Other relevant threats: Although agriculture changes and intensification can be considered the main drivers of large-scale declines in the Little Bustard, other threats have been identified across the species' world range. In certain areas like central Spain, urban sprawl has been important in recent years, causing direct habitat disappearance and loss of suitability due to fragmentation and edge effects, since breeding Little Bustards avoid the proximity of large linear infrastructures and urbanized areas (Suárez-Seoane *et al.* 2002, 2008, Silva *et al.* 2010). Indeed, collision with powerlines and hunting pressure have also been identified as relevant risks for the Little Bustard across its distribution range (De Juana and Martínez 2001, Íñigo and Barov 2010, Silva *et al.* 2010). For example, 42% of mortality recorded in 139 birds that were satellite- and radio-tracked in Iberia were human-caused, with poaching accounting for 32% of total mortality (Marcelino *et al.* 2018), although collision with powerlines (see also Silva *et al.* 2010) and vehicles were also relevant (6.45 and 3.23%, respectively; Marcelino *et al.* 2018). While shooting seems to be related to poaching and opportunistic hunting in Europe (De Juana and Martínez 2001), legal hunting is still an important pressure for wintering eastern populations. For instance, the species is legally shot in Iran (Sehhatisabet *et al.* 2012), and probably also in Azerbaijan, as well as in passage and wintering sites of the Middle East, although no quantitative estimates are available (Gauger 2007, Ramadan-Jaradi *et al.* 2017, Collar *et al.* 2017). Human presence, which increases near urbanized areas, has been shown to induce physiological stress in Little Bustards (Tarjuelo *et al.* 2015), a threat difficult to assess at large scales, but potentially important in the increasingly human-frequented European rural landscape.

Climate change is another potential new threat for the Little Bustard. The species' climate niche requirements may not be met under climate conditions forecast for the end of this century in its current range (Gudka *et al.* 2019). Indeed, the Little Bustard's European range was predicted to shift northwards (Huntley *et al.* 2007). However, when forecasts incorporate suitable habitat availability and spatial proxies of philopatry and conspecific attraction, the favourable range predicted remains fairly unchanged (Estrada *et al.* 2016), so that the Little Bustard ends up trapped in regions with a growing mismatch with the species' climate requirements.

Conflicting conservation status

The evidence reviewed here highlights the different population dynamics experienced by the two Little Bustard sub-populations. These have been isolated, with presumably no, or sporadic

