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Male post-breeding movements and stopover habitat selection of an endangered short-distance migrant, the Little Bustard *Tetrax tetrax*

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Migration decisions, such as the selection of stopover sites, is critical for the success of post-breeding movements, also affecting subsequent survival and reproductive success. Recent advances in biologging are unveiling the stopover strategies of many long-distance travelers but far less attention has been given to short-distance migrants. In this study, we investigate the stopover ecology of an endangered grassland bird, the Little Bustard, a short-distance migrant in Iberia. Using a high resolution spatial dataset, derived from GPS/GSM tracking data of 27 male Little Bustards breeding in southern Portugal and covering three years (2009 to 2011), we studied the post-breeding movements of Little Bustards using Dynamic Brownian Bridges models to identify the main stopover sites. Generalized Linear Mixed Models were then used to examine habitat selection in stopovers. During their post-breeding movements, male Little Bustards were essentially nocturnal migrants, making frequent stopovers (mean per movement = 2.5) while maintaining a relatively fast pace to reach more productive agricultural post-breeding areas. Stopovers occurred in most post-breeding movements (83 %) regardless of the total distance covered (average 64.3 km) and most stopovers (84 %) lasted less than 24 hours. Land cover and topography influenced the selection of stopover sites, with birds using mostly agricultural non-irrigated and irrigated croplands and avoiding other land uses and rugged terrain. There was a negative relationship between stopovers and the proximity to roads, but not to power lines. The high frequency of stopovers during post-breeding movements,

despite the short distances travelled, together with the nocturnal migratory behaviour of bustards, may impose additional risks to a bird mainly threatened by collision with power lines in non-breeding areas. We also conclude that even when dealing with short distance migrants, habitat connectivity between breeding and post-breeding areas is likely to be a key conservation concern.

Key words: grassland bird, movement ecology, habitat selection, stopover selection, connectivity

Post-breeding migratory movements are usually associated to a predictable seasonal change of environmental conditions and/or food availability (Dingle & Drake 2007, Hedenström 2008), but are also influenced by individual factors such as sex, age or role specialization during reproduction (e.g., Palacín *et al.* 2009). Migratory strategies and decisions along the trajectory, such as interrupting migration at particular stopover sites for resting and/or refueling (Newton 2008), play a key role in the success of the movement and subsequent survival (Alerstam *et al.* 2003, Legagneux *et al.* 2012). Therefore, understanding migratory decisions including stopover use and habitat selection on route, is crucial to to estimate population trends and risks, predict changes in migratory behaviour and develop appropriate conservation strategies (Shuter *et al.* 2011). In this context, a good knowledge of migratory connectivity, which refers to the extent to which animals from the same breeding area move to the same non-breeding areas (Newton 2008), is also important, especially for species with highly selective habitat preferences (e.g., Briedis et al. 2016).

Recent advances in tracking technology opened a new door for the study of avian migration (Robinson *et al.* 2010) and stopover ecology of a wider number of migrant species (e.g., Eraud *et al.* 2013, Lemke *et al.* 2013, Evens *et al.* 2017). Despite that, the knowledge on the stopover ecology of many avian groups and species, and particularly of short-distance migrants, is still very limited (but see Strandberg *et al.* 2009, Newton *et al.* 2017, Röseler *et al.* 2017).

The Little Bustard *Tetrax tetrax* is a medium-sized grassland bird, whose distribution is fragmented across the Palearctic range. Spain and Portugal are the stronghold of its western distribution, where the main breeding populations are mostly concentrated in the Extremadura, Castilla La Mancha (Spain) and Alentejo (Portugal) regions (De Juana & Martínez 1996, García de la Morena *et al.* 2006, Equipa Atlas 2008). The species has a Vulnerable conservation status in Europe, where it is mainly threatened by habitat loss and degradation (Silva *et al.* 2018), illegal killing and collision with power lines (Marcelino *et al.* 2017), and recent trends indicate a severe decline in their breeding numbers in parts of their range (Silva *et al.* 2018). Although Iberian Little Bustards have been considered mostly sedentary (e.g., Cramp & Simmons 1980, Villers *et al.* 2010) a recent and comprehensive tracking study found that most populations in the region are actually migratory or partially migratory (89 % of all tracked individuals, García de la Morena *et al.* 2015), performing regular short or medium-distance movements to post-breeding and/or wintering sites (Silva *et al.* 2007, García de la Morena *et al.* 2015). The majority of male Little Bustards engage in these migratory movements in June/July, right after the breeding season and during the Iberian summer (García de la Morena *et al.* 2015) when temperatures and vegetation dryness reach their peak (Silva *et al.* 2007). In these post-breeding movements, birds head to northern, coastal or higher-altitude areas, where food availability and environmental conditions are expected to be more favorable (Silva *et al.* 2007, 2015, García de la Morena *et al.* 2015). Studies on stopover ecology of bustards are scarce and limited to a few long-distance bustard species/populations, such the Asian Houbara Bustard *Chlamydotis macqueenii* (e.g., Combreau *et al.* 1999, Tourenq *et al.* 2004, Burnside *et al.* 2017) or the Asian Great Bustard *Otis tarda dybowskii* (Kessler *et al.* 2013). The stopover ecology of short-distance migratory bustards, such as the Iberian Little Bustard population, is completely unknown.

In the present study, we use a high-resolution tracking dataset, collected over a four-year period, to investigate the stopover ecology of Iberian Little Bustards during their post-breeding movements. Our specific aims were to characterize their migratory behaviour (route consistency) and use of stopovers (occurrence, number, duration and site-fidelity), and to study the influence of habitat structure (land cover and topography) and linear infrastructures (roads and power lines) in stopover habitat selection during post-breeding movements.

Material and methods

Fieldwork

Capture and tagging of Little Bustards were carried out in several sites located in two main breeding areas, Castro Verde and Vila Fernando SPAs (Special Protected Areas) (Figure 1), in the early breeding period (April to early May) of three consecutive years, from 2009 to 2011 (14, 7 and 6 individuals, respectively). The capture method was aimed at males, using snares and a female decoy (Ponjoan *et al*. 2010). A Solar GPS Platform Transmitter Terminal (30 g PTT; Microwave Telemetry Inc.) was deployed on 27 adult breeding males, using a full harness made of Ribbon Teflon, weighing less than 4.7 % of the birds' mass. Transmitters were programmed to record a GPS position every 2 hours, with an accuracy of ± 18 m (Microwave Telemetry 2014). Eight of the 27 birds were tracked for more than one year (in one case up to three years).

Pre-analysis of tracking data

Spatial data from the PTTs and cartographic data were handled with Quantum GIS 2.2.12 (QGIS Development Team 2013). Birds were considered sedentary whenever they remained within 15 km from their breeding site throughout the year (see García de la Morena *et al.* 2015). A quarter of the post-breeding movements (25.7 %, n = 35) were preceded by a long-term permanence in pre-migratory staging areas (or secondary breeding areas) (average duration = 26.1 days, range = 10.7 - 38.9 days). These areas were close, although clearly separated from the main breeding area (average distance ± SD = 13.4 ± 4.8 km) and were not considered part of the subsequent post-breeding movement.

