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Enduring the heat: the microclimate characteristics that determine site suitability for an endangered grassland bird during post-breeding

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ABSTRACT

Environmental changes, including habitat loss and fragmentation in combination with climate change, have increased population reliance on protected areas (PAs) while also requiring individuals to adapt to changing local conditions or search for refugia when conditions deteriorate. Microclimate refugia within PAs may be critical for allowing species to persist when exposed to extreme thermal conditions, yet the availability of microclimate refugia and the ability of PAs to protect species from extremes has rarely been considered. We GPS-tracked 47 little bustards (*Tetrax tetrax*) in the Iberian Peninsula in 2009–2019, to understand their micro-scale climate and habitat use in the warmest period of the year, the post-breeding season. We compared post-breeding conditions at locations used in that period with those not used after breeding. We found that increasing temperature may reduce site suitability, while sites with greater microclimate refugia availability were more likely to be used by little bustards post-breeding. Although dispersed shrubs may provide micro-refugia, dense shrubby patches were avoided. While almost 63 % of the breeding locations were in PAs, only under 7 % of all post-breeding locations were within these key conservation areas, showing this species is not well protected across its life cycle. We assessed the impact of expected increasing temperatures from climate change scenarios and found that up to 15 % of currently used locations are predicted to become unsuitable, including those falling within PAs. Habitat management strategies should maintain landscapes with diverse characteristics that may provide shelter from extreme temperatures, such as scarce patches of low-density shrubs.

1. Introduction

Through global warming and the increasingly frequent occurrence of heatwaves, many areas may become uninhabitable for the species that have previously occupied them. Some habitat characteristics may provide shelter from the negative effects of climate warming by providing small-scale refuge from extreme conditions and allowing sites to be utilized when the surrounding landscape has become inhospitable (Ramos et al., 2023a; Suggitt et al., 2018). These microclimate refugia may take the form of habitat patches, such as wetland and forest areas, shielded cliff edges, or individual habitat features like rock structures or vegetation (García et al., 2020; Williamson et al., 2021). They can be used as nesting sites, or for resting during foraging, and provide shelter from high temperatures (Ramos et al., 2023a). The presence of microclimate refugia has been shown to improve individual survival in areas particularly exposed to high temperatures (Lima et al., 2016). Furthermore, refugia are expected to be crucial landscape features for allowing population persistence despite global warming (Stark and Fridley, 2022;

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Suggitt et al., 2018). This has been shown across different bird species, populations of which have already been negatively affected by rising temperatures. For example, bird populations in areas with microclimate refugia were less likely to be declining (Kim et al., 2022). Thus, microclimate availability can be a key buffer against elevated temperatures and play an important role in habitat management and conservation to increase ecosystems' resilience to climate change (Jones et al., 2023).

Protected areas (PAs) are a cornerstone of biodiversity conservation and key to protecting endangered species. These areas may shield species from the negative effects of anthropogenic activities (e.g. hunting and land-use change; Buchan et al., 2023) as well as promote population recovery and increase (Wauchope et al., 2022). Through the widespread and pervasive impact of habitat degradation, PAs often become patches of fragmented natural or semi-natural habitats in otherwise inhospitable landscapes (Brennan et al., 2022; Ward et al., 2020), producing isolated populations of species they were designated to protect (Méndez et al., 2011; Santiago-Ramos and Feria-Toribio, 2021). Furthermore, as local conditions become seasonally unfavourable, individuals may move to new areas and return once conditions improve (Cohen and Jetz, 2023; Zurell et al., 2018). However, such movements pose challenges for species conservation within static protected areas, as individuals may be forced to move outside of these areas in order to find sites with suitable conditions (Pérez-Granados et al., 2025; Santiago-Ramos and Feria-Toribio, 2021). Furthermore, the recent fast speed of climate change (IPCC, 2023) can render previously occupied distribution areas climatically unsuitable, driving a shift in species distributions (Chen et al., 2011) through movement, local extinctions, and population declines (Pearce-Higgins and Green, 2014). Thus, the effective management of protected areas for species conservations needs to consider not only the prevention of habitat loss and elimination of threat exposure, but also individual seasonal movement patterns and distributional shifts in response to climate change (Garden et al., 2015; Pérez-Granados et al., 2025; Thomas et al., 2012).

Grassland-associated bird species are experiencing disproportionately high population declines compared to other bird groups (Gregory et al., 2019; Rigal et al., 2023; Voříšek et al., 2010). These declines are attributed to a combination of factors, including changes in land use and the intensification of farming practices, which can also occur within PAs (Gameiro et al., 2024). Additionally, shifts in crop phenology, such as earlier harvesting dates in response to climate change, can lead to nest destruction, abandonment, and increased juvenile mortality (Stanton et al., 2018). The little bustard (*Tetrax tetrax*) is a grassland-associated bird species, with the most important part of its European range found within the Iberian Peninsula. Little bustard populations within this area display a diversity of movement strategies, with few individuals remaining in the same areas throughout the year, and most individuals being short distance migrants (García de la Morena et al., 2015). In recent years, the species has faced dramatic declines within the Iberian Peninsula, including population reductions of up to 59 % in Spain (Morales and Bretagnolle, 2022) and 77 % in Portugal (Silva et al., 2023). These population declines have been associated with frequent exposure to extremely high temperatures and habitat loss through changes in land use and agricultural (Alonso et al., 2020; González del Portillo et al., 2024; Gudka et al., 2019; Silva et al., 2023). However, these studies do not consider microclimate availability within habitats used by the little bustards, particularly during the post-breeding season, when temperatures can be extremely high and detrimentally affect individuals. This is especially relevant, as the little bustard has been shown to use microclimate refugia as temperatures increase (Ramos et al., 2023a) and the timing of their post-breeding dispersive movements as well as the distance moved have been associated with the availability of refugia within their breeding areas (Ramos et al., 2023b; Ramos et al., 2025).

To halt the declines of species such as the little bustard, conservation action must prioritise managing directed at maintaining or creating sites with characteristics crucial for individual persistence, as well as increasing the connectivity between these patches, and reducing anthropogenic disturbance (Marcolin et al., 2021; Pérez-Granados et al., 2025; Silva et al., 2024). However, studies investigating patterns of space usage, which are frequently used to inform management strategies, are often carried out at coarse spatial scales (Maclean and Early, 2023). Micro-scale site characteristics, such as refugia, may be decoupled from broad scale climatic trends at landscape level (De Frenne et al., 2021). Omitting this heterogeneity may exaggerate the role of environmental variables as well as the estimation of threats posed by climate change, possibly due to the lack of consideration of important features such as microclimate refugia (Maclean and Early, 2023; Stark and Fridley, 2022).

