

1 **Microclimate refugia shapes microclimatic niches and predicts individual variability in post-**
2 **breeding migration in a partially migratory species**

3 **Abstract**

- 4 1. The characterisation of species' environmental niches can help predict biodiversity responses
5 to global environmental change and identify areas where environmental suitability declines
6 as the conditions change. However, environmental niches, i.e. the full range of conditions a
7 species experiences, are frequently described at coarse spatial and temporal scales, thus are
8 unlikely to capture the across-individual variability in exposure to microclimate conditions.
9 Within species ranges and even within populations, individuals may vary in their ability to
10 access microclimate refugia or may adopt different movement strategies to avoid exposure
11 to unsuitable conditions. This individual variability currently remains unclear but could help
12 us understand species' capacity to adjust to changes in climate.
- 13 2. We used an 11-year satellite tracking dataset and high-resolution remotely sensed habitat and
14 climate information to investigate the microclimatic niche of a partially migratory grassland
15 bird, the endangered little bustard (*Tetrax tetrax*) in the species western stronghold
16 populations, in Southern Europe. Our study, including both breeding and post-breeding
17 seasons, aimed to determine if the local conditions experienced by individuals during the
18 breeding season can be used to predict individual movement strategies after breeding.
19 Furthermore, we examined if the distance travelled during post-breeding dispersive migration
20 influenced the level of dissimilarity between seasonal niches experienced by individuals.
- 21 3. The little bustard microclimatic niche was characterized along a gradient of temperature and
22 microclimate refugia availability. Our results revealed that individuals occupying breeding
23 areas with low microclimate refugia availability were more likely to move longer distances
24 after breeding. Furthermore, long-distance migratory individuals maintained similar
25 microclimatic niches across seasons, whereas short-distance migrants predominantly
26 displayed a higher niche dissimilarity between seasons.

27 4. Temperature and microclimate refugia availability during the breeding season can help
28 predict individual differences in migratory behaviour of little bustards and their niche
29 dissimilarity across seasons.

30 5. Global warming and subsequent declines in microclimate refugia availability may force this
31 species to move earlier and travel longer distances after breeding. This study provides
32 information that can help design conservation strategies for little bustards and other
33 endangered grassland bird species exposed to high temperatures.

34

35 **Keywords:** microclimatic niche, seasonal movements, movement strategy, niche tracking, partial
36 migration, seasonal niche

37

38 **Introduction**

39 A species' niche can have multiple interconnected dimensions, including environmental, ecological
40 and biogeographic factors (Soberón, 2007). The combination of all niche dimensions limits species
41 distributions to a fraction of the fundamental niche - the realised niche (Hutchinson, 1978). The extent
42 of any given niche dimension may vary between individuals and across populations due to individual
43 variability in physiological, biological and behavioural traits (Soberón, 2007). Some individuals may be
44 niche specialists, having a narrow niche relative to their population or species, while others may be
45 generalists with relatively broad niches (Bolnick et al., 2003). The occurrence of both specialist and
46 generalist individuals within populations is a source of species diversity (Araújo et al., 2011; Carlson et
47 al., 2021) that may allow species to better adjust to environmental changes (Bolnick et al., 2007).
48 Understanding the underlying factors affecting individual variability and its demographic
49 consequences can aid the design of targeted conservation measures aiming to help species adapt to
50 the current fast rate of environmental change.

51 Species and individual niches may also vary throughout the annual cycle induced by seasonal
52 differences in environmental conditions (Cohen & Jetz, 2023; Winger et al., 2018), especially at higher

53 latitudes. Through migration, individuals can either maintain their environmental niche throughout
54 the year, by moving between areas with similar environmental characteristics, a phenomenon
55 referred to as “niche tracking” (Gomez et al., 2016), or undergo a complete niche change, known as
56 “niche switching” (Ponti et al., 2020). These seasonal niches play a crucial role in individual fitness and
57 survival, with the breeding season often being the most critical period (Harrison et al., 2011) when
58 individuals may require access to specific habitats, food resources, or social conditions (Ponti et al.,
59 2020). In the post-breeding period individuals can be more mobile, utilizing different combinations of
60 environmental conditions, and therefore have broader niches (Suárez-Seoane et al., 2008). The
61 movement strategies that enable niche tracking or switching can also vary between individuals within
62 populations and species (Fandos et al., 2020; Illán et al., 2022).

63 Partial migration, where some individuals within a population migrate, while others remain resident
64 at their breeding sites throughout the year, is more common than previously thought (Buchan et al.,
65 2020; Chapman et al., 2011; Newton, 2010; Reid et al., 2018). For the two strategies (residency and
66 migration) to be maintained within a population, both need to yield similar fitness or relative benefits
67 (Buchan et al., 2020; Lundberg, 1988). Migration may have a higher cost than residency, as migratory
68 individuals, especially those performing long distance movements, face high energetic costs and an
69 increased probability of encountering threats both during migration and at post-breeding sites
70 (Alerstam et al., 2012; Buchan et al., 2023; Wikelski et al., 2003). However, moving also allows
71 individuals to access new resources and maintain their niche, while residents and short-distance
72 migrants may be exposed to seasonal changes and unsuitable conditions at their year-round sites, and
73 consequently occupy different niches across their annual cycle (Alerstam et al., 2012). The
74 mechanisms and drivers underlying between-individual variability in movement behaviour and niche
75 tracking strategies are still poorly understood (but see Illan et al., 2022) or have mostly been examined
76 at coarse scales (Fandos et al., 2020; Zurell et al., 2018) but have a wide interest when planning
77 conservation measures.

78 The emergence of microclimate and high-resolution environmental data, including information at the
79 scale at which individuals experience their environments (Carlson et al., 2021; Suggitt et al., 2018), is
80 opening new research opportunities and increasingly being used to understand responses to
81 environmental change (Maclean & Early, 2023; Massimino et al., 2020; Potter et al., 2013) and
82 variability in individual behaviour (Ramos et al., 2023b). This has been facilitated by recent advances
83 in animal tracking technologies (e.g. Nathan et al., 2022), increased availability of remotely sensed
84 habitat information (Petorelli et al., 2005; Valerio et al., 2020), and lower costs of cloud computing,
85 which were major limitations just a few years ago (Schulte to Buhne & Pettoelli, 2017).

86 In this study, we analyse movement data of 46 little bustards (*Tetrax tetrax*), satellite tracked over 11
87 years, in five Southern European breeding populations and characterise individual and population
88 realised microclimatic niches, characterised using the microclimatic temperature and refugia
89 conditions that are utilised across the breeding and post-breeding seasons. We determine the micro-
90 scale environmental factors (e.g. temperature, microclimate refugia and food availability) that may
91 influence individual migratory distances and subsequent seasonal niche dissimilarities of this partially
92 migratory species. We hypothesise that (1) increased access to microclimate refugia and food
93 availability within breeding areas reduces post-breeding migratory distances, since access to
94 temperature refugia sites and foraging resources are expected to be available locally; (2) individuals
95 exposed to higher temperatures during the breeding season will undergo longer post-breeding
96 dispersive migrations as physiological limits may be reached at the breeding sites forcing individuals
97 to move; and (3) individuals moving relatively shorter distances will have more dissimilar breeding and
98 post-breeding niches than those dispersing farther from the breeding areas, this is expected because
99 individuals moving longer distances may be able to find optimal microclimate and foraging conditions
100 (similar to the breeding areas), while those moving shorter distances may be using local refugia in
101 suboptimal sites but do not experience the cost of moving to new areas.

