Wildlife Research Monographs 5

Vincent Bretagnolle
Juan Traba
Manuel B. Morales *Editors*

Little Bustard: Ecology and Conservation

Springer

Wildlife Research Monographs

Volume 5

Series Editors:

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

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

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

The book series on “Wildlife Research Monographs” focuses on all aspects of wildlife biology to fill a vital niche at the intersection of several disciplines. The aim of the series is to summarize knowledge about interaction between wildlife species, their habitats, as well as human activities. Main areas are: wildlife ecology, diseases, toxicology, conservation, management, and the sustainable use of natural resources. The series addresses graduate students, university teachers, scientists and professionals.

More information about this series at http://www.springer.com/series/8826

Vincent Bretagnolle • Juan Traba •
Manuel B. Morales
Editors

Little Bustard: Ecology and Conservation

Springer

Editors
Vincent Bretagnolle
Centre d'Etudes Biologiques de Chizé,
CNRS & La Rochelle Université
Beauvoir sur Niort, France

Juan Traba
Department of Ecology
Universidad Autónoma de Madrid
Madrid, Spain

Manuel B. Morales
Department of Ecology and Research
Centre for Biodiversity and Global Change
Universidad Autónoma de Madrid
Madrid, Spain

ISSN 2366-8733 ISSN 2366-8741 (electronic)
Wildlife Research Monographs
ISBN 978-3-030-84901-6 ISBN 978-3-030-84902-3 (eBook)
https://doi.org/10.1007/978-3-030-84902-3

Author of the picture: Dr. Vincent Bretagnolle

Foreword

Paul F. Donald

Few bird families illustrate the world's conservation problems better than the bustards. Of the 26 species recognized by BirdLife International, more than half are globally threatened or near threatened with extinction. They owe this parlous conservation status to the full panoply of threats facing wildlife today: habitat loss, degradation and fragmentation, hunting, infrastructure (particularly power lines), disturbance, agricultural intensification, road traffic, predation and climate change have all played a part in driving many species to the edge of extinction. Bustards have few natural defences against predators and therefore rely on flat, open undisturbed expanses of grassland or other low habitats that allow them to see, and keep, danger at a distance. Unfortunately, these are exactly the sorts of habitats that are most easily converted to other purposes, and many of the natural grasslands of Europe and Asia have been ploughed up for arable cultivation. Some African species remain relatively common and thrive in large national parks and undisturbed desert and semi-desert areas, but all the European and Asian species are now listed as globally threatened or near threatened.

Despite their often large size (the family contains the world's heaviest flying birds), an evolutionary trajectory that has placed a great deal of emphasis on crypsis means that bustards are often hard to observe and to study, and our state of knowledge for many species is poor. It has only been in the last few years, for example, that satellite tracking has revealed that, outside the breeding season, Bengal floricans leave the few protected areas they still nest in and move considerable distances into quite different habitats. The little bustard, being as its name suggests one of the smaller members of the family, is particularly hard to study, but this has not prevented a great deal of research effort being invested in the species, particularly in the European parts of its range. Here, its population has collapsed due to changes in agriculture, and little bustard has become a model species in research assessing the environmental impacts of farming, as the skylark has become

elsewhere in Europe. It is therefore both a species of high conservation concern in its own right and an important indicator of the health of the wider landscape. The last two decades have seen a surge in research work on this species, particularly in Spain, Portugal, France and Italy, where it is now restricted to an isolated and threatened population on Sardinia. The recent loss of the species from mainland Italy marks the most recent extinction in a long-term decline that has seen the little bustard being lost as a breeding bird from Germany, Greece, Poland, Slovakia and a number of other European countries. It is no wonder that the little bustard has attracted so much attention from the continent's ornithologists. The results of all their work have thus far been published largely in scientific articles, spread across many national and international journals. What has been lacking, until now, is a comprehensive synthesis of this great body of research.

The western European population is extremely important, but the bulk of the little bustard's global population lies far to the east, especially in the vastness of the Pontic-Caspian steppes. These cover an area of nearly a million square kilometres between eastern Europe and western China. Here, the species is even more difficult to study; not only are these areas remote and often inaccessible but many populations are migratory, adding a further complication to assessing their conservation status and exposing them to many more threats. Massive changes in steppe management since the collapse of the Soviet Union have led to both gains and losses for little bustards in this region, but much of this information has until now been buried in scientific papers (including in the Russian journal *Strepet*, the local name for little bustard).

This remarkable publication, 6 years in the making, represents a landmark in the study of little bustards, for it collects and summarises this mass of disparate information between the covers of a single book, and then uses this synthesis to identify research and conservation priorities to guide future work. The book's chapters are authored by the world's leading authorities on the species and between them they cover a very wide range of subjects, from sexual dimorphism to sex ratios, from phylogeography to phenology, and from national populations to national action plans. What makes the book even more authoritative is that all the chapters have been independently reviewed by other experts in the ecology and conservation of farmland and steppe birds, thus bringing in an even wider range of expertise. This book will serve as the primary reference on the little bustard for many years to come, and I am delighted to have been asked to introduce it.

Contents

Why a Monograph on Little Bustard?

Juan Traba, Manuel B. Morales, and Vincent Bretagnolle

> In its full nuptial plumage the male of this species is to my mind the most beautiful of game-birds found in Europe. It is extremely abundant on the low undulating hills and grass-grown plains of south-west Andalucia, but owing to its peculiar habits of flight is very rarely shot by the sportsman

This is how the British soldier, writer and naturalist Willoughby Verner began his chapter on the little bustard *Tetrax tetrax* in his memoir "My Life among the Wild Birds of Spain", published in 1909. Verner summarizes in a short paragraph all the little bustards' traits that have attracted the attention of ornithologists and naturalists for years, both professional and amateur: their beauty, despite being a bird of flat and treeless landscapes, their surprising behaviour, and their once incredible abundance. We would dare to say that these are, in short, the main motivations to write and edit this book. As ornithologists, we are ceaselessly amazed by the male's clownlike postures and the astonishing camouflage of the females. As ecologists, we have always been fascinated by the species' morphology and spectacular displays, the products of the evolutionary forces at play in its peculiar mating system. As conservation biologists, we see in its current population crash a perfect though pitiful example of the "abundant species paradigm": it is not the scarcity but the speed of decline of a species that should warn us, as mere numbers can be misleading when considering species still abundant in at least some areas, as they can suggest

J. Traba (✉) · M. B. Morales
Terrestrial Ecology Group, Departamento de Ecología, Universidad Autónoma de Madrid (TEG-UAM), Madrid, Spain

Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain
e-mail: juan.traba@uam.es; manuel.morales@uam.es

V. Bretagnolle
Centre d'Etudes Biologiques de Chizé, CNRS & La Rochelle Université, Beauvoir sur Niort, France
e-mail: vincent.bretagnolle@cebc.cnrs.fr

V. Bretagnolle et al. (eds.), *Little Bustard: Ecology and Conservation*, Wildlife Research Monographs 5, https://doi.org/10.1007/978-3-030-84902-3_1

only a minor conservation emergency. There is perhaps, a fourth motivation. For us editors, and for sure for all contributors to this monograph, the little bustard is an icon of the vanishing traditional agricultural landscapes of Europe and other parts of the world, once biologically so rich and diverse, and currently so sadly replaced by industrial farmland. This book is a plea for urgent action to recover a biologically friendly agriculture compatible with the existence of the little bustard and so many other wonderful farmland and steppe species.

