Movement, behaviour and microclimate habitat requirements of endangered grassland birds in a warming world

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Abstract

Species distribution worldwide is intricately connected to the environmental conditions' individuals experience. Despite many ecological studies tackling this subject, many overlook the inclusion of information at the scale individuals experience their environment, resulting in inaccurate estimations of species range shifts. This thesis addresses this gap by utilizing state-of-the-art tracking devices and analysis software to investigate the movement strategies, fine-scale habitat utilization, and microrefugia preferences of an endangered grassland bird. This study focused on the little bustard (*Tetrax tetrax*), benefiting from data from a long-term tracking project in the Iberian Peninsula. Additionally, the partial migratory behaviour of the species provides unique insights into the effects of environmental changes on movement strategies, both at broader and more detailed scales.

At a fine scale, my investigation into little bustards' microclimate refugia use revealed their active search for cooler sites characterized by heterogeneous vegetation cover. I further investigated the consistency in little bustard's migratory behaviour and the significance of microclimate refugia in regulating migratory timings. My findings revealed that post-breeding migration timing correlates with the declines in food availability, although microclimate refugia availability may extent the breeding season for longer. Finally, when looking at the environmental niche of this species, I identified a gradient of temperature and microclimate refugia availability as primary determinants, suggesting a crucial role for refugia in niche tracking and adoption of different migratory strategies.

A broader analysis of the species foraging movements uncovered year-round movements dependent on sparsely and randomly distributed resources. Breeding and winter movements were associated with higher soil and vegetation moisture levels, while the post-breeding season, showed optimal search patterns in more productive areas.

Overall, this thesis enhances our understanding of the importance of fine-scale environmental variability in species distribution and movement strategies and also provides new tools for planning conservation measures to create more resilient habitats.

Resumo

A distribuição das espécies está intimamente ligada às condições ambientais que os indivíduos enfrentam. No entanto, muitos estudos negligenciam a informações à escala em que os indivíduos experienciam o ambiente, podendo estimar incorretamente as mudanças na distribuição das espécies. Esta tese aborda essa lacuna, utilizando tecnologia de ponta para investigar as estratégias de movimento, a utilização do micro-habitat e as preferências de micro-refúgios do sisão (*Tetrax tetrax*), uma ave estepária ameaçada. O estudo, realizado na Península Ibérica, beneficia de dados de um projeto de seguimento de longa duração que permite estudar o comportamento migratório da espécie, fornecendo conhecimentos sobre os efeitos das mudanças ambientais nas estratégias de movimento em diferentes escalas.

Numa escala fina, a investigação sobre o uso de micro-refúgios revelou uma busca ativa por locais mais frescos, com uma cobertura vegetal heterogénea. O estudo da consistência do comportamento migratório e da importância dos micro-refúgios demonstrou que o tempo da migração pós-reprodutora está correlacionado com a diminuição da disponibilidade de alimentos, e que a disponibilidade de micro-refúgios pode prolongar a época de reprodução. Finalmente, a análise do nicho ambiental identificou um gradiente de temperatura e disponibilidade de micro-refúgios como os principais determinantes, sugerindo um papel crucial dos micro-refúgios na manutenção do nicho e na adoção de diferentes estratégias migratórias.

Uma análise dos movimentos de forrageamento da espécie revelou movimentos anuais dependentes de recursos distribuídos de forma esparsa e aleatória. Os movimentos durante a reprodução e inverno estão associados a níveis mais elevados de humidade do solo e na vegetação, enquanto na pós-reprodução observam-se padrões de procura-ótima em áreas mais produtivas.

No geral, esta tese contribui para a compreensão da importância da variabilidade ambiental em pequena escala na distribuição de espécies e nas estratégias de movimento, fornecendo novos conhecimentos para o planeamento de medidas de conservação visando a criação de habitats mais resilientes.

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— Chapter 1 —

General Introduction

"As the journey begins, embrace the lockdown and the new normal, for within challenges lie opportunities to grow and emerge stronger."

1.1 Species responses to environmental change

Across the globe, species distributions are intricately linked to the environmental conditions and their evolutionary history within biogeographic realms (Wallace, 2011). To understand ecosystems and how they function it is crucial to identify the factors that determine species distributions, and this has been the focus of many ecological studies (Elith & Franklin, 2013; Miller, 2010). However, in a world where human-induced changes to the environment are growing in scale and importance (Pörtner et al., 2022), it is imperative not only to comprehend the environmental characteristics shaping species distribution and abundance but also to grasp the impacts of environmental change (Cohen et al., 2018; Ehrlen & Morris, 2015).

Habitat destruction and fragmentation, pollution, invasive species, and climate change, are widely acknowledged as pivotal drivers of biodiversity loss, exerting varied influences on species distribution and abundance (WWF, 2022). Nonetheless, species have been adapting to changing environments through time. Insights from paleorecords, combined with a multidisciplinary approach involving paleoecology, paleoclimatology and macroecology have shed light on species' adaptations during the Pleistocene glaciations and the late Quaternary (Foedham et al., 2020; Pardi & Smith, 2012). These records substantiate the notion that, despite the escalating threats, species exhibit remarkable adaptability, thereby shaping ecosystems through alterations in timing of the life cycles, changes in abundance and distributions. As environmental conditions change species are compelled to explore new distribution areas, adjusting to new feeding resources, predator-prey interactions, competition with novel species, and shifts in breeding and movement patterns (Jiguet et al., 2007; Sanz, 2002). Additionally, these changes may manifest as physiological adaptations, such as thermoregulation; behavioural shifts, including reduced activity levels, refugia use, and migration; and broader evolutionary responses, such as genetic diversity - all contributing collectively to a species' ability to adjust to changes (Huey et al., 2012; Rastogi, 2007).

Despite the extensive body of literature on species adaptations to environmental change, much remains to be understood, as different species, populations and individuals may exhibit diverse responses to changes in their environment (Cox, 2010). Moreover, some adaptive behaviours, like migration are complex and individual variability in migratory behaviour within populations is still poorly understood but likely linked to how individuals experience their environment.

Migration

Migration, observed as a repeatable seasonal behaviour performed by numerous species globally, ranging from small insects to large mammals (Dingle, 2014; Reid et al., 2018), is a complex response to ecological, environmental, and physiological factors that have changed over time (Newton, 2010). It is linked to fluctuations in resource availability due to seasonality and is particularly prevalent at higher latitudes. Migratory behaviour is intricate and diverse, expressed in a wide variety of forms, making its precise definition difficult (Dingle, 2014). Traditionally, migration has been associated with the long-distance round-trip movements undertaken by many bird species across the globe (Dingle, 2014). However, there are various other migratory behaviours, including short-distance migrants, such as species that migrate within the same continent or country (Newton, 2010); altitudinal migrants, like bats and other large vertebrates (McGuire & Boyle, 2013); and even the shorter-term diel vertical migration performed daily by zooplankton in the water column (Russel, 1926).

Within the same species, it is documented that different populations can adopt different migratory strategies, like white storks (C*iconia ciconia*), where northern-European populations are fully migratory while southern populations are transitioning towards residency (Catry et al., 2017; Flack et al., 2016; Gilbert et al., 2016). This within-population migratory variation is known as partial migration where some individuals migrate while others remain residents year-round (Chapman, 2011; Newton, 2010). Partial migration is now known to be widespread across multiple taxa and the coexistence of individuals with distinct migratory behaviours enhances resilience and grants species and populations the necessary plasticity to adapt to changing conditions (Gilroy et al., 2016). While migration may entail high costs, especially for birds covering long distances, including elevated energetic costs and exposure to threats, it also allows birds to explore different resources not available in breeding areas throughout the year, thereby increasing fitness for subsequent breeding seasons (Alerstam et al., 2012; Buchan et al., 2020; Wilkelski et al., 2003). On another hand, while residents do not face the threats and energetic costs of migrations, they are constrained by the environmental conditions and resource availability at the breeding site, however, they can start breeding earlier in the year which may bring higher reproductive success (Grist et al., 2017; Lok et al., 2017). Likely, residency and migratory behaviours confer different benefits to individuals with overall equivalent fitness (Buchan et al., 2020; Chapman et al., 2011; Lundberg, 1988), explaining why both strategies are maintained.

While declines in resource availability are pivotal triggers for migration, enabling individuals to evade unsuitable environments and ultimately enhancing survival and fitness (Dingle, 2014; Reid et al., 2018), factors such as sex, age and individual experiences collectively contribute to shape migratory behaviour (Baert et al., 2018; Fudickar et al., 2013; Martín et al., 2016). In the case of resident individuals, behavioural adaptations enable them to remain in the same areas year-round. Some of those adaptations, such as shifts in diet and use of anthropogenic food subsidies (Gilbert et al., 2016), are advantageous and enable individuals that remain at the breeding areas to respond more quickly to changes in environmental conditions at the start of the breeding season (Buchan et al., 2020).

The intricacies surrounding migratory behaviour, encompassing its diverse definitions and the factors influencing individuals' decisions to migrate, as well as within-species variations are likely associated with individual experiences and small-scale environmental variation. This is a captivating research area within animal behaviour and movement ecology and is the focus of this PhD study. Understanding how fine-scale information, such as microrefugia, can contribute to shaping individuals' decisions to move or migrate is essential to design effective conservation strategies in a changing world.

Microrefugia and microclimate

Microrefugia sites are areas of relative climatic stability within species' ranges, and where species can retreat to and persist when conditions become unsuitable, for example under severe climate change (Ashcroft, 2010; Keppel et al., 2012). Microrefugia has been traditionally studied for its role in species resilience during climate change events such as the Quaternary (Ashcroft, 2010; Bennett & Provan, 2008,). This study focuses on microclimate refugia, which can also be sites used by individuals on a daily basis to shelter from extreme environmental conditions, rest or avoid predation (Powers et al., 2017; Smith et al., 2019). These dynamic features in space and time are experienced by individuals at the metre scale or smaller (Suggitt et al., 2011) and can help species persist in areas where environmental conditions fluctuate or become unsuitable (e.g. in certain times of the day or the year) (Hampe et al., 2011; Maclean et al., 2015). These local level microrefugia areas are attributed to the interplay of topography, soil composition and vegetation characteristics, creating a fine-scale heterogeneous thermal landscape (Suggitt et al., 2018).