Post-breeding movements were therefore only considered to occur when birds moved more than 15 km away from their breeding areas, between May and August. To set the limits of each individual post-breeding movement, we considered their breeding site or pre-migratory staging area as the 'origin point' of the migratory movement while the 'end point' coincided with the arrival to the main post-breeding area, the furthest location from the breeding site, where the majority of birds stayed for at least two or three months. The boundaries of the movements were the last and first two fixes in the same position or close to each other, located in the departure and destination areas, respectively. In a few cases (n = 6) birds had more than one main post-breeding areas, and their movement was subdivided accordingly, which in all cases were two post-breeding areas. Those movements were included in all analyses, except for the estimation of arrival and departure dates, from breeding and to post-breeding areas, respectively.

Identification and characterization of stopovers

Movements and stopovers were characterized (occurrence, number and duration) through visual inspection of each individual movement. We considered as stopover sites, areas in which birds stayed for at least two consecutive fixes, along each individual's post-breeding movement, excluding the departure and destination areas. Our data collection settings (see above) did not allow for the detection of stopovers with duration inferior to two hours.

Habitat selection

To identify the stopover locations to be included in the habitat modeling analysis, we used Brownian Bridge Movement Models (BBMMs) (Horne *et al.* 2007, Sawyer *et al.* 2009, 2011). The BBMM were used to estimate the utilization distribution (UD) of individual bustards along the movement route, incorporating the distance and elapsed time between successive fixes, as well as the location error and the Brownian motion variance (BMV) (see details in Horne *et al.* 2007, Sawyer *et al.* 2009).

Since there is evidence that Little Bustards may migrate preferentially during the night (Silva *et al.* 2014), we assumed that their migratory behaviour was likely to differ between day and night. For that reason, we used Dynamic BBMM which is a version of

BBMM that considers changes in behaviour when moving, namely changes in speed and direction, which can be defined for different time-windows (12 h in our case, to differentiate the expected night and day periods). Within the sliding window, Dynamic BBMM calculates different BMV values and compares the model fit using one or two estimates of BMV (Kranstauber *et al.* 2012, Lai *et al.* 2015, Palm *et al.* 2015). UDs between 50 and 75 % were used to outline the stopover areas, as they showed a good adjustment to the stopover relocations. The decision of using 50 or 75 UD was dependent on the extension of the movement, where after visual inspection, BBMM analysis of shorter post-breeding movements generally resulted in a good adjustment with 50 % UD; while longer post-breeding movements showed better adjustments at the 75 % UD level. Departure and arrival site locations (six fixes each) were included in the movement path considered in the Dynamic BBMM analysis, as a margin of fixes is required on each end of the window, depending on window and margin sizes (Kranstauber *et al.* 2012).

To characterize stopover habitat selection, Little Bustard fixes inside stopover areas were compared to an equal number of random points located in a region defined as a 2-km buffer outside these areas – these locations were considered pseudo-absences for modelling purposes. This approach was selected for two key reasons. Firstly, the goal of this analysis was to explore stopover habitat selection in the context of the migratory corridor rather than within the stopover site and selecting potentially unused areas within the stopovers is likely to underestimate the availability of habitats in the surrounding landscape. Secondly, given that stopover areas were selected according to high UD areas and considering the time interval between relocations (2 hours), this approach also maximizes the likelihood that locations selected as pseudo-absences represent unused, although available, locations.

Habitat selection analysis was then carried out with presence / absence locations in relation to landscape variables known to be relevant for the Little Bustard (Silva *et al.* 2004, 2007, 2010). Land cover data was originally obtained from CORINE Land Cover (CLC) 2012 version 18.5 (EEA 2016). Level 3 categories were reclassified into three relevant land cover categories: dry cropland, irrigated cropland, and other land uses (see Table 1 for details). Terrain ruggedness was calculated as the mean of absolute differences between the elevation of a cell and that of its surrounding cells (Wilson *et al.* 2007), using data from ASTER Global Digital Elevation Model (NASA 2009) and the function 'terrain' from the Raster package (Hijmans 2017) for R statistical software. Finally, we collected information on the distribution of the main roads from "© OpenStreetMap contributors" (classes: motorway, trunk, primary and secondary; Haklay & Weber 2008), distribution power lines for the whole study area and classified each point according to its distance to the nearest road and power line.

Consistency in the use of breeding, post-breeding areas and stopovers

To quantify the fidelity to breeding and post-breeding areas, we calculated the percentage of spatial overlap between consecutive years of the same individual, given by the 95 % UD (estimated by Brownian Bridges Models) in the breeding area (from 1 April to departure date) and post-breeding areas (see above) in each year. Similarly, the repeated use of stopover sites by the same individual in consecutive years was assessed by quantifying the overlap between stopover areas previously identified in the post-breeding movements (delimited by the 50-75 % UD).

Statistical analyses

The effects of habitat, landscape and human infrastructures were tested using the presence and absence locations at stopover sites. We calculated the Pearson correlation coefficient and the variance inflation factor (VIF) between the explanatory variables to evaluate correlation and collinearity (Zuur *et al.* 2009). VIF values (all < 1.2) and pairwise correlation between explanatory variables (all $|r| < 0.60$) were low for our dataset, so all variables were used in the analysis.

Stopover habitat selection was modeled using Generalized Linear Mixed Models (GLMMs) with a binomial error distribution (Zuur *et al.* 2009). Bird identity was included as a random factor to address the spatial and temporal dependency of the replicated measures from each individual (Zuur *et al.* 2009). As we expected a response at short ranges from the linear infrastructures, we applied a log-transformation (log x+1) to the variables distance to roads and distance to power lines, so that short distances were more influent in the analysis. We computed GLMMs with all possible variable combinations, resulting in a total of sixteen models. To decrease model selection uncertainty and increase robustness of parameter estimates, we performed model averaging using an information theoretical approach by computing averaged parameter estimates from the best-selected models with ΔAICc < 10 (Burnham *et al.* 2011). Model performance was assessed through the deviance explained and conditional R^2 of each selected model (Nakagawa & Schielzeth 2013, Johnson 2014).

Analysis were done in R (R Core Development Team 2014), using the package usdm to calculate VIF (Naimi *et al.* 2014), the package lme4 to calculate GLMMs (Bates *et al.* 2016) and the package MuMIn for multimodel selection and model averaging (Bartón 2013).