In this study, we aimed to compare the microclimate and microhabitat characteristics of sites used during the post-breeding season with the post-breeding conditions at sites that have been used exclusively in the breeding season. In particular, we examined how temperature, microclimate refugia availability, and vegetation greenness (as a proxy for food availability) affected site usage during the post-breeding (summer) season, when individuals were exposed to extreme thermal conditions and the importance of microclimate availability may be highest. Furthermore, we predicted how availability of suitable sites, both within and outside of key conservation areas, including protected areas, may change as a result of different global warming scenarios. We hypothesise that sites used by little bustards during the post-breeding season will have lower temperatures and greater microrefugia availability, associated with the presence of arboreous or shrubby cover, compared to sites not used after breeding, and that global warming will reduce sites suitability for little bustards during the post-breeding season. This knowledge can help identify management actions to improve the resilience of protected areas for little bustards and promote their year-round use, aiding conservation.

2. Methods

2.1. Study species and tracking data

Tracking devices were deployed on 47 male little bustards, collecting data between 2009 and 2019 (Supporting Information). Trapping was carried out in April, in the Alentejo (Portugal) and Extremadura (Spain) regions. The individuals were tagged with either Platform Transmitter Terminal (PTT; Microwave Telemetry Solar Argos/GPS 30 g) or Global System for Mobile Communications (GSM; Movetech Telemetry Flyway 38 g) devices using a Teflon harness with a weak link to prevent lifelong deployment. The tracking devices weighed less than 4 % of the birds' body mass (Ramos et al., 2023a) and were programmed to collect GPS fixes either every two hours (PTT) or 10, 20 or 30 min (GSM). Approval for the capture of little bustards and the deployment of GPS tracking devices was obtained from Instituto da Conservação da Natureza e das Florestas (ICNF/CAPT/2014, ICNF/CAPT/2015) and Consejería de Medio Ambiente y Rural, Políticas Agrarias y Territorio of the Junta de Extremadura. Full details of capturing and deployment methods are available in (Ramos et al., 2023a).

All statistical analyses, and data handling, were carried out in R v.4.2.1 (R Core Team, 2022).

All in-flight locations obtained, identified from ground speed, were removed from the analysis. Furthermore, any night or crepuscular locations collected between the hours of 20:00 and 07:00 were removed, as the focus of this study was to determine the effect of warm temperatures on habitat selection and microclimate refugia usage after the breeding season, and little bustards are unlikely to be utilizing microclimate refugia sites at night, when temperatures rarely exceed 25 °C. This temperature threshold has been identified as one beyond which little bustard activity is significantly reduced (Silva et al., 2015).

The little bustard breeding season starts in April and ends, on average, in June. The post-breeding (summer) season in this study includes the months of July, August, and September (15th July - 15th

September; Ramos et al., 2023a). This is the period corresponding to peak temperatures within the Iberian Peninsula. To increase consistency between individuals the data acquisition for the breeding period only included tracking data from the 1st of May, as the timings of tag deployment could occur throughout April.

To determine whether a GPS location obtained during breeding was also used in the post-breeding season, we produced a circular buffer, with a radius of 500 m, around each GPS location and examined the buffer overlap between breeding (i.e. any GPS location collected by any individual during the breeding season) and post-breeding (i.e. any GPS location collected by an individual during the post-breeding season) locations across all birds. Hence, in this study a location (also referred to as site or area) is defined as the GPS location and the corresponding 500 m buffer around it. If a breeding location buffer overlapped at least 50 % with a post-breeding location buffer, this would be classified as used in both the breeding and post-breeding seasons. Otherwise, the breeding location would be assigned as used by individuals in this study exclusively in the breeding season (hereafter referred to as 'non-used in post-breeding' or 'non-used') and the post-breeding location would be classed as used by focal individuals in the post-breeding season only (hereafter referred to as 'used in post-breeding' or 'used'). Due to the relatively low number of locations used in both seasons ($N = 1253$ out of 85,759 GPS locations), and as the aim of this study was to investigate the conditions at used and non-used sites during the post-breeding season, the locations used in both breeding and post-breeding and those used in the post-breeding only were combined for the purpose of analysis and are referred to as 'used' in this study. The distribution of the GPS locations obtained and whether they are used or non-used in the post-