connections between them, at least since the mid-20th century (see Table 2). Western and eastern populations may present some level of evolutionary divergence. Though not currently recognized, taxonomists formerly considered two different subspecies based on perceived morphological differences (Collar *et al.* 1996). Recent morphological analyses indicate differences between north-eastern and south-western localities of the range (Bretagnolle *et al.* 2021). Moreover, a phylogeographic study using mtDNA samples from France and Iberia found a low but significant level of structure at that geographical scale (García *et al.* 2011), which suggests that a larger-scale study might also find genetic structure. Further genetic evidence covering the main western and eastern nuclei is required. But overall, the existence of such morphological differences, possible genetic structuring, along with the observed ecological differences (i.e. western population mainly dependent on agricultural habitats vs the eastern one largely dependent on steppe), and the contrasting migratory behaviour (mainly resident with a single migratory populations in the west *vs* fully migratory in the east), all together strongly advocate for considering the two subpopulations as different evolutionary units. While the lack of a global phylogeography prevents the definition of evolutionary significant units *sensu stricto* (Moritz 1994), these two subpopulations show opposite overall trends (i.e. clearly diverging extinction risks), are ecologically distinct and suffer threats with different intensities. Therefore, we argue that they should be considered as independent conservation units, through their treatment as different designable units for conservation status assessment (Green 2005). Moreover, these two designable units closely fit the concept of 'Geographically Separate Subpopulations' (i.e. "populations that are so isolated from others of the same species that it is extremely unlikely that there is any genetic interchange"), recognized by IUCN as assessable for conservation status (https://www.iucnredlist.org/resources/tax-sources). In this context, we recommend treating each Little Bustard sub-range as a Geographically Separate Subpopulation with its own world status. Moreover, we consider the results presented in this review may be useful to update the global situation of the species with an eye on the on the eventual classification of the rapidly vanishing western population in the 'Endangered' IUCN category, which would allow more coordinated, ambitious, and urgent conservation action, particularly in Iberia, where trends seem most concerning. This classification may meet several IUCN criteria based on the reasonable premise that the population dynamics of the western population are governed by Iberian trends, since the Spanish and Portuguese populations (which represent a single and well connected metapopulation) account for c.95% of Little Bustard numbers in the western range, as shown in this review. In this context, the Iberian population has been declining by more than 50% for 10 years, as well as its area of occupancy (criteria A2a, b; García de la Morena *et al.* 2018, Silva *et al.* 2018). Furthermore, the quality of Little Bustard habitat in Iberia seems to have dramatically worsened (criterion A2c), due to the marked decrease of grass-covered fallow land (and other grassland types), the species' most used and selected habitat in Iberia, which declined by c.58% between 2000 and 2017, although the steepest fall (c.31%) occurred after 2008 (Traba and Morales 2019). The decline of the Little Bustard in Spain was strongly correlated with the loss of fallow land over that period (Traba and Morales 2019). According to Silva *et al.* (2018), habitat quality has similarly degraded in Portugal. Finally, population projection results forecast population decreases of c.57–74% over a 10-year period (Criterion A3b; García de la Morena *et al.* 2018, Traba *et al.* 2020). Given the geographical and ecological continuity with the Portuguese population and provided the similarly negative past trends reported by Silva *et al.* (2018), there is no reason to believe that Little Bustard numbers in that country should follow a different path. In summary around 95% of the western population is expected to have decreased by more than 50% in 2026 if current habitat conditions do not improve.

Regarding the eastern population, our suggestion for this Geographically Separate Subpopulation would be maintaining its current global classification as 'Near Threatened', unless more solid evidence advising otherwise is reported in the coming years. Any further reassessment must be accompanied by population monitoring and studies on eastern Little Bustard genetic relationships, ecology (very poorly known) and requirements, consistent with the designable unit update protocol advised by Green (2005). In our view, this might be a reasonable and consistent alternative to

the actual species' classification since (i) it would increase the protection status of the strongly declining western population, (ii) it does not imply changing the status of the eastern population, given the lack of more solid evidence and (iii) it may help avoiding the pitfall of global categorization by giving priority at world level to the most threatened population.

Acknowledgements

Nuno Faria kindly provided census data for two Portuguese localities. NGO Charente-Nature kindly made accessible long-term data and counts to VB. Sarah Young reviewed the English before ms submission. We are thankful to three anonymous reviewers for their useful comments on a previous version of the ms. This paper is a contribution to Excellence Network Remedinal 3CM (S2013/MAE2719), supported by Comunidad de Madrid.

References

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

André, R. (1985) Some aspects of reproduction in the Little Bustard and a contribution to an estimate of its population in France in 1978-1979. *Bustard Stud.* 2: 153–159.

Andryushchenko, Y.L. and Stadnichenko, I. S. (1999) The current state of bustard, Little Bustard, and stone curlew in the south of the left-bank Ukraine. *Branta* 2: 135–151.

Antonchikov, A. (2011) Little Bustard: current status and conservation prospects. *Steppe Bull.* 31: 33–38. (In Russian).

Ayé, F., Schwizer, M. and Roth, T. (2014) *Birds of Central Asia*. London: Christopher Helm.

BirdLife International (2004) *Birds in Europe: population estimates, trends and conservation status*. Cambridge: BirdLife International.

BirdLife International (2015) *European Red List of birds*. Luxembourg: Office for Official Publications of the European Communities.

BirdLife International (2018) *State of the world's birds: taking the pulse of the planet*. Cambridge: BirdLife International.