Despite the undeniable potential of microrefugia in maintaining suitable environmental conditions for species in their current distribution ranges, the majority of the studies evaluating species distribution models within various climate change scenarios, focus on the coarse resolution of several kilometres (Araújo et al., 2007; Garcia et al., 2011). Many of those studies predict that future suitable conditions will cease to overlap with the current species distribution ranges, potentially leading to rapid adaptations or extinctions, especially among populations at the edges of species ranges (Chen et al., 2011; Lenoir & Svenning, 2015; Thomas et al., 2004). A contrasting viewpoint posits that by neglecting fine-scale environmental variation, distribution models might exaggerate species range shifts (Maclean & Early, 2023) and overestimate the effects of climate change. This dichotomy highlights the significance of acknowledging fine-scale environmental variation, particularly in heterogeneous landscapes that can offer substantial variability at a finer resolution, surpassing that found at coarser scales (Maclean et al., 2017; Suggitt et al., 2018).

This intricate variation plays a critical role in buffering species against the impacts of ongoing climate change. Moreover, as species experience their environment at fine scales, microrefugia can have an important role in triggering species responses to changes despite that most studies fail to include fine-scale information (Shaw, 2016). Recently, this fine scale environmental information started to be integrated in broad scale ecological studies (Bramer et al., 2018; Maclean et al., 2017), but there is still much to be understood. Specifically, it can be used to understand individual variability in behaviour and responses to environmental change within species and populations. By understanding the role of microclimate refugia in buffering species against ongoing climate and environmental changes, effective conservation measures can be implemented, especially for populations at the warm edge of the species range.

In this thesis, I focus three chapters in understanding the role and importance of microclimate refugia for a grassland specialist species that is facing significant population declines due to climate and environmental changes (García de la Morena, 2018; Silva et al., 2022; Silva et al., 2023).

1.2 Individual variability

While migratory behaviour and microrefugia use are two crucial mechanisms for species to adapt under environmental change, individual variability is a fundamental trait amongst species and populations and facilitates fast species responses to changing conditions. As environmental cues can be perceived differently by individuals (Mueller et al., 2013; Newton, 2010), and exposure to environmental variables varies at small scales, hence individuals may adopt different strategies to adapt to similar changes and conditions which increases species resilience to unfavourable or changing environments.

Individual movement strategies and behaviour are influenced by intrinsic and external factors. When intrinsic factors dominate, individuals are more likely to exhibit repeatable behaviours between years (Kürten et al., 2022; Newton, 2010; Reid et al., 2020). Conversely, when external factors have a greater influence, changes in environmental conditions can influence the timing of migration, breeding, and moulting (Tomotani et al., 2018; Zaifman et al., 2017). However, individuals' behaviours and decisions typically result from the interplay of both intrinsic and external factors exhibited at different ratios, leading to a diverse range of responses among individuals exposed to the same environments.

The between-individual variation confers resilience to a species, enabling it to adapt to rapid environmental changes and playing a crucial role in species evolutionary processes (Shaw, 2020). As seen before, the between-individual variation in migratory behaviour and coexistence of migratory and resident strategies within partial-migratory species is a remarkable example of long-term adaptation to environmental change. Additionally, studies from several species across multiple years have shown that migratory movements are a plastic behaviour which depends on the degree that external factors, like environmental conditions, and individuals' life history, like age and experience, influence the migratory behaviour (Franklin et al., 2022; Hasselquist et al., 2017; Reid et al., 2020; Soriano-Redondo et al., 2023). The interplay of these different aspects, shape each individual's migratory behaviour along with individual plasticity, which emerges from within-individual variability. All aspects considered help individuals adapt to yearly changes in their environment, increasing their fitness and survival and confers the flexibility needed at the species and population levels to adapt to environmental change.

1.3 Foraging movements

Animals continuously adapt to changes in their environment by adopting different movement strategies or fine-scale habitat use to shelter from unfavourable conditions. A crucial adaptation needed relates with foraging, where individuals need to constantly make decisions to find the resources needed to survive. The foraging term relates to all aspects of food acquisition by animals and focus on where and when to search for food, which resources to consume and how to efficiently perform that search (e.g. when to search and when to move to new feeding areas) (Pike et al., 1977; Stephens & Krebs, 1986).

As food resources are often irregularly distributed (Weimerskirch et al., 2005), the optimal foraging theory states that, when information about resource availability is limited, individuals are expected to adopt a specialized random walk known as Lévy walks (or Lévy flights) (Viswanathan et al., 2011). Lévy flights are random walks consisting of clusters of numerous small steps, with longer steps interspersed between them (Viswanathan et al., 1999). This foraging movement strategy is highly efficient and increases the probability of encounters with sparsely and randomly distributed resources (Focardi & Cecere, 2014). Contrastingly, when resources are abundant and predictable, Brownian motion is the most effective strategy to adopt (Humphries et al., 2010; Sims et al., 2012). Brownian motions are characterized by steps of similar and constant length with random turning angles, making them an irregular search pattern (Turchin, 1996).

According to the Lévy flight foraging (LFF) hypothesis, animals should adopt a Lévy flight pattern while foraging, maximizing resource encounter probabilities (Viswanathan et al., 2011). This pattern is adopted by a vast array of species, from small insects to large marine predators, as demonstrated by many studies (Hays et al., 2012; Humphries et al., 2012; Reynolds et al., 2007; Sims et al., 2012). Thus, understanding species foraging strategies is of great importance to understand individual movement decisions and how resources availability may limit them. As these decisions can change over time in response to fluctuations in resource distribution, the study of foraging movements should encompass different temporal scales, ranging from annual to within-season adaptations. Despite this, most investigations into animal foraging behaviour have been conducted at fine spatial and temporal scales, typically utilizing focal observation methods. However, the recent developments of tracking technology and remote sensing data allow us to obtain detailed information on environmental characteristics for areas that can coincide with the distribution of an entire species (Valerio et al., 2020). In the fifth chapter I take advantage of those technological advancements to study within season foraging movements in more detail.

1.4 Technology advancements

Until recently, obtaining fine-scale environmental information over large areas was constrained in both space and time, requiring extensive fieldwork to obtain reliable fine-scale information. However, the recent availability of fine-scale remote sensing data and advancements in microclimate modelling (Maclean et al., 2019; Suggitt et al., 2018) have ushered in new opportunities to integrate both coarse and fine-scale environmental data into species distribution models. This integration is not only a crucial and a necessary development in ecological studies but also aligns more closely with the diverse scales at which individuals experience their environment (Bütikofer et al., 2020).

In this thesis, I investigate how microrefugia and fine-scale temperature information contribute to species movement decisions, particularly regarding the timing and distance of migrations, and how they shape the species environmental niche. Additionally, I examine within season foraging movement using high temporal resolution GPS data, remote sensing data and state-of-the-art statistical tools.

To achieve these, I leveraged the growing capability to track species movements across their entire range, capitalising on advancements in ringing, radio tagging, and satellite technology. With these tools we now possess sophisticated software that enables the detailed tracking of even the smallest species throughout their migratory journeys (Cagnacci et al., 2010). The continuous development of tracking devices plays a crucial role, allowing us to reduce the risk of impacting individuals' well-being by attaching smaller, lighter, and more efficient and accurate devices (Acácio et al., 2022; Kays et al., 2015).

Nonetheless, despite the significant advancements in tracking technology over the past decades the bottleneck has, until recently, been data processing. Despite the ability to track species at 1-second intervals, computer software and RAM are not yet optimised to handle such amounts of data. However, ongoing technological developments now empower scientists to efficiently process tracking data and capitalise on the detailed information it provides (Schulte to Buhne & Pettorelli, 2017). Additionally, it is now feasible to match tracking data with new generation satellite imagery, offering detailed insights into habitat and weather information at approximately 10-meter resolution (Valerio et al., 2020) while covering large enough areas that encompass the species' entire range (Bütikofer et al., 2020; Kays et al., 2015; Potter et al., 2013).

With these advancements, we now have the necessary tools to study species movement ecology at the scale individuals experience their habitat. By integrating fine-scale habitat information with individual movement data and combining this information with broader and coarse ecological features, we can gain a more comprehensive understanding of species behaviour and adaptation to environmental changes. Beyond that, this holistic approach allows us to identify more effective conservation strategies, informed by a nuanced understanding of the intricacies of species movement and habitat dynamics.

1.5 Study system and tracking technology

The species

This thesis examines the behavioural and movement responses of little bustards, *Tetrax tetrax* (Linnaeus, 1759) to environmental variables and variability. Little bustard is a medium-sized grassland specialist bird classified globally as 'Near Threatened' (BirdLife Internationalt, 2023). Its present breeding distribution is fragmented into two main regions: one centred in south-eastern European Russia and Kazakhstan and a second in south-western Europe (BirdLife International, 2023; Cramp and Simmons, 1980; del Hoyo et al., 1996) (Figure 1.1). While the eastern population is mostly fully-migrant, the western population is considered mostly resident (BirdLife International, 2023) (Figure 1.1).

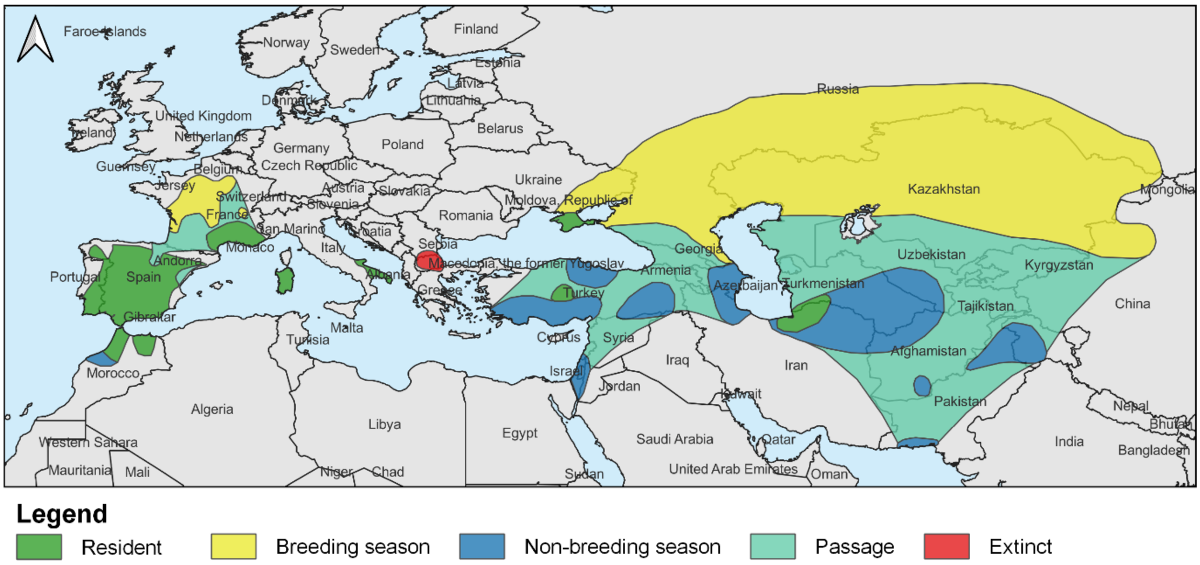

Figure 1.1– Little bustard (*Tetrax tetrax*) distribution map (BirdLife International, 2021). Map made with QGIS 3.22.7 (www.qgis.org).