102

103 **Materials and Methods**

104 **(a) Study site and target species**

105 The Iberian Peninsula is simultaneously a global biodiversity hotspot and one of the world's most
106 vulnerable regions to climate change (Pörtner et al., 2022). The region is expected to suffer from
107 extensive warming and increasing drought frequency in the near future (Jones et al., 2020), which is
108 expected to cause habitat changes, species range contractions or even (local) extinctions (Pörtner et
109 al., 2022). Conditions are particularly rough in flat and open areas with low vegetation cover, such as
110 semi-natural grasslands, where species are exposed to high temperatures throughout most of the
111 year. Within the Iberian Peninsula, semi-natural grasslands are one of the most climate change
112 sensitive habitats, due to their ecological characteristics and dependency on human management
113 through agriculture activities and livestock grazing (Emanuelsson, 2008).

114 Semi-natural grasslands in Iberia are crucial for grassland birds, including several endangered species
115 that use this habitat mainly during the breeding period. Among those species, the little bustard, *Tetrax*
116 *tetrax* (Linnaeus, 1758), which is a medium-sized grassland specialist bird classified as 'Near
117 Threatened' (BirdLife International, 2021). Recent studies indicate a severe decline in little bustard
118 breeding numbers in the Iberian Peninsula (Morales & Bretagnolle, 2022a; Silva et al., 2023), which
119 used to be a stronghold of this species' western distribution (García de la Morena, 2018; Silva et al.,
120 2018). The main Iberian breeding populations are predominantly concentrated in the Extremadura,
121 Castilla La Mancha (Spain), and Alentejo (Portugal) regions (Equipa Atlas, 2008; García de la Morena
122 et al., 2018), all of which are affected by elevated temperatures and vulnerable to climate change
123 (Pörtner et al., 2022, Ramos et al., 2023a).

124 Little bustards are a partially migratory species (García de la Morena et al., 2015), where many
125 individuals move to northern or coastal post-breeding areas, where the temperatures are milder and
126 the food availability is higher (García de La Morena et al., 2015; Silva et al., 2007). These post-breeding
127 movements occur between June and August and are mostly triggered by food shortages, increased
128 levels of exposure to high temperatures, and a lack of microclimate refugia in the breeding areas
129 (Ramos et al., 2023b). This species is known to decrease their activity patterns at temperatures above

130 25 °C (Silva et al., 2015) and make use of microclimate refugia sites during the warmer parts of the
131 year (Ramos et al., 2023a).

132

133 **(b) Tracking and location data**

134 Between 2009 and 2019, 46 male little bustards were captured and tagged in five distinct breeding
135 areas across the southwest Iberian Peninsula, in Alentejo (Portugal) and Extremadura (Spain), during
136 the breeding season (April and May). Breeding males were attracted by a stuffed female acting as a
137 decoy and trapped with snares (Ponjoan et al., 2010; Ramos et al., 2023a). GPS tracking devices
138 varying between 2% and 4% (\bar{x} = 3.2%) of the birds' mass (Kenward, 2000), were deployed using a
139 thoracic harness made of Teflon Ribbon with a weak link to avoid lifelong deployment. Two types of
140 solar GPS devices were used. Platform Transmitter Terminal (Solar Argos/GPS 30_g PTT - Microwave
141 Telemetry) devices were deployed on 19 birds between 2009 and 2011, and Global System for Mobile
142 Communications (GSM) devices (Flyway 38g - Movetech Telemetry) were deployed on 28 birds
143 between 2014 and 2019. Transmitters were programmed to record a GPS position every 2 hours (PTT)
144 or 10 to 30 minutes (GSM).

145 Bird trapping and the deployment of GPS devices were approved by the Instituto da Conservação da
146 Natureza e das Florestas (Portuguese Government agency responsible for Wildlife and Forests
147 Management and Conservation) through licenses to João Paulo Silva (ICNF/CAPT/2014,
148 ICNF/CAPT/2015) and Consejería de Medio Ambiente y Rural, Políticas Agrarias y Territorio of the
149 Junta de Extremadura (Spanish Ministry of Environment and Rural, Agrarian Policies and Territory of
150 the Extremadura region) through the license to José M^a Abad-Gómez.

151 We filtered the GPS locations dataset to only include locations on the ground with null velocity.
152 Moreover, we included only daylight locations collected between 6 am and 5 pm (breeding) and 7 am
153 and 8 pm (post-breeding) to avoid capturing nocturnal roost sites. Only individuals captured before
154 the 1st of May and with at least seven days of data prior to departure from the breeding areas were
155 included in the analysis. This threshold was defined to reduce the influence of the tagging date, which

156 can vary greatly between individuals, as well as to avoid characterising the breeding season based on
157 a relatively low sample size from individuals captured later in the season. As a result, for consistency,
158 we defined the breeding season as starting from the 1st of May for all individuals. The end of breeding
159 and the start of post-breeding season was the date when each tracked little bustard left the breeding
160 area and moved to a non-breeding area for a minimum period of 30 days. Birds that used the breeding
161 area during the whole year were considered residents (Jiguet & Bretagnolle, 2001) and the post-
162 breeding season was defined as their period between the 15th of July and the 15th of September. This
163 represents the hottest period of the year in the Iberian Peninsula, when little bustards are exposed to
164 extreme temperatures, as well as a period of food shortage (Ramos et al. 2023a, Silva et al. 2007).

165

166 (c) Environmental data

167 We obtained micro-scale environmental data for all little bustard GPS locations as well as within a 500
168 m buffer around each GPS location. Hourly temperatures were extracted at a 30 x 30 m resolution at
169 20 cm above ground (Ramos et al. 2023a) using the *microclima* (Maclean et al., 2019) and *NicheMapR*
170 (Kearney & Porter, 2017) packages in R version 4.1.0 software (R Core Team, 2016). We used the fully
171 automated microclimate model, which generated temperatures at the 30 m scale while accounting
172 for terrain characteristics, habitat type, and vegetation information (such as canopy and shading
173 effects). Within the buffer around each GPS location, we also calculated the minimum, maximum,
174 mean, median, and standard deviation of the hourly temperature.

175 Microclimate refugia are small patches within the broader landscape with features that may provide
176 shelter from unfavourable, particularly high temperatures (Rull, 2009). For the studied species,
177 microclimate refugia is characterized by small patches of non-herbaceous vegetation, usually trees
178 and shrubs, in an herbaceous matrix, which creates a more heterogeneous thermal landscape (Ramos
179 et al. 2023a).