BirdLife International (2020) Species factsheet: *Tetrax tetrax*. Downloaded from http://www.birdlife.org on 29/01/2020.

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

Bretagnolle, V., Denonfoux, L. and Villers, A. (2018) Are farming and birds irreconcilable? A 21–year study of bustard nesting ecology in intensive agrosystems. *Biol. Conserv.* 228: 27–35.

Bretagnolle, V., Mañosa, S. and Morales, M. B. (2021) Natural history of the Little Bustard: morphology, biometry, diet, sexual dimorphism, and social and breeding behaviour. In V. Bretagnolle, J. Traba and M. B. Morales, eds. *Little Bustard ecology and conservation*. Berlin: Springer. (In press).

Brotons, L., Mañosa, S. and Estrada, J. (2004) Modelling the effects of irrigation schemes on the distribution of steppe birds in Mediterranean farmland. *Biodivers. Conserv.* 13: 1039–1058.

Burfield, I. (2005) The conservation status of steppic birds in Europe. Pp 119-131 in G. Bota, M. B. Morales, S. Mañosa and J. Capmrodon, eds. *Ecology and conservation of steppe-land birds*. Barcelona: Lynx Edicions.

Casas, F., Mougeot, F., Arroyo, B., Morales, M. B., Hervás, I., García de La Morena, E. L., Fagan, W. F. and Viñuela, J. (2019) Opposing population trajectories in two Bustard species: A long-term study in a protected area in Central Spain. *Bird Conserv. Internatn.* In press: https://doi.org/10.1017/S0959270918000254.

Cherkaoui, S. D., El Yaacoubi, A., Aghzar, A., El Yousfi, L. and Qninba, A. (2020) Rapid extirpation of a newly discovered

population of Little Bustard Tetrax tetrax in "Central plateau" (Morocco): lessons for conservation. *Bull. Institut Scientifique, Rabat, Section Science de la Vie* 42: 15–22.

Collar, N. J. (1996) Family Otididae (bustards). Pp. 240–273 in J. Del Hoyo, A. Elliot, and J. Sargatal, eds. *Handbook of the birds of the world vol 3. Hoatzin to auks*. Barcelona: Lynx Edicions.

Collar, N. J., Garcia, E. F. J. and De Juana, E. (2016) Little Bustard (*Tetrax tetrax*). In: J. del Hoyo, A. Elliot, J. Sargatal, D. A. Christie and E. De Juana, eds. *Handbook of the birds of the world alive*. Barcelona: Lynx Edicions. http://www.hbw.com/node/53736. Accessed 21 July 2016.

Collar, N. J., Baral, H. S., Batbayar, N., Bhardwaj, G. S., Brahma, N., Burnside, R. J., Choudhury, A. U., Combreau, O., Dolman, P. M., Donald, P. F., Dutta, S., Gadhavi, D., Gore, K., Goroshko, O. A., Hong, C., Jathar, G. A., Jha, R. R. S., Jhala, Y. V., Koshkin, M. A., Lahkar, B. P., Liu, G., Mahood, S. P., Morales, M. B., Narwade, S. S., Natsagdorj, T., Nefedov, A. A., Silva, J. P., Thakuri, J.J., Wang, M., Zhang, Y. and Kessler, A. E. 2017. Averting the extinction of bustards in Asia. *Forktail* 33: 1–26.

Cramp, S. and Simmons, K. E. L. (1980) *The birds of the Western Palearctic. Vol* 2. Oxford: Oxford University Press.

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

De Juana, E. and Martínez, C. (1996) Distribution and conservation status of the Little Bustard *Tetrax tetrax* in the Iberian Peninsula. *Ardeola* 43: 157–167.

De Juana, E. and Martínez, C. (2001) *Action Plan for the conservation of Little Bustard (Tetrax tetrax)*. Strasbourg: BirdLife International and the European Commission.