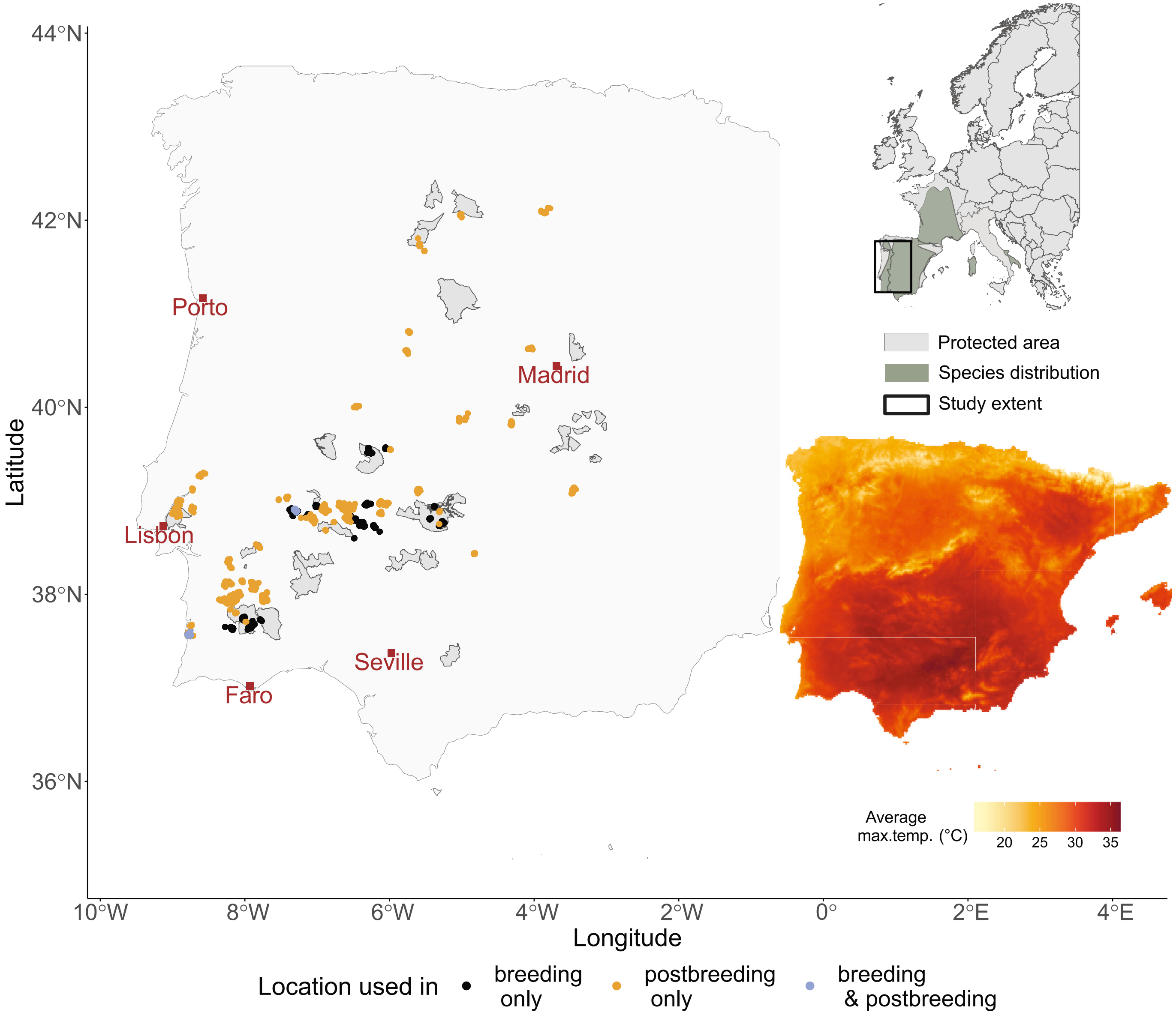

Fig. 1. Little bustard GPS locations collected from 47 individuals between years 2009–2019, the little bustard range within Europe (top right; shaded area; BirdLife International 2020), and the average maximum monthly temperature for July – September 2009–2019 for the Iberian Peninsula (bottom right; produced using the CRU-TS 4.06 dataset downscaled with WorldClim 2.1; Fick and Hijmans, 2017; Harris et al., 2020). Black points show locations used in the breeding season only ($N = 53,158$) 63 % of these are within protected areas (PAs), in orange are the locations occupied only in the post-breeding season ($N = 31,348$) 4.4 % within PAs, and in blue those used in both breeding and post-breeding ($N = 1253$) 61.2 % within SPAs. The darker grey areas show the selected protected areas with agro-steppe habitat used by little bustards based on (Gameiro et al., 2020), using data obtained from European Environmental Agency (EEA). Vector data for mapping were obtained from *rnaturalearth* (Massicotte et al., 2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

breeding season is shown in Fig. 1. The proportion of used and non-used locations within the designated Special Protected Areas (SPAs) identified based on Gameiro et al. (2020), was determined. We did not assess the change in suitability of habitats within PAs as well as any potential resulting change in usage frequency of these areas over the study period, as detecting major climatic and microclimatic changes may be unlikely over this relatively short period.

2.2. Environmental data

To characterise the microclimatic conditions at each site we first obtained microclimate temperatures at a 30 m resolution and 20 cm above ground using the fully automated microclimate modelling procedure from the *microclima* package (Maclean et al., 2019). To generate these temperatures, the microclimate model used National Centers for Environmental Prediction climate reanalysis data (NCEP) (Kanamitsu et al., 2002; Kemp et al., 2012), and accounted for terrain characteristics through a digital elevation model from Amazon Web Services (AWS) and habitat type. Temperature was extracted at the GPS location and in each 30 m cell within a 500 m buffer around the GPS location. Microclimate refugia availability was defined as the difference between the minimum and median temperature available within the buffer of each GPS location. A more negative value represented a larger difference between the minimum and median temperature within the buffer, and therefore, a greater availability of microclimate refugia. To characterise the microscale habitat at each site we used CORINE land cover maps at 100 m resolution for reference years 2012 and 2018 (European Environment Agency. European Union's Copernicus Land Monitoring Service). All land use types were simplified into one of the four categories: arboreous, herbaceous, shrubby, or other habitat (Supporting Information). To ensure that these land use datasets are sufficient to represent the habitat across the study period we compared the proportion of land use change between the 2012 and 2018 datasets across the four habitat categories (herbaceous, shrubby, arboreous, other habitat) in a 500 m buffer around all GPS locations collected. We found that the overall number of locations with a change in habitat cover proportion was low, with a change in shrubby cover occurring at 3.30 % ($N = 2871$; 80.21 % increase and 19.79 % decrease in shrubby cover), change in herbaceous at 6.65 % ($N = 5757$; 18.84 % increase and 81.16 % decrease in herbaceous cover), and change in proportion of arboreous cover within 4.59 % ($N = 3987$; 73.86 % increase and 26.14 % decrease in arboreous cover) of all buffers. This relatively low number of sites at which the proportion of habitat cover changed suggest that the two datasets are sufficient to represent the habitat cover within our study area during this period. For data collected between 2009 and 2014 we used the 2012 dataset, and for data collected in 2015–2019 we used the 2018 land use dataset. We extracted the proportion of each habitat type category within a 500 m buffer around each GPS location. The proportion was arcsine square-root transformed due to large skew towards extreme ends of the proportion range (i.e. large number of near-zero or near-one values). Site usage decisions may be in part driven by the availability of resources such as food. Hence, we included the Normalized Vegetation Index (NDVI) for every GPS location as an approximation of food availability (Pettorelli et al., 2005; Ramos et al., 2023b). Little bustards feed predominantly on green plants, as well as on arthropods (Bretagnolle et al., 2022), therefore, NDVI provides a direct (i.e. indicating the presence of green plants) and indirect (i.e. indicating presence of patch characteristics favourable for arthropods) approximation of food availability at each location. To calculate NDVI we extracted near infra-red (NIR) and red (R) reflectance values at each GPS location from an 8-day average Moderate Resolution Imagining Spectroradiometer (MODIS) surface reflectance images at a 250 m resolution using Google Earth Engine (Didan, 2015; Gorelick et al., 2017). The NDVI at each location was calculated as the difference between the near infra-red and red reflectance (NIR – R) divided by the sum of near infra-red and red reflectance (NIR + R; Huete et al., 2002). Full details of producing the dataset are available in (Ramos et al., 2023a) and (Ramos et al., 2023b).