180 Previous studies have highlighted the importance of the availability of such sites for the little bustard
181 (Ramos et al. 2023). Hence, we calculated two metrics: refugia availability and refugia use and included

182 them in subsequent analyses. Refugia use was calculated as the difference between the estimated
183 temperature at the GPS location and median temperature of the 500 m buffer area, while refugia
184 availability was defined by the difference between the minimum and the median temperature within
185 the buffer (Ramos et al. 2023a):

$$186 \quad \text{REFUGIA USE} = \text{Temperature GPS Location} - \text{Buffer Median Temperature}$$

$$187 \quad \text{REFUGIA AVAILABILITY} = \text{Buffer Minimum Temperature} - \text{Buffer Median Temperature}$$

188

189 Greater negative values of both variables indicate more microclimate refugia use and availability
190 (Ramos et al. 2023a), since it translates in point temperatures cooler than the median of the buffer.

191 We also extracted the Normalized Difference Vegetation Index (NDVI) values for all little bustard GPS
192 locations. Satellite-derived NDVI is a measure of vegetation greenness and biomass which is widely
193 used to examine patterns of vegetation productivity and biodiversity distribution at large spatial and
194 temporal scales (Pettorelli et al., 2005). As green plants are an important component of the little
195 bustard's diet, especially during the breeding season, NDVI has been broadly used as a predictor of
196 food availability (Pettorelli et al., 2005). Moreover, precipitation acts as a stimulus for vegetation
197 growth, and therefore, is highly correlated with NDVI (Li et al., 2019; Schultz & Halpert, 1993). Thus,
198 NDVI is both a good indicator of precipitation patterns in the previous months (Pettorelli et al., 2005)
199 and a proxy of food availability, which is a key determinant of little bustard movements and space use
200 (Ramos et al., 2023b). NDVI was extracted from MODIS satellite imagery at a 250 m resolution and 8-
201 day interval, using the Google Earth Engine (Didan, 2015; Gorelick et al., 2017). We evaluated all
202 images retrieved to ensure that their quality was sufficient to be used in the study (Didan, 2015). We
203 calculate the average NDVI of the last eight days before an individual departed its breeding area (or
204 the end of the individual's breeding season). This was done to account for the immediate conditions
205 an individual may be experiencing before leaving the breeding area.

206

207 **(d) Micro-climate and the realised microclimatic niche**

208 The little bustard's realised microclimatic niche was characterised using the Principal Component
209 Analysis (PCA-occ) approach outlined by Broennimann et al. (2012). This method transforms the
210 correlated environmental variables into independent principal components, generating a multi-
211 dimensional shape, representing the microclimatic niche. The number of dimensions considered was
212 determined by the number of principal components cumulatively explaining over 70% of the variance
213 within the initial dataset. The PCA-occ was calculated using the *ade4* package (Dray & Dufour, 2007)
214 and the *ecospat* (Broennimann et al., 2014) R packages, and using the temperature- and refugia-
215 related variables outline above for all little bustard's GPS location data included in this study (Table 1).
216 The PCA scores corresponding to observations belonging to each individual, population, and season,
217 both across the entire study period and for each year, were extracted. The microclimatic space
218 (hereafter designated the realised microclimatic niche or microclimatic niche) utilized by little
219 bustards in different parts of the range and annual cycle, was determined by estimating the 99.5%
220 bivariate normal kernel (to eliminate outliers) of the corresponding PCA scores on the retained first
221 two principal components, using the package *adehabitatHR* (Calenge, 2006). This produces a two-
222 dimensional representation of the microclimatic niche. We then overlapped each population's
223 breeding and post-breeding niches with the total species' breeding and post-breeding niche,
224 respectively. We also calculated the percentage of overlap of the seasonal niches across all
225 populations, as well as between the seasonal niches and the overall little bustard niche. At individual
226 level, the overlaps were carried out separately for each population and each year that a given
227 individual was tracked for, i.e. the seasonal niche of any individual in any year was overlapped with
228 the niche of the same year and season of the population that that individual belonged to. Finally, we
229 determined, for each individual, the percentage of the total seasonal microclimatic niche occupied.

230

231 Table 1 – Description and spatial resolution of the micro-scale temperature and microclimate refugia variables
232 included in the Principal Component Analysis (PCA-occ), used to characterise the little bustard's realised
233 microclimatic niche.

Variable	Description
Point temp.	Temperature at the GPS location (°C), measured at 30 m scale and 20 cm above ground
Mean temp.	Mean temperature within the 500 m buffer around the GPS location (°C), measured at a 30 m scale.
Median temp.	Median temperature within the 500 m buffer around the GPS location (°C), measured at a 30 m scale.
Max. temp.	Maximum temperature within the 500 m buffer around the GPS location (°C), measured at a 30 m scale.
Min. temp.	Minimum temperature within the 500 m buffer around the GPS location (°C), measured at a 30 m scale.
Temp. Std	Temperature standard deviation within the 500 m buffer around the GPS location (°C), measured at a 30 m scale.
(Microclimate) refugia use	Difference between temperature at GPS location and Median temperature of the 500 m buffer
(Microclimate) refugia availability	Difference between the Minimum temperature of the 500m buffer and the Median temperature of the 500 m buffer, for the GPS location.

234

235 **Statistical analysis**

236 Adult little bustards tend to have a strong site fidelity in both breeding and post-breeding seasons
 237 (Alonso et al., 2020; García de La Morena et al., 2015), which can be derived from a learning process
 238 while they are immature birds, as documented in other bustard species (Burnside et al., 2017; Newton,
 239 2010). Moreover, previous studies showed that distance travelled during the post-breeding
 240 movements, tends to be relatively consistent between years for the same individual (Ramos et al.
 241 2023b). Since little bustard age is difficult to estimate, for birds with multiple years of data, only data
 242 from the last, most recent year of tracking was used in the analyses below. By including only the most

243 recent year of data for each individual we maximise the chance of capturing the consistent behaviour
244 that characterises adult individuals.

245 We obtained the centroids of each individual's daily utilization distribution (calculated as the 90%
246 bivariate normal kernel of the individual's relocations). For the breeding season, we calculated the
247 mean centroid across each individual's daily utilization distributions of that season. The distance
248 travelled by the individual to the post-breeding areas was calculated as the Euclidean distance
249 between the individual's mean breeding centroid and the centroids of each daily post-breeding
250 utilization distribution (for more details see Ramos et al., 2023b). The mean centroid for the breeding
251 distribution was used because, within a season, individuals consistently use the same areas, however,
252 during the post-breeding season some individuals may move and use more than one area, and
253 therefore, the movement distance was calculated for each daily utilization distribution during the
254 post-breeding. The distances calculated were then summed to obtain the total distance travelled by
255 each individual.