The little bustard was so common in France and Iberia until the late 1960s and 1980s, respectively, that nobody would have ever believed that the situation could become so critical in only about 15–20 years. However, this is what happened: in Italy, France, Spain, Portugal and Morocco, at slightly different times but during periods that never exceeded two decades, the little bustard populations of these countries just crashed, and in some cases vanished. The red flag was first raised in France, with warning signals by ornithologists in the late 1980s, when the little bustard became scarce or even extinct in former strongholds in the country. This and other bustard species were already the focus of a small network of scientists and conservationists concerned about the alarming status shown by bustards worldwide. They edited a dedicated journal, *Bustard Studies*, published irregularly when funds were available, which contributed to an increased awareness of the fragile conservation status of several bustard species and helped creating an IUCN specialist group. In 1990, the situation was seriously alarming for the little bustard in France, although admittedly, at that time, trend data or long-term surveys were still not available. Thanks to pioneering conservationists a first LIFE programme was set in 1996 in France and dedicated solely to the conservation of the little bustard, a project that included a significant part of research on basic breeding biology, virtually unknown at that time.

The dramatic situation of the little bustard was however not restricted to France. In 1997, a technical international workshop was held in Trujillo, Spain, to discuss the global status of the little bustard in Europe, and to establish conservation priorities. In 2001, as an output of this workshop, a preliminary draft of the European Species Action Plan was elaborated (De Juana 2001). This document highlighted the threatened conservation status of the species in Europe, even though at that time the Iberian population was considered healthy and abundant, and encouraged public administrations to take a series of urgent measures to avoid local and regional extinctions (De Juana 2001). Such actions targeted little bustard habitat, considering the Common Agricultural Policy (CAP) as a potential key tool to promote environmentally friendly practices as well as, at the same time, banning harmful subsidies such as those for afforestation or sunflower crops in steppe or pseudosteppe areas in Spain (De Juana 2001).

In 2010, the European Species Action Plan (SAP) was finally officially released (Íñigo and Barov 2010), trying to put forward specific actions and measures in order to reverse the now dramatic trend undergone by the species during the previous 20 years in most of its range. In 2011, a rapid assessment of the implementation of such measures revealed that almost none of the targets of the draft SAP from 2001 had been achieved, and recommended revising the conservation status category of

the species, as well improving implementation of measures throughout the whole range of the species (Barov and Derhé 2011).

Twenty-three years after the 1997 workshop, the situation of the little bustard in Europe has worsened, mainly as a result of continuing destruction of favourable habitats (particularly after the suppression of CAP mandatory fallows after 2008, Traba and Morales 2019), and increasing agricultural intensification at field and landscape scales (to be described in this volume). Results of the second Spanish census of the species, carried out during 2016, revealed a dramatic decline in its main stronghold in Western Europe, with a reduction of 50% in just 10 years (García de la Morena et al. 2018; see also chapter "The little bustard around the world: distribution, global conservation status, threats and population trends"). Wintering censuses showed very similar trends (García de la Morena et al. 2018), as well as an extremely worrying bias in sex-ratio. Indeed, all factors already mentioned in the first draft of the SAP (De Juana 2001) threatening little bustard populations are still active (Morales et al. 2015). Main measures aimed at improving the conservation status of the little bustard were related to land-use policy and modifications of the CAP (Barov and Derhé 2011). However, as necessary as they are, their implementation in a multinational context has proved difficult, due both to the complexity of European legislation and to national particularities. As a consequence, land management measures addressing little bustard conservation have been of limited success, especially outside protected areas. And currently all countries in the Western Palearctic have seen either sharp declines or extinction of the little bustard over the last 75 years, some of them quite recent, like extinctions in north Africa and continental Italy (Morales and Bretagnolle 2021). However, some successful conservation projects were implemented during that period, which provides some hope.

When a species is declining rapidly, there is in general an increase in research effort, both on the causes of decline and on basic breeding biology (to better target conservation effort). The little bustard is no exception. Almost nothing was known of its breeding biology, either in France or in Spain, in the 1980s. Then, following some pioneering studies (e.g. Schulz 1985; De Juana and Martínez 1996; Salamolard and Moreau 1999), the interest in the species has significantly grown, as shown by the papers published in scientific journals (Fig. 1).

Beside conservation issues, the little bustard is an interesting study model for its rather unusual mating system, its suitability to study aspects of sexual selection given its features intermediate between classical leks and resource-based polygyny, and its rather complex habitat requirements and migration patterns (Collar et al. 2016). The biological interest of the little bustard has stimulated a good deal of basic and applied research, as summarized below and displayed throughout this book. The interest is regionally biased, however, as studies carried out in Spain account for nearly 44% of the total number of published papers, France 21% and Portugal 20% (Table 1). This geographic bias is even higher when considering that 89% of the literature comes from the western range of the species, while only 11% comes from countries in the eastern range, which highlights the knowledge gap regarding eastern populations and the need to fill it. In a literature survey aimed at identifying priorities

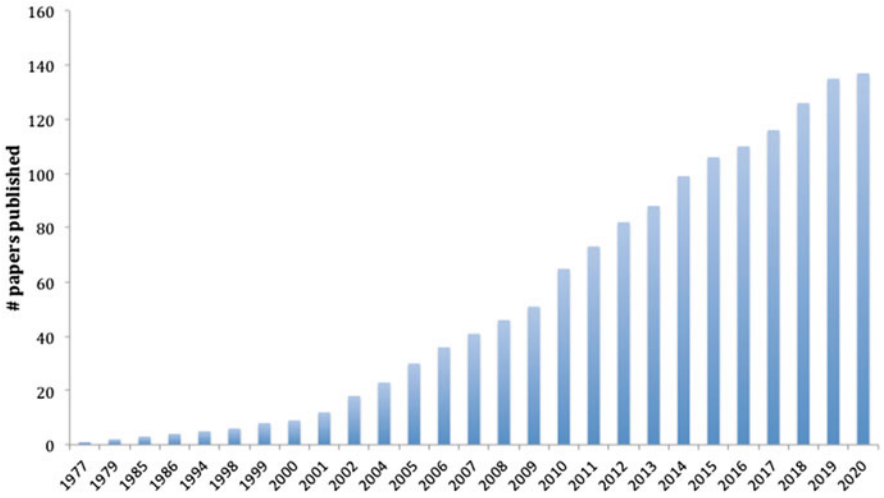

Fig. 1 Cumulative number of published papers per year (1977–2019) about little bustard *Tetrax tetrax* in scientific journals until 2019. Source search: Web Of Science (WOS) with keyword: "little bustard" (updated April 2020)