To obtain comparable environmental data for locations not used after the breeding season, a date within the post-breeding season (15th July to 15th September) was randomly generated. The environmental variables for each abandoned GPS location were then extracted following the methods outlined above, for a given random date and at the same time of day as the original breeding point was recorded. Hence, all environmental data was extracted for dates during the post-breeding (summer) season, as the aim of this study is to compare what the conditions at those non-used sites are when the individuals are using the other, post-breeding locations.

2.3. Statistical analyses

The GPS location data are largely clustered, and the dataset includes spatial overlap due to the individuals remaining in or returning to roughly the same place for long periods. Locations in close proximity have partially overlapping 500 m buffers, resulting in highly similar values for the environmental variables of interest. This poses a problem as high spatial autocorrelation and pseudoreplication violate the model assumptions. Hence the data was spatially thinned, to randomly retain only locations with a minimum distance of 500 m between them, therefore, preventing the same location from being included in the dataset more than once, and ensuring all observations used to fit the model are independent. Furthermore, this procedure allowed us to prevent over-representation of sites due to varying sample size across individuals as a result of the different data collection schedules for different devices (10–120 min). The study area was sub-divided using a 0.5° resolution 12 × 12 square grid (144 cells, approximately 40 km^2 each) and within each grid cell, the locations were thinned to a minimum distance of 500 m using the ‘thin’ function from the *spThin* package (Aiello-Lammens et al., 2015). The procedure was repeated 20 times to ensure the largest possible sample size retained, and we ensured that the resulting sample size was unaffected if the number of repeats was greater than this. The full dataset contained 85,759 data locations, the thinned datasets had approximately 1.3 % of the data ($N = 1140$). Thinning was carried out separately for the GPS locations that were abandoned and used after breeding to prevent loss of data due to proximity between them. To avoid a biased subsample being used for analysis, the thinning procedure was further randomised. Out of the 20 subsets generated through the thinning procedure, only those with the maximum sample size were retained. Then, for each of the 144 grid cells, one dataset was randomly selected, producing an overall dataset that was further cleaned using *CoordinateCleaner* (Zizka et al., 2019) to check for invalid coordinates, and then used for modelling (details described below). This procedure was repeated 100 times to minimise the likelihood of a biased sample being selected. The model coefficients for the 100 models were stored, and model averaging was carried out using the ‘model.avg’ function from the *MuMIn* package (Bartoń, 2023) with equal weights given to each model, to produce the average model coefficients. The output is presented in Supporting information. As the variability in model coefficients produced by the 100 models was low, to simplify the modelling and prediction process, a single thinned dataset was randomly selected out of the 100 repetitions of the thinning procedure and used in subsequent analysis, the results of which are presented below.

Diurnal variation in the data, particularly with regards to temperature, is likely, and the range of possible temperatures may differ depend on the time of day. To account for this, we calculated the maximum average temperature at each hour of the day across all locations collected and found that on average, the highest temperatures occur at 1 PM (Supporting information). Then, we calculated the time since the warmest hour of the day as the absolute difference in minutes between 1 PM and the time at which each location was collected.

To compare the sites used in the post-breeding to those abandoned after breeding and to model the probability of a given site being used during the post-breeding season, we fitted a generalized linear model (GLM) with a binomial error distribution and logit link. The response variable used in this model was the use status of a site, i.e. either 'non-used' (0; i.e. locations used exclusively in breeding) or 'used' (1; i.e. locations used in post-breeding). The explanatory variables were temperature at location (i.e. GPS location), microclimate refugia availability, proportion of shrubby cover within the 500 m buffer (arcsine transformed), proportion of arboreous cover within the 500 m buffer (arcsine transformed), NDVI, and time since the warmest hour of the day (in minutes). The environmental variables were selected for consistency with and findings of previous research (Ramos et al., 2023a, 2023b). See Section 2.2 Environmental data for information on how the variables were obtained.

To investigate how climate change and in particular increasing temperatures, may affect the potential future usage of sites currently utilized by little bustard, we used the model above to generate predictions of site usage probability, and therefore, changes in availability of suitable sites at three levels of climate warming. For this purpose, we used all known locations used in the post-breeding season (i.e. all 'used' sites in the non-thinned data, $N = 32{,}601$). We assume that if a location is currently used, it is suitable. All the habitat (proportion shrubby cover, proportion arboreous cover) and NDVI values obtained at each site were maintained constant while the microclimate temperature obtained from the microclimate model was increased by 1.5, 2.7, or 3.6 °C to correspond to the IPCC GCM warming scenarios (IPCC, 2023). This new dataset was used to generate predictions from the model to obtain the probability of site usage at all 'used' sites for each scenario. To determine whether a site is predicted to be 'used' or non-used, we first generated an ROC curve and calculated a probability cut-off corresponding to equal model specificity and sensitivity. This point serves as an optimal cut-off threshold for distinguishing between the two possible binary outcomes (Youden, 1950). The calculated cut-off threshold was equal to 0.6. Any site with a predicted usage probability equal to or above this threshold was predicted to be used (probability $\geq$0.6), while a predicted usage probability below this threshold indicated that the site was predicted to not be used (non-used; probability $<$0.6). We then calculate how many sites were predicted to remain suitable (i.e. those with a predicted probability $\geq$0.6) and calculate the percentage lost out of the total 32,601 currently used sites. To summarise the changes in suitability across the study area, we produced a 0.1° grid (approx. 8km^2) across the study extent. Within each grid cell, we summed the total number of current 'used' locations, then counted the number of locations predicted to remain used under each warming scenario. The percentage suitability lost was determined by the difference between the number of locations predicted to be used (i.e. those with predicted usage probability $\geq$0.6) under the three warming scenarios and the number of currently used locations. We use the non-thinned dataset for this purpose to obtain the number of available locations out of all known used locations, that remain suitable, and therefore, the percentage of loss in suitability.

3. Results

The final dataset consisted of 1140 location records obtained from 47 tracked little bustards between 2009 and 2019, of which 754 were used, and 386 were abandoned in the post-breeding season. The probability of a location being used by little bustards in the post-breeding season decreased with increasing temperatures, but little bustards were more likely to use locations with higher NDVI and greater microclimate refugia availability (Table 1, Fig. 2a-c). Site usage probability was significantly higher in locations with low shrubby cover and exhibited a steep decline with increasing shrub density (Fig. 2d). In contrast, the proportion of arboreous cover did not significantly affect site usage during the post-breeding season (Table 1).