Devoucoux, P. (2014) Conséquences et impacts prévisibles d'une perte d'habitat majeure sur une espèce menacée aux exigences écologiques complexes: effets de la mise en place du contournement ferroviaire à grande vitesse Nîmes-Montpellier sur la dynamique de la population d'outarde canepetière des Costières de Nîmes. Dissertation, University of Poitiers.

Díaz, M., Concepción, E. D., Morales, M. B., Alonso, J. C., Azcárate, F. M., Bartomeus, I., Bota, G., Brotons, L., García, D., Giralt, D., Gutiérrez, J. E., López-Bao, J. V., Mañosa, S., Milla, R., Miñarro, M., Navarro, A., Olea, P. P., Palacín, C., Peco, B., Rey, P. J., Seoane, J., Suárez-Seoane, S., Schöb, C., Tarjuelo, R., Traba, J., Valera, F. and Velado-Alonso, E. (2021) Environmental objectives of Spanish agriculture: scientific guidelines for their effective implementation under the Common Agricultural Policy 2023-2030. *Ardeola*. In press.

Donald, P. F., Evans, A. D., Muirhead, L. B., Buckingham, D. L., Kirby, W. B. and Schmitt, S. I. A. (2002) Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis* 144: 652–664.

Donald, P. F., Sanderson, F. J., Burfield, I. and van Bommel, F. P. J. (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agric. Ecosyst. Environ.* 116: 189–196.

Eken, G. and Magnin, G. (2000) *A preliminary biodiversity atlas of the Konya Basin, central Turkey*. Istanbul: Dogal Hayati Koruma Dernegi.

Estrada, A., Delgado, M. P., Arroyo, B., Traba, J. and Morales, M. B. (2016) Forecasting large-scale habitat suitability of European bustards under climate change: the role of environmental and geographic variables. *PLoS ONE* 11(3): e0149810.

Evans, M. (1994) *Important bird areas in the Middle East*. Cambridge: BirdLife International.

Faria, N. (2015) Implications of dry grassland management in the ecology and conservation of grassland birds in south Portugal. PhD Dissertation. Autónoma University of Madrid.

Faria, N., Rabaça, J. and Morales, M. B. (2012) Linking plant composition and arthropod abundance to establish Little Bustard breeding requirements in pastureland dominated landscapes. *Biodivers. Conserv.* 21: 2109–2125.

Faria, N., Morales, M. B. and Rabaca, J. E. (2016) Exploring nest destruction and bird mortality in mown Mediterranean dry

grasslands: an increasing threat to grassland bird conservation. *Eur. J. Wildl. Res.* 62: 663–670.

Fedosov, V. N., Fedosov, A. V. and Antonchikvo, A. (2016) Surveys of Little Bustard in Orenburg Province and species conservation prospects. *Steppe Bull.* 49: 55–58. (In Russian).

Gaba, S. and Bretagnolle, V. (2020) Social–ecological experiments to foster agroecological transition. *People and Nature* 2: 317–327.

Gao, X., Yang, W., Qiao, J., Yao, J. and Xu, K. (2008) Distribution and status of bustards in China. *Front. Biol. China* 3: 385–391.

García, J. T., Mañosa, S., Morales, M. B., Ponjoan, A., García de la Morena,E., Bota, G., Bretagnolle, V. and Dávila, J. A. (2011) Genetic consequences of interglacial isolation in a steppe bird. *Mol. Phyl. Evol.* 61: 671–676.

García de La Morena,E., De Juana, E., Suárez, F., Morales, M. B. and Martínez, C. (2003) Sisón común (Tetrax tetrax). Pp. 232–233 in R. Martí and J. C. del Moral, eds. *Atlas de las aves reproductoras de España*. Madrid: SEO/Birdlife-Ministerio de Medioambiente.

García de La Morena,E., De Juana, E., Suárez, F., Morales, M. B. and Martínez, C. (2004) Sisón común (Tetrax tetrax). Pp. 202–207 in A. Madroño and R. Martí, eds. *Libro Rojo de las aves de España*. Madrid: SEO/BirdLife-Ministerio de Medioambiente.