Results

Post-breeding movements

From the 27 male Little Bustards tracked in the course of this study, only one individual from Vila Fernando showed a clear sedentary behaviour, remaining close to the breeding site all year round, during two consecutive years (maximum distance from the breeding site = 7.7 km). All other individuals (96.3 %) performed seasonal movements (Figure 1**,** mean departure date: 29 June), moving to areas further than 35 km (79 % of all birds) from their breeding sites during the post-breeding period (average = 77.5 ± 65.5 km; range = 19.0 - 303.7 km). Most birds captured in Castro Verde (52 %) headed north to post-breeding areas where irrigated agriculture is the dominant land use, while other individuals flew to more distant coastal SPAs (21 %), such as the Tagus estuary and the Portuguese Southwest coast, also areas with a very high proportion of irrigated crops. Most birds from Vila Fernando moved east to the irrigated crops that surround the Guadiana river (70 %). One individual engaged in a long-distance movement (of more than 300 km) reaching a post-breeding area located north of Plasencia, Spain. The large majority of post-breeding movements occurred during the night with 78 % of these movements starting already in the night period and the remaining (22 %) in late afternoon (roughly between 17:00 and 20:00) and finishing in the first hours of daylight or late night (Table 2). No birds were recorded flying in the hottest hours of the day, between 11 and 16h (considering all periods of continuous flight, including partial movements between stopovers and movements without stopovers, n = 124).

Stopovers

Stopovers occurred in more than 80 % of the post-breeding movements (Table 2) and 76 % of birds made one to three stopovers during their movements. There was a significant positive relation between the distance travelled and the number of stopovers made by the birds (Pearson's correlation: $r = 0.38$, d.f. = 32. $p = 0.028$) although the occurrence of stopovers was still high (75 %) in shorter-distance movements (< 50 km).

The vast majority of stopovers (84 %) were of short duration (Figures 2 and 3), lasting less than 24 hours (see Table 2). These short stopovers lasted most of the daylight period (64 % of short stopovers), with birds arriving at late night/early morning and departing in the late afternoon or during the night (Table 2). Despite that, a substantial part of these short stopovers were carried out exclusively during night time (36 %) lasting only a few hours (88 % of these nocturnal stopovers lasted up to 4 h). The distance travelled between stopovers (including departure and arrival to post-breeding areas) was different in diurnal and nocturnal stopovers. While only 48 % of diurnal stopovers were followed by a stop within the following ten kilometers of the movement, over 80 % of night stopovers had a subsequent stop within the same distance (median distance travelled = 10.20 and 3.70 km, respectively; Mann-Whitney $U = 445.0$, $n = 83$, $p = 0.008$).

The majority of stopover locations during these post-breeding movements were located outside SPAs (82.2 %), contrasting with locations during the breeding period, mostly located within SPAs (85.4 %, this dataset).

Most birds tracked over consecutive years maintained a similar migratory behaviour (Figure 5 and Table 4), using the same breeding (88 % of birds, n = 8) and post-breeding areas (63 % of birds). An exception was a bird that in the second year dispersed to a new breeding site, 87 km away from its previous breeding area. Despite the fidelity to the same post-breeding areas over consecutive years (Figure 5), there were no repetitions in the use of stopover sites by the same individuals (Table 4).

Habitat selection on route

The stopover habitat selection model averaging process retained 4 models (ΔAICc < 10; AIC range: 932.94 - 942.21; deviance explained: 0.11 – 0.13; r^2: 0.20 – 0.23). The selection of stopover sites was mostly influenced by land use and distance to roads, with the maximum relative importance of 1, followed by terrain ruggedness with 0.97 (Table 3). In their stopover sites, little bustards used mostly irrigated cropland and non-irrigated areas composed by extensive traditional farming and pastures (see Figure 4). While there were no significant differences in the selection of the above land uses, other land uses were avoided as well as the proximity of the main roads and more rugged landscapes (Table 3). The selection of stopover sites was not influenced by the distance to power lines (see Table 3).

Discussion

Post-breeding movements and stopovers

Although there is some evidence that Little Bustards migrate during the night (Villers *et al.* 2010), in contrast to other bustard species (e.g., Kessler *et al.* 2013), there is little information whether this is an obligatory or flexible migratory strategy. In this study, the great majority of male post-breeding movements were nocturnal or partially nocturnal (89.5 %, n = 124) and birds avoided to fly during most of the daylight period. One of the main potential advantages of nocturnal migration is to avoid predation (Alerstam 2009), but there are other compensations, such as using daylight hours to forage and refuel, minimizing load costs (e.g. Delingat *et al.* 2006). Furthermore, nocturnal migration has metabolic advantages, particularly for birds with an active flapping flight, as it is possible to minimize water loss (Klaassen 1996). Summer temperatures in Southern Portugal frequently exceed 35°C, particularly during midday hours and Little Bustards are known to reduce their activity levels in response to extreme hot weather (Silva *et al.* 2015). For this large bird species, flying preferentially during the night period will probably help to prevent water loss and avoid overheating during migratory movements. A potential disadvantage of night migration is an increased risk of collision with anthropogenic infrastructures, such as power lines, as many avian species show a weak or slower reaction to less-visible barriers during nocturnal flights, compared to daylight time (e.g., Deng & Frederik 2001, Murphy *et al.* 2016).

During their post-breeding movements, male Little Bustards made one to three diurnal stopovers, which frequently lasted less than 24h (84 %), between nocturnal flights. Overall, the occurrence of stopovers was high (> 80 % of movements) even when the birds were covering a short migratory distance. The species is known to perform migratory movements of 400-600 km in a single night when crossing the Pyrenees (Villers *et al.* 2010), which is a much larger distance than the one covered by Little Bustards in the south Portuguese plains during the post-breeding period. Additionally, with a ground flight speed of 65 km per hour (Villers *et al.* 2010) and no evident geographic barriers (except for one individual that crossed Sierra de Gredos, Spain), most of the tracked birds could have completed their post-breeding movements in a single nocturnal flight of a couple of hours. This raises the question: Why do male bustards make stopovers in these short-distance migratory movements?

The breeding period is an extremely demanding phase for male Little Bustards. Food resources are expected to decline throughout the breeding season (Silva *et al.* 2007) and their foraging activity is likely restricted due to high temperatures in early summer (Silva *et al.* 2015). In these short-distance movements birds are also likely to perform their journeys in active flapping flight mode, not flying at appropriate altitudes to take advantage of tail winds and therefore with high energy expenditure (Liechti & Schmaljohann 2007, Mateos-Rodríguez & Liechti 2011). It is thus likely that the birds need to make stopovers to refuel and rest, even during relatively short migratory flights. By making these “obligate” diurnal stops and moving preferentially during the night, Little Bustards may avoid unnecessary costs, while resting and refueling (also minimizing load costs) to resume the migratory movement in the subsequent night.

It remains uncertain whether this migratory strategy is also used by female Little Bustards, considering not only their distinct breeding phenology (females remain in breeding areas for longer periods, due to parental care duties), smaller body size, as well as the potential higher flexibility in their migratory behaviour (e.g., Palacín *et al.* 2009). Indeed, in the sympatric Great Bustard, who share a similar breeding phenology and habitat, females tend to remain sedentary in years when they are raising young (Palacín *et al.* 2009, 2011).