256 We obtained the centroids of the individual breeding and post-breeding microclimatic niches and
257 calculated the Euclidean distance between them for each individual. This distance represents the
258 dissimilarity between individual seasonal niches, where higher values mean more dissimilar niches.

259 We fitted two Linear Mixed-effects Models (LMM) using the *lme4* package (Bates et al., 2014). The
260 first model analysed the influence of the individual breeding niche on the dispersive migration
261 distance travelled, by using the coordinates of the centroids of each individual's breeding
262 microclimatic niche (scaled) and the average NDVI of the last eight days before departure from
263 breeding area (or last eight days of breeding season), to explain the distance travelled (natural
264 logarithm-transformed). The second model examined the effect of individual used niche as well as the
265 distance travelled on the dissimilarity between seasonal niches. To analyse this, we use the
266 dissimilarity between each individual's breeding and post-breeding niche (calculated as the distance
267 between niche centroids, see above) as a response variable, and include the percentage of overlap
268 between the individual's breeding niche and the breeding niche of its breeding population in the same

269 year, the scaled x (temperature) and y (microclimate refugia availability) coordinates (in PC units) of
270 the centroids of each individual's breeding microclimatic niche, as well as the distance travelled by
271 that individual during its dispersive migration (natural logarithm-transformed). In both models, we
272 included the breeding population as an independent random intercept effect.

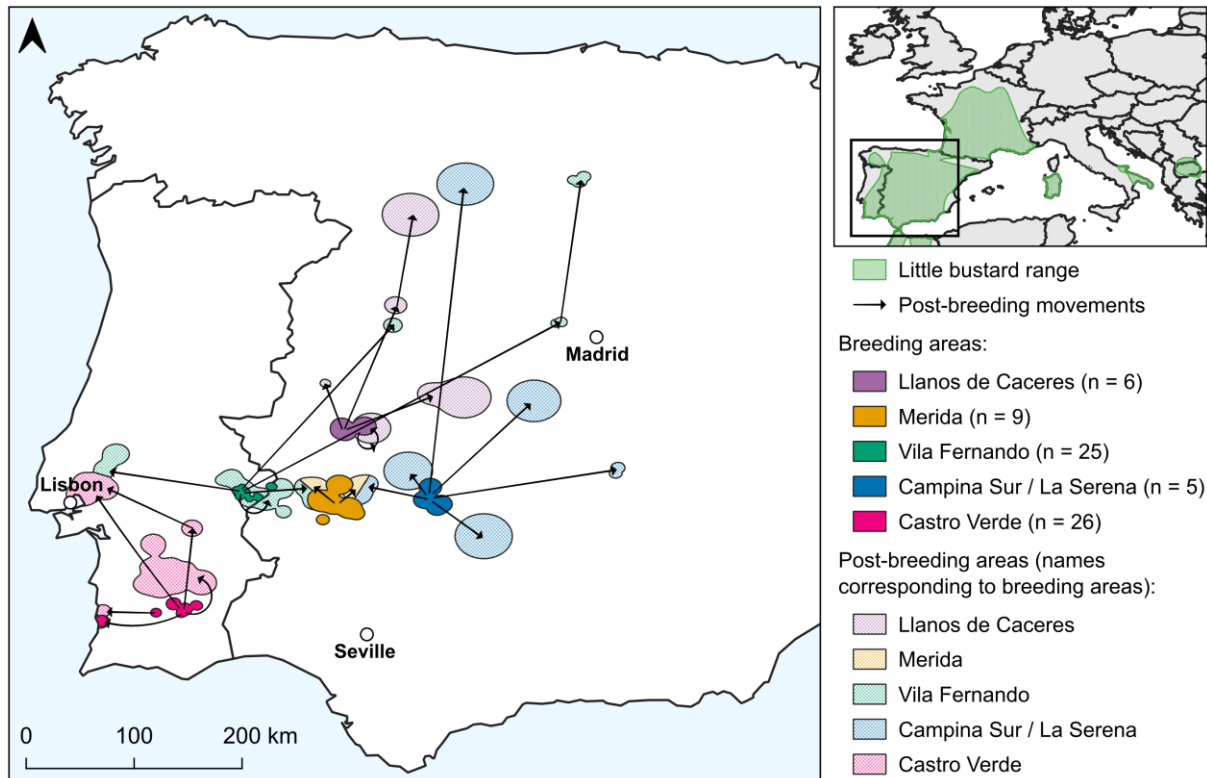
273 Some populations had a relatively small number of tracked individuals, and this low sample size could
274 potentially bias our results. To test whether a lower sample size is sufficient to produce an adequate
275 representation of the population niche, we randomly selected five individuals from populations with
276 a larger number of tracked individuals (Merida, Vila Fernando and Castro Verde) and repeated the
277 seasonal niche overlap analysis only using data for the selected five individuals. We repeated this
278 process for each possible combination of five individuals within each population (up to 10,000
279 combinations; see Supplementary Information: S3 for details). We then compared the population
280 seasonal niches produced using all data with those obtained using data from only five individuals and
281 found that the extent of seasonal niche overlap obtained for populations consisting of only five
282 individuals matches the seasonal niches produced with all available data. This suggests that five
283 individuals may be a representative sample of the populations included in this study.

284

285 **Results**

286 During the 11-year study, we captured and deployed GPS tracking devices on 46 male little bustards
287 in five different populations. We collected more than 30,000 GPS locations in both breeding and post-
288 breeding seasons, which we used to build the high-spatial resolution realised microclimatic niche. The
289 breeding areas used by the little bustards varied between 36,123 ha, in Vila Fernando and 162,547 ha,
290 in Merida (Figure 1, Table 2). The distance travelled to the post-breeding sites varied greatly between
291 individuals, with movements ranging from 1 to 421 km (median = 36 km) and with some birds using
292 more than one post-breeding area (Figure 1).

293



294

295 Figure 1 – Migratory movements of 46 male little bustards from breeding (full) to post-breeding (transparent)
 296 areas in the Iberian Peninsula obtained from GPS tracking data. Each colour represents a breeding population,
 297 and the number of individual/years tracked within each population is showed in paratheses (total of 71
 298 individual/years). The arrows show movements to post-breeding areas. The little bustard’s range within Europe
 299 (BirdLife International, 2021) is shown in green in the inset map.