García de la Morena,E. L., Bota, G., Ponjoan, A. and Morales, M. B. (2006) *El sisón común en España. I censo nacional*. Madrid: SEO/BirdLife.

García de la Morena, E. L., Bota, G., Mañosa, S. and Morales, M. B. (2018) *El Sisón Común en España. II Censo Nacional (2016)*. Madrid: SEO-Birdlife.

Gauger, K. (2007) Occurrence, ecology and conservation of wintering Little Bustards *Tetrax tetrax* in Azerbaijan. *Archiv für Naturschutz und Landschaftsforschung* 46: 5–27.

Gendre, N., Éraud, C., Bretagnolle, V. and Dalloyau, S. (2018) L'Outarde canepetière Tetrax tetrax en France en 2012 et 2016: effectifs et répartition. *Ornithos* 25-5: 290–302.

Goriup, P. (1994) Little Bustard *Tetrax tetrax*. Pp. 236–237 in G. M. Tucker and M. F. Heath, eds. *Birds in Europe: their conservation status*. Cambridge: BirdLife International.

Goriup, P. and Parr, D. (1985) Results of the ICBP bustard survey of Turkey, 1981. *Bustard Stud.* 2: 77–98.

Green, D. M. (2005) Designatable units for status assessment of endangered species. *Conserv. Biol.* 19: 1813–1820.

Grimmett, R., Roberts, T. and Inskipp, T. (2009) *Birds of Pakistan*. London: Christopher Helm.

Grüebler, M. U., Schuler, H., Horch, P. and Spaar, R. (2012) The effectiveness of conservation measures to enhance nest survival in a meadow bird suffering from anthropogenic nest loss. *Biol. Cons.* 146: 197–203.

Gudka, M., Santos, C. D., Dolman, P. M., Abad-Gómez, J. M. and Silva, J. P. (2019) Feeling the heat: Elevated temperature affects male display activity of a lekking grassland bird. *PLoS ONE* 14(9): e0221999.

Hagemeijer, W. J. M. and Blair, M. J. (1997) *The EBCC Atlas of European breeding birds: their distribution and abundance*. London: T. and A. D. Poyser and European Bird Census Council.

Heiss, M. (2013) The importance of Besh Barmag bottleneck (Azerbaijan) for Eurasian migrant birds. *Acta Ornithol.* 48: 151–164.

Heiss, M. (2016) Records of globally Red-listed bird species migrating through the Besh Barmag bottleneck, Azerbaijan Republic. *Podoces* 11: 43–52.

Huntley, B., Green, R. E., Collingham, Y. C. and Willis, S. G. (2007) *A climatic atlas of European breeding birds*. Barcelona: Lynx Edicions.

Inchausti, P. and Bretagnolle, V. (2005) Predicting short-term extinction risk for the declining Little Bustard (Tetrax tetrax) in intensive agricultural habitats. *Biol. Conserv.* 122: 375–384.

Inger, R., Gregory, R., Duffy, J. P., Stott, I., Voříšek, P. and Gaston, K. J. (2015) Common European birds are declining rapidly whilst less abundant species' numbers are rising. *Ecol. Lett.* 18: 28–36.

Iñigo, A. and Barov, B. (2010) *Action plan for the Little Bustard Tetrax terax in the*

European Union. SEO/BirdLife and BirdLife International for the European Commission.

Issa, N. and Muller, Y. (2015) *Atlas des oiseaux de France métropolitaine; nidification et présence hivernale*. Paris: Delachaux & Niestlé.

Isenmann, P. and Moali, A. (2000) *Birds of Algeria*. Paris : Société d'Etudes Ornithologiques de France.

Isenmann, P., Gaultier, T., El Hili, A., Azafzaf, H., Dlensi, H. and Smart, M. (2005) *Oiseaux de Tunisie/Birds of Tunisia*. Paris: SEOF Editions.

