Differential migration of Little Bustard *Tetrax tetrax* at the fringes of its eastern range

LOUIS-PHILIPPE CAMPEAU & MIMI KESSLER

Summary: Although differential migration is widely observed in birds, including other species of bustards, it has not yet been described in the Little Bustard *Tetrax tetrax*. Using photographic evidence from 2008 to 2025, we investigate differential migration within the eastern population of Little Bustards as they move through and overwinter in countries beyond the limits of their usual wintering range in Azerbaijan, eastern Georgia and northern Iran. We find a high likelihood that these birds are of female-type plumage (*ie* adult females or juveniles of either sex) during both regular and irruptive winters, such as that of 2024/25. Using a more limited dataset of photographs in which the age of individuals is discernible, we find that this differential migration is both sex-based and age-based, with adult females and juveniles undertaking the most distant migratory movements in a 40:60 ratio. Likely increased female mortality during these journeys is expected to impact population demographics.

INTRODUCTION

Following a series of national extinctions in central and eastern Europe in the 19th and 20th centuries, the range of the Little Bustard *Tetrax tetrax* is now split between a mostly resident western population centred on the Iberian peninsula and southern France (with a small migratory population in north-west France), and a mostly migratory eastern one ranging from the Black Sea to the west of Xinjiang, China (with a small resident population in Crimea). To the best of our knowledge, different migration patterns between sexes and age classes have not been described in any Little Bustard population exhibiting migratory behaviour. Little Bustards from the eastern population have been assumed to form mixed post-breeding flocks towards the end of the summer before migrating south and congregating in larger groups on wintering grounds (Potapov & Flint 1987). In their comprehensive edited volume on the Little Bustard, Morales *et al* (2022) hinted at this knowledge gap, writing that 'although much of what we know from their movements [is] based on tagged males, there is no evidence of differential migration of the sexes, as described for other bustard species'. Indeed, in species such as the Great Bustard *Otis tarda*, which exhibits a high degree of sexual dimorphism, the much larger males are observed to winter further north than females, giving them an advantage in returning early to their breeding grounds (Wang *et al* 2023). Male Little Bustards, however, are on average only slightly heavier than the females (Bretagnolle *et al* 2022).

In their review of the status of the Little Bustard in Iraq, Syria, Lebanon and Jordan, Aidek *et al* (2025) noted that all records of hunted Little Bustards in Syria seemed to be of females or juveniles ('female-type' birds). The winter of 2024/25 saw a large irruption of Little Bustards from their eastern range with many records from outside the species' current wintering areas, from Romania and Greece to Türkiye and Israel (ebird, Özgencil *et al* 2025, Perlman 2025). The causes of these longer-than-usual movements remain unclear. A sudden change in weather patterns could account not only for irruptions but also for the record observation of 101 530 Little Bustards at the Beshbarmag bottleneck observation site in Azerbaijan on 22 October 2024 (Farajli 2024). Alternatively, high breeding productivity could account for both phenomena; if extremely low percentages of the total population occasionally reach distant wintering grounds, a greater population size would increase the numbers of birds observed there. While more research will be needed to explain these irruptions, we used the opportunity to investigate and compare sex and age ratios of overwintering Little Bustards between irruptive and non-irruptive winters, and between typical winter range states and extralimital areas.

Plate 1. Left: A juvenile Little Bustard, characterised by the contrastingly darker head-cap and scapulars against the paler beige median coverts bearing an '*x*' pattern. © *Mark Easterbrook*. Upper right: A typical adult female, uniformly darker than the juvenile, lacking the '*x*' pattern, and with a streaked breast. © *Gültekin Yazıcıoğlu*. Lower right: Adult male Little Bustard in flight, 5 May 2025, Bouches-du-Rhône, Provence-Alpes-Côte d'Azur, France. © *Yann Muzika*