300

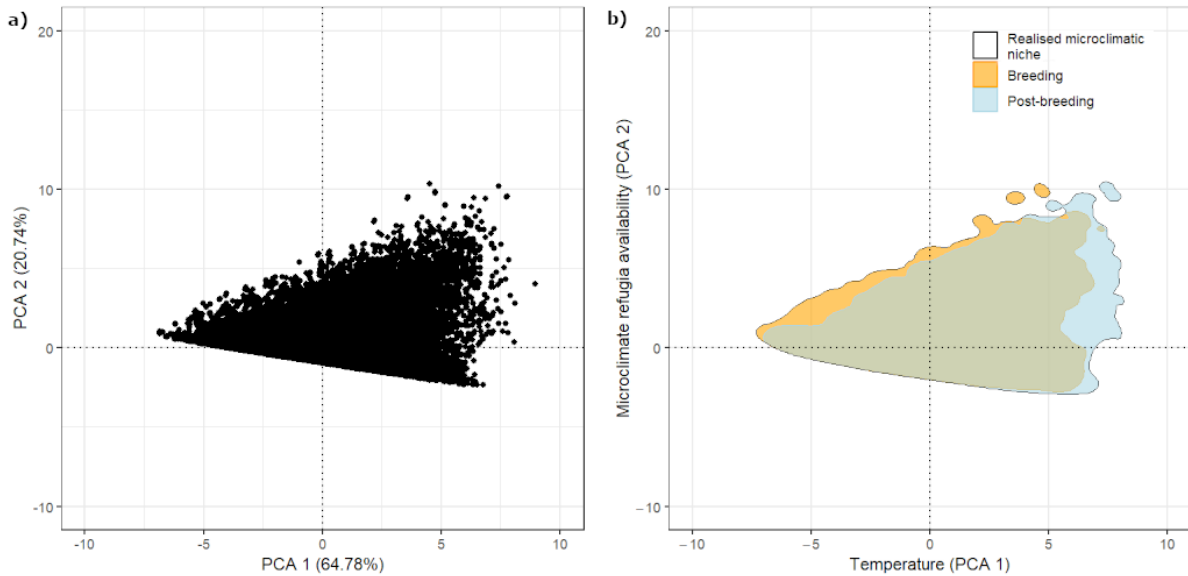
301 **(a) Realised microclimatic niche**

302 The little bustard realised microclimatic niche was characterised by the first two PC axes, capturing
 303 85.53% of the variation in the data (64.78% by the first and 20.74% by the second component,
 304 Figure 2a). The first axis was strongly and positively associated with temperature (point temperature,
 305 mean temperature, median temperature, minimum temperature, and maximum temperature). The
 306 second principal component had a strong positive association with increasing refugia availability and
 307 temperature standard deviation (Supplementary Information: S1).

308 The breeding season niche represented 85.72% of the total realised microclimatic niche, while post-
 309 breeding represented 91.00% (Figure 2b). The post-breeding niche overlapped in 89.55% with the

310 breeding niche (Figure 2b). Overall, the post-breeding niches were characterised by higher
 311 temperatures with more microclimate refugia availability compared to the breeding niches.

312



313

314 Figure 2 – a) Principal component scores representing the little bustard realised microclimatic niche determined
 315 based on GPS locations obtained in the Iberian Peninsula; b) Realised microclimatic niche during the breeding
 316 (orange) and post-breeding (blue) seasons.

317

318 Out of the five breeding populations tracked in this study, three had a breeding niche smaller than
 319 50% of the overall used niche (Campina Sur/La Serena, Castro Verde and Llanos de Caceres) (Table 2,
 320 Supplementary Information: S2). The two other breeding populations (Merida and Vila Fernando) had
 321 a wide breeding niche, representing more than 95% of the season’s used niche (Table 2, Figure 2).

322

323 Table 2 – General spatial (areas used, total number of individuals, and GPS locations) and realised microclimatic
 324 niche (overlap of breeding and post-breeding season microclimatic niches) information for each breeding
 325 population. ^a Number of individual/years in relation to the overall breeding season microclimatic niche. ^b
 326 Percentage of overlap with the post-breeding season’s overall microclimatic niche.

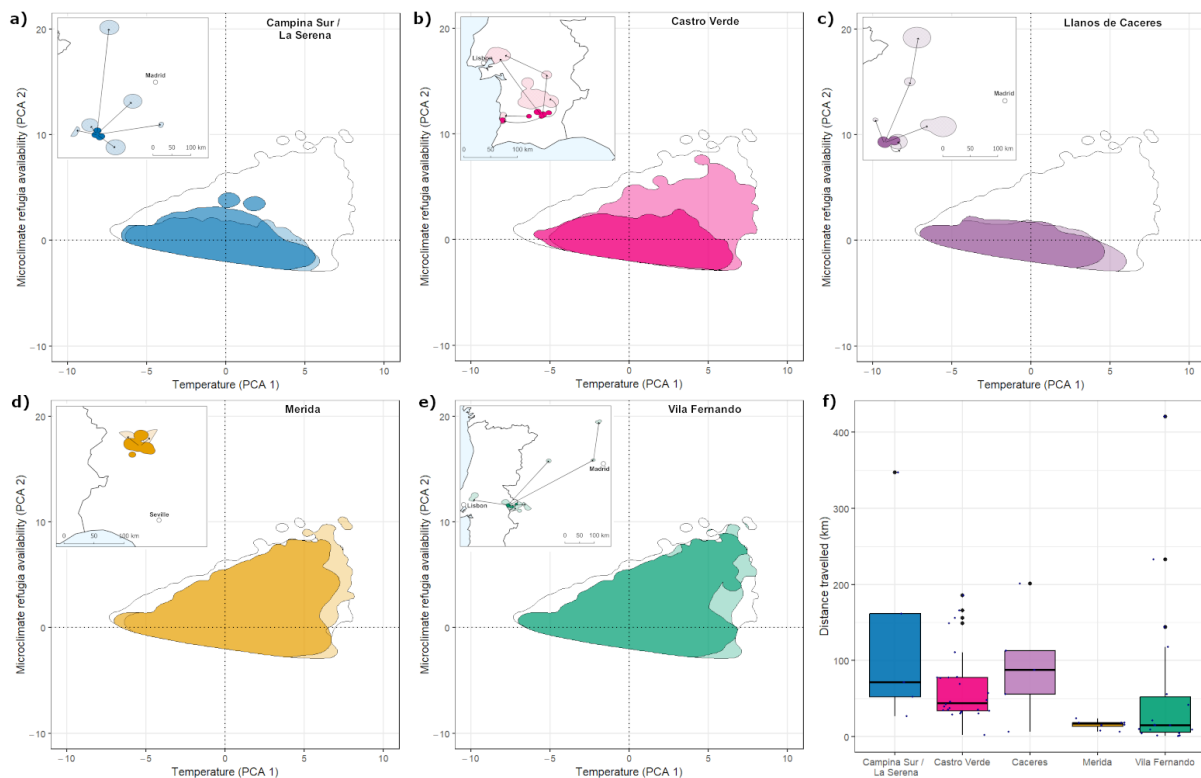
Capture site	Breeding used area (ha)	Num. ind. ^a	Num. GPS locations ^a	Breeding season overlap ^b	Post-breeding season overlap ^b
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Llanos de Caceres	77 846	6	1728	35.83	35.13
Merida	162 547	9	7197	98.15	97.14
Vila Fernando	36 123	25	9931	96.49	94.27
Campina Sur / La Serena	91 923	5	3170	47.00	37.22
Castro Verde	57 996	26	8296	44.52	78.30

327

328 For most breeding populations, the microclimatic niche remained similar in both seasons, despite the
329 post-breeding movements performed by the individuals (Figure 3). The majority of populations
330 maintained a similar percentage of niche occupied across seasons, except Castro Verde, for which the
331 seasonal microclimatic niche increased from 44.52% of the overall species niche in the breeding to
332 78.30% in the post-breeding season (Table 2, Supplementary Information: S2, S4), with the expansion
333 occurring towards areas with more microclimate refugia availability (Figure 3b).