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

Kamp, J., Urazaliev, R., Donald, P. F. and Hölzel, N. (2011) Post-Soviet agricultural change predicts future declines after recent recovery in Eurasian steppe bird populations. *Biol. Conserv.* 144: 2607–2614.

Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvaňová, A., Kalyakin, M. V., Bauer, H. G. and Foppen, R. P. B. (2020) *European breeding bird atlas 2: Distribution, abundance and change*. Barcelona: European Bird Census Council and Lynx Edicions.

Kirwan, G. M., Byla, K., Castell, P., Demirci, B., Özen, M., Welch, H. and Marlow, T. (2008) *The birds of Turkey*. London: Helm.

Kornev, S. V. and Gavlyuk, J. V. (2017) Little Bustard. In A. V. Davygora, ed. *Red Book of Orenburg Oblast. Vol 1: Animals*. Orenburg, Russia: Orenburg Publishing.

Korovin, V. A. (2014) Restoration of the Little Bustard population in the northern Steppe Trans-Urals. *Biol. Bull.* 41: 856–861.

Mañosa, S., Bota, G., Estrada, J. and Cuscó, F. (2015) Una oportunidad para el sisón en Cataluña. *Quercus* 356: 24–35.

Marcelino, J., Moreira, F., Mañosa, S., Cuscó F., Morales, M. B., García de la Morena,E. L., Bota, G., Palmeirim, J. M. and Silva, J. P. (2018) Long term tracking study of the Little Bustard in Iberia shows high anthropogenic mortality. *Bird Conserv. Internatn.* 28: 509–520.

Massa, B. and La Mantia, T. (2007) Forestry, pasture, agriculture and fauna correlated to recent changes in Sicily. *Foresta* 4: 418–438.

Morales, M. B., Bretagnolle, V. and Arroyo, B. (2005) Viability of the endangered Little Bustard Tetrax tetrax population of western France. *Biodivers. Conserv.* 14: 3135–3150.

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

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

Morales, M. B., Arroyo, B. and Traba, J. (2015) El declive del sisón en el centro de España. *Quercus* 356: 36–43.

Morales, M. B., Mañosa, S., Villers, A., García de la Morena, E. L. and Bretagnolle, V. (2021) Migration, movements and non-breeding ecology. In V. Bretagnolle, J. Traba and M. B. Morales,eds. *Little Bustard ecology and conservation*. Berlin: Springer. (In press).

Moritz, C. (1994) Defining 'Evolutionary Significant Units' for conservation. *Trends Ecol. Evol.* 9: 373–375.

Nissardi, S. and Zucca, C. (2011) *Risultati del primo censimento completo dei maschi territoriali di gallina prataiola tetrax tetrax in Sardegna (2009-2011)*. Cervia: Atti del Convegno Italiano di Ornitologia.

Onrubia, A. and Andrés, T. (2005) Impact of human activities on steppic-land birds: a review in the context of the Western Palearctic. Pp 185–210 in G. Bota, M. B. Morales, S. Mañosa, and J. Camprodon, eds. *Ecology and conservation of steppe-land birds*. Barcelona: Lynx Edicions.

Oparin, M. L., Kondratenkov, I. A., Oparina, O. S. and Mamayev, A. B. (2018) Abundance of the Little Bustard *Tetrax tetrax* L. 1758 (Otididae, Aves) in Saratov Oblast. *Biol. Bull.*45: 1165–1173.

Palacín, C. and Alonso, J. C. (2008) An updated estimate of the world status and population trends of the Great Bustard *Otis tarda*. *Ardeola* 55: 13–25.

Palacín, C. and Alonso, J. C. (2009) Probable population decline of the Little Bustard *Tetrax tetrax* in north-west Africa. *Ostrich* 80: 165–170.

Patrikeev, M. (2004) *The birds of Azerbaijan*. Sofia: Pensoft.

Petretti, F. (1985) Preliminary data on the status of the Little Bustard in Italy. *Bustard Studies* 2: 165–170.