METHODS

LPC systematically reviewed all photographic records of Little Bustards from a series of citizen science platforms for the winters of 2008 (the first in which photographic records were available) to 2025, including ebird.org, inaturalist.org, rombird.ro, azerbaijan.birding.day, kz.birding.day, russia.birding.day, uzbekistan.birding.day and uabirds.org. We also invited authors of papers submitted to Kessler *et al* (2025a) to share photographs (Aidek *et al* 2025, Ashoori *et al* 2025, Campbell & Kessler 2025, Özgencil *et al* 2025, Khan *et al* 2025, Ten *et al* 2025). Extralimital migrating and wintering birds were defined as those observed from October to March beyond the areas of Little Bustard mass overwintering in Azerbaijan, eastern Georgia, northern Iran, Turkmenistan and Uzbekistan. In total, 136 extralimital and 71 intralimital records were reviewed, taking care to avoid double-counts. From these, 381 extralimital (including 24 hunted) and 2320 intralimital birds were photographed with sufficient detail to characterise them as adult male or female-type.

Even in non-breeding plumage, adult male Little Bustards on the ground can be identified by a combination of finer vermiculation on their backs, clear-cut delimitation between brown chest and white belly, and larger necks/heads (Jiguet & Wolff 2000). In flight, male Little Bustards show a conspicuously shorter 7th primary, which produces a whistling sound when flying and remains surprisingly visible on photographs of large flocks in the air. Males only acquire this characteristic in July or August of their second year, well outside the seasonal range of this study. While these criteria make the separation of adult males from female-type birds relatively straightforward, differentiating between

adult females and juveniles (of both sexes) during the winter season is more difficult, with only a handful of high-quality photos showing the juvenile characters of darker head-cap and scapulars contrasting with paler face and covert feathers, combined with the distinctive 'x' pattern on the median coverts of the closed wings (Plate 1). It is almost impossible to distinguish between male and female juveniles in winter. As the quality of the photograph permitted, individuals were identified as (adult) male, female-type or unknown. A separate tally was kept for the smaller number of cases in which females and juveniles were distinguishable.

For each country, records were summed and those from winter 2024/25 totalled separately to examine patterns in ratio of males to female-type Little Bustards during that winter's remarkable irruption (Table 1). Pearson Chi-square tests with Yates's continuity correction were conducted in R (base package, v4.2.1) to assess differences in the ratio of males to female-type Little Bustards (1) between intralimital and extralimital countries during typical winters; (2) between typical and irruptive winters in extralimital areas; and (3) in intralimital areas.

RESULTS

Overall, of the 381 extralimital birds from all winters for which a determination could be made, 27 were adult males and 354 were female-types, a 0.076 male per female-type ratio (Table 1). Of these 27 males, 7 were recorded alone, with all others mixed among female-type birds. This contrasts sharply with the intralimital range, where this ratio is 0.62, based on analysis of 2320 individuals. Our analyses of the data in Table 1 yield three statistically significant results:

1. During typical winters, a bird wintering outside the species' core winter range is significantly more likely to be of female-type than one wintering within the usual limits (χ^2= 34.44, *df* = 1, *P* = <0.0001). Excluding Crimea, due to the presence of a small sedentary population, ratios in the extralimital areas during normal winters vary from a maximum of 0.43 males per female to as low as 0.077, or even 0 in many cases where males were not recorded. In contrast, during typical winters in Azerbaijan, eastern Georgia, and northern Iran—areas that regularly host large wintering flocks—we find strikingly similar ratios of between 0.66–0.7 male to female-type Little Bustards. The male to female-type ratio is lower (0.39) in Uzbekistan, in the south of which Little Bustards have only in the last two decades resumed wintering in good numbers, and to the north of which the species has only recently expanded its wintering range (Ten *et al* 2025).
2. During the irruptive winter 2024/25, the ratio of adult male to female-type Little Bustards in extralimital areas was more extreme than in typical winters (χ^2= 13.38, *df* = 1, *P* <0.0005). Moreover, decreasing ratios of adult male to female-type birds are observed in more southerly extralimital range states. Most extreme are Greece and Türkiye during the 2024/25 irruption, with 2 males recorded each for 65 and 86 female-type respectively, as well as Israel where none of the 22 Little Bustards was an adult male. Extralimital records from the irruptive winter from southern Iran and Pakistan are scarce; nevertheless, an observation in February 2025 at the Kamjan International Wetland in southern Iran was of a female-type, as are all 11 twenty-first century records of hunted Little Bustards in Pakistan (Khan *et al* 2025).
3. During the irruptive winter 2024/25, there were relatively more female-type birds on the wintering grounds in intralimital states than during typical winters (χ^2= 8.38, *df* = 1, *p* <0.01). Ratios during the irruptive winter in intralimital wintering grounds of Azerbaijan and eastern Georgia were 0.37 and 0.54, respectively. In comparison, the