Table 1 Number of papers published per country between 1978 and 2019

	N studies	%	Distribution range
Azerbaijan	1	0.7	East
Europe	2	1.5	West
France	29	21.2	West
Iran	2	1.5	East
Italy	2	1.5	West
Morocco	1	0.7	West
Portugal	28	20.4	West
Romania	1	0.7	East
Russia	11	8.0	East
Spain	60	43.8	West

Same source as Fig. 1

in conservation-oriented research about steppe birds in Spain, Morales and Traba (2016) considered that little bustard had received a level of scientific attention consistent with its conservation status as Vulnerable in Spain. Research on little bustard has covered all major topics, including population sizes, habitat selection, habitat management, agri-enviromental schemes associated with the CAP and its effects on the species, movements, food requirements, breeding biology and behaviour. In addition, a rather high number of PhD theses have been defended in recent years (Table 2). As a consequence of this collective effort, our knowledge about the basics of the species and its requirements is high enough to propose and implement science-based conservation measures.

Table 2 Number and dates of PhD thesis dedicated to little bustard

Country	Author	Year
France	Frédéric Jiguet	2001
France	Axel Wolf	2001
France	Alex Villers	2010
France	Pierrick Devoucoux	2014
Spain	Paula Delgado	2009
Spain	Anna Ponjoan	2012
Spain	Rocío Tarjuelo	2015
Spain	Eladio L. García de La Morena	2016
Spain	Francesc Cuscó	2019
Portugal (though defended in Germany)	Holger Schulz	1985
Portugal	Joao Paulo Silva	2010
Portugal (though defended in Spain)	Nuno Faria	2015

It was therefore time to synthesize all this breadth of information. The idea of writing this book first came in 2006, when an international workshop was organized in Chizé at the end of the second French LIFE project. Then, Vincent Bretagnolle and Manuel B. Morales thought about writing a monograph on Western Palearctic bustards. However, the idea did not develop, but was never entirely dropped. So, when Beatriz Arroyo and Jesús T. García, as editors of the Wildlife Research Monographs Series, suggested that we could perhaps think of such a book, but focused on little bustard, a very rapid decision was made between all of us: go ahead. It took however 2 further years to gather all authors, write and review the 12 chapters forming the core of this volume.

This book collects, reports and updates all the available information on the species, putting everything together in a comprehensive and compact volume. It starts with a necessary full review of the Otididae family, including origins, phylogeny and systematics (chapter "The little bustard and its family: an overview of relationships") and continues with two general chapters about life history traits (chapter "Natural history of the little bustard: morphology, biometry, diet, sexual dimorphism, and social and breeding behaviour") and the most updated data about distribution, global conservation status, threats and population trends (chapter "The little bustard around the world: distribution, global conservation status, threats and population trends"). Chapter "Breeding biology and demographic traits: population parameters, reproduction and survival" deepens our knowledge of breeding biology, providing recent and novel results about nesting phenology, clutch size, mating system, sex-ratio, productivity and survival rates. Some of these demographic parameters, which are key for population viability, seem to be severely skewed (sex-ratio) or show poor values (productivity), critically affecting recruitment and long-term persistence (see also chapter "Little bustard population dynamics"). The low availability and quality of preferred habitats is behind this poor demographic performance, as the little bustard is a specialist of natural and agrarian steppes and grasslands. Chapter "Habitat selection and space use" makes a thorough revision of habitat selection at large and local scales. Post-breeding movements and migration,

which show differences among individuals and populations, are analysed in chapter "Migration, movements and non-breeding ecology". All other aspects relating to behavioural ecology, such as sexual display, mate choice, territoriality and personality traits, are included in chapter "Behavioural ecology of the little bustard: sexual selection and mating systems". Interspecific relationships, including predation, competition with coexisting birds and the effects of parasites, are treated in chapter "Interspecific relationships: predation, competition or coexistence, parasites". Chapter "Captive breeding, handling and care, and the impact of releases on wild populations" evaluates the experience of captive breeding and population reinforcement carried out in France. This chapter also provides useful information about individual handling (capture and tagging). Chapter "Little bustard population dynamics" aims to evaluate population viability, highlighting the effect of key demographic parameters (see above) as well the effects of density dependence, and to explore the causes of adult and chick mortality and dispersal (natal and adult). The relationships of the species with humans are analysed in the next two chapters: chapter "Threats affecting little bustards: human impacts" is centred on threats, reviewing the general causes of the species' decline, as well as recent results about anthropogenic disturbance and stress responses. Chapter "Little bustard and humans: conservation and management" makes a thorough review of conservation initiatives specifically addressing the species, including protected areas, agri-environmental schemes, action plans and LIFE projects. It provides some insights for the European CAP regulations after 2020 to improve the conservation status of the little bustard: mainly, agrarian extensification and the maintenance of fallows, set-asides and grazed pastures, which means a drastic reduction in the application of agrochemicals. Chapter "Conclusions and perspective" summarizes the main conclusions of the book and provides a general prospectus of the species' future.

At this very moment, in winter 2021, there is no doubt about the critical status of the species and the urgent need to undertake major conservation measures. At the time of writing these lines, the little bustard has been included in Appendix I of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), which requires parties to the convention to provide it with the strictest protection. In Spain, an academic initiative has drafted the National Conservation Strategy of the species, in the hope of facilitating public administrations to evaluate periodically the status and viability of the population, its distribution changes, habitat extent and quality and risk factors, and successfully requested the re-listing of the species as "Endangered" in Spain. So far, too few national and international initiatives have been implemented, perhaps with the exception of some LIFE projects in France and Portugal. We hope this book, by providing the most up-to-date review of knowledge of the biology, threats and conservation initiatives for the little bustard all over the world, will boost new projects and management programmes. The decline of little bustard is an allegory of the dramatic decay of natural and agrarian steppes in Europe, and probably in the rest of the world. Little bustard is a recipient not only of the usual threats to agricultural systems, such as agricultural intensification, but also of new ones, such as the expansion of large solar photovoltaic and wind energy installations. The little bustard is an ecological umbrella species; but we confidently feel it is also a conservation umbrella species, representing many others showing the

same or even worse trends, perhaps even better than other famous species (Tarjuelo et al. 2014), as its specific habitat requirements match those of other threatened steppe birds such as pin-tailed and black-bellied sandgrouse (*Pterocles alchata* and *P. orientalis*), Eurasian stone-curlew (*Burhinus oedicnemus*), great bustard (*Otis tarda*), Montagu's harrier (*Circus pygargus*) and several passerines (Morales and Bretagnolle 2021). The conservation of the little bustard means the conservation of the steppe bird community and their habitats. It has to be now.