The little bustard inhabits both natural and semi-natural grasslands, the last being mostly represented by agricultural and pastoral landscapes, highly dependent on human management (Emanuelsson, 2008). Along with the Great bustard (*Otis tarda*), the little bustard is one of the iconic species of European grasslands and it is considered an umbrella species, particularly for species linked to cereal and grassland-dominated landscapes (Morales et al., 2023). As umbrella species, little bustards are considered good indicators of ecosystem's health (Bretagnolle et al., 2018; Traba & Morales, 2019), and have ecological characteristics and requirements that overlap with other species in the community (Caro, 2010). Moreover, research done with little bustards, and conservation measures will likely benefit many other species that inhabit grassland and low intensive cereal-production ecosystems.

In recent decades the little bustard's European population has been declining, being currently classified as 'Vulnerable' and considered a priority species under the European Union Wild Birds Directive (2009/147/EC). This species main threats are habitat loss and degradation (Silva et al., 2022), illegal hunting and collision with power lines (Marcelino et al., 2017), with recent studies indicating a severe decline in breeding numbers in parts of their range (García de la Morena et al., 2018; Santangeli et al., 2023; Silva et al., 2023). Within Europe, the Iberian Peninsula is considered a stronghold of this species western distribution, where the main breeding populations are mostly concentrated in Extremadura and Castilla La Mancha (Spain), and Alentejo (Portugal) (García de la Morena et al., 2018; Silva et al., 2018).

This species breeds in an exploded lekking system (Ponjoan et al., 2012), characterised by loose aggregations of displaying males that are visited by females with the single purpose of mating (Höglund and Alatalo, 2014; Morales et al., 2001). In traditional lekking areas, it is possible to find territorial males that are fateful to their lekking site throughout the season and in subsequent years, and by satellite males that can visit several territorial males as well as different lekking areas in the same season (Silva et al., 2017). However, declines in breeding populations make it hard for lekking areas to be maintained with this traditional structure. This type of breeding strategy makes the species extremely vulnerable to changes in their breeding habitat, since once a lekking area is lost it is unlikely to be recolonised by other males, which can compromise the site for future breeding attempts (Silva et al., 2017).

Despite previously being considered as sedentary, the little bustard Iberian population is now known to be mostly migratory or partially migratory, with birds performing regular short-medium distance movements within Iberia to post-breeding and wintering sites (García de la Morena et al., 2015; Silva et al., 2007). Most of the movements occur after the breeding season, between June and July, when temperatures increase and the vegetation dries, limiting the activity period and food availability (Silva et al., 2015). Usually, the post-breeding sites are areas where food availability and environmental conditions are expected to be more favourable, generally in northern Iberia, near the coast or in higher-altitude areas (García de la Morena et al., 2015; Silva et al., 2007; Silva et al., 2015), or, still, in nearby irrigation areas. The drivers that influence migratory strategies, both timings and distance travelled, are addressed in the third chapter with a focus on the fine-scale environmental characteristics.

Previous studies with little bustards in the Iberian Peninsula showed that elevated temperatures (above 25°C) inhibit activity (Silva et al., 2015) which may pose serious time constraints, particularly during breeding and foraging, with potential consequences for individual fitness and population dynamics. In these situations, the use of microrefugia can be crucial, since it allows for individuals to shelter against detrimental condition and help reduce the risk of overheating and costly metabolic functions to thermoregulate (Gudka et al., 2019; Rastogi, 2007). Identifying the use and availability of microclimate refugia areas in both breeding and post-breeding seasons is the focus of the second chapter.

Since 2009 our team has been tagging little bustards with solar GPS tracking devices. From 2009 to 2011, 28 little bustards were tagged with Platform Transmitter Terminal (Solar Argos/GPS 30 g PTT—Microwave Telemetry) devices. From 2014 onwards, 74 birds were tagged with Global

System for Mobile Communications (GSM) devices, which were used as the source of little bustards' movement information for the different chapters of this thesis.

The study area

This thesis uses movement data from birds tagged in the Iberian Peninsula, which is part of the Mediterranean ecosystem and one of the world's regions most vulnerable to climate change (Pörtner et al., 2022). In the past few decades this region has experienced an increase in the mean air temperature, as well as extensive warming, drought and heat wave frequency (Fick et al., 2017; Jones et al., 2020; Pörtner et al., 2022). This poses an imminent threat to species that depend on open flat habitats with low vegetation cover like the little bustard, especially during breeding and post-breeding seasons (Gudka et al., 2019; Sanz et al., 2003), due to temperature homogenization.

These open habitats with low vegetation cover in the Iberian Peninsula are known as semi-natural grasslands. Created and maintained by agricultural activity and livestock grazing, these areas are highly dependent on human management (Emanuelsson, 2008), as to avoid the development of vegetation succession that creates heterogeneous areas of shrubs and herbaceous vegetation. Once one of the most important cereal production landscapes of Iberia, grasslands are currently under high livestock pressure (Faria et al., 2012; Reino et al., 2010) due to the current European Union Common Agricultural Policy (CAP), which has been promoting the replacement of traditional cereal-based systems by livestock-based systems (especially based on cattle production) and the increase of permanent pastures (Faria & Morales, 2020; Ramos et al., 2021; Ribeiro et al., 2014).

The little bustards' capture locations included important grassland special protected areas (SPAs), from Natura 2000 (Castro Verde, Piçarras, Vale do Guadiana, Torre da Bolsa and Vila Fernando, in Alentejo - Portugal; La Serena y Sierras Periféricas, Magasca, Llanos de Cáceres y Sierra de Fuentes and Sierras Centrales y Embalse de Alange, in Extremadura - Spain). These are the most important breeding locations for this species in the Iberian Peninsula (Equipa Atlas, 2008; García de la Morena et al., 2018). After the breeding season many individuals moved away from breeding locations and used non-breeding areas inside but mostly outside SPAs, mainly in the north and coastal areas across Iberia (see Figure 2.1). The study area of all subsequent chapters is focused on the GPS locations of the tagged little bustards, as well as its surrounding area (see *Methods* section of Chapter 2).

The technology and capture method used

In this thesis, I used GPS tracking devices to obtain high resolution movement information and habitat used of little bustards, acquire a comprehensive long-term database. I used data from two types of GPS devices from four different suppliers. Between 2009 and 2011, little bustards were tagged with Platform Transmitter Terminal (Solar Argos/GPS 30g PTT) from Microwave Telemetry, for which the horizontal accuracy was set at 24m (Silva et al., 2015). From 2014 to 2018 birds were tagged using Global System for Mobile Communications (GSM) devices, from Movetech Telemetry (Flyway-38 - discontinued - and Flyway-23). These devices present a horizontal accuracy between 3.4 and 6.5m (Acácio et al., 2022). From 2019 onwards little bustards were tagged with GPS/GSM devices, from three suppliers, Movetech Telemetry (Flyway-23), E-obs (25g), and Ornitela (OrniTrack-15, -20 and -25). All these devices are GPS/GSM and 87% of locations have less than 10m error in horizontal accuracy as described in Acácio et al. (2022).

To gain a deeper knowledge on how tracking devices operate, I was involved in the assembling, lab testing and deployment of several new models from Movetech Telemetry (https://movetech-telemetry.com/), an academic consortium that develops low-cost tracking tags.

I tested all the tracking devices components (e.g. different batteries and solar panels) in order to understand their efficiency, how different settings could affect the charging cycles and to detect possible malfunctions of the components before assembling them (Figure 1.2). This is an important knowledge to gain when working with movement data and devices in order to understand and troubleshoot potential errors after deployment.

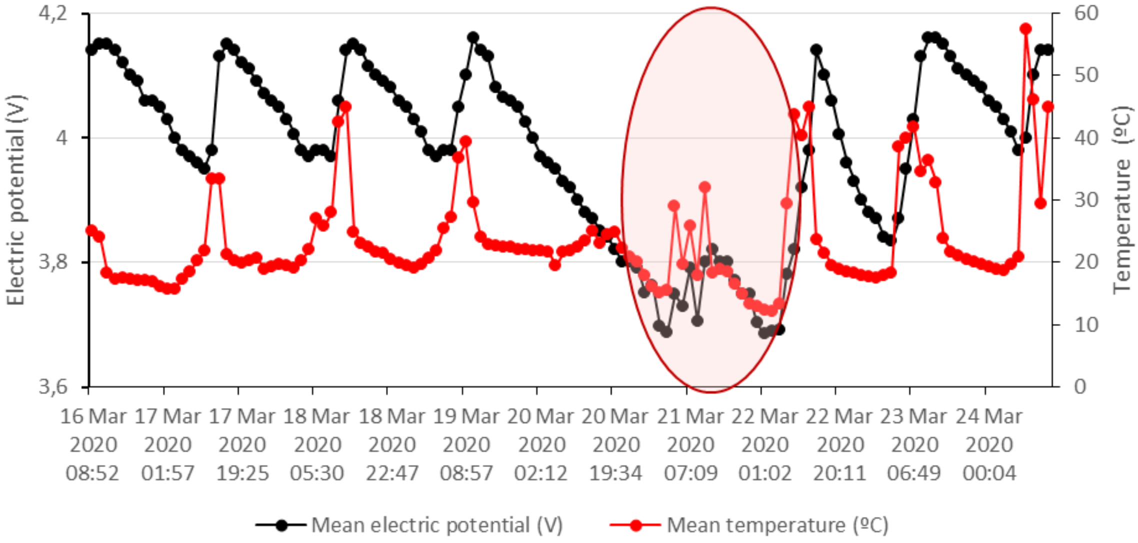

Figure 1.2 – Electric potential (V) and temperature (ºC) measured by the PCB, showing regular charging cycles and an abnormal one starting on the 20th of March 2020

Besides the testing of the components, I helped assemble Movetech GPS devices raging from 6g to 90g, with both GSM and LoRa data transmission (Gauld et al., 2023). All the assemblages were done at controlled environmental conditions in different laboratories. I started by glueing the solar panel to the casing, and waterproofed all the device, while being cautious about the 3% weight limit of the intended species (Kenward, 2000). The devices were deployed in white storks (*Ciconia ciconia*), as part of an ongoing project, “Birds on the move” (https://whitestork.org/index.php/birds-on-the-move/); in Eurasian stone curlews (*Burhinus oedicnemus*), as a pilot of the “BIOTRANS – Transnational conservation of Steppe birds” from the Steppe birds move team in which I participated in the tagging; and in common kestrel (*Falco tinnunculus*), as part of a PhD project aiming to investigate behavioural responses to extreme temperatures (Figure 1.3).