Petretti, F. (2006) Conservation of steppe birdlife in Italy. Pp 235–239 in D. Gafta and J. Akeroyd, eds. *Nature conservation. Concepts and practice*. Heidelberg: Springer.

Petretti, F. (2007) The situation of the Little Bustard in Italy. Pp. 65–69 in D. Leitão, C. Jolivet, M. Rodríguez and J. Tavares, eds. *Bustard conservation in Europe in the last 15 years: current trends, best practice and future priorities*. Sandy: RSPB/BirdLife.

Ramadan-Jaradi, G., Itani, F. and Serhal, A. (2017) Interesting bird records from Lebanon. *Sandgrouse* 39: 187–192.

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M. and Marra P. P. (2019) Decline of the North American Avifauna. *Science* 366: 120–124.

Santangeli, A. and Dolman, P. M. (2011) Density and habitat preferences of male Little Bustard across contrasting agro-pastoral landscapes in Sardinia (Italy). *Eur. J. Wildl. Res.* 57: 805–815

Schenk, H. and Aresu, M. (1985) On the distribution, number and conservation of Little Bustard in Sardinia (Italy). *Bustard Stud.* 2: 161–164.

Schulz, H. (1985) A review of the world status and breeding distribution of the Little Bustard. *Bustard Stud.* 2: 131–152.

Scott, D. A. (1995) *A directory of wetlands in the Middle East*. Slimbridge: IUCN and IWRB.

Sehhatisabet, M. E., Abdi, F., Ashoori, A., Khaleghizadeh, A., Khani, A., Rabiei, K. and Shakiba, M. (2012) Preliminary assessment of distribution and population size of wintering Little Bustards *Tetrax tetrax* in Iran. *Bird Conserv. Internatn.* 22: 279– 287.

SEO/BirdLife (2018) SACRE. https://www.seo.org/sacre/. (Last accessed 31.10.2018).

Serrano-Davies, E., Traba, J., Arroyo, B., Mougeot, F., Cuscó, F., Mañosa, S., Bota, G., Faria, N., Villers, A., Casas, F., Devoucoux, P., Bretagnolle, V. and Morales, M. B. (In review). Biased sex ratios in Western Europe populations of Little Bustard (*Tetrax tetrax*) confirm their unviable status. *Avian Conserv. Ecol.*

Shlyakhtin, G. V., Tabachishin, V. G., Khrustov, A. V. and Zav'yalov, E. V. (2004) Ecological segregation of bustards (Otididae) in the north of the lower Volga region: evolutionary and adaptive aspects. *Russ. J. Ecol.* 35: 247–253

Silva, J. P. (2010) Factors affecting the abundance of the Little Bustard *Tetrax tetrax*: implications for conservation. PhD Dissertation, University of Lisbon.

Silva J. P. and Pinto, P. (2006) Final report of Action 2 of the Project LIFE02NAT/P/8476: Conservation of the Little Bustard in Alentejo. Institute for Nature Conservation. Available via http://portal.icnb.pt/NR/rdonlyres/783CA43B-7C0E-4FA4-8286-F4EB120C4A49/0/Life_SISAO.pdf. Accessed 17 Jan 2011.

Silva, J. P., Santos, M., Queirós, L., Leitão, D., Moreira, F., Pinto, M., Leqoc, M. and Cabral, J. A. (2010) Estimating the influence of overhead transmission power lines and landscape context on the density of Little Bustard *Tetrax tetrax* breeding populations. *Ecol. Mod.* 221: 1954–1963.

Silva, J. P., Correia, R., Alonso, H., Martins, R. C. D'Amico, M., Delgado,A., Sampaio,H., Godinho, C. and Moreira, F. (2018) EU protected area network did not prevent a country wide population decline in a threatened grassland bird. *PeerJ* 6: e4284.

Smelansky, I. E. and Tishkov, A. A. (2012) The steppe biome in Russia: ecosystem services, conservation Status, and actual challenges. Pp. 45–101 in M. J. A. Werger and M. A. van Staalduinen, eds. *Eurasian steppes. Ecological problems and livelihoods in a changing world*. Heidelberg: Springer.