Habitat selection during stopovers

Little bustards, as other species from the Otitidae family, are extremely selective in relation to their habitat, particularly in the breeding and post-breeding seasons (e.g., Martínez 1994, Faria & Rabaça 2004, Silva *et al.* 2004, 2007). In southern Portugal, breeding Little Bustards tend to prefer agricultural fallow lands or extensive pastures, while in the post-breeding season birds move to more productive areas, usually occupied by irrigated fields (Silva *et al.* 2007). In stopover sites, dry crops and irrigated crops were both used by Little Bustards. Irrigated croplands were not significantly preferred in stopovers (compared to dry crops), which may be an indication that most birds were on the move, instead of prospecting potentially good foraging grounds or evaluating post-breeding areas. During stopovers, birds did avoid "other land uses" as well as rugged terrain. These results suggest that male Little Bustards are being less selective during short stopovers than in other periods of the year (showing a mixed preference for dry and irrigated crops), but still occupy areas that warrant a minimum protection from predators (areas with good horizontal visibility allow the early detection of predators, Metcalfe 1984) and potential foraging habitat.

Linear human infrastructures, such as roads and power lines, are known to negatively impact populations of many vertebrate species through habitat loss and degradation, barrier effect, increased human disturbance and mortality (Janss *et al.* 2000, Benítez-López *et al.* 2010, Silva *et al.* 2010, Barrientos *et al.* 2012). During the breeding season, Little Bustards seem to avoid the proximity of roads and power lines (Suárez-Soane *et al.* 2002, Silva *et al.* 2010; but see Martínez 1994, Faria & Rabaça 2004 for divergent results), and in the winter, when food resources are abundant, bustards have been found to avoid the proximity of roads and inhabited houses (Silva *et al.* 2004). In contrast, during the post-breeding period, these birds tend to use areas of intensified agriculture, moving closer to roads, which are abundant in those areas (Silva *et al.* 2007). Considering such variability regarding the response to linear infrastructures and human presence, it is likely that the importance of such drivers may vary according with the ecological context and individual requirements. The negative response of Little Bustards to roads suggests that during stopovers they still avoid proximity to some human infrastructures, also favoring areas with greater availability of food and cover. Nevertheless, bustards showed a lack of response to the presence of power lines and, as other heavy flight birds (e.g., Sandhill Cranes *Antigone canadensis*, Murphy *et al.* 2016), may be less able to detect the presence of these linear infrastructures during nocturnal flights.

Individual consistency in migratory behaviour

To our knowledge, this is the first study quantifying the fidelity of male Little Bustards to their post-breeding areas, revealing a high level of fidelity to those areas (see also García de la Morena *et al.* 2015). This pattern is similar to that found in other short-distance migrant steppe birds in Iberia (Great Bustard, Morales *et al.* 2000, Alonso *et al.* 2001) and supports a strong migratory connectivity between Little Bustards breeding and non-breeding areas. Despite the similar migratory routes and high fidelity to post-breeding areas, there was no repetition by individuals in the use of stopover sites in consecutive years. Stopover site fidelity was never investigated in short-distance migrants but is known to occur in long-distance migrants that are highly selective in relation to habitat, such as waterfowl and shorebirds (e.g., Fox et al. 2002). Little bustards are highly selective in relation to their habitat but have shown to be less selective during post-breeding stopovers (see above). The short-time spent in these post-breeding migratory stopovers (less than 24 hours) and availability of potential areas with adequate habitat may influence the non-repetition of the same stopover sites, but further studies are needed to support this hypothesis.

Implications for conservation

A good knowledge of the spatial distribution of migrant populations across the entire annual cycle is critical for their conservation (Shuter *et al.* 2011). Migratory strategies and decisions of long-distance migrants are known to have important impacts on the timing and success of breeding (Klaassen *et al.* 2014, Hewson *et al.* 2016) and also on survival (e.g., Klaassen *et al.* 2014, Lok *et al.* 2015). Much less is known about the impacts of migratory choices in short-distance migrants, but those are expected to be lower since the time window of the movement is relatively short and moving smaller distances decreases the risks associated to crossing large ecological barriers or the probability of facing unexpected changes in weather conditions. On the other hand, short-distance migrants tend to show more flexibility to deal with environmental changes (e.g., Newton 2008, Doxa *et al.* 2012, Clark *et al.*

2014). For migrant species that use human-associated habitats, the negative impact of human infrastructures may also increase the costs of migration, but this topic has been seldom studied (e.g., Palacín *et al.* 2017).

We found that male Little Bustards perform frequent stopovers during their post-breeding movements, despite the short-distances travelled, moving mostly during nighttime. At the same time, Little Bustards seem to be less responsive to certain habitat features at these stopover sites, namely to power lines, when compared to other stages of the annual cycle. Moreover, stopovers were mostly located outside SPAs and individuals did not use the same stopover sites over consecutive years, despite the similar migratory routes and fidelity to post-breeding areas. Little Bustards, as most bustard species, are very prone to collision with overhead wires, particularly with power lines (Barrientos *et al.* 2012, Silva *et al.* 2014) due to their narrow binocular field of view, low flight maneuverability, gregarious behaviour and high flight speed (Martin & Shaw 2010, Barrientos *et al.* 2012). For a collision-prone species, this migratory strategy (short nocturnal flights interspersed with several stops) may impose additional risks during this particular stage of year, since birds may be crossing unknown areas, likely at collision-risk altitudes (see Silva *et al.* 2014) and under low light conditions. For the Great Bustard *Otis tarda*, also a short-distance migrant in Iberia and a collision-prone species, mortality is 2.4 to 3.5 times higher in migrants than in sedentary individuals, mostly due to collision with power lines (Palacín et al. 2017).

The maintenance of open habitats in the agricultural plains of south Portugal is determinant for the conservation of grassland bird populations. The rapid expansion of agricultural intensification in these areas, particularly of permanent crops, has been very significant over the last decade (e.g., Ribeiro *et al.* 2014). This widespread change in the agricultural systems is affecting grassland birds' populations all over Europe (Donald *et al.* 2006) and in Portugal, over the last decade, Little Bustards have declined ca 50 %, possibly linked to habitat loss and degradation (Silva *et al.* 2018). This intensification of agriculture may not only affect bustards during their breeding and post-breeding periods, but also during their migratory movements, by reducing the availability of potential stopover areas. Therefore, the preservation of open habitat areas between their main breeding sites and post-breeding areas is a key conservation measure to ensure connectivity between breeding and post-breeding areas and which should be considered in future management and conservation plans.

Final considerations

Nowadays, due to the fast development of human infrastructures, including power lines, the migratory strategy of this short-distance migrant, based on nocturnal flights interspersed with frequent stops, may impose additional risks to a collision-prone species and possibly increase their human-induced mortality. In the near future, the development and widespread of intensive agriculture practices may also affect the availability of adequate stopover sites and non-protected post-breeding areas and overall connectivity between breeding and post-breeding areas. For a better understanding of actual population trends and its relation with migration, it will be relevant to monitor the mortality of Little Bustards associated with migratory movements, considering also factors such as age and sex, and assess the demographic effects of their migratory strategies.