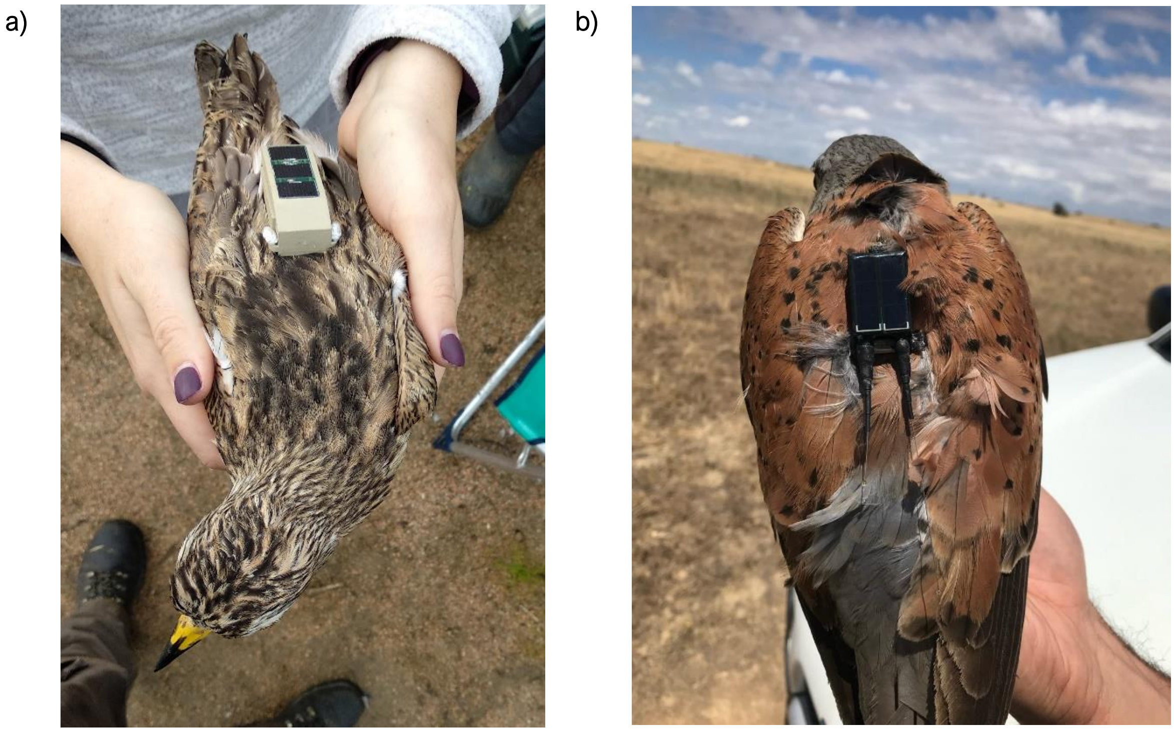

Figure 1.3 – Deployed tracking devices a) 13.5g GPS/GSM device deployed in a Eurasian stone curlew; b) 6g GPS/LoRa and GSM device deployed in a common kestrel

Male little bustards were captured during the breeding season in the lekking areas (Morales et al., 2001) using a stuffed female that acted as a decoy. The team placed snares around the decoy with the main objective of capturing males (Ponjoan et al. 2010). After capture, a GPS tracking device was deployed using a thoracic harness made of Teflon Ribbon with a weak. The GPS devices varied between 2% and 4% ($\bar{x}$ = 3.2%) of the birds' body mass, as recommended by the guidelines (Kenward, 2000).

1.6 Thesis structure and chapters rationale

This thesis aims to understand how species respond to environmental changes with a particular focus on the contribution of microclimate refugia in different movement behaviours and migration, while also considering individual variability. The research presented uses the little bustard as a case study since it is an iconic yet endangered grassland specialist bird and examine environmental information at the scale at which individuals experience their habitat. All the chapters leverage long-term, high-resolution tracking data of little bustards in the Iberian Peninsula, carried out by the Steppe Bird MOVE group (https://steppebirdsmove.com; CIBIO-UP). Although I only contributed for the fieldwork seasons of 2019 and 2020, I was able use the data collected by the supervisory team since 2009. These data are integrated with state-of-the-art modelling to address major threats affecting the species and identify effective, high-resolution conservation actions (Potter et al., 2013).

Most of the thesis is focused on the novel topic of microclimate refugia, in Chapter 2 I start by testing whether little bustards use microclimate refugia by employing a novel methodology. I aimed to use GPS location data of little bustards to identify microclimate refugia and microclimate refugia use, at a fine scale, approaching the scale species usually experience in their habitat (Suggitt et al., 2011). I also determine the main landscape and climatic features that increase the availability of microclimate refugia opportunities. For this chapter, I used pre-existing data from the Steppe birds MOVE group, which was then extracted from movebank (https://www.movebank.org). I then proceed with data cleaning, removing all the GPS points prior of tagging and after the birds died (when applicable) and any errors in the data. I then defined, with the help of João P. Silva the phenology of each tagged individual in order to identify the main period within the bird annual cycle (breeding, migration and post-breeding/winter periods). I also obtained the temperature information for each GPS point from the package *microclima*, developed by Ilya Maclean (Maclean et al., 2019), using the High-Performance Computing Cluster (at the University of East Anglia) and with James Gilroy's help to develop the initial R script. I retrieved all the other relevant variables and performed the statistical analysis, as well as the writing. This chapter is published in *Scientific Reports*.

In Chapters 3 and 4 I used the previous chapter and the microclimate data generated to explore the importance of microclimate refugia in little bustards' migratory behaviour and habitat use. Chapter 3 aimed to additionally understand if microclimate refugia availability combined with food availability influences this species' migratory behaviour. I started by testing individual consistency across multiple migratory events for both timing and distance travelled. I then analysed the main environmental features that can influence little bustards' migratory timings for both departure and return to the breeding areas. I retrieved all the variables (except NDVI, which was done by Ana Teresa Marques) and performed all the statistical analysis, plots and maps. Additionally, I wrote the manuscript having received and incorporated the suggestions from all co-authors. This paper is published in *Movement Ecology*.

In Chapter 4 I use microclimate refugia, temperature and food availability to determine the experienced ecological niche in the Iberian Peninsula, during the breeding and post-breeding, two seasons little bustards are exposed to high temperatures and food shortage (Silva et al., 2007; Silva et al., 2017). I further identify the differences in niche between breeding and post-breeding, looking at the broader Iberian region but also of five populations, while exploring the relation between individual migratory strategy and post-breeding experienced environmental niche. The variables for this chapter were already collected (from the previous chapters). I developed the R code together with Karolina Zalewska. I performed all the data treatment and statistical analysis, as well as interpretation and writing. I aim to submit this chapter to *Journal of Animal Ecology*.

In Chapter 5, I looked at monthly foraging movements of little bustards tagged between 2017 and 2022 throughout the whole yearly cycle, to identify different movement strategies (Viswanathan et al., 2011). I then examine the possible relation between the different movement strategies and, the environmental and habitat characteristics, taking advantage of state-of-the-art remote sensing information. The aim was to understand how little bustard movement strategies change between seasons in relation with the available environment. For this chapter I started by understanding the MLE analysis program and outputs. I did all the data cleaning to guarantee only reliable data was used, by calculating the mean speed between two consecutive GPS locations (considering time and distance) and removing unrealistic speeds and associated locations. With guidance from Nuno Queiroz, I ran all the MLE analysis. All the remote sensing variables were obtained by Francesco Valerio, but I was responsible for ruining the statistical analysis and validating the models as well as writing the manuscript. All authors provided their input in interpreting the results. I aim to submit this chapter to *Movement Ecology*.

In Chapter 6, the general conclusions of this thesis, I summarise the results presented in each chapter and discuss the broader implications of the research and how it can be combined with existing knowledge and available ecological information in order to design more effective conservation measures. I further identified questions that arise from this thesis that remain to be answered but can greatly benefit this endangered species conservation.

Each chapter is presented in the style of a standalone publication, with references and supplementary information provided at the end of each chapter.

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— Chapter 2 —

Combining bird tracking data with high-resolution thermal mapping to identify microclimate refugia

"In the realm of fieldwork- (deep in Alentejo), discover the joy
that fuels your strength to conquer it all."

Combining bird tracking data with high-resolution thermal mapping to identify microclimate refugia

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Authors' contributions

RFR, AMAF and JPS conceived the overall study. JPS was responsible for capturing and tagging the little bustards. RFR prepared the dataset, coded the models, and analysed the data, assisted by JJG and AMAF. RFR wrote the manuscript assisted by AMAF with revisions of JPS, JJG. All authors gave final approval for publication.

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Abstract

Elevated temperatures can have a range of fitness impacts, including high metabolic cost of thermoregulation, hence access to microclimate refugia may buffer individuals against exposure to high temperatures. However, studies examining the use of microclimate refugia, remain scarce.

We combined high resolution microclimate modelling with GPS tracking data as a novel approach to identify the use and availability of cooler microclimate refugia (sites > 0.5˚C cooler than the surrounding landscape) at the scales experienced by individual animals.

77 little bustards (*Tetrax tetrax*) were tracked between 2009 and 2019. The 92,685 GPS locations obtained and their surrounding 500m areas were characterised with hourly temperature and habitat information at 30m x 30m and used to determine microclimate refugia availability and use.

We found that the semi-natural grassland landscapes used by little bustards have limited availability of cooler microclimate areas – fewer than 30% of the locations. The use of cooler microclimate sites by little bustards increased at higher ambient temperatures, suggesting that individuals actively utilise microclimate refugia in extreme heat conditions. Microclimate refugia availability and use were greater in areas with heterogeneous vegetation cover, and in coastal areas.

This study identified the landscape characteristics that provide microclimate opportunities and shelter from extreme heat conditions. Little bustards made greater use of microclimate refugia with increasing temperatures, particularly during the breeding season, when individuals are highly site faithful. This information can help identify areas where populations might be particularly exposed to climate extremes due to a lack of microclimate refugia, and which habitat management measures may buffer populations from expected increased exposure to temperature extremes.