334



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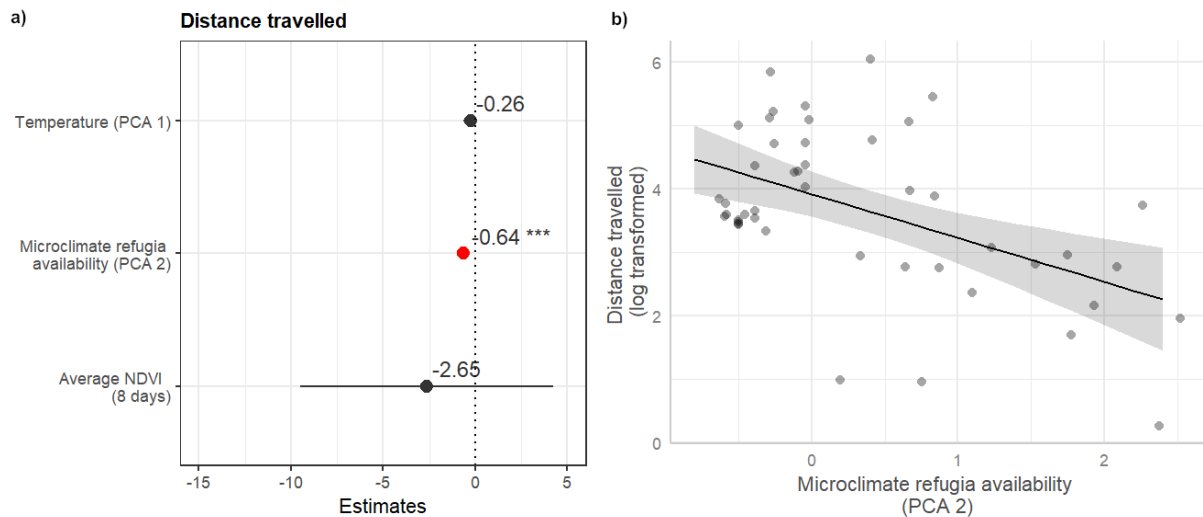
336 Figure 3 – Breeding (full colour) and post-breeding (transparent colour) microclimatic niche used by each
 337 breeding population with information of the post-breeding locations and movements (inset map), and the
 338 distances travelled (f). From top left to bottom right: Campina Sur/La Serena, Castro Verde, Llanos de Caceres,
 339 Merida, and Vila Fernando. Black outline shows the realised microclimatic niche across all populations and
 340 seasons. See Supplementary Information S4 for details on each individual and population.

341

342 **(b) Distance travelled and niche dissimilarity in relation to the breeding microclimatic niche**
 343 **characteristics**

344 Distance travelled was negatively associated with microclimate refugia availability (the PC2; estimate
 345 = -0.638, SE = 0.168, $p < 0.001$), while there was no significant association with temperature (PC1;
 346 estimate = -0.261, SE = 0.182, $p = 0.158$), or NDVI (estimate = -2.648, SE = 3.395, $p = 0.440$; Figure 4).

347



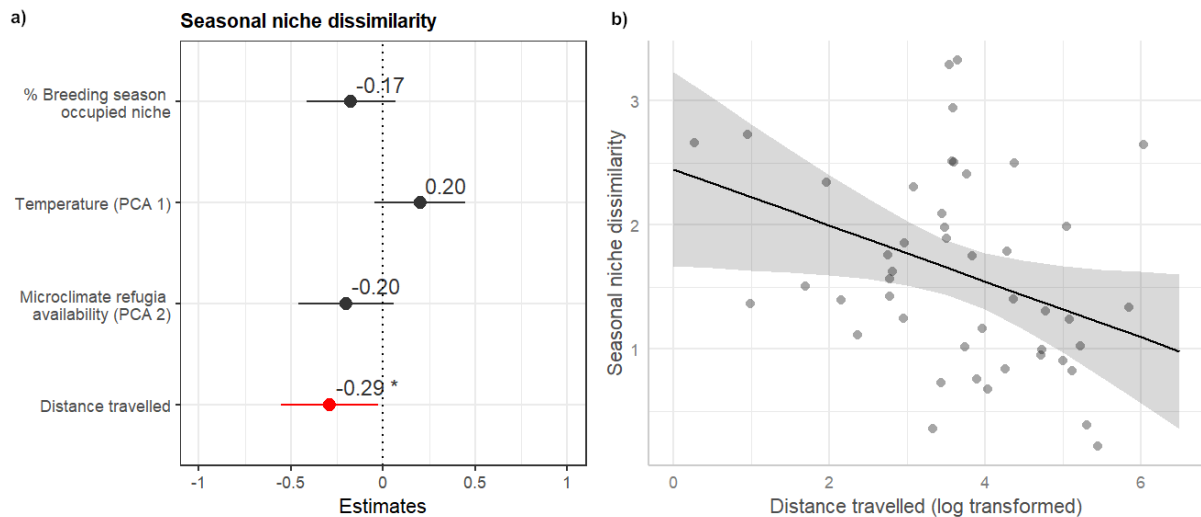
348

349 Figure 4 – a) Coefficient estimates, from LMM, explaining the individual distance travelled using microclimatic
 350 niche dimensions (temperature (PC1) and microclimate refugia availability (PC2)) and NDVI (R^2 presented Figure
 351 S5.1). Covariate significance is shown: *** $p < 0.01$; * $0.01 < p < 0.05$; none/otherwise, $p > 0.05$.; and b) the
 352 relationship between distance travelled and microclimate refugia availability (PC2).

353

354 Seasonal niches were more dissimilar as the distance travelled in the post-breeding migration
 355 decreased (estimate = -0.289, SE = 0.130, $p = 0.032$), while there was no significant association with
 356 any microclimatic niche axis (PC1 estimate = 0.200, SE = 0.122, $p = 0.108$; PC2 estimate = -0.201, SE =
 357 0.127, $p = 0.122$) or the individual’s breeding microclimatic niche (estimate = -0.175, SE = 0.119, $p =$
 358 0.149; Figure 5).

359



360

361 Figure 5 – a) Coefficient estimates from LMM for the effect of niche characteristics and migratory distance
 362 travelled on niche dissimilarity between seasons (R^2 presented Figure S5.2). Covariate significance is shown: ***
 363 $p < 0.01$; * $0.01 < p < 0.05$; none/otherwise, $p > 0.05$. b) Dissimilarity between the seasonal niches in relation to
 364 the distance travelled in the post-breeding dispersive migration.