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References

Alerstam T (2009) Flight by night or day? Optimal daily timing of bird migration. Journal of Theoretical Biology 258: 530-536.

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103: 247-260.

Alonso JA, Martín CA, Alonso JC, Morales MB, Lane SJ (2001) Seasonal movements of male Great Bustards in central Spain. Journal of Field Ornithology 72: 504-508.

Barrientos R, Ponce C, Palacín C, Martín CA, Martín B, Alonso JC (2012) Wire marking results in a small but significant reduction in avian mortality at power lines: a BACI designed study. PLoS One 7: e32569.

Bartón K (2013) MuMIn: Multi-model inference. R package version 1.9. 13. The Comprehensive R Archive Network (CRAN), Vienna, Austria.

Bates D, Maechler M, Bolker B, Walker S (2016) lme4: Linear mixed-effects models using Eigen and S4 (R package version 1.1-12).

Benítez-López A, Alkemade R, Verweij PA (2010) The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biological Conservation 143: 1307-1316.

Briedis M, Beran V, Hahn S, Adamík P (2016) Annual cycle and migration strategies of a habitat specialist, the Tawny Pipit *Anthus campestris*, revealed by geolocators. Journal of Ornithology 157: 619-626.

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65: 23-35.

Burnside RJ, Collar NJ, Dolman PM (2017) Comparative migration strategies of wild and captive-bred Asian *Houbara Chlamydotis macqueenii*. Ibis 159: 374-389.

Clark RG, Pöysä H, Runko P, Paasivaara A (2014) Spring phenology and timing of breeding in short-distance migrant birds: phenotypic responses and offspring recruitment patterns in common goldeneyes. Journal of Avian Biology 45: 457-465.

Combreau O, Launay F, Al Bowardi M, Gubin B (1999) Outward migration of houbara bustards from two breeding areas in Kazakhstan. Condor 101: 159-164.

Cramp S, Simmons KEL (1980) *Handbook of the Birds of Europe the Middle East and North Africa: The Birds of the Western Paleartic*, Vol II, Hawks to Bustards. Oxford University Press, London.

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

Delingat J, Dierschke V, Schmaljohann H, Mendel B, Bairlein F (2006) Daily stopovers as optimal migration strategy in a long-distance migrating passerine; the northern wheatear *Oenanthe oenanthe*. Ardea 94: 593-605.

Deng J, Frederick P (2001) Nocturnal flight behavior of waterbirds in close proximity to a transmission powerline in the Florida Everglades. Waterbirds 24: 419-424.

Dingle H, Drake VA (2007) What is migration? Bioscience 57: 113-121.

Donald PF, Sanderson FJ, Burfield IJ, Van Bommel FP (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems & Environment 116: 189-196.

Doxa A, Robert A, Crivelli A, Catsadorakis G, Naziridis T, Nikolaou H, Jiguet F, Theodorou K (2012) Shifts in breeding phenology as a response to population size and climatic change: a comparison between short-and long-distance migrant species. The Auk 129: 753-762.

EEA (2016) Corine Land Cover. https://www.eea.europa.eu/data-and-maps/data/clc-2012-raster.

Equipa Atlas (2008) Atlas das aves nidificantes em Portugal (1999-2005). Assírio & Alvim, Lisboa.

Evens R, Conway GJ, Henderson IG, Cresswell B, Jiguet F, Moussy C, Sénecal D, Witters N, Beenaerts N, Artois T (2017) Migratory pathways, stopover zones and wintering destinations of Western European nightjars *Caprimulgus europaeus*. Ibis 159: 680-686.

Eraud C, Rivière M, Lormée H, Fox JW, Ducamp JJ, Boutin JM (2013) Migration routes and staging areas of trans-Saharan Turtle Doves appraised from light-level geolocators. PloS one 8: e59396.

Faria N, Rabaça JE (2004) Breeding habitat modelling of the little bustard *Tetrax tetrax* in the site of community importance of Cabrela (Portugal). Ardeola 51: 331-343.

Fox AD, Hilmarsson JO, Einarsson O, Walsh AJ, Boyd H, Kristiansen JN (2002) Staging site fidelity of Greenland White-fronted Geese *Anser albifrons flavirostris* in Iceland. *Bird Study 49*: 42-49.

García de la Morena EL, Bota G, Ponjoan A, Morales MB (2006) El sisón común en España. I Censo Nacional (2005). SEO/BirdLife. Madrid.

García de la Morena EL, Morales MB, Bota G, Silva JP, Ponjoan A, Suárez F, Mañosa S, de Juana E (2015) Migration Patterns of Iberian little bustards *Tetrax tetrax*. Ardeola 62: 95-112.

Haklay M, Weber P (2008) Openstreetmap: User-generated street maps. IEEE Pervasive Computing 7: 12-18.

Hedenström A (2008) Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society of London B: Biological Sciences 363: 287-299.

Hewson CM, Thorup K, Pearce-Higgins JW, Atkinson PW (2016) Population decline is linked to migration route in the Common Cuckoo. Nature Communications 7: 12296.

Hijmans RJ (2017) raster: Geographic Data Analysis and Modeling. R package version 2.6-7. https://CRAN.R-project.org/package=raster

Horne JS, Garton EO, Krone SM, Lewis JS (2007) Analyzing animal movements using Brownian bridges. Ecology 88: 2354-2363.

Janss GF (2000) Avian mortality from power lines: a morphologic approach of a species-specific mortality. Biological Conservation 95: 353-359.

Johnson PCD (2014) Extension Nakagawa & Schielzeth's R_GLMM^2 to random slopes models. Methods in Ecology and Evolution 5: 44-946.

Kessler AE, Batbayar N, Natsagdorj T, Batsuur D, Smith AT (2013) Satellite telemetry reveals long-distance migration in the Asian great bustard *Otis tarda dybowskii*. Journal of Avian Biology 44: 311-320.

Klaassen M (1996) Metabolic constraints on long-distance migration in birds. Journal of Experimental Biology 199: 57-64.

Klaassen RHG, Hake M, Strandberg R, Koks B, Trierweiler C, Exo KM, Bairlein F, Alerstam T (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 83: 176–184.

Kranstauber B, Kays R, LaPoint SD, Wikelski M, Safi K (2012) A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. Journal of Animal Ecology 81: 738-746.

Lai S, Bêty J, Berteaux D (2015) Spatio–temporal hotspots of satellite–tracked arctic foxes reveal a large detection range in a mammalian predator. Movement Ecology 3: 37.

Legagneux P, Fast PL, Gauthier G, Bêty J (2012) Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proceedings of the Royal Society of London B: Biological Sciences 279: 876-883.

Lemke HW, Tarka M, Klaassen RH, Åkesson M, Bensch S, Hasselquist D, Hansson B (2013) Annual cycle and migration strategies of a trans-Saharan migratory songbird: a geolocator study in the great reed warbler. PLoS One 8: e79209.

Liechti F, Schmaljohann H (2007) Wind-governed flight altitudes of nocturnal spring migrants over the Sahara. Ostrich 78: 337-341.