ratios in the same states in typical winters were 0.66, and similar ratios were observed in northern Iran and Kazakhstan.

Table 1. Number and ratio of adult male and female-type Little Bustards per country, based on photographic evidence. Records were collected from the months October to March during the years 2008–2025. Data from winter 2024/25, an irruption year, are presented separately. Ins data = There were insufficient records to calculate a ratio. *Others include one female-type each for Austria, Croatia and Cyprus, one male for Saudi Arabia (a bird captured in unclear circumstances; Campbell & Kessler 2025), one male and one female-type for the Czech Republic, two female-types for Russia (Black Sea coast) and the United Arab Emirates and one male and three female-types for mainland Ukraine. **Crimea is reported to have a very small resident population (Kessler *et al* 2025b), but we include data from the 2024/25 irruption when Crimea received a large influx of wintering birds. ***Kazakhstan had its first winter record of a flock of 141 birds on 14 January 2024. Its population is otherwise entirely migratory.

Country	Number of records	Males		Female-types		M/Female-type ratio	
		Pre-2024	2024-5	Pre-2024	2024-5	Pre-2024	2024-5
Extralimital states							
Romania	21	5	3	33	17	0.15	0.18
Bulgaria	6	0	0	5	1	0	0
Albania	2	0	0	1	9	0	0
Greece	19	4	2	20	65	0.2	0.031
Türkiye	33	2	2	26	86	0.077	0.023
Georgia (Black Sea)	4	0	0	3	9	0	0
Syria	4	No data	0	No data	8	Ins data	0
Israel	15	2	0	12	22	0.17	0
Iran (south)	3	0	1	2	1	0	Ins data
Pakistan	10	0	0	8	3	0	0
Others*	13	3	0	7	4	0.43	0
Crimea**	6	3	0	1	11	N/A	0
Intralimital states							
Azerbaijan	16	159	44	241	120	0.66	0.37
Georgia (east)	25	481	52	730	96	0.66	0.54
Iran (north)	16	114	2	164	1	0.7	Ins data
Uzbekistan	14	27	0	69	4	0.39	Ins data
Kazakhstan***	1	7	No data	9	No data	0.78	Ins data

Discrimination of adult females from juveniles

The category 'female-type' includes not only females but also juvenile (first-winter) males. To test whether the differential migration described above occurs on the basis of age or sex, it is necessary to use the more limited set of photographs that contain sufficient level of detail to age the birds as juveniles or adults. Only 54 of the 354 female-type Little Bustards photographed across the extralimital range could be aged with a good degree of confidence. Of these, 21 were adult females and 33 were juveniles. On the intralimital wintering grounds, there is a lack of good quality photographs allowing reliable identification of age.

DISCUSSION

Through this review of photographic evidence, we find that within the eastern range, Little Bustards observed on extralimital wintering grounds are mostly female-type. Data from a smaller subset of photographs indicate that roughly 40% of these female-type birds are adult females. The trend towards female-type bias on extralimital wintering grounds was exaggerated during the irruptive winter of 2024/25. These demographic patterns are consistent with observations of differential migration and irruption in other bird species, in that males and adults typically overwinter closer to breeding sites (Gauthreaux 1982). Similar patterns are observed in other bustard species in Eurasia, *eg* longer-distance migration by female than male Asian Houbara *Chlamydotis macqueenii* (Combreau & Al Baidani 2015) and Great Bustard *Otis tarda* (Streich *et al* 2006, Wang *et al* 2023), and bias in irruptive movements in Great Bustard (Streich *et al* 2006).