Snow, D. W. and Perrins, C. M. (1998) *The birds of the Western Palearctic (Concise Edition). Vol 1. Non-Passerines*. Oxford: Oxford University Press.

Spangenberg, E. P. (1951) Order Otidiformes. Pp. 139–168 in P*titsy Sovetskogo Soyuza (Birds of the Soviet Union). Vol.* 2. Moscow: Sovetskaya Nauka.

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

Suárez-Seoane, S., Garcia de la Morena, E. L., Morales, M. B., Osborne, P. E. and De Juana, E. (2008) Maximum entropy niche-based modelling of seasonal changes in Little Bustard (*Tetrax tetrax*) distribution. *Ecol. Mod.* 219: 17–29.

Suvorov, P. and Svobodová, J. (2012) The occurrence of ecological traps in bird populations: is our knowledge sufficient? A review. *J. Landsc. Ecol.* 5: 36–56.

Tarjuelo, R., Barja, I., Morales, M. B., Traba, J., Benítez-López, A., Casas, F., Arroyo, B., Delgado, M. P. and Mougeot, F. (2015) Effects of human activity on physiological and behavioural responses of an endangered steppe bird. *Behav. Ecol.* 26: 828–838.

Ternier, L. (1892) L*a sauvagine en France. Oiseaux de mer, de rivières et de marais.* Paris : Firmin-Didot.

Thévenot, M., Vernon, R. and Bergier, P. (2003) *The birds of Morocco*. London: British Ornithologists' Union and British Ornithologists' Club. (BOU checklist No. 20).

Traba, J. and Morales, M. B. (2019) The decline of farmland birds in Spain is strongly associated to the loss of fallowland. *Sci. Repts.* 9: 9473.

Traba, J., Bota, G., Mañosa, S., García de la Morena, E. and Morales, M. B. (2020) Análisis de viabilidad de la población de Sisón Común en España. Documento anexo a las Bases Científicas para la Elaboración de la Estrategia Nacional de Conservación del Sisón Común (Tetrax tetrax). Madrid: Fundación Biodiversidad and Ministerio para la Transformación Ecológica (MITECO). Unpublished report.

Villers, A., Millon, A., Jiguet, F., Lett, J. M., Attié, C., Morales, M. B. and Bretagnolle, V. (2010) Tracking of wild and captive-bred Little Bustards *Tetrax tetrax* from western France, and implications for reinforcement programmes. *Ibis* 152: 254–261.

Vorisek, P., Jiguet, F., van Strien, A., Skorpilova, J., Klvanova, A. and Gregory, R. D. (2010) Trends in abundance and biomass of widespread European farmland birds: how much have we lost? In: British Ornithologists' Union, eds. *Lowland Farmland Birds III: Delivering Solutions in an uncertain World, Online Conference Proceedings.* http://www.bou.org.uk/bouproc-net/lfb3/vorisek-etal.pdf

Wassink, A. (2016) *The new birds of Kazakhstan*. Texel: Arend Wassink, privately published.

Wassink, A. and Oreel, G. J. (2007) *The birds of Kazakhstan*. Texel: De Cocksdorp.

Wolff, A., Paul, J. P., Martin, J. L. and Bretagnolle, V. (2001) The benefits of extensive agriculture to birds: the case of the Little Bustard. *J. Appl. Ecol.* 38: 963–975.

Yeatman, L. (1976) *Atlas des oiseaux nicheurs de France*. Paris : Société Ornithologique de France/ Ministère de la Qualité de la Vie Environnement.

Yousefi, M., Kafash, A., Malakoutikhah, S., Ashoori, A., Khani, A., Mehdizade, Y., Ataei, F., Ilanloo, S. S., Rezaie, H. R. and Silva, J. P. (2017) Distance to international border shapes the distribution pattern of the growing Little Bustard *Tetrax tetrax* winter population in northern Iran. *Bird Conserv. Internatn.* 28: 499–508.