365

366 **Discussion**

367 Our study, utilizing a robust dataset of 11 years of tracking data with more than 30,000 GPS locations,
 368 primarily focused on understanding the realised microclimatic niche of an endangered grassland bird
 369 specialist. Our study characterised the little bustard’s microclimatic niche within the southern part of
 370 the Iberian Peninsula across gradients of temperature and microclimate refugia availability. While
 371 there was a significant overlap of the seasonal niches at the species level, some populations were
 372 restricted to smaller sections of the species niche in southern Iberian Peninsula. At individual level, we
 373 observed a negative relationship between distance travelled and microclimate refugia availability
 374 during the breeding season, whereby individuals with less refugia available within their breeding sites
 375 tend to move longer distances. Additionally, distance travelled was also negatively related to niche
 376 dissimilarity between seasons, as birds that performed longer movements maintained a similar
 377 realised microclimatic niche across seasons.

378 Not surprisingly, temperature (thermal component of the niche) explained more than half of the
 379 variation within the data, representing the first axis of the niche. This finding is consistent with

380 previous studies that have identified temperature as a critical factor in determining the macro-scale
381 environmental niches of species, including that of the little bustard (Delgado et al., 2011; Fandos &
382 Telleria, 2020; Ponti et al., 2020). Temperature is a well-known driver and limiting factor at both
383 species- and individual-levels, frequently shown to have direct effects on individuals through thermal
384 stress, as well as affecting them indirectly, by reducing food availability (Breed et al., 2013; Chen et
385 al., 2011; Hao et al., 2012; Rastogi et al., 2007). Furthermore, extreme temperatures have also been
386 linked to changes in individual breeding and migratory behaviour (Tomotani et al., 2018).

387 Microclimate refugia availability was the main variable defining the second dimension (component)
388 of the microclimatic niche. Although little bustards only occasionally use microclimate refugia (Ramos
389 et al., 2023a), these areas may become crucial during the post-breeding season when temperatures
390 increase, and food becomes scarce (Silva et al., 2007). Areas of microclimate refugia availability can
391 provide necessary shelter from high temperatures for both little bustards, as well as for arthropods,
392 which are an important food source for this species, especially in drier habitats (González del Portillo
393 et al., 2021; Jiguet, 2002; Suggitt et al., 2018). Given that little bustards show reduced activity levels
394 when temperatures are above 25 °C and can experience temperatures of up to 40 °C during the post-
395 breeding season in the Iberian Peninsula (Ramos et al., 2023a; Silva et al., 2015), it is unsurprising that
396 microclimate refugia availability may be an important component of the little bustard's realised
397 microclimatic niche. Areas with microclimate refugia availability are usually characterized by small
398 patches of shrubs and trees in a generally herbaceous matrix (Ramos et al. 2023a), creating a
399 heterogeneous thermal landscape.

400 The population microclimatic niches varied mainly across the second principal component, which was
401 associated with microclimate refugia availability. During the breeding season, microclimate refugia
402 were relatively limited for three breeding populations (Llanos de Caceres, Campina Sur/La Serena, and
403 Castro Verde), compared to the Merida and Vila Fernando populations, which had a broad breeding
404 niche in terms of refugia availability. In the post-breeding season, however, while both Llanos de
405 Caceres and Campina Sur/La Serena populations seemed to have maintained an almost identical

406 microclimatic niche, the niche of the Castro Verde population expanded in terms of refugia availability.
407 On average, individuals from the Campina Sur/La Serena and Llanos de Caceres populations move
408 farther north during the post-breeding season than individuals from Castro Verde, or any of the other
409 breeding populations studied here. Northern areas are characterised by temperatures up to 10 °C
410 lower compared to the more southern post-breeding areas (Ramos et al. 2023a). The lower
411 temperatures associated with Northern post-breeding areas are more similar to the temperature
412 range that the individuals are exposed to during breeding, and therefore, the relative thermal strain
413 is lower. Hence, these individuals that travel longer distances to areas with lower temperatures may
414 be less dependent on the availability of microclimate refugia (Ramos et al. 2023a) and are usually
415 niche trackers, a behaviour already documented at the species level for multiple species (Fandos &
416 Tellería, 2020; Somveille et al., 2019). The opposite may be true for birds that do not move as far
417 north, such as the Castro Verde breeding population, as the exposure to relatively higher
418 temperatures within their post-breeding areas may potentially increase the need for microclimate
419 refugia. Castro Verde is one of the warmest areas within the little bustard's range in the Iberian
420 Peninsula and has had the highest temperature anomaly, reaching 2 °C during the breeding season,
421 over the past 30 years (Ramos et al., 2023a). Hence, individuals from this breeding population migrate
422 to areas with more microclimate refugia available (near the coast) and have a more dissimilar post-
423 breeding niche, as finding shelter from the extreme heat within the area may be necessary to maintain
424 fitness and for their survival. Finally, both the Merida and Vila Fernando populations had broad
425 microclimatic niches with relatively more microclimate refugia available across both the breeding and
426 post-breeding seasons. The greater refugia availability may allow individuals from these populations
427 to cope with increasing temperatures throughout the summer (the post-breeding season) and remain
428 in similar areas in both seasons. Thus, these breeding populations have, in general, more similar
429 seasonal niches. These across-population differences result from diverse individual movement
430 strategies and use of microclimate refugia, which have been associated with increased resilience to
431 environmental change (Gilroy et al 2016, Ramos et al. 2023b).

432 While previous studies compared long-distance migrants to resident birds (Cohen & Jetz, 2023; Gomez
433 et al., 2016; Ponti et al., 2020), this study analysed individual GPS data and the gradient of distances
434 individuals moved, including resident, short-, medium-, and long-distance migrants. At individual level,
435 the availability of microclimate refugia during the breeding season was negatively associated with the
436 migration distance of male little bustards, with longer distance migrants having less microclimate
437 refugia availability during breeding. Although microclimate refugia availability is dynamic over time,
438 areas with low availability during the breeding season are likely to remain so in post-breeding (Ramos
439 et al., 2023a). Furthermore, during the breeding season, male little bustards are restricted to lekking
440 areas, which are characterized by open sites that allow birds to be seen by conspecifics but also expose
441 them to elevated temperatures due to the lack of features that may shield them from the heat (Silva
442 et al., 2015; Silva et al., 2017; Ramos et al. 2023a). Post-breeding movements may be the most
443 advantageous strategy for birds experiencing low microclimate refugia availability during their
444 breeding season, allowing them to move to cooler areas or areas with refugia available. Moreover,
445 migration has other benefits such as access to sites with higher food availability (Fandos & Telleria,
446 2020; Somveille et al., 2019), however, it can also have a potentially detrimental effect on fitness due
447 to its high energetic cost and the increased exposure to potential hazards (Dingle, 2014; Wikelski et
448 al., 2003). On the other hand, individuals that move short distances or are resident are likely exposed
449 to harsh conditions during the warmest period of the year, the post-breeding season (Fandos &
450 Tellería, 2020). Thus, remaining stationary requires a higher tolerance to sub-optimal conditions and
451 may involve behavioural and physiological adaptations to cope with unfavourable conditions (Cohen
452 & Jetz, 2023). However, remaining closer to the breeding sites can also be advantageous, as it removes
453 the additional physiological strain of movement which could otherwise have a negative effect on
454 individual fitness during the subsequent breeding season.