Three major hypotheses, relating to physiology, dominance and spring arrival times, have been posited to explain differential migration (Cristol *et al* 1999). Because male and female Little Bustards are of similar size, the physiological hypothesis, which argues that larger individuals are better able to endure a period of cold and food scarcity, is not supported. The dominance hypothesis contends that dominant (typically larger) individuals monopolise winter food resources, forcing less dominant classes to migrate. However, Little Bustard winter food resources are neither scarce nor easily defensible. The arrival-time hypothesis proposes that individuals arriving earliest on breeding grounds will overwinter closer to breeding grounds. This explanation is most compelling for Little Bustards, as lekking males arrive well before females to establish display territories.

During an irruption winter, even on intralimital wintering grounds we observe a decrease in the ratio of male to female-type birds (ratios 0.37–0.54). This suggests that a greater number of juveniles were present during the irruption winter than in other years. Studies of avian irruption ecology have largely focused on boreal seed and fruit-eating species, and on raptors (Newton 2006). In contrast, the Little Bustard's diet consists primarily of invertebrates and ground vegetation, resources that are subject to less interannual variation in winter (Cabodevilla *et al* 2024). Nevertheless, in his multi-decadal study of the steppe birds of northern Kazakhstan, Ryabov (1949) noted high interannual variation in Little Bustard populations, which he attributed to low reproductive success in years of drought. It may be possible that in 2024, beneficial conditions resulted in high breeding productivity in some parts of the Little Bustard's eastern range. Of note, the 2024 growing season in northern Kazakhstan was marked by above-average rainfall (https://ipad.fas.usda.gov). The high levels of primary productivity which resulted in high wheat crop yields (ibid) could also have supported higher invertebrate densities for growing chicks.

The issue of where adult males winter is unresolved. There was no site at which the number of adult males was greater than the number of female-types. Seven lone adult males were recorded at extralimital sites, and four at intralimital. The largest male-only flock consisted of six birds and was recorded in January 2024 in Georgia. Males were most commonly observed in mixed flocks containing female-type birds. Of individual records we reviewed (208 in total), none from extralimital wintering sites, and only five from intralimital wintering sites, reported more adult males than female-type birds (male:female-type ratios from 1.2–2.3). Although our study excluded records from most of Kazakhstan and Xinjiang as non-wintering areas, there were few records from winter months, and those we scrutinised did not contain large numbers of males. Systematic and comprehensive winter surveys, and satellite telemetry can help to answer this question, and may reveal other aspects of differential sexual migration in the eastern population of Little Bustards.

Increased risks, including powerline collisions and hunting, are encountered by Little Bustards migrating longer distances (Aidek *et al* 2025, Cambell & Kessler 2025, Kessler *et al* 2025b, Khan *et al* 2025). Such mortality could contribute to a higher female mortality rate, with negative demographic implications for this lekking species, in which females are already disproportionally killed during the breeding season by agricultural machinery (Campeau & Kulagin 2022). In contrast, we are not aware of reports of male-biased winter mortality, nor of specific high-mortality factors at more northern overwintering sites (*eg* northern Caucasus & Uzbekistan; Oparin *et al* 2025, Ten *et al* 2025). However, mass mortality of birds at one of the southern wintering sites (Turkmenistan; Rustamov & Shcherbina 2025) was reported in years of harsh winter weather, and as discussed above, the wintering areas used by male Little Bustards are not well understood.

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Louis-Philippe Campeau, IUCN Bustard Specialist Group, Bishkek, Kyrgyzstan. louisphilippecampeau@gmail.com

Mimi Kessler, IUCN Bustard Specialist Group, Riyadh, Saudi Arabia. mimi@eurasianbustardalliance.org