To end, we the editors wish to thank the numerous researchers, from many countries and institutions, who have contributed selflessly to this book. Similarly, every chapter has been revised by external reviewers, to which we want to extend our thanks. Nigel Collar, besides being the main author of chapter "The little bustard and its family: an overview of relationships", made a thorough English revision of the book, and made many important comments. Nigel has also been keen on bustard conservation worldwide, a leader in bird conservation and BirdLife International, and has inspired all of us for the many years we have spent in bustard conservation. We owe him a particular thank you.

References

Barov B, Derhé M (2011) Review of the implementation of species action plans of threatened birds in the European Union (2004–2010). BirdLife International

Collar NJ, Garcia EFJ, De Juana E (2016) Little bustard (*Tetrax tetrax*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, De Juana E (eds) Handbook of the birds of the world alive. Lynx Edicions, Barcelona

de Juana E (2001) European species action plan. Little Bustard *Tetrax tetrax*: draft action plan. BirdLife International, Cambridge

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

García de la Morena EL, Bota G, Mañosa S, Morales MB (2018) El sisón común en España. II Censo Nacional (2016). SEO/BirdLife, Madrid

Iñigo A, Barov B (2010) Action plan for the Little Bustard Tetrax tetrax in the European Union. SEO/BirdLife and BirdLife International for the European Commission

Morales MB, Bretagnolle V (2021) An update on the conservation status of the Little Bustard Tetrax tetrax: global and local population estimates, trends, and threats. Bird Conserv Int:1–23. https://doi.org/10.1017/S0959270921000423

Morales MB, Traba J (2016) Prioritizing research in steppe bird conservation: a literature survey. Ardeola 63:5–18

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

Salamolard M, Moreau C (1999) Habitat selection by Little Bustard *Tetrax tetrax* in a cultivated area of France. Bird Study 46:25–33

Schulz H (1985) A review of the world status and breeding distribution of the Little Bustard. Bustard Stud 2:131–151

Tarjuelo R, Morales MB, Traba J, Delgado MP (2014) Are species coexistence areas a good option for conservation management? Applications from fine scale modeling in two steppe birds. PLoS One 9:e87847

Traba J, Morales MB (2019) The decline of farmland birds in Spain is strongly associated to the loss of fallow-land. Sci Rep 9:9473

The Little Bustard and Its Family: An Overview of Relationships

Nigel J. Collar and Manuel B. Morales

The Bustard Family: General Traits

The little bustard belongs to the Otididae, a distinctive Old World family of non-passerine birds known in English as bustards, floricans and korhaans, and comprising (by the most recent taxonomic arrangement) 26 species in 12 genera (del Hoyo and Collar 2014; see Table 1 for some of their basic morphological, biological and ecological traits). The earliest presumed bustard fossil dates from the Middle Eocene (48–38 million years ago) (Olson 1985), although now-discredited DNA–DNA hybridisation techniques suggested the family arose as many as 77 million years ago (Sibley and Ahlquist 1985).

Members of the bustard family share a range of features which, in combination, are fully diagnostic, involving moderate to very large body sizes, rather long necks and legs, relatively short bill (never more than the length of the head), powder-down and photoreactive porphyrins at the base of feathers, no uropygial gland, no hind toe (hence no ability to perch in trees) and nidifugous young. They occupy habitats from dry open woodland and high scrub through savanna and steppe to semi-desert and the fringes of desert, based mainly in Africa: the genera *Lissotis* (two species), *Neotis* (four species), *Lophotis* (three species), *Heterotetrax* (three species), *Afrotis* (two species) and *Eupodotis* (two species) are confined to the Afrotropical region, while

N. J. Collar (✉)
BirdLife International, Cambridge, UK

Bird Group, Natural History Museum, Tring, UK
e-mail: Nigel.Collar@birdlife.org

M. B. Morales
Terrestrial Ecology Group, Departamento de Ecología and Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain
e-mail: manuel.morales@uam.es

V. Bretagnolle et al. (eds.), *Little Bustard: Ecology and Conservation*, Wildlife Research Monographs 5, https://doi.org/10.1007/978-3-030-84902-3_2

Table 1 Some basic morphological, reproductive and ecological traits of bustard species

Common name	Scientific name	Authority	Weight (g) males/females	Height (cm) males/ females	Clutch size	Distribution	Main habitat	Diet	IUCN Red List category
Little bustard	*Tetrax tetrax*	Linnaeus, 1758	761–1012/ 680–945	43/43	2–6	Eurasia and N Africa	Steppe, pasture-land, cereal farmland	Mainly herbivo-rous, insectivorous in breeding	NT (2018)
Great bustard	*Otis tarda*	Linnaeus, 1758	5800–18,000/ 3300–5300	105/75	2–4	Eurasia and N Africa	Steppe, pasture-land, cereal farmland	Mainly herbivo-rous, insectivorous in breeding, also small vertebrates	VU (2017)
African houbara	*Chlamydotis undulata*	Jacquin, 1784	1800–3200/ 1200–1700	65–75/ 55–65	1–3	N Africa and Canary Islands	Semi-desert, shrub-steppe	Mixed insectivo-rous-herbivorous	VU (2016)
Asian houbara	*C. macqueenii*	Gray, 1832	1500–3175/ 1100–1250	65–75/ 55–65	2–5	Middle East and C Asia	Shrub-steppe, semi-desert, desert	Mixed insectivorous-herbivorous, also small vertebrates	VU (2016)
Hartlaub's bustard	*Lissotis hartlaubii*	Heuglin, 1863	1500–1600/–	60/–	–	E Africa	Grassland and savanna	Mixed insectivo-rous-herbivorous	LC (2016)
Black-bel-lied bustard	*L. melanogaster*	Rüppell, 1835	1800–2700/ 1400	60/60	1–2	W, C, E and SW Africa	Grassland, savanna, open woodland, pas-tureland and farmland	Mainly insectivo-rous, complemented with plants	LC (2016)
Ludwig's bustard	*Neotis ludwigii*	Rüppell, 1837	4200–6000/ 2200–2500	85/–	2	SW Africa	Semi-desert, arid grassland	Mixed insectivorous-	EN (2016)