Table 1
Parameter estimates from a generalized linear model (GLM) explaining the probability of site usage by little bustards during the post-breeding season as a function of temperature, microclimate refugia availability (difference between the minimum and median temperature within 500 m buffer), the proportion of arboreous and shrubby cover within 500 m buffer around the GPS location (arcsine square-root transformed), NDVI, and time (in minutes) since the warmest hour of the day.

Parameter	Estimate	Std. Error	z value	p value
Intercept	5.091	0.586	8.687	<0.001
Temperature (°C)	−0.110	0.015	−7.199	<0.001
Microclimate refugia availability (°C)	−0.337	0.131	−2.571	0.010
Prop. arboreous cover (arcsine transformed)	0.371	0.228	1.631	0.103
Prop. shrubby cover (arcsine transformed)	−1.604	0.302	−5.311	<0.001
NDVI (scaled and centred)	2.116	0.195	10.847	<0.001
Time since warmest hour of day (min)	−0.003	0.001	−3.894	<0.001

From all locations used in the post-breeding season, only approximately 6.6 % locations (pre-thinned sample size, 2144 out of 32,601) fall within PAs (Fig. 3). Out of these, 9.3 % (157) would lose suitability if temperatures increased by 1.5 °C, 11.5 % (247) with a 2.7 °C temperature increase, and 14.4 % (309) locations would be lost if the temperature was increased by 3.6 °C.

The predicted number of sites used decreased for all warming scenarios: at 1.5 °C temperature increase approximately 9.3 % (3017) locations were expected to be lost, 11.2 % (3665) lost at 2.7 °C, and 12.8 % (4172) locations lost with a 3.6 °C temperature increase. When GPS locations were combined into a grid (0.1°resolution), some spatial differences were observed. Across all temperature increase scenarios, over two-thirds (70.3–77.23 %) of grid cells were predicted to have up to 10 % declines in the number of suitable locations. However, some grid cells were predicted to experience major losses in suitability, with a 65.6 % decline in the predicted number of suitable locations when the temperature was increased by 1.5 °C, 75.0 % with an increase of 2.7 °C, and 78.1 % loss predicted when point temperatures were increased by 3.6 °C (Fig. 4). Losses of more than 50 % of used locations were predicted in approximately 4 % of the grid cells in all temperature increase scenarios.

4. Discussion

The sites used in the warm post-breeding season were characterised by lower temperatures, higher availability of microclimate refugia, and increased NDVI, but reduced shrub cover compared to shite that were not used after breeding. Predictions from our model, show consistent declines in post-breeding site suitability across all future temperature increase scenarios, highlighting that parts of the little bustard distribution which are already characterised by relatively low suitability, such as central and southern parts of the Iberian Peninsula, will continue to decline in suitability due to increasing temperatures. Consequently, this reduction in site suitability may induce little bustards to move earlier to find cooler conditions (Ramos et al., 2023b).

Conservation efforts of grassland birds in Europe, including the little bustard, have led to the designation of a network of Special Protection Areas (SPAs), which were designed for the protection of the species during the breeding season but not during other phenological stages. Protected areas, and particularly SPAs, have been shown to increase rare species abundance and the likelihood of them colonising these areas (Barnes et al., 2023). Our study shows that these grassland SPAs indeed protect a large proportion of the little bustard breeding occurrences, however, in the post-breeding season, only approximately 6.6 % of the recorded locations fell within the protected areas.

Between July and September, a time characterised by particularly high temperatures, little bustards seem to use these SPAs sparingly, and instead move to nearby areas. The drivers of habitat selection are likely