Lok T, Overdijk O, Piersma T (2015) The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. Biology letters 11: 20140944.

Marcelino J, Moreira F, Mañosa S, Cuscó F, Morales MB, García de la Morena EL, Bota G, Palmeirim JM, Silva JP (2017) Tracking data of the Little Bustard *Tetrax tetrax* in Iberia shows high anthropogenic mortality. Bird Conservation International 1-12.Martin GR, Shaw JM (2010) Bird collisions with power lines: failing to see the way ahead? Biological Conservation 143: 2695-2702.

Martínez C (1994) Habitat selection by the little bustard *Tetrax tetrax* in cultivated areas of central Spain. Biological Conservation 67: 125-128.

Mateos-Rodríguez M, Liechti F (2011) How do diurnal long-distance migrants select flight altitude in relation to wind? Behavioral Ecology 23: 403-409.

Metcalfe NB (1984) The effects of habitat on the vigilance of shorebirds: is visibility important? Animal Behaviour 32: 981-985.

Microwave Telemetry (2014) PTT-100 30 gram Solar Argos/GPS PTT. http://www.microwavetelemetry.com/bird/solarArgosGPS_30g.cfm

Morales MB, Alonso JC, Alonso JA, Martín E (2000) Migration patterns in male great bustards (*Otis tarda*). The Auk 117: 493-498.

Murphy RK, Dwyer JF, Mojica EK, McPherron MM, Harness RE (2016) Reactions of Sandhill cranes approaching a marked transmission power line. Journal of Fish and Wildlife Management 7: 480-489.

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from Generalized Linear Mixed-effects Models. Methods in Ecology and Evolution 4: 133-142.

Naimi B, Hamm NA, Groen TA, Skidmore AK, Toxopeus AG (2014) Where is positional uncertainty a problem for species distribution modelling. Ecography 37: 191-203.

NASA JPL (2009) ASTER Global Digital Elevation Model [Data set]. NASA JPL. https://doi.org/10.5067/aster/astgtm.002

Newton I (2008) The ecology of bird migration. Academic Press, London.

Newton RE, Tack JD, Carlson JC, Matchett MR, Fargey PJ, Naugle DE (2017). Longest sage-grouse migratory behavior sustained by intact pathways. The Journal of Wildlife Management 81: 962-972.

Palacín C, Alonso JC, Alonso JA, Martín CA, Magaña M, Martin B (2009) Differential migration by sex in the great bustard: possible consequences of an extreme sexual size dimorphism. Ethology 115: 617-626.

Palacín C, Alonso JC, Alonso JA, Magaña M, Martín CA (2011) Cultural transmission and flexibility of partial migration patterns in a long-lived bird, the great bustard *Otis tarda*. Journal of Avian Biology 42: 301-308.

Palacín C, Alonso JC, Martín CA, Alonso JA (2017) Changes in bird-migration patterns associated with human-induced mortality. Conservation Biology 31: 106-115.

Palm EC, Newman SH, Prosser DJ, Xiao X, Ze L, Batbayar N, Balachandran S, Takekawa JY (2015) Mapping migratory flyways in Asia using dynamic Brownian bridge movement models. Movement Ecology 3: 3.

Ponjoan A, Bota G, Mañosa S (2010) Trapping techniques for little bustards *Tetrax tetrax* according to age, sex and season. Bird Study 57: 252-255.

QGIS Development Team (2013) QGIS geographic information system. Open Source Geospatial Foundation Project.

R Core Development Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Ribeiro PF, Santos JL, Bugalho MN, Santana J, Reino L, Beja P, Moreira F (2014) Modelling farming system dynamics in High Nature Value Farmland under policy change. Agriculture, Ecosystems & Environment 183: 138-144.

Robinson WD, Bowlin MS, Bisson I, Shamoun-Baranes J, Thorup K, Diehl RH, Kunz TH, Mabey S, Winkler DW (2010) Integrating concepts and technologies to advance the study of bird migration. Frontiers in Ecology and the Environment 8: 354-361.

Röseler D, Schmaljohann H, Bairlein F (2017) Timing of migration, routes and wintering grounds of a short-distance diurnal migrant revealed by geolocation: a case study of Linnets *Carduelis cannabina*. Journal of Ornithology 158: 875-880.

Sawyer H, Kauffman MJ, Nielson RM, Horne JS (2009) Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19: 2016-2025.

Sawyer H, Kauffman MJ (2011) Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80: 1078-1087.

Shuter JL, Broderick AC, Agnew DJ, Jonzén N, Godley BJ, Milner-Gulland EJ, Thirgood S (2011) Conservation and management of migratory species. In: Milner-Gullard EJ, Fryxell JM, Sinclair ARE (eds)Animal migration: a synthesis. pp 172–206, Oxford University Press, Oxford.

Silva JP, Catry I, Palmeirim JM, Moreira F (2015) Freezing heat: thermally imposed constraints on the daily activity patterns of a free-ranging grassland bird. Ecosphere 6: 1-13.

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

Silva JP, Faria N, Catry T (2007) Summer habitat selection and abundance of the threatened little bustard in Iberian agricultural landscapes. Biological Conservation 139: 186-194.

Silva JP, Pinto M, Palmeirim JM (2004) Managing landscapes for the little bustard *Tetrax tetrax*: lessons from the study of winter habitat selection. Biological Conservation 117: 521-528.

Silva JP, Santos M, Queirós L, Leitão D, Moreira F, Pinto M, Lecoq M, Cabral JA (2010) Estimating the influence of overhead transmission power lines and landscape context on the density of little bustard *Tetrax tetrax* breeding populations. Ecological Modelling 221: 1954-1963.

Silva JP, Palmeirim JM, Alcazar R, Correia R, Delgado A, Moreira F (2014) A spatially explicit approach to assess the collision risk between birds and overhead power lines: A case study with the little bustard. Biological Conservation 170: 256-263.

Strandberg R, Alerstam T, Hake M, Kjellén N (2009) Short-distance migration of the Common Buzzard *Buteo buteo* recorded by satellite tracking. Ibis 151: 200-206.

Suárez-Seoane S, Osborne PE, Alonso JC (2002) Large-scale habitat selection by agricultural steppe birds in Spain: identifying species–habitat responses using generalized additive models. Journal of Applied Ecology 39: 755-771.

Tourenq C, Combreau O, Lawrence M, Launay F (2004) Migration patterns of four Asian houbara *Chlamydotis macqueenii* wintering in the Cholistan Desert, Punjab, Pakistan. Bird Conservation International 14: 1-10.

Villers A, Millon A, Jiguet F, Lett JM, Attié C, Morales MB, Bretagnolle V (2010) Migration of wild and captive-bred little bustards *Tetrax tetrax*: releasing birds from Spain threatens attempts to conserve declining French populations. Ibis 152: 254-261.

Wilson MFJ, O'Connell B, Brown C, Guinan JC, Grehan AJ (2007) Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Marine Geodesy 30: 3-35.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York.