								herbivorous, also small vertebrates	
Denham's bustard	*N. denhami*	Children & Vigors, 1826	9000–10,000/ 3000	100/80	1–2	W, C, E and S Africa	Grassland, savanna and open woodland	Mixed insectivorous-herbivorous, also small vertebrates	NT (2016)
Heuglin's bustard	*N. heuglinii*	Hartlaub, 1859	4000–8000/ 2600–3000	–/–	2	Kenya and Horn of Africa	Desert, semi-desert, arid grassland	Mixed insectivorous-herbivorous, also small vertebrates	LC (2016)
Nubian bustard	*N. nuba*	Cretzschmar, 1826	5400/–	70/50	2	Sahel	Semi-arid scrub-land and savanna	Mixed insectivo-rous-herbivorous	NT (2016)
Arabian bustard	*Ardeotis arabs*	Linnaeus, 1758	5700–10,000/ 4500	100/75	1–2	Sahel and SW Arabia	Semi-desert, arid grasslands, savanna	Mixed insectivorous-herbivorous, also small vertebrates	NT (2018)
Kori bustard	*A. kori*	Burchell, 1822	10,900–19,000/ 5900	120/90	1–2	E and S Africa	Open grassland and savanna	Mixed insectivorous-herbivorous, also small vertebrates	NT (2016)
Great Indian bustard	*A. nigriceps*	Vigors, 1831	8000–14,500/ 3500–6750	120/90	1–2	N and C India	Semi-desert, open and wooded grassland	Mixed insectivorous-herbivorous, also small vertebrates	CR (2018)
Australian bustard	*A. australis*	Gray, 1829	4300–9300/ 2400–4200	120/90	1–2	N, W and C Australia and S New Guinea	Grasslands, semi-desert and savanna	Mixed insectivorous-herbivorous, also small vertebrates	LC (2016)
Bengal florican	*Houbaropsis bengalensis*	Gmelin, 1789	1250–1700/ 1700–2250	64/68	1–2	S Nepal and N India	Moist grassland, pastureland	Mixed insectivorous-	CR (2018)

(continued)

Table 1 (continued)

Common name	Scientific name	Authority	Weight (g) males/females	Height (cm) males/ females	Clutch size	Distribution	Main habitat	Diet	IUCN Red List category
								herbivorous, also small vertebrates	
Lesser florican	*Sypheotides indicus*	Miller, 1782	450/–	46/51	3–5	India	Grassland, scrub-land and farmland	Mixed insectivorous-herbivorous, also small vertebrates	EN (2016)
Savile's bustard	*Lophotis savilei*	Lynes, 1920	–/–	42	–	Sahel	Arid scrubland and savanna	Unknown	LC (2016)
Buff-crested bustard	*L. gindiana*	Oustalet, 1881	675–900	50	1–2	E Africa	Arid scrubland	Mixed insectivo-rous-herbivorous	LC (2016)
Red-crested bustard	*L. ruficrista*	Smith, 1836	680	50	1–2	E Angola to S Mozambique and N South Africa	Dry grassland, scrubland and savanna	Mixed insectivo-rous-herbivorous	LC (2016)
Karoo bustard	*Heterotetrax vigorsii*	Smith, 1831	1600/1350	60	1–2	SW Africa (Cape Province)	Desert and semi-desert	Mainly herbivo-rous, complemented with arthropods	LC (2016)
Rüppell's bustard	*H. rueppelii*	Wahlberg, 1856	–/–	60	1	SW to NW Namibia	Desert and semi-desert	Mixed insectivorous-herbivorous, also small vertebrates	LC (2016)
Little brown bustard	*H. humilis*	Blyth, 1856	700	40	2	Horn of Africa	Semi-desert, arid grassland	Mixed insectivo-rous-herbivorous	NT (2016)
	Afrotis afra		700	50	1–2	Cape region			

Southern black bustard		Linnaeus, 1766					Semi-arid scrubland and farmland	Mixed insectivorous-herbivorous	VU (2016)
Northern black bustard	*A. afraoides*	Smith, 1831	700	50	1–2	Inland S Africa	Desert, semi-desert, dry grassland and savanna	Mainly insectivorous, complemented with plants	LC (2016)
White-bellied bustard	*Eupodotis senegalensis*	Vieillot, 1820	1400–1500/ <1400	50–60/ <50	1–3	Sahel, C, E and S Africa	Grassland and savanna, farmland	Mixed insectivorous-herbivorous	LC (2016)
Blue bustard	*E. caerulescens*	Vieillot, 1820	1120–1612	55	1–3	SE Africa	Grassland, pastureland, farmland	Mixed insectivorous-herbivorous, also small vertebrates	NT (2017)

Data are compiled from Collar et al. (1986), superseded by Ziembicki (2010) for Australian bustard, Cramp and Simmons (1980) for Asian houbara and various sources (including M.B. Morales own data) for little bustard. The most recent classification in IUCN world conservation status categories is also presented, along with year of last assessment in parentheses (IUCN Red List; *CR* Critically Endangered, *EN* Endangered, *VU* Vulnerable, *NT* Near Threatened, *LC* Least Concern)

Ardeotis has two species in the Afrotropics (one penetrating the Arabian peninsula), one in the Indian subcontinent and one in Australia and southernmost New Guinea. The monotypic *Tetrax* and *Otis* plus *Chlamydotis* (two species) are Palearctic, but all have populations in North Africa; only *Sypheotides* and *Houbaropsis* occur entirely outside Africa, both in the Indian subcontinent but the latter also in Cambodia (Table 1).

Phylogenetic Relationships and Life-History Traits

Unsuspected Relatives

Increasingly confident broad-scale studies of the relationships of birds have in the past 10 years redefined the longstanding working assumption in avian taxonomy that bustards are part of or close to the Gruiformes (cranes, crakes and various allies). Hackett et al. (2008) located '*Choriotis*' (= *Ardeotis*) and *Eupodotis* between *Opisthocomus* (Hoatzin) and the Cuculiformes (cuckoos), with 'Gruiformes' (sic, in inverted commas) sister to Cuculiformes and with Musophagiformes (turacos) also distantly indicated. Building on this, McCormack et al. (2013) found 'surprisingly close relationships between phenotypically divergent bird families, such as bustards (Otididae) and turacos (Musophagidae)'. Moreover, Prum et al. (2015) produced a cladogram which inserts *Ardeotis* between the turacos and the cuckoos in what they call an 'Otidimorph' clade, sister to a 'Columbimorph' clade of mesites, sandgrouse and pigeons and grouping with these latter in a wider category named 'Columbaves', this being sister to Gruiformes on the one side and to 'Strisores' (nightjars, hummingbirds, swifts) on the other. These are unsettling findings: the notion that bustards are potentially closest to such ecologically and phenotypically divergent birds as cuckoos and turacos is very hard to credit, but the evidence appears to be consistent (Jetz et al. 2012; Jarvis et al. 2014; Prum et al. 2015).