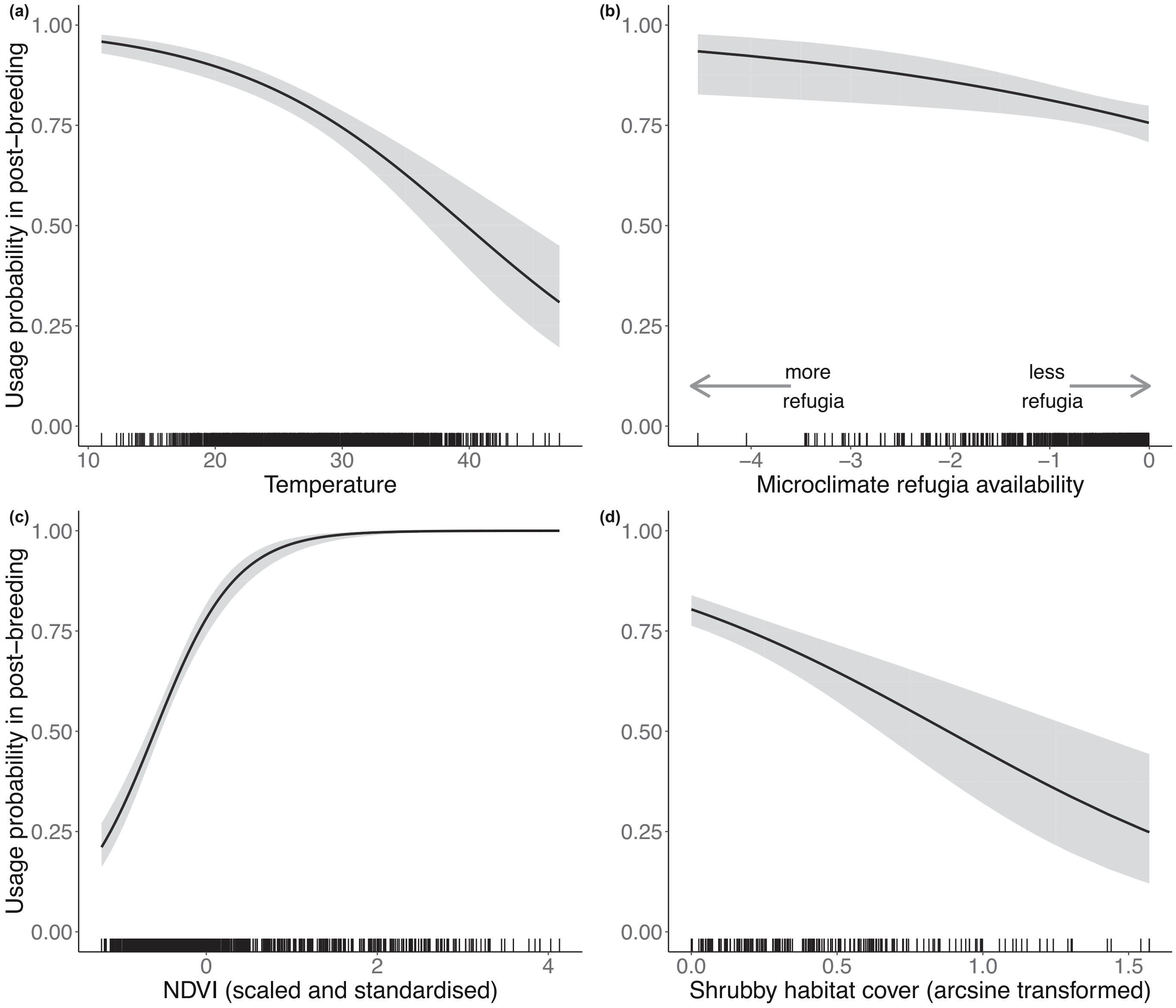

Fig. 2. Model predictions from generalized linear model (GLM) of current site usage probability in the summer (post-breeding season) by the little bustards in relation to temperature at point (a), microclimate refugia availability (calculated as the difference between the minimum and median temperatures within a 500-m buffer; b), NDVI (c), and the proportion of shrubby cover within 500-m buffer around GPS location (d). Shaded areas represent the 95 % confidence intervals and rug shows raw data distribution.

to differ between the breeding and post-breeding seasons. Food availability is much more limited in the post-breeding than the breeding season, and movement between patches may be relatively greater as individuals are not restricted to more limited habitats, e.g. those suitable for lekking (Traba et al., 2022). Using areas outside of the SPAs may expose individuals to a range of anthropogenic disturbances and threats which are absent in protected areas, such as hunting, as well as the presence of roads or powerlines, which are known causes of increased mortality (Silva et al., 2023). Furthermore, the landscape within the SPAs is managed to maintain suitable, open grassland habitats for this species. Surrounding areas, on the other hand, have seen considerable land use changes in previous years, with land conversion into irrigation areas, increase in grazing pastures at the expense of cereal fields, and high intensity agricultural production (Gameiro et al., 2020; Silva et al., 2023). This intricate interplay between agricultural practices, habitat management, and the species' exposure to potential threats highlights the complexities of conserving protected species throughout the year.

Refugia availability within the grassland habitats of the Iberian Peninsula can be linked to isolated patches of shrub and trees in otherwise open habitats, and it has been shown that little bustards tend to select sites with these habitat features (Ramos et al., 2023a). At the same time, usage of sites with higher herbaceous vegetation cover is also crucial, as these are where food availability may be highest. After the breeding season, in the summer months, food availability is greatly reduced within the SPAs, which is likely one of the major reasons for little bustards moving away from these areas during the post-breeding migration (Crispim-Mendes et al., 2024; Silva et al., 2023). This introduces a trade-off and explains the negative relationship between site usage and shrubby cover we find in this study. Use of shrubs as microclimate refugia has previously been shown (e.g. Shelef and Groner, 2011; Ruth et al., 2020), and the availability of scarce shrubby patches providing refugia will likely increase in importance with global warming. Furthermore, microclimate refugia availability has been shown to increase with increasing shrubby cover (Ramos et al., 2023a). However, sites with high shrubby cover during the post-breeding season tend to be drier, possibly abandoned fields, which may provide abundant