455 Similarly, migratory distance was also a good predictor of seasonal dissimilarity in the individual's
456 microclimatic niche. Individuals that travel longer distances have low seasonal niche dissimilarity,
457 indicating potential niche tracking. On the other hand, individuals that choose post-breeding locations

458 closer to the breeding areas, may display niche switching strategies (Martínez-Meyer et al., 2004;
459 Nakazawa et al., 2004). This behaviour has already been documented at the species level for multiple
460 species (Fandos & Tellería, 2020; Somveille et al., 2019). For the studied populations of male little
461 bustards, our results suggest that individuals with less microclimate refugia available during the
462 breeding season move farther away to cooler locations, which can be considered macro scale refugia
463 and are characterised by conditions similar to those experienced by the individual during breeding.
464 While little bustards exhibit high site fidelity during both breeding and post-breeding seasons, and
465 migratory behaviour is likely a genetic trait (Alonso et al., 2020; Burnside et al., 2017; Villers et al.,
466 2010), migratory behaviour and migratory distance are plastic behaviours that vary between
467 individuals in partially migratory species (Pulido, 2007; Salewski & Bruderer, 2007). As such, a
468 dispersive migration strategy may persist if individuals adopting different movement strategies gain
469 fitness benefits under distinct environmental conditions, and environmental variability and selection
470 do not favour one single strategy (Buchan et al. 2021).

471 The average NDVI of the last 8 days of each individual's breeding season, had no significant effect on
472 the distance travelled by individuals. In southern Iberian Peninsula, NDVI peaks during April and May
473 and decreases steeply from May to June, as temperature increases (Marcelino et al. 2020). Male little
474 bustards are highly affected by this fluctuation. In areas where NDVI decreases rapidly, they migrate
475 early, whereas areas with higher NDVI allow for a longer breeding period (Ramos et al. 2023b).
476 Towards the end of the breeding season, NDVI is relatively low across all breeding sites, and therefore,
477 all individuals within our study area are likely exposed to similar, low availability of green plants.
478 Furthermore, despite the well-known importance of green plants in little bustard's diet, during
479 reproduction and periods of food shortage (Jiguet 2002, Bretagnolle et a. 2022, Silva et al. 2015),
480 recent studies reinforce that arthropods also form an important part of the little bustard diet
481 (Cabodevilla et al. 2021, González del Portillo et al. 2024), indicating that NDVI alone may not capture
482 the full extent of food availability. This could explain why male little bustards, like other bustard
483 species, have a high site fidelity in both breeding and post-breeding season (Alonso et al. 2020,

484 Burnside et al. 2017), which is also linked with relatively high repeatability of the distance travelled
485 between years (Ramos et al. 2023b).

486 Nevertheless, caution is needed when extrapolating these findings. During the non-breeding period,
487 little bustards gather in mixed flocks, including males, females and juvenile individuals (Morales et al.
488 2022), and thus, all individuals, may have similar microclimatic requirements, as well as limitations.
489 However, since only females participate in chick-rearing, they tend to stay longer in the breeding areas
490 (Schulz 1986). As the summer progresses and temperatures increase, females and juveniles will
491 potentially experience detrimental environmental conditions, which may be different to those
492 experienced by males. Additionally, the knowledge of female little bustards' movement strategies,
493 such as timings, distance travelled, and stopovers, is still largely limited, and may differ from the
494 migratory strategies of males, which are better understood (Morales et al. 2022). Thus, we can expect
495 that the post-breeding microclimatic niche will be similar across males and females, however, during
496 the breeding season, their niches may be significantly different, and therefore, the relationship
497 between the seasons and movement strategies of females may be different from that reported in this
498 study.

499 This study focuses on birds captured in Southwest Iberian Peninsula, which exhibit two main migration
500 patterns described for the Iberian populations: resident/sedentary and summer migrants (García de
501 la Morena et al. 2015). However, other dispersive migratory strategies are known within the
502 populations of the Iberian Peninsula (García de la Morena et al. 2015). In particular, populations in the
503 north of Iberia, have higher proportions of summer-winter and winter migrants (Morales et al. 2022,)
504 which may display different microclimatic niches and niche similarities between seasons, since they
505 are exposed to lower temperatures across the year (Ramos et al. 2023a). Hence, our findings may be
506 extrapolated to other populations with the same migratory strategies but not to all populations within
507 the Iberian Peninsula.

508 Finally, the metric used in this study to quantify seasonal differences in microclimatic niches captures
509 a limited representation of a potentially more complex ecological relationship. Seasonal niche

510 dissimilarity, measured as the Euclidean distance between the centroids of the seasonal microclimatic
511 niches, represents the difference between the average position of each niche within the
512 environmental space, however, it does not capture other potentially important niche characteristics,
513 such as niche size or shape. For example, the range of post-breeding conditions may be completely
514 within the range of breeding conditions, and the two niches may fully overlap, but the centroid
515 distance may be relatively large. Furthermore, niche shifts may be determined by the availability
516 within the environmental space, and this availability is likely to differ seasonally. An individual may
517 select different conditions due to differences in requirements at different stages of the annual cycle,
518 or experience seasonal changes in conditions. Thus, accounting for niche position within the total
519 available environmental space would provide a more complete overview of the seasonal niche
520 dynamics. Our approach only partially included this, as the range of microclimatic conditions observed
521 across all individuals and seasons is used to define the range of the two principal component axes.
522 Although quantifying niche overlap while explicitly accounting for the range of conditions that are
523 utilised out of those available would provide a more complete and nuanced overview of seasonal niche
524 dynamics, it is not possible given how computationally intensive microclimate modelling is. For our
525 study it would require generating the hourly microclimate temperatures at a 30 m scale, across the
526 whole study extent, in this case the Iberian Peninsula. Our centroid distance approach, while limited,
527 still allows us to reliably quantify dissimilarity between seasonal niches and draw inference on
528 similarity between conditions experienced by individuals in the two seasons, despite not accounting
529 for the available environmental conditions. Our results suggest that migratory distance can determine
530 individual niche similarity between seasons, with short distance migrants usually having more
531 dissimilar niches. However, other factors such as niche breadth or breeding latitude are known to
532 influence seasonal niche strategy at the species level (Gomez et al., 2016) and should be considered
533 in future studies. We demonstrated that microclimate refugia availability, particularly during the
534 breeding season, plays a key role in defining microclimatic niche dissimilarity between seasons and

535 can help predict individual movement strategies, which to our knowledge, has not been demonstrated
536 before.

537

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