An Unresolved Family Tree

No satisfactory molecular phylogeny of the Otididae has been published, and the work that has been done to date leaves as many questions as answers over the relationships of the species. Two papers appearing within a year of each other have been the only contributions that address the family as a taxonomic entity. Pitra et al. (2002), using both mitochondrial (cytochrome b, cyt_b, for all taxa, and control region for a subset of 10 taxa) and nuclear (CHD1_Z intron, for 9 taxa) evidence, sampled the most species, only missing two (*Heterotetrax humilis* and *H. vigorsii*). Based on cyt_b evidence, they found that the genera *Neotis* and *Ardeotis* did not separate out into two clades; in their tree *Neotis heuglinii* sits between the two Afrotropical *Ardeotis* and the two from Asia and Australia (the latter two are very

similar but structurally very distinct from the Afrotropical species, and very possibly merit their own genus); the two *Lissotis* were sister to the clade with *Neotis* and *Ardeotis*. In a separate clade from all these came *Otis* and *Chlamydotis*, as sisters, along with *Afrotis* and *Eupodotis* (sensu del Hoyo and Collar 2014); *Houbaropsis* and *Sypheotides* were—albeit not closely—related to each other and together were sister to *Lophotis*, while *Tetrax* emerged as an isolated form but sister to the previous three genera. Most unexpectedly and inexplicably, *Eupodotis* (now *Heterotetrax*) *rueppelii* was recovered as basal to all other bustards.

Broders et al. (2003) used only the cytochrome *b* gene to determine the relationships of seven genera, but the sequences were more than twice as large as Pitra et al. (2002), i.e. 1143 bp instead of 444. They also found that *Otis* and *Chlamydotis* cluster together, and again detected a link between *Lophotis* and *Tetrax*. However, in their tree *Afrotis* emerged as basal to the other taxa studied, while *Eupodotis* (now *Heterotetrax*) *rueppelii* was sister to *Ardeotis* (at least the two Afrotropical species); they judged that *rueppelii*'s anomalous position in the Pitra tree was probably attributable to degraded DNA or a mislabelled sample. However, *Eupodotis senegalensis* emerged as the next closest relative of *Afrotis* and far from *E. rueppelii*, and for this reason Broders et al. suggested the adoption of *Heterotetrax* for *rueppelii* and its relatives (a proposal followed by Dickinson and Remsen 2013; del Hoyo and Collar 2014).

It is the inconsistencies rather than the consistencies between these two studies that matter; they undermine the confidence with which any of the findings can be treated. Regrettably this did not trigger a more comprehensive review of the family, but one further piece of work produced another unexpected result. In seeking to add *Heterotetrax humilis* to the Pitra et al. tree, and using the same sequence and bp length from cytochrome b as in that study, Horreo et al. (2014) discovered that much its closest relative was *Tetrax* rather than other *Heterotetrax*. The authors therefore speculated that these two species, very different phenotypically, shared a recent common ancestor and that the distinct sexual plumage dimorphism in *Tetrax* must have evolved over a very short period of time (riskily inferring that 'many of the phenotypic traits used to classify members of the Otididae are not phylogenetically informative'). However, they also wisely concluded that errors in process may have occurred and 'further analyses including additional sequence from unlinked nuclear genome markers will be necessary to confirm phylogenetic relationships in the family Otididae'. Figure 1 compiles the phylogenies, respectively, produced by Pitra et al. (2002), Broders et al. (2003) and Horreo et al. (2014), highlighting the position of the little bustard in each tree.

In fact, advances of this type had already been made, but the results have so far remained unpublished except as a PhD thesis. Cohen (2011) used mitochondrial and nuclear DNA (5341 nucleotide bp; three mitochondrial markers: cyt_b, NADH, Ctr_II; five nuclear markers: Fib5, TGFB,GAPDH, ODC, CHD1Z) as well as a morphological/behavioural dataset of 'all 27 species of Otididae' (he recognised *Eupodotis senegalensis barrowii* as a full species) to arrive at a series of alternative but largely complementary conclusions concerning the relationships of the bustards, synthesised in a consensus phylogenetic tree, reproduced in Fig. 2. In his phylogeny