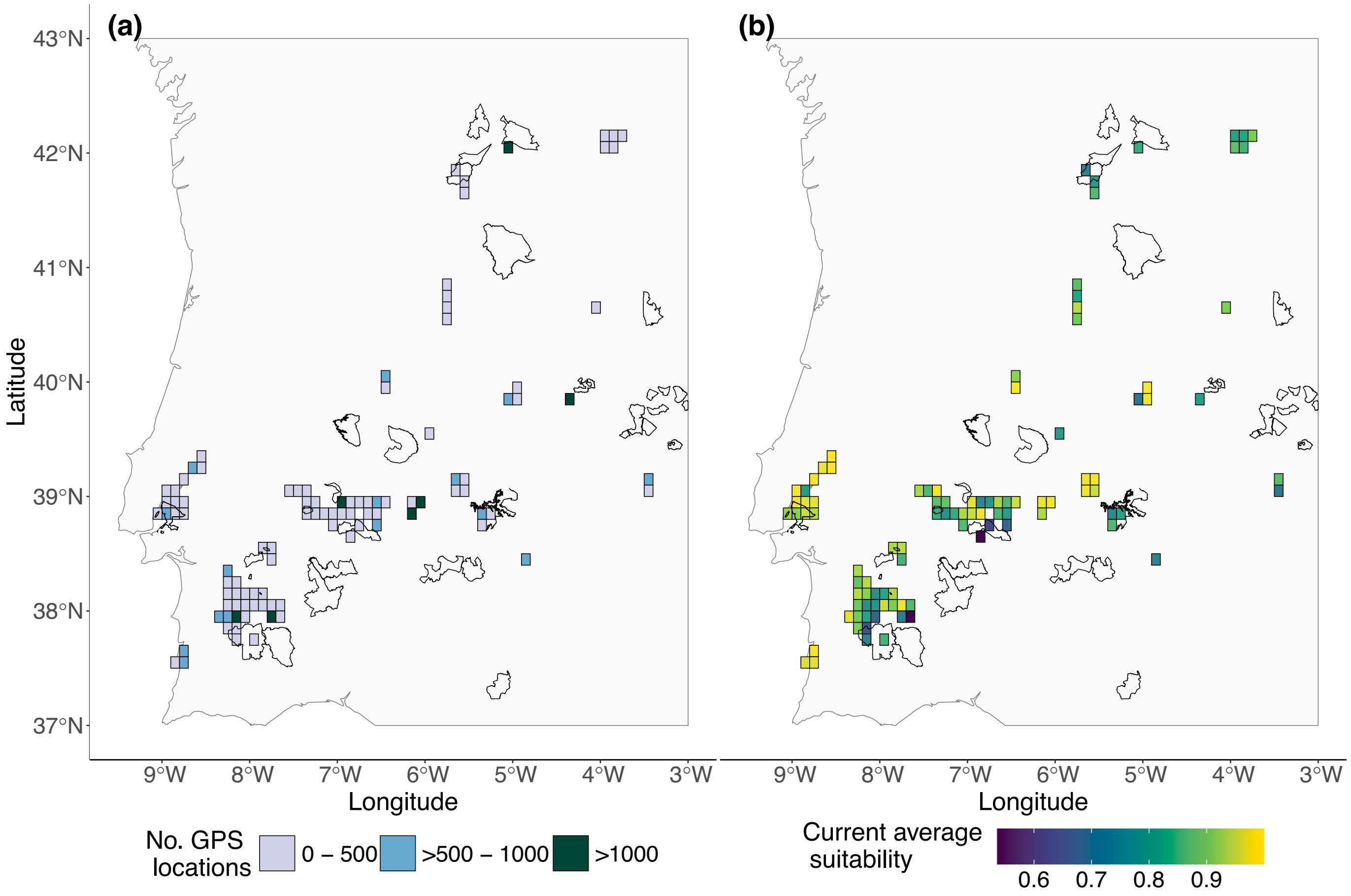

Fig. 3. The number of GPS locations used in the post-breeding season within each grid cell (cell resolution = 0.1°; $N = 32{,}601$; a), and current (2009–2019) average suitability during the post-breeding season within each grid cell as predicted by the generalized linear model using current site characteristics (b).

microclimate refugia but limited food sources. Hence, while the presence of scattered shrubby patches across that do not significantly disrupt the open habitats may generally be beneficial for little bustards, by significantly increasing microclimate refugia availability (Ramos et al., 2023a), a high proportion of them within the habitat may make the patch less favourable for the species.

The finding that sites preferred by little bustard during post-breeding are characterised by greater microclimate refugia availability aligns with previous studies that indicate the need for habitat patches providing adequate shelter from extreme heat (Ramos et al., 2023a; Suggitt et al., 2018). Generally, microclimate refugia have been shown to potentially buffer against broad scale extreme temperature events (Finocchiaro et al., 2024). Furthermore, a recent study of habitat suitability within the Iberian range of the little bustard showed that during the post-breeding season, individuals are likely to select habitat with more varied characteristics (Crispim-Mendes et al., 2024), and these areas may be more likely to have greater refugia availability. Similarly, meadow pipits were found to use microclimate refugia such shaded, cooler slopes within an upland landscape when macro-scale climatic conditions were unsuitable (Massimino et al., 2020). Our results contribute to the growing evidence for the necessity of refugia for the survival of species exposed to high temperatures and in the face of global warming (Nadeau et al., 2022; Ramos et al., 2023a; Suggitt et al., 2018).

We show that low density of shrub cover may provide microclimate refugia for little bustards. Like other grassland-associated birds, this species has been affected by habitat degradation and loss as a result of changes in and the intensification of agricultural practices (Gameiro et al., 2024; Silva et al., 2024). In the Iberian Peninsula, conversion of cereal fields to permanent pastures has led to the homogenisation of the landscape, with the quality of these habitats often being further degraded through overgrazing (Silva et al., 2023). Furthermore, habitat fragmentation as a result of land use changes may further reduce and isolate patches of suitable habitat, negatively affecting little bustard populations (Gameiro et al., 2020; Moreira et al., 2012; Santiago-Ramos and Feria-Toribio, 2021). In addition, climate change, and in particular increased occurrence of extreme events such as droughts and heatwaves, may have a further negative impact on habitat quality, while a lack of micro-refugia features may cause areas to become uninhabitable due to exposure to extreme thermal conditions (Ramos et al., 2023a). Management is required to maintain large-scale grassland areas, with features that improve habitat quality (e.g. through maintaining suitable vegetation height) and provide microclimate refugia features such as sparse shrubs that to not fragment the grassland habitat but may be used as shelter from the heat.

The Iberian Peninsula has already experienced changes related to global warming, and these are expected to continue in the next decades (IPCC, 2023). In addition to thermal strain on individuals, increasing temperatures, particularly earlier in the year, may result in vegetation drying out sooner, which may limit food availability. Furthermore, the threat may not be solely linked with year-to-year warming, but also with the increase in the occurrence of extreme events, such as draughts or heatwaves (Marcelino et al., 2020; Maresh Nelson et al., 2024). These more short-term events have been shown to have a particularly negative impact on grassland birds (Maresh Nelson et al., 2024). Based on our predictions, areas which are already experiencing more extreme temperatures, will continue to “deteriorate” in the future. This is particularly true for the centre and southwest part of the species' distribution range in Iberia, which coincides with important little bustard breeding