2.1 Introduction

Microrefugia are localised areas of climatic stability where species can persist under climate change (Rull, 2009). Microrefugia may be experienced by individuals at the meter scale or smaller (Suggitt et al., 2011). In contrast, macrorefugia is measured at scales of hundreds of kilometres (Massimino et al., 2020; Potter et al., 2013). Many species use microclimate refugia daily, either to rest, or to avoid periods of high temperatures during the day or low temperatures during the night (Powers et al., 2017; Smith et al., 2019). This dynamic temporal use of microclimate refugia enables species to persist in areas where environmental conditions fluctuate or become unsuitable in parts of the day or the year (Hampe & Jump, 2011; Maclean et al., 2015). Thus, microclimate refugia use may allow populations to persist in areas where larger-scale climate conditions are becoming unsuitable.

Use of microrefugia by individual animals is still poorly understood, especially for large mobile taxa. However, the combination of new tracking technologies and novel tools for temperature modelling at finer scales (Maclean et al., 2019) is opening up new avenues for research, enabling researchers to quantify the importance of small-scale climate refugia for population persistence under climate change.

Recent studies modelling microclimate at a fine scale have demonstrated how habitat structure and topography can be combined to provide significant microclimate refugia, with ground-level temperatures varying by up to 5°C across scales of a few meters in some landscapes (Massimino et al., 2020; Suggitt et al., 2011). This variation has important consequences for local-scale species occurrence patterns. For example, in Meadow pipits (*Anthus pratensis*) microclimate conditions had a stronger effect than macroclimate and accounted for approximately a third of the variation in occupancy probability across the United Kingdom (Massimino et al., 2020). These findings highlight the importance of microclimate in facilitating species persistence in areas where macro-scale conditions may not (or no longer) be suitable. Microclimate refugia may be particularly critical for population persistence at the edge of species ranges (Oliver et al., 2009; Thomas et al., 1999) or in areas predicted to be exposed to high variability due to climate change (IPCC, 2017).

Mediterranean ecosystems, like the Iberian Peninsula in western Europe, are among the world's most vulnerable ecosystems to climate change (IPCC, 2017) and are expected to continue to suffer from extensive warming and increasing drought and heat wave frequency (Jones et al., 2020). Climatic conditions are expected to become particularly extreme in flat, open areas with low vegetation cover, as is the case of semi-natural grasslands. Microclimate refugia may therefore be crucial for the persistence of many endangered species in the Mediterranean region, but our understanding of the characteristics of important microrefugia remains limited particularly for large mobile taxa.

This study examines availability and use of microclimate refugia using the little bustard, *Tetrax tetrax* as a case study. This grassland specialist is classified as 'Near Threatened' (BirdLife International, 2020) and the Iberian Peninsula is considered the stronghold of the species' European distribution, however, recent studies indicate a severe decline of breeding numbers in the region, despite conservation efforts (García de la Morena et al., 2018; Silva et al., 2018).

As a grassland specialist inhabiting open areas with short vegetation, the little bustard is a good model species to understand use of microclimate refugia in landscapes with limited refugia opportunities that are warming due to climate change. Research have showed that little bustard daily activity levels decrease when temperatures exceed 25°C (Silva et al., 2015), which are frequent both in breeding and post-breeding seasons. In addition, as shown for other bird species, little bustards are likely to experience thermal stress above approximately 37°C, and lethal body temperature at 46°C (King, 1964; McKechnie & Wolf, 2019; Whittow, 1986). We hypothesis that little bustards use microclimate refugia to avoid detrimental effects of exposure to thermic stress. We test the prediction that increasing exposure to high temperatures, particularly during the breeding and post-breeding seasons, will require little bustards to make more use of microclimate refugia (where available) to minimise the impacts of thermal stress.

We used long-term high-resolution GPS-tracking data to quantify microclimate refugia use across a large area of the little bustard's western European range. Our objectives are to i) identify microclimate refugia using high spatial and temporal resolution environmental and tracking data, ii) determine if the use of microclimate refugia increases with exposure to high temperatures, and iii) identify the characteristics of landscape areas that provide microclimate refugia opportunities.

2.2. Methods

Study area and study system

Between 2009 and 2019, 77 male little bustards were captured and tagged in five breeding areas across the southwestern Iberian Peninsula, in Alentejo (Portugal) and Extremadura (Spain) during the breeding season (April and May; Figure 2.1). In this area of Europe, temperatures often exceed 37°C and heat waves have increased in frequency in the last three decades (Paredes et al., 2021). Little bustards breed in an exploded lekking system (Morales et al., 2001), which consists in males defending their territories from other males in wide areas while showing an exuberant displaying behaviour to attract visiting females and mate (for more details see Morales et al., 2001). Once breeding is completed, most little bustards migrate to post-breeding areas scattered across Iberia.

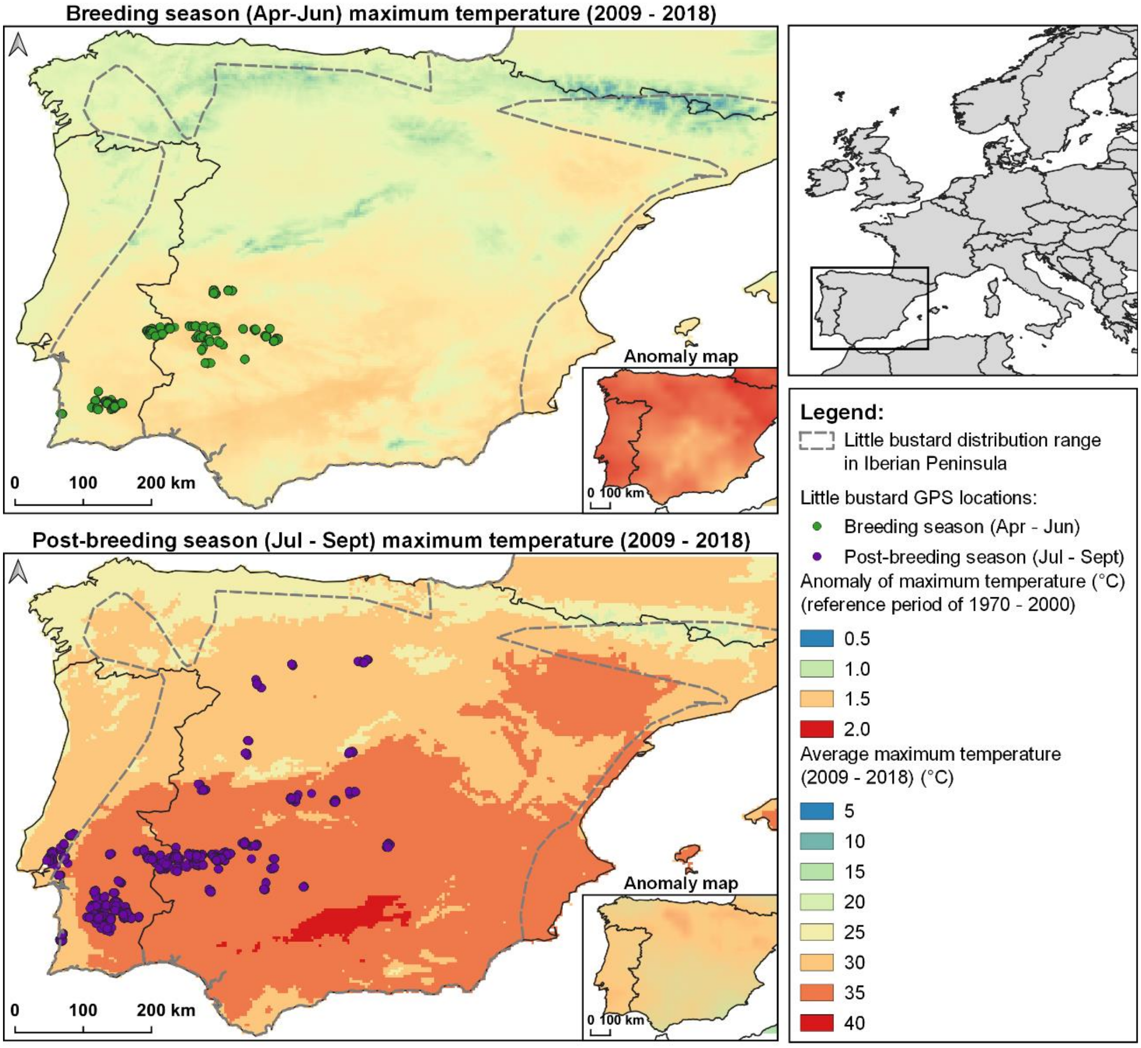

Figure 2.1 – Clusters of little bustards' GPS locations displayed over the average daily maximum temperature between 2009 and 2018 for breeding season (April – June) and post-breeding (July – September). Corresponding anomaly maps using the reference period of 1970 – 2000 are shown. Dashed grey line represents the little bustard distribution in the Iberian Peninsula (BirdLife International, 2021). Temperature data obtained from the WorldClim (Fick & Hijmans, 2017). Map made with QGIS 3.28.2 (www.qgis.com)

Breeding males were captured using decoys and snares at the start of the breeding season. Although some females were attracted to the decoy, they were not the targeted sex, due to different behaviours, which require more complex capture techniques. Males were attracted by a stuffed female acting as a decoy and trapped with snares, placed around the decoy (Ponjoan et al., 2010). GPS tracking devices varied between 2% and 4% ($\bar{x}$ = 3.2%) of the birds' mass (Kenward, 2000), were deployed using a thoracic harness made of Ribbon Teflon with a weak link to avoid lifelong deployment.

Two types of Solar GPS devices were used. Platform Transmitter Terminal (Solar Argos/GPS 30g PTT - Microwave Telemetry) were deployed on 28 birds between 2009 and 2011, and Global System for Mobile Communications (GSM) devices (Flyway 38g - Movetech Telemetry) were deployed in 49 birds between 2014 and 2019. Transmitters were programmed to record a GPS position every 2 hours (PPT) or 10 to 30 minutes (GSM). Bird trapping and GPS tagging were approved by the 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.