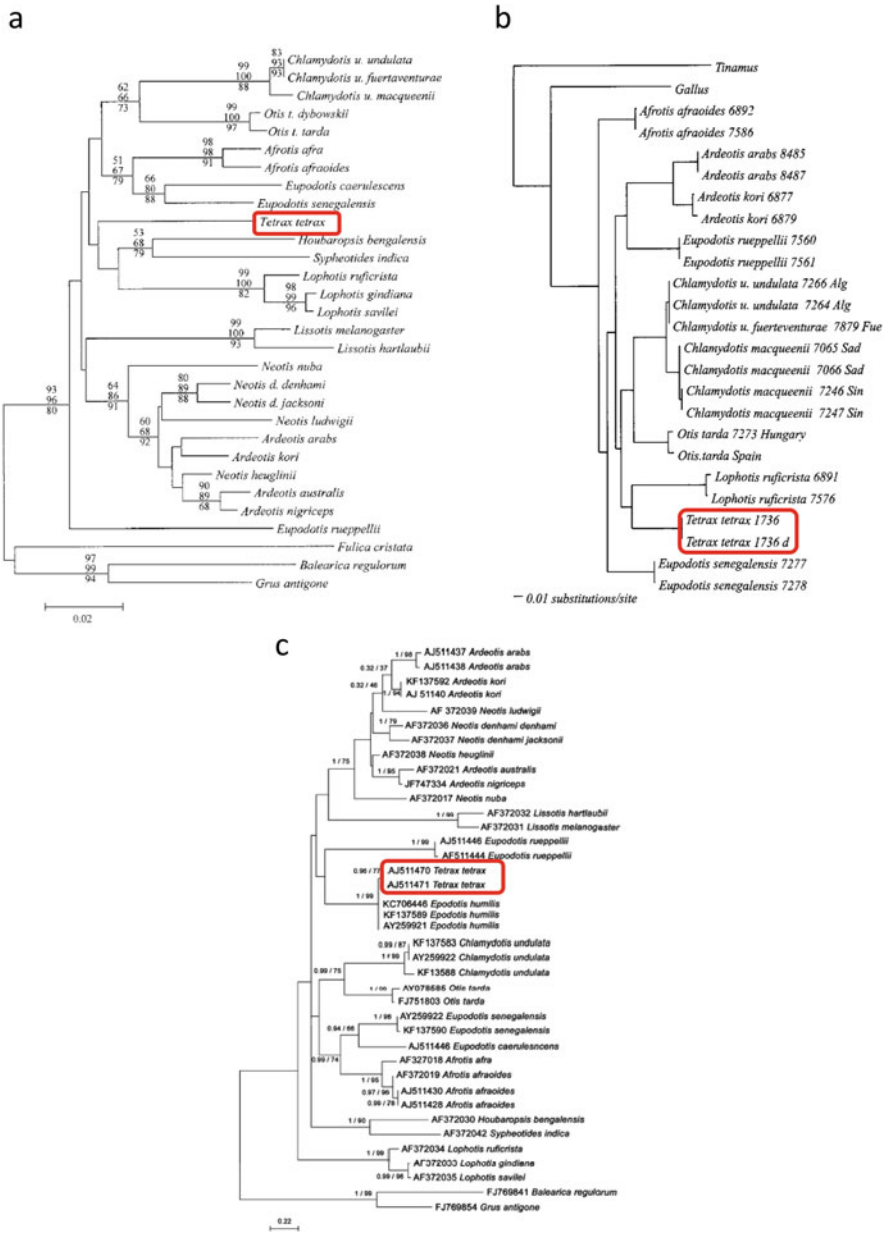

Fig. 1 Compilation of three phylogenetic trees of the Otididae using the mitochondrial cyt_b marker, highlighting the position of the little bustard in each phylogeny. Composed figure based on Pitra et al. (2002) (**a**), Broders et al. (2003) (**b**) and Horreo et al. (2014) (**c**). See text for marker sequence details. In tree (**c**) '*Epodotis*' should be read '*Eupodotis*'

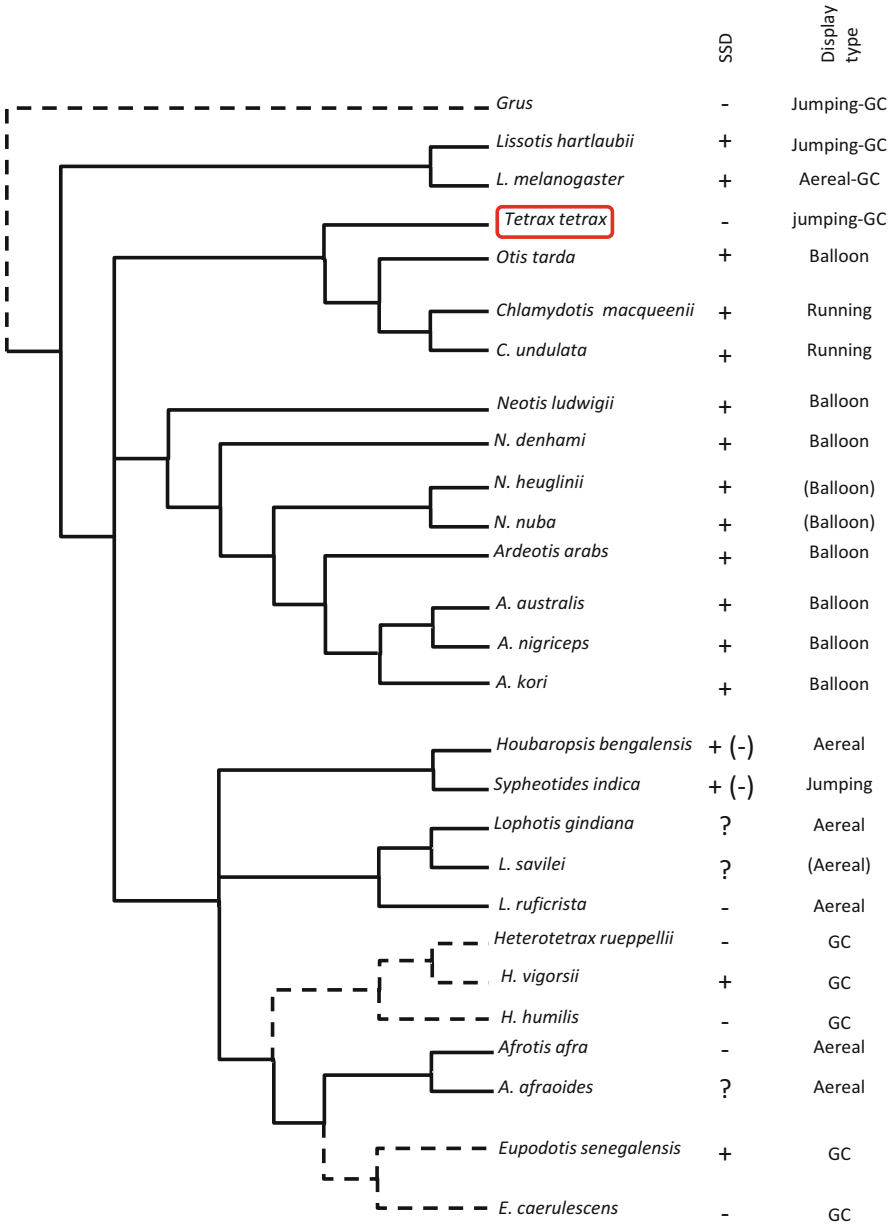

Fig. 2 Variation of sexual size dimorphism (SSD; present: +, absent: −), type of sexual display (GC = ground-calling) and mating strategy across the bustard phylogenetic tree (based on the consensus phylogeny provided by Cohen 2011, see text for details). On the basis of values provided in Table 3, a species is considered dimorphic when the percentage difference is larger than 10% for body weight and/ or larger than 5% for wing length (see Höglund 1989). Cases of inverse SSD (females larger than males) are indicated as (−), while interrogation marks denote lack of information. Solid branches indicate polygynous (i.e. exploded lek) lineages, while dashed branches denote monogamous lineages. The position of the little bustard in the tree is highlighted

Table 2 Position of genus *Tetrax* in bustard phylogeny according to existing studies

Source	Position in phylogenetic tree	Closest genera
Pitra et al. (2002)	Derived isolated single-genus clade	*Houbaropsis*, *Sypheotides*, *Lophotis* forming sister clade
Broders et al. (2003)	In small clade sister to large one formed by *Ardeotis*, *Heterotetrax rueppelii*, *Chlamydotis* and *Otis*	*Lophotis* as sister genus in clade
Cohen (2011)	In small basal clade	*Otis* and *Chlamydotis* in sister sub-clade
Horreo et al. (2014)	In small derived clade sister to *H. rueppelii*	*Heterotetrax humilis* as sister in clade

Sources are ordered chronologically

Lissotis tended to emerge as basal, *Tetrax* (highlighted) grouped with *Otis* and *Chlamydotis*, *Neotis* and *Ardeotis* again failed to emerge as two separate lineages, and the split between *Eupodotis* and *Heterotetrax* was upheld, albeit with *H. humilis* proving close to both *H. rueppelii* and *H. vigorsii* and having nothing to do with *Tetrax*. Table 2 summarises the different positions of *Tetrax*, the genus of our subject species, assigned in the four phylogenetic studies reviewed here.