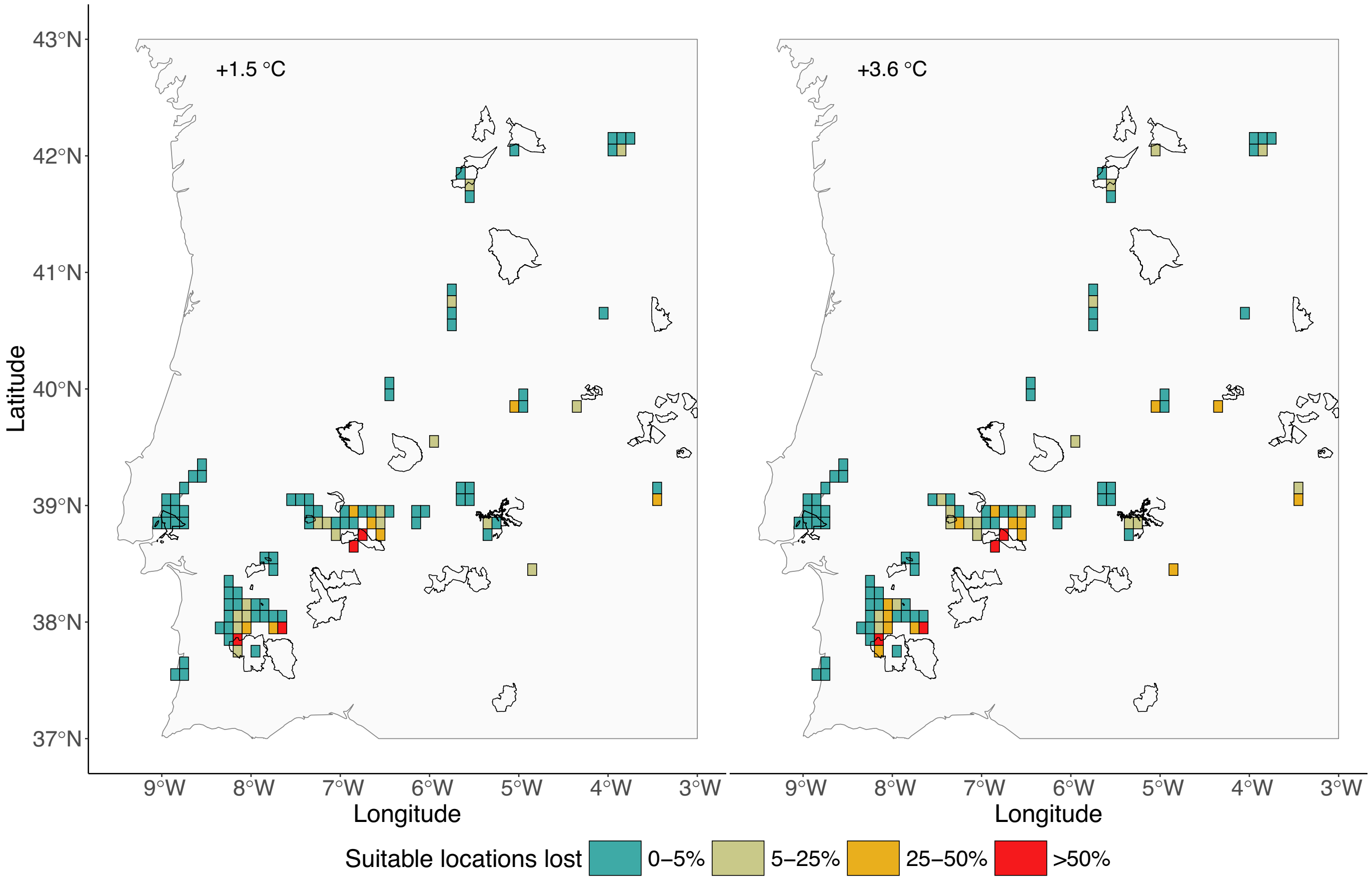

Fig. 4. The proportion of locations that become unsuitable for little bustards with a 1.5 °C or 3.6 °C temperature increase within each grid cell (resolution = 0.1°), predicted from the generalized linear model. Predicted site usage determined using a probability cut-off of 0.6. Within PAs, 3.5 % of sites are predicted to become unsuitable with an average warming of 1.5 °C, while with a 3.6 °C temperature increase this loss in suitability is expected to be 10.6 %.

sites within its Iberian range – Alentejo (Portugal) and Extremadura (Spain). Hence, habitat management to provide microclimate refugia will likely be key for enabling species, such as the little bustard, to survive these now unavoidable warming temperatures and increasingly frequent extreme events. The availability of fine-scale GPS tracking data allows us to identify which locations are used by the little bustards, and in combination with micro-scale environmental characteristics, we are able to determine the features of the habitats used. Furthermore, while breeding areas are relatively well protected, this is not the case for the sites used in the post-breeding season. However, during this time individuals are exposed to particularly high temperatures, which are likely to increase with global warming. Hence, the post-breeding areas that offer microclimate refugia shielding individuals from the heat urgently need to be protected to aid species conservation and prevent further rapid declines of the little bustard within the Iberian Peninsula.

The variables used to define site characteristics used in this study are not without limitations. Presence of green vegetation is associated with food availability for little bustard throughout their annual cycle (Bretagnolle et al., 2022), and therefore, NDVI has been included in this analysis. NDVI provides a measure of greenness but does not differentiate from where the greenness originates. This means that herbaceous, shrubby, or arboreous vegetation will be cumulatively and indiscriminately included, and therefore, higher NDVI may not always translate to greater food availability if the vegetation type is not suitable. A further limitation of our study is that it presents an over-simplified approach to predicting climate change. In each scenario considered, all site characteristics except for temperature are kept as those corresponding to the site characteristics at the time of tracking data collection. This is unlikely to be a realistic representation of how the landscape will change with climate change, but while temperature predictions exist, the same is not possible for habitat cover or NDVI. Linked to this, we assume an even warming across the area and the same level of presence of habitat characteristics providing microclimate refugia (i.e. microclimate refugia availability). However, it is not possible to obtain forecasts at microclimate level – while global monthly temperature predictions up to 2100 are available, they are at a relatively lower spatial resolution, and therefore, were not suitable for use in this study. Finally, this study has not explored past change in suitability within PAs. We show predicted declines in suitability across the study area with future warming, however, identifying changes which have already occurred may help to better understand the extent to which PAs have been impacted by ongoing climate change.

5. Conclusions

As global temperatures continue to rise and extreme weather events such as heatwaves and droughts increase in frequency, protected areas which enable year-round conservation of threatened species are of key importance. However, understanding the characteristics that make sites suitable for species conservation is crucial to help design conservation actions and management strategies for these areas. We show, that during the post-breeding season – a period of limited food availability and particularly high temperatures, sites used by little bustards are characterised by lower temperatures and greater availability of microclimate refugia. These sites correspond to low shrubby cover and higher NDVI. This highlights the trade-off between selecting sites with greater food availability, i.e. open, green areas (including irrigated areas), and using sites with characteristics offering refugia from high temperatures, such as drier sites with sparce shrubs. Our study contributes to the growing evidence of the crucial role of microclimate refugia for the persistence of species in areas already exposed to extreme thermal conditions, such as the little bustard.

CRediT authorship contribution statement

Karolina Zalewska: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Rita F. Ramos:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Inês Catry:** Writing – review & editing, Supervision, Funding acquisition. **James J. Gilroy:** Writing – review & editing, Supervision, Methodology, Funding acquisition. **João P. Silva:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Aldina M.A. Franco:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Ethical approval

All captures and handling of little bustards, and deployment of GPS tracking devices were performed under license and in accordance with relevant guidelines and regulations. Licenses were issued by Instituto da Conservação da Natureza e das Florestas (Portuguese Government agency responsible for Wildlife and Forests Management and Conservation) through licenses to João Paulo Silva (ICNF/CAPT/2014, ICNF/CAPT/2015) and Consejería de Medio Ambiente y Rural, Políticas Agrarias y Territorio of the Junta de Extremadura (Spanish Ministry of Environment and Rural, Agrarian Policies and Territory of the Extremadura region) through the license to José Mª Abad-Gómez.

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Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111557.

Data availability

The tracking data used in this study is available in the Movebank Data Repository (Little Bustard movement ecology; study IDs: 56464697, 20047912, 56464970, 253940991, 461568973).

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