We filtered the GPS dataset to only include locations on the ground with null velocity, removing all in-flight fixes. The dataset was then subdivided into two seasons - breeding and post-breeding – the temporal limits of which were defined for each breeding area independently, as the breeding phenology and movement dates of the little bustards to post-breeding areas vary geographically. We defined the start of the breeding season uniformly as the 1st of April and defined the end of the breeding season for each breeding areas as the day the first tracked male moved from that area towards its post-breeding area, ensuring we captured the core period of the breeding season while avoiding capturing migratory movements and stopover sites (García de la Morena et al., 2015). The post-breeding season was defined uniformly for all breeding areas, from 15th of July to 15th of September, representing the hottest period of the year (Figure 2.1) when exposure to extreme heat is highest, and food shortages occur (Silva et al., 2007). The dates selected for two seasons guaranteed temporal independence as there was no overlap between breeding and post-breeding seasons across all birds.

The highest temperatures recorded in Iberia occur in the southwestern region which coincides with the little bustard Iberian population stronghold (Equipa Atlas, 2008; García de la Morena et al., 2018). The landscape is characterised by semi-natural grasslands created and maintained by agricultural activities and livestock grazing and are thus dependent on human management of the landscape (Emanuelsson, 2008).

During the 11-year period the birds were tracked, the average maximum air temperatures varied between 6.8-28.7°C in the breeding season (April to June) and 15.8-36.3°C in the post-breeding (July to September). Relative to a reference period of 1970 – 2000, there was a 1 to 2°C increase in temperature across the whole region (Figure 2.1), with greatest increases during the breeding season (1.5 to 2°C; Figure 2.1) (Fick & Hijmans, 2017; Harris et al., 2014).

Quantifying micro-climatic conditions

We estimated the hourly temperature at 20cm above ground level for all bird GPS locations using the R packages *microclima* (Maclean et al., 2019) and *NicheMapR* (Kearney & Porter, 2017; Kearney et al., 2020). Microclimate temperature account for the effects of net radiation, coastal influence and cold air drainage into consideration (from *NicheMapR*). These variables are determined at microscale accounting for terrain information such as slope, aspect and hill shade, and canopy shading effects resulting from different habitat types as defined by the International Geosphere-Biosphere Program (IGBP) (from *microclima*). We used the fully automated model, where National Centers for Environmental Prediction (NCEP; Kanamitsu et al., 2002; Kemp et al., 2012) climate reanalysis data is downscaled and interpolated to provide hourly information on the reference temperatures and atmospheric forcing conditions that are used to parameterise the model.

We used 30m x 30m resolution habitat information from CORINE Land Cover map 2018 (EEA, 2018) to account for canopy shading effects, matching CORINE habitat categories to their equivalent MODIS / IGBP categories using the schema provided in Table S2.1 (Strahler et al., 1999).

For each GPS location we retrieved the temperature information at the focal point, as well as for the surrounding area of 500 meters (mapped at 30 x 30m resolution), for the hour at which the GPS location was obtained. We used the 500m area (here onwards called buffer area) to evaluate how climatically different a bird’s location was from its nearby surroundings at each point in time using this distance threshold as across the annual cycle, little bustards typically move less than 300m between two consecutive hourly points (Table S2.2).

Classifying habitat conditions

We mapped habitat conditions across each buffer area using the 2012 and 2018 CORINE land cover maps (EEA, 2007; EEA, 2018), selecting the 2012 map for GPS locations between 2009 and 2014, and the 2018 map for locations from 2015 onwards, to account for land use changes that may have occurred during the eleven-year tracking period (see Table S2.4).

To capture habitat variation relevant to little bustards, we simplified the CORINE land cover classes into four categories: herbaceous, shrubby, arboreous vegetation and “other land uses” (this includes urban areas, roads and water bodies). The study area is dominated by herbaceous vegetation (Emanuelsson, 2008), but a complete description of CORINE land cover correspondence classes can be seen in Table S2.3. In addition to extracting the land use information at the GPS location point, we also calculated the percentage of each type of land use in the buffer area.

Defining microclimate refugia

We defined microclimate refugia as locations that were at least 0.5°C cooler than the median temperature of the surrounding 500m buffer area. This half degree difference reflects the magnitude of variation that is likely to be perceived by animals (Scheffers et al., 2014), birds in particular, and lead to significant changes in behaviour, thermoregulation and survival (Rastogi, 2007; Scheffers et al., 2014). We determined the availability of microclimate refugia around each GPS fix (obtained above 25°C), by calculating the difference between the minimum and the median temperatures within the 500m buffer. Microclimate refugia was considered to be available when this difference exceeded 0.5°C. We considered that little bustards were using microclimate refugia when the focal location was at least 0.5°C cooler than the median temperature of their surrounding buffer area.

Statistical analysis

We used Generalized Linear Mixed Models (Bolker et al., 2009) (GLMM) with a binomial error distribution and a logit-link function (Zuur et al., 2009), to analyse the environmental characteristics of sites that provide microclimate refugia (i.e. their availability was coded as 1 or 0 depending on the presence of refugia within the 500m buffer), and how environmental conditions influence the probability that refugia are used by little bustards (coded as 1 or 0 depending on whether the focal point was > 0.5°C cooler than the median of the buffer). We modelled breeding and post-breeding seasons separately, resulting in four GLMMs.

We hypothesised that both availability and use of refugia may vary seasonally, so we included Julian day as an independent variable. Moreover, little bustards' daily activity patterns may influence refugia use, so we included a binary variable representing active or inactive periods during daytime hours, which have been previously established for the species using tracking data (Silva et al., 2015). The inactive periods were between 11am to 4pm during the breeding season and between 10am to 4pm in the post-breeding season, and we expected birds to be more likely to use microrefugia in the inactive periods.

We also included the longitude and latitude coordinates of each individual's core area in each season determined by the centroid of the 50% Minimum Convex Polygon (MCP) (Heupel et al., 2004; Kenward, 2000). This was done to account for larger-scale gradients of environmental variation across the Iberian Peninsula (Figure 2.1).

For each of our four models (microclimate refugia availability and use, for both breeding and post-breeding seasons), we included variables capturing variation in temperature and habitat, as spatial and temporal thermal variability (Table 2.1). We tested for multicollinearity between variables, aiming for -0.7 > r < 0.7 and a variance inflation factor (VIF) smaller than 3 (Zuur et al., 2009). A high negative correlation between the proportion of herbaceous and arboreous habitat was detected, and of these we chose to use the proportion of arboreous habitat in the models.

Table 2.1 - Explanatory variables used in the models of microclimate refugia availability and use, for both breeding and post-breeding seasons

Variable name	Description
Temp. median buffer (ºC)	Median of the temperature data in the buffer area
Temp. SD buffer (ºC)	Log (+1) transformation of the standard deviation of the temperature data in the buffer area
Hour	Hourly period (category), either active or inactive (García de la Morena et al., 2018)
Julian day	Julian day of the GPS locations point
Point land use	Land use of the location (category), either herbaceous, arboreous or shrubby
Prop. herbaceous	Arcsine (square root) transformation of the proportion of herbaceous land use in the buffer area
Prop. arboreous	Arcsine (square root) transformation of the proportion of arboreous land use in the buffer area
Prop. shrubby	Arcsine (square root) transformation of the proportion of shrubby land use in the buffer area
50 MCP long.	Longitude of the centroid of the 50% MCP of each individual per year
50 MCP lat.	Latitude of the centroid of the 50% MCP of each individual per year

We also used individual ID nested within year as a random factor (with 103 and 90 groups for the breeding and post-breeding seasons, respectively). We filtered the data to only include GPS locations with temperatures above 25°C prior to modelling (Silva et al., 2015), and only included daylight locations between 6am and 5pm (breeding) and 7am and 8pm (post-breeding) to avoid capturing nocturnal roost sites that could have microclimate characteristics.

To account for the potential spatial autocorrelation (expected in spatially clustered data), we introduced a spatial autocovariate term (RAC) (Crase et al., 2012; Dormann, 2007) with a neighbourhood of 300 meters, calculated from the residuals of a GLMM including all other explanatory variables (i.e., the global model). By using the RAC term, we account for autocorrelation in the response variable, only after fitting the other explanatory variables first (Crase et al., 2012). RAC was calculated using the *autocov_dist* function from the *spdep* package in R (Bivand & Piras, 2015).

The models including the RAC term were compared against both the null and global model using Akaike's Information Criterion and ANOVA test (Zuur et al., 2007) (AIC). The fit of models was evaluated using the Area Under the Curve (AUC) (Fielding & Bell, 1997).

All models and summary statistics were run in the R version 3.6.2 (R Core Team, 2016) in the *lme4* package (Bates et al., 2015).

2.3 Results

Identifying microclimate refugia availability and use

The dataset included 43,500 GPS locations obtained during the breeding season and 49,185 locations in post-breeding (Figure 2.2, Table S2.5). In total we obtained 102 bird/year of data in the breeding season and 90 bird/year in the post-breeding. Most of the GPS locations (97% for breeding and 98% for post-breeding seasons) were within -0.5 and 0.5°C of the median temperature of the 500m surrounding landscape (Figure 2.2), indicating little bustards use areas with similar temperatures to their surroundings.

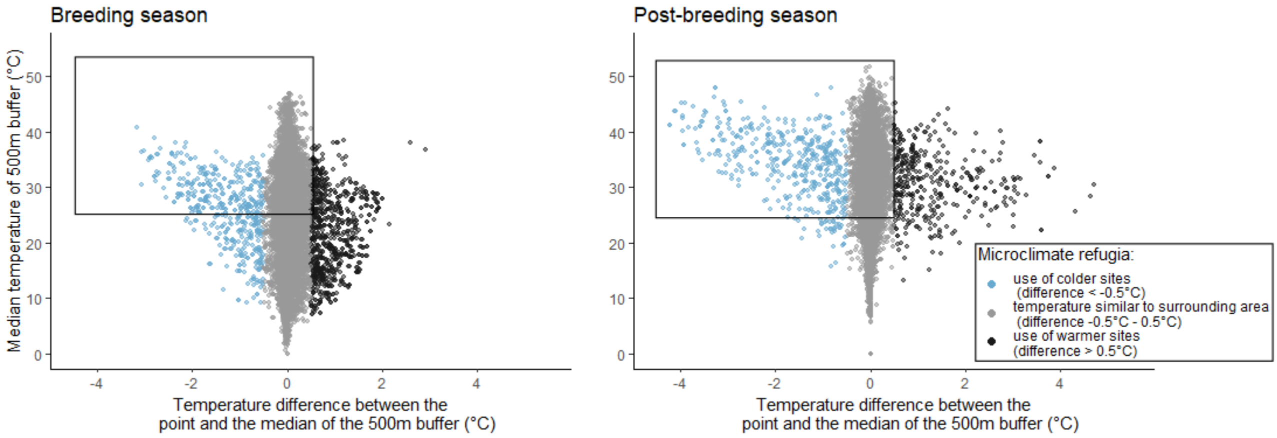

Figure 2.2 - Difference between the temperature of the little bustard locations and the median temperature of the buffer area, for both breeding and post-breeding seasons. The black squares identify the GPS location data used to understand microclimate refugia availability and use by little bustards. Only locations obtained at ambient temperature above 25°C are included in the analysis where sites with and without cooler microclimate refugia opportunities are compared.