Yang et al. (2010) sequenced the whole mitochondrial genome (16,849 bp) for *Otis tarda*, and used 12S, 16S and VAL sequences on four other bustard species to produce a tree, in which *Tetrax tetrax* was basal. The sequence of species generated by Pitra et al. (2002) formed the basis for the treatment of the family in Dickinson and Remsen (2013), whereas Cohen's (2011) multiple arrangements were used to decide the sequence in del Hoyo and Collar (2014). This latter places the little bustard first, implying a basal position. Next to it is the great bustard *Otis tarda*, reaffirming a relationship that was expressed for many decades by the frequent placement of little bustard in *Otis* (an assuredly mistaken habit which persisted into the 1970s; see, e.g., Harrison 1978). These two species share several characteristics: a relatively short bill with distinctly decurved upper mandible, a proportionately rather less elongate neck and slightly shorter legs than in other species, stockier, less tapered build, marked seasonal sexual plumage dimorphism, and largely overlapping herb-rich steppeland/farmland habitats and distributions. They diverge sharply in their self-advertisement behaviour (Table 3 and Fig. 2), the little bustard performing a striking but little-known display that involves accelerating food-stamping, a little leap, wing-flash and simultaneous call from a small prepared display-point in low light conditions (see chapter 'Natural history of the little bustard: morphology, biometry, diet, sexual dimorphism, and social and breeding behaviour'), the great bustard undertaking a celebrated 'balloon-display' with extraordinary contortions of wings and tail at various apparently random points within a lekking ground (see, for example, Cramp and Simmons 1980).

The African Houbara *Chlamydotis undulata* and Asian Houbara *C. macqueenii*, clearly very closely related to each other, replace the great and little bustard in the more arid areas of the Palearctic. There is some potential for temporary sympatry

Table 3 Degree of body weight and wing length sexual dimorphism, dominant mating system and type of courtship display in bustard species

Species		Weight dimorphism (%)	Wing length[a] dimorphism (%)	Mating system	Type of display[b]
Common name	Scientific name				
Little bustard	*Tetrax tetrax*	9.11[c, d]	0.99	Exploded lek[e]	Jumping and ground-calling
Great bustard	*Otis tarda*	176.74[c]	21.26	Exploded lek[f]	Balloon
African houbara	*Chlamydotis undulata*	72.41[c]	8.7	Exploded lek[e, g]	Running
Asian houbara	*Chlamydotis macqueenii*	72.41[c]	8.7	Exploded lek[h]	Running
Hartlaub's bustard	*Lissotis hartlaubii*	–	7.4	(Exploded lek)[e]	Aerial and ground-calling
Black-bellied bustard	*L. melanogaster*	60.71[c]	8.26	Exploded lek[e]	Aerial and ground-calling
Ludwig's bustard	*Neotis ludwigii*	56.92[c]	15.97	Exploded lek[e]	Balloon
Denham's bustard	*N. denhami*	216.67[c]	17.35	Exploded lek[e]	Balloon
Heuglin's bustard	*N. heuglinii*	114.29[c]	14.53	Exploded lek[e]	(Balloon)
Nubian bustard	*N. nuba*	–	15.25	(Exploded lek)[e]	(Balloon)
Arabian bustard	*Ardeotis arabs*	74.44[c]	13.04	(Exploded lek)[e)]	Balloon
Kori bustard	*A. kori*	77.12[i]	16.12[i]	Exploded lek[e]	Balloon
Great Indian bustard	*A. nigriceps*	119.51[c]	27.00	Exploded lek[e]	Balloon
Australian bustard	*A. australis*	106.06[c]	11.5	Exploded lek[j]	Balloon
Bengal florican	*Houbaropsis bengalensis*	−25.32[c]	−19.04	Exploded lek[e]	Aerial
Lesser florican	*Sypheotides indica*	–	−6.38	Exploded lek[e]	Jumping
Savile's bustard	*Lophotis savilei*	–	–	(Exploded lek)[e]	(Aerial)
Buff-crested bustard	*L. gindiana*	–	–	(Exploded lek)[e]	Aerial
Red-crested bustard	*L. ruficrista*	–	2.91	Exploded lek[e]	Aerial

(continued)

Table 3 (continued)

Species		Weight dimorphism (%)	Wing length[a] dimorphism (%)	Mating system	Type of display[b]
Common name	Scientific name				
Karoo bustard	*Heterotetrax vigorsii*	18.52[c]	6.5	Monogamy[e]	Ground-calling
Rüppell's bustard	*H. rueppelii*	–	4.76	Monogamy[e]	Ground-calling
Little brown bustard	*H. humilis*	–	1.96	Monogamy[e]	Ground-calling
Southern black bustard	*Afrotis afra*	–	3.03	Exploded lek[e]	Aerial
Northern black bustard	*A. afraoides*	–	–	(Exploded lek)[e]	Aerial
White-bellied bustard	*Eupodotis senegalensis*	–	8.26	Monogamy[e]	Ground-calling
Blue bustard	*E. caerulescens*	–	0.99	Monogamy[e]	Ground-calling

Degree of dimorphism is calculated as the percent increase of male relative to female body weight. Data used for weight calculations are the median of male and female weight ranges provided in Table 1, while those for wing length are based on Johnsgard (1994), except for the case of Kori bustard, which are provided by Osborne and Osborne (1998). Dashes denote insufficient information for dimorphism calculation. Parentheses in mating system and display type categories indicate only (educated) guessed information

[a]Johnsgard (1994)
[b]Osborne et al. (1984)
[c]Collar et al. (1986)
[d]M. B. Morales unpublished data
[e]Corresponding reference in Morales et al. (2001)
[f]Morales and Martin (2002)
[g]Hingrat and Jalme (2005)
[h]Riou and Combreau (2014)
[i]Osborne and Osborne (1998)
[j]Ziembicki (2010)

between members of these four species in places, but the ecological niche of *Chlamydotis* is distinct; the ability of bustards to survive without water is particularly marked in these two species and in their Sahelian equivalent the Nubian bustard *Neotis nuba* Collar et al. (1986). Male *Chlamydotis* perform a remarkable self-advertising display in which they erect their black-and-white neck-side ruffs so that these billow over the retracted head while the bird runs at speed, seemingly unable to see where it is going but in fact highly alert to the environment, in lines and circles across a considerable area of terrain (for differences in the displays of the two species, see Collar and Combreau 2017).