Figures and Tables

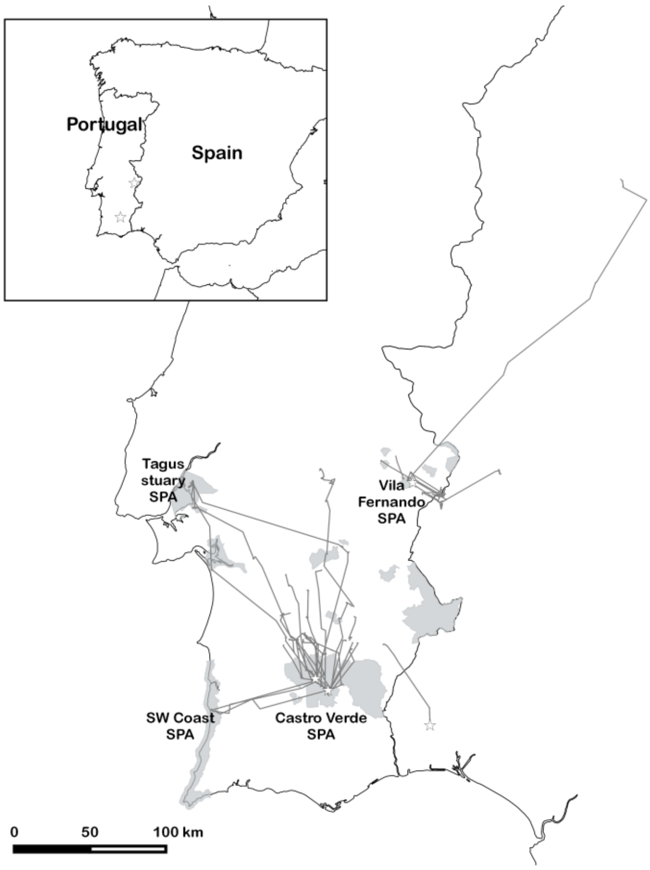

Figure 1 Outward post-breeding movements (n = 40) of little bustards *Tetrax tetrax* breeding at Castro Verde and Vila Fernando SPAs. Capture locations (breeding sites) are indicated by white stars and special protected areas with importance for grassland birds are shown in grey.

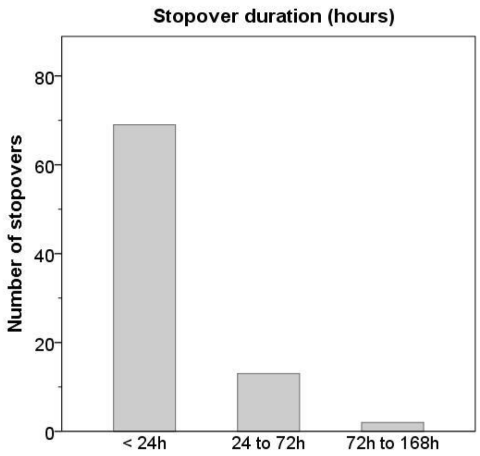

Figure 2 Number and duration (in hours) of stopovers (n = 84) during the post-breeding movements (n = 40) of little bustards *Tetrax tetrax.*

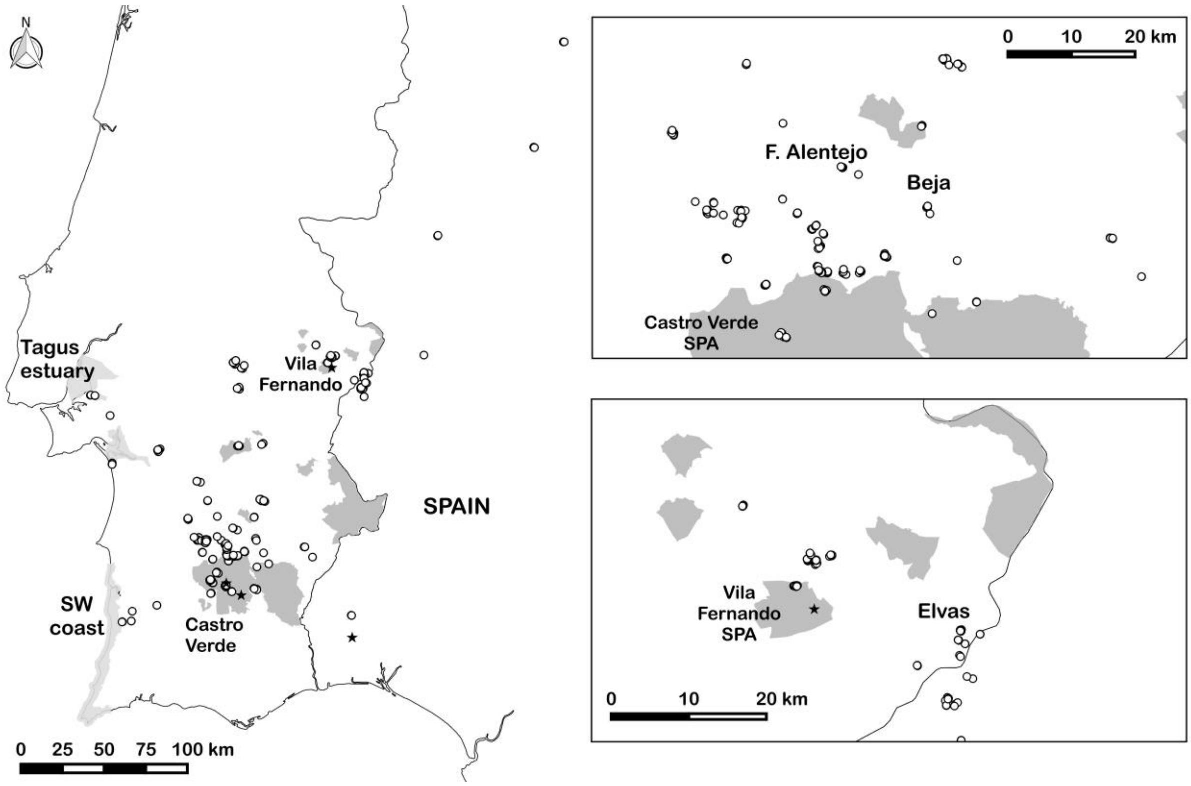

Figure 3 Stopover locations of little bustards during their outward post-breeding movements. Capture locations (breeding sites) are indicated by black stars and special protected areas with importance for grassland birds are shown in grey.