Half of the little bustard locations (35% in the breeding and 63% in the post-breeding) were at ambient temperatures above 25°C, and approximately a quarter of the GPS locations (26.7% of breeding and 29.5% of post-breeding) were identified as having microclimate refugia available within the buffer area (Table 2.2, Figure 2.3). At very high temperatures (above 37°C), microclimate refugia were available within 500m of 24.9% and 36.2% of the little bustard GPS locations obtained for breeding and post-breeding seasons, respectively (Table 2.2). Microrefugia sites provided temperatures up to 4°C cooler than the surrounding landscape and the largest temperature differences obtained were for locations at more than 40°C and during the post-breeding season.

Table 2.2 - Summary information of microclimate refugia availability in the buffer area and use by little bustard at above optimal temperature (25-37°C) and at thermal stress temperature (> 37°C), for both breeding and post-breeding seasons (Figure 2.3). Number and percentage of GPS locations in each temperature range; GPS locations with microclimate refugia availability; and GPS locations with microclimate refugia use. Percentages of 'availability' and 'use' calculated as: % Availability = n° 'Availability' GPS location / Total n° GPS location; % Use = n° 'Use' GPS locations / n° 'Availability' GPS locations.

Temperature (°C)	Breeding			Post-breeding		
	Total (%)	Availability (%)	Use (%)	Total (%)	Availability (%)	Use (%)
25-37	14,491 (94.9%)	3,876 (26.8%)	291 (7.5%)	25,861 (82.9%)	7,286 (28.2%)	264 (3.6%)
≥ 37	780 (5.1%)	194 (24.9%)	5 (2.6%)	5,337 (17.1%)	1,933 (36.2%)	158 (8.2%)
Total	15,271 (100%)	4,070 (26.7%)	296 (7.3%)	31,198 (100%)	9,219 (29.5%)	422 (4.6%)

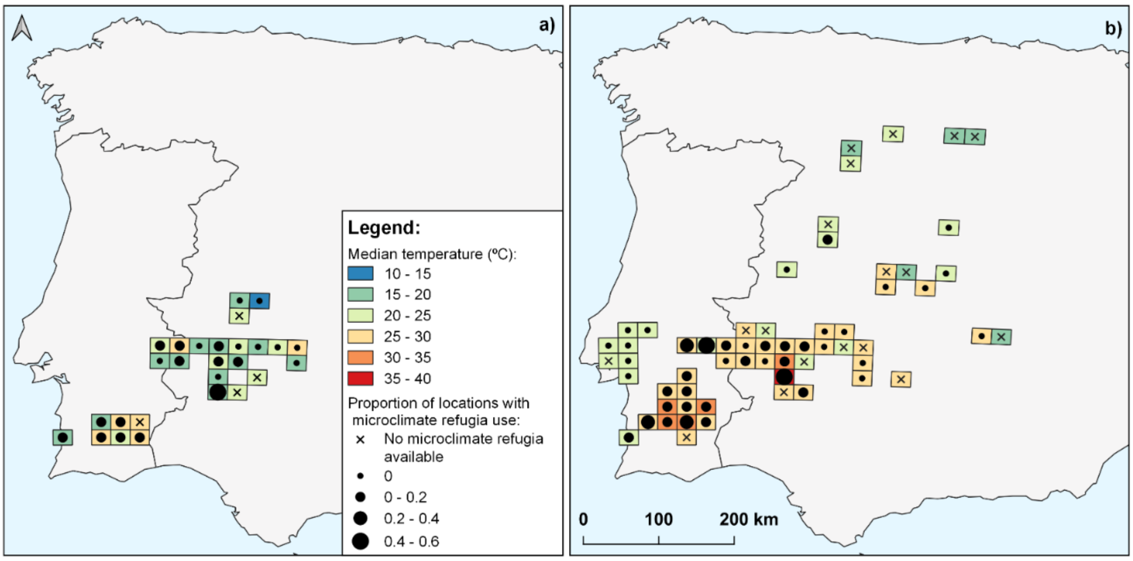

Figure 2.3 - Mean median temperature for little bustard locations in the 25x25 km grid cells occupied and proportion of locations where microclimate refugia was used by little bustards (circles), in both a) breeding and b) post-breeding seasons. The "x" shows the grids were there was no microclimate refugia available. Map made with QGIS 3.28.2 (www.qgis.org)

The temporal use of microclimate refugia was low (7.3% of breeding and 4.6% of post-breeding locations where microclimate refugia were available) but peaked during the post-breeding season when ambient temperatures exceeded 37°C (use at 8.2% of the locations) (Table 2.2, Figure 2.3).

Determinants of microclimate refugia availability

During the breeding season, availability of microclimate refugia was negatively associated with longitude (F = -1.33, p < 0.01) and positively associated with latitude (F = 1.40, p < 0.01) indicating general trends towards higher availability of microclimate refugia in areas occupied by little bustards within northern and western regions (Figure 2.4, Table S2.6). Microclimate refugia availability was negatively associated with proportion of arboreous land use within the buffer area (F = -0.47, p < 0.01) and positively associated with proportion of shrubby land use (F = 0.40, p < 0.01) (Figure 2.4, Table S2.6). In the post-breeding, microclimate refugia availability was positively associated with higher proportions of both shrubby and arboreous land uses (F = 0.10, p < 0.01 and F = 0.07) (Figure 2.4, Table S2.6).

At higher ambient temperatures in the post-breeding season, little bustards used sites with greater microclimate refugia availability (F = 0.11, p < 0.01). Locations with higher availability of microclimate refugia also showed greater temperature standard deviations across the 500m area surrounding the bird locations, for both breeding (F = 2.10, p < 0.01) and post-breeding seasons (F = 2.01, p < 0.01) (Figure 2.4, Table S2.6).

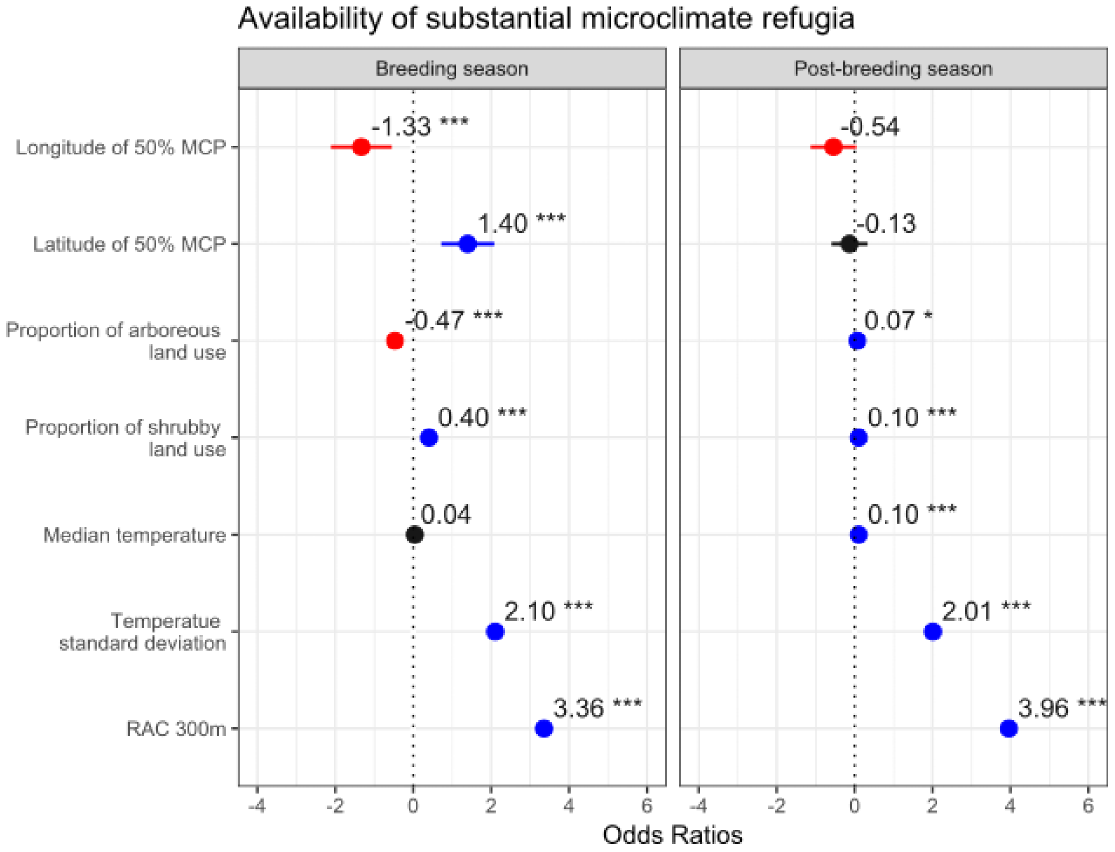

Figure 2.4 - GLMM results for the predictors of availability of microclimate refugia, for both breeding and post-breeding seasons. Variable significancy is shown: *** $p < 0.01$; * $0.01 < p < 0.05$; others, $p > 0.05$. Positive effects are shown in blue, negative effects in red and not significant effects in black

Determinants of microclimate refugia use

The use of microclimate refugia was negatively associated with longitude, for both breeding and post-breeding seasons (F = -1.17, p = 0.03; F = -1.26, p = 0.01, respectively), and was positively associated with latitude during breeding season (F = 1.48, p < 0.01), indicating higher microclimate refugia use in more northern and coastal areas of the Iberian Peninsula (Figure 2.5, Table S2.7), mirroring patterns for microclimate refugia availability.

Microclimate refugia use was positively associated with arboreous locations in both seasons (F = 5.72, p < 0.01, for breeding; F = 6.99, p < 0.01, for post-breeding), as well as with shrubby locations during post-breeding (F = 6.10, p < 0.01) (Figure 2.5, Table S2.7). Additionally, it was negatively associated with high proportions of arboreous land use in the surrounding 500m in both seasons (F = -0.82, p < 0.01, for breeding; F = -2.07, p < 0.01, for post-breeding), as well as with high proportions of surrounding shrubby land use, during post-breeding (F = -0.64, p < 0.01). Sites that were used as microclimate refugia therefore tended to be focal locations with some arboreous or shrubby cover sitting within areas dominated by other more open habitats.