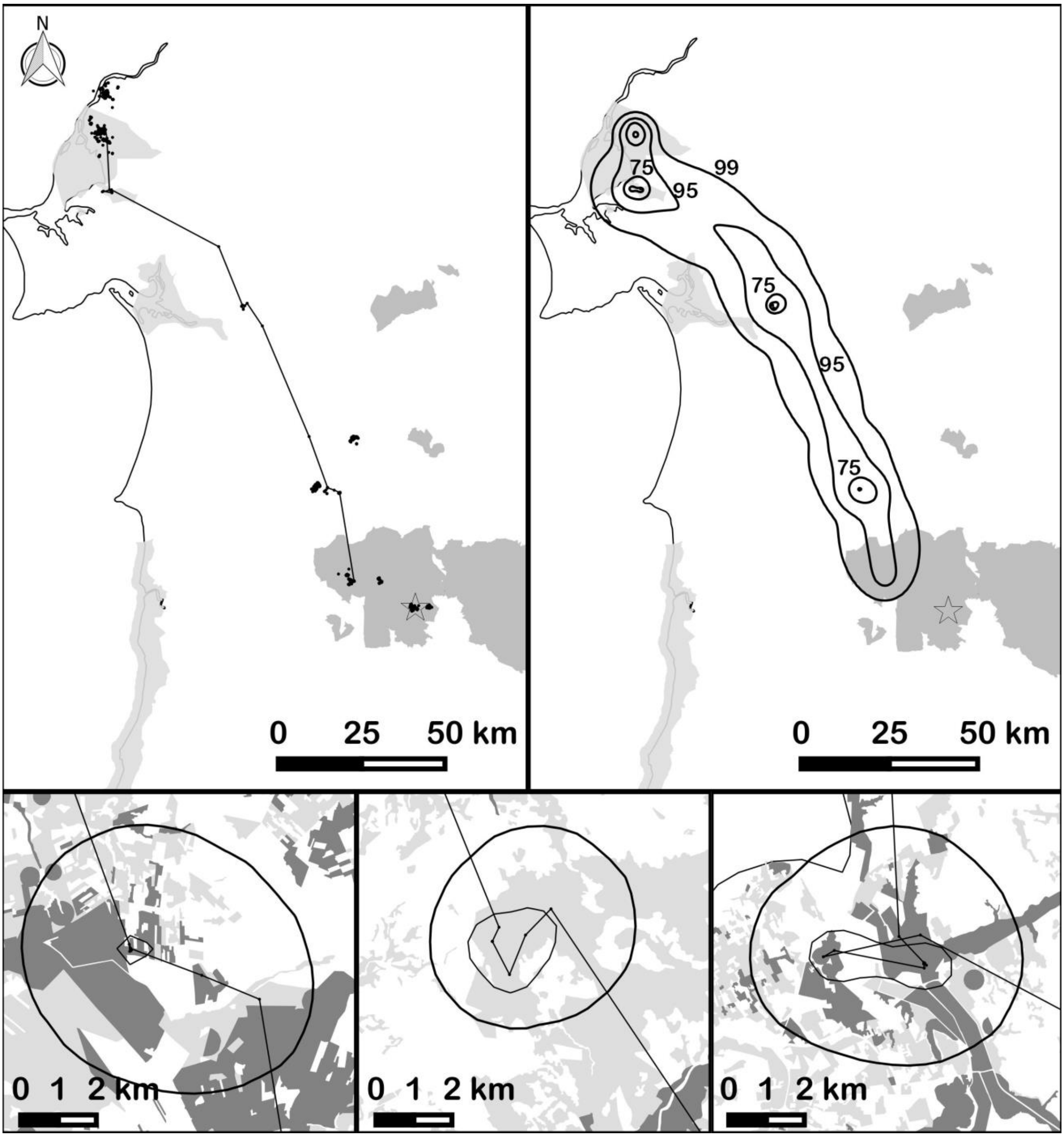

Figure 4 Example of a post-breeding movement of a little bustard *Tetrax tetrax* (individual 91469_1_2009) that bred in Castro Verde in 2009: a) All fixes (black dots) during the year and post-breeding movement (black line); b) Utilization distribution (UD) during the post-breeding movement estimated from Dynamic Brownian Bridge models (stopover areas were identified using the 50 - 75 % kernel UD); c) d) e) Stopover locations and land use (Light grey – Pastures and non-irrigated crops, Dark

grey – irrigated crops, White – other land use). Star indicates breeding location. Note that the post-breeding movement was delimited between a pre-migratory/second breeding area (see methods) and the main post-breeding area.

Table 1 Description and summary statistics of the predictor variables used to model the habitat selection of little bustard at stopover sites (n = 61) during post-breeding movements. Means and range are provided for the continuous variables and frequency per classes is presented for the categorical variables.

Variable	**Description (units)**	**Mean (SD) / Frequency**	**Range**
Land cover	Corine Land Cover 2012 classes: Dry croplands (non-irrigated arable land 2.1.1, pastures 2.3.1, natural grasslands 3.2.1); Irrigated croplands (permanently irrigated land 2.1.2, rice fields 2.1.3) and Other land uses (all remaining land cover classes)	Dry croplands: 620 Irrigated croplands: 153 Other land uses: 271	-
Ruggedness	Terrain ruggedness (30 m spatial resolution)	-0.43 (0.31)	-0.94 - 1.49
Distance to power lines	Distance to distribution power lines (m)	777.9 (666.3)	0 - 4801
Distance to roads	Distance to the main roads (m) (classes: motorway, trunk, primary and secondary of © OpenStreetMap (Haklay & Weber 2008)	2581 (1940.1)	0 - 11000

Table 2 Description of stopovers during post-breeding movements of little bustards *Tetrax tetrax*.

	Number of post-breeding movements	40
	Number of stopovers[1]	84
	Number of tracked individuals	27
Movement	**Departure date[2]**	179.5 ± 22.2 (184)
	Arrival date[2]	184.0 ± 23.4 (189)
	Duration of movements (days)[3]	2.4 ± 2.4 (1.4)
	Movement range (km)	64.3 ± 55.7 (41.5)
	Time of departure	23:21 ± 03:24 (00:00)
	Time of arrival	06:24 ± 03:47 (07:00)
Stopovers	**Occurrence of stopovers[1]**	83.0 %
	Number of stopovers per movement[1]	2.5 ± 1.4 (2.0)
	Duration of stopovers (hours)	20.5 ± 24.6 (16.0)
	Time of departure	23:57 ± 04:09 (01:00)
	Time of arrival	05:53 ± 03:28 (06:00)
	Distance travelled between stops (km)	23.4 ± 27.8 (12.4)

[1] estimated from BBMM analysis and visual inspection; [2] Julian date; [3] Including stopovers; mean ± standard deviation, with median in brackets

Table 3 Estimated coefficients of the model averaging procedure, indicating the relative importance of the variable and the number of containing models.

(Conditional average)	**Estimate**	**Std. Error**	**z value**	**p-value**	**Relative variable**	**No. of containing**

					importance	models
Intercept	1.623	0.584	2.774	0.006	-	-
Land cover:					1	4
Irrigated lands	0.219	0.255	0.855	0.392		
Other land use	-1.706	0.209	8.152	<0.001		
Ruggedness	-0.839	0.287	2.924	0.003	0.97	2
Log (Distance to power lines + 1)	-0.005	0.056	0.090	0.928	0.27	2
Log (Distance to roads + 1)	0.238	0.075	3.166	0.002	1	4

The category non-irrigated lands is represented by the intercept values