In the post-breeding season, microclimate refugia use was positively associated with the little bustard active period (F = 1.09, p < 0.01) and the Julian day (F = 0.21, p = 0.02) (Figure 2.5, Table S2.7).

Lastly, little bustard use of microclimate refugia during post-breeding was positively associated with the median temperature of the surrounding area (F = 0.31, p < 0.01), and with the temperature standard deviation, for both breeding (F = 0.79, p < 0.01) and post-breeding seasons (F = 1.15, p < 0.01) (Figure 2.5, Table S2.7).

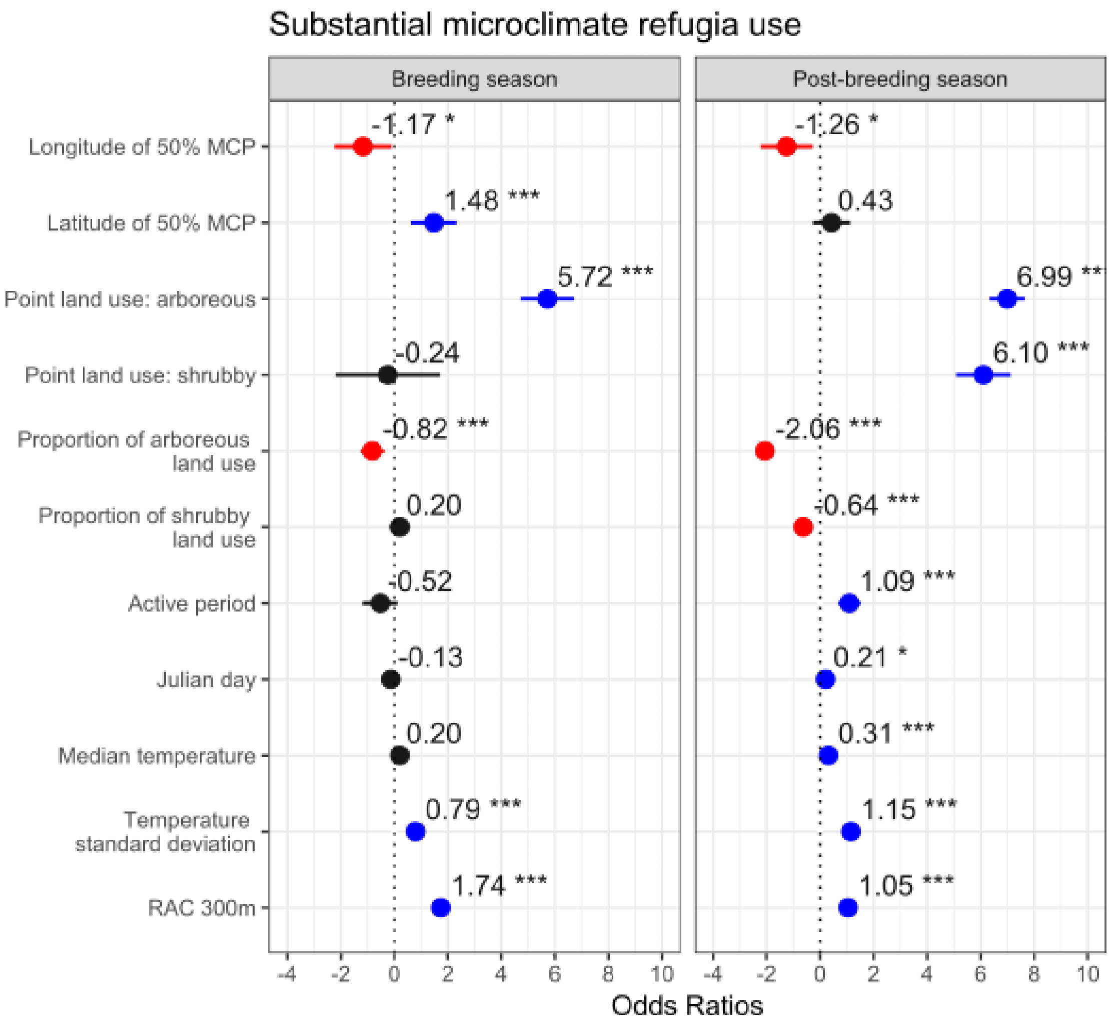

Figure 2.5 - GLMM results for the predictors of microclimate refugia use, for both breeding and post-breeding seasons. Variable significancy is shown: *** p < 0.01; * 0.01 < p < 0.05; others, p > 0.05. Positive effects are shown in blue, negative effects in red and not significant effects in black

2.4 Discussion

Our 11-year tracking dataset reveals the use and availability of microclimate refugia of a threatened grassland species in areas exposed to high and increasing temperatures, extreme drought, and frequent heat waves (IPCC, 2017). We find that little bustards use microclimate refugia in both breeding and post-breeding seasons, especially when exposed to higher temperatures. The microclimate refugia sites used are characterized by small patches of shrubs and trees in an herbaceous landscape, which promotes heterogeneous temperatures. This heterogeneous thermal landscape can mitigate against detrimental effects of increasing temperatures observed across the Iberian Peninsula over the past 30 years (Figure 2.1) which are expected to continue under climate change (IPCC, 2017). Additionally, microclimate refugia can shelter individuals from high temperatures during critical parts of the annual cycle (Gudka et al., 2019). Nonetheless, further research on the physiological, behavioural and fitness consequences of exposure to temperature extremes is needed to ascertain the extent to which microclimate refugia availability may provide effective conservation measures.

Birds can use thermoregulation mechanisms (e.g. evaporating water through the skin) and behavioural changes (e.g. decreasing activity levels when temperatures are higher) to respond to temperature extremes, but all these can impact their fitness (Gudka et al., 2019; Rastogi, 2007; Silva et al., 2015). The apparent use of microclimate refugia by little bustards was low in comparison to its availability. Nonetheless the use increased when ambient temperature rose. The percentage of use of microclimate refugia above 37°C was greatest during post-breeding (8.2%) when ambient temperatures tend to peak, and when the birds are not actively breeding, and therefore are less site faithful. Little bustards show a strong site fidelity during the breeding season, even when their display areas undergo major land use changes (Faria & Rabaça, 2004; Salamolard & Moreau, 1999). Males remain in their display areas characterized by low vegetation cover (Silva et al., 2010), making this species particularly vulnerable to temperature extremes. Although in our study, temperatures above 37°C during breeding season represent only 5% of the data, the higher temperature anomalies registered during this period (Figure 2.1), suggest that microrefugia may play an important role in buffering high temperatures. This buffering effect reduces the risk of overheating and costly metabolic functions to thermoregulate, and consequently may prevent fitness depletion (du Plessis et al., 2012).

Little bustards were often exposed to temperatures above 25°C in the post-breeding, the temperature above which little bustards drastically reduce their activity patterns (Silva et al., 2015). In the summer months (post-breeding season) temperatures often exceeded 40°C. This was associated with an increase in the use of microclimate refugia which was observed at very high temperatures (> 37°C).

An alternative strategy many individuals adopt to cope with extreme temperatures is to migrate to milder areas in the Iberian Peninsula. The little bustard is a partial-migratory species, with most Iberian individuals performing short- to medium-distance movements during post-breeding (García de la Morena et al., 2015). These milder areas are mainly located at the northern range of the species' Iberian distribution and in coastal areas (e.g., estuaries).

This movement strategy enables individuals to avoid the extreme temperature conditions experienced in some post-breeding areas. Northern and western areas can be up to 10°C colder than inland southwestern areas, and thus can act as macro-scale refugia. This may help explain why, despite an increase in microclimate refugia use above 37°C, the overall (above 25°C) percentage of microclimate refugia use in the post-breeding season decreases. During post-breeding, little bustards are less dependent on grasslands, and can use areas with different land uses where they may be less exposed to high temperatures, such as irrigated fields and olive groves with more heterogeneous temperatures (Alonso et al., 2020). Perhaps unsurprisingly, we found that microclimate refugia availability was higher in areas with more shrubby or arboreous cover during the post-breeding, which correspond to the non-grassland areas little bustards' resort to during the post-breeding season. By contrast, during the breeding season, little bustards are restricted to sites that maximise their ability to be seen by conspecifics (Silva et al., 2015). This need to be conspicuous and strong site fidelity behaviour to lekking areas (Silva et al., 2017) likely exposes little bustards to elevated temperatures in the breeding season.

This season is also the period with the highest temperature anomalies, hence if this trend continues, availability of small-scale microclimate refugia may become even more important in the future due to climate change.

Our results suggest that the presence of small patches of trees and shrubs within landscapes dominated by herbaceous vegetation can provide microclimate refugia, as even in smaller patches the canopies' shade allows for lower temperatures (Carroll et al., 2016). Furthermore, the heterogeneous thermal landscape that is created by shaded areas protects our study species from exposure to high temperatures as well as insects that the little bustard may consume (Jiguet, 2002; Suggitt et al., 2018). This is an indirect positive effect of microclimate refugia availability, that benefits this endangered species.

Both microclimate refugia availability and use increase in northern and western areas of southwestern Iberia during breeding season. The southern populations in the Baixo Alentejo (Portugal) region have little microclimate refugia overall, despite being one of the species' most important breeding areas in Iberia (Grimmet & Jones, 1989; Silva et al., 2010). Landscapes there are less topographically diverse and more dominated by open areas than other parts of the range (Ribeiro et al., 2016), offering fewer microclimate refugia.

Microclimate refugia availability was higher in both seasons when temperatures in the 500m buffer area were more heterogenous. These temperature-heterogeneous areas may allow little bustards to have quick access to cooler areas that enable them to reduce metabolic heat production and to thermoregulate (Whittow, 1986).

In the post-breeding, little bustards used more microclimate refugia during their active period of the day and towards the end of the post-breeding season. These results may be explained by high temperature variation during the active period, as the temperature rises at different rates from early morning until the middle of the day and decrease at different rates in the second part of the day. Additionally, in the Iberian Peninsula, temperatures can reach 40°C during the post-breading season (between July and August). These periods of high temperature in the middle of the day correspond to little bustards' inactive period (Silva et al., 2015).

Lower refugia use during the inactive period suggests that little bustards may be adopting other strategies to cool down. For instance, they may be keeping activities to a minimum to reduce metabolic heat production or using behavioural thermoregulation (Powers et al., 2017; Rastogi, 2007). Additionally, areas with microclimate refugia may have increased foraging resource availability (Jiguet, 2002; Suggitt et al., 2018) and thus are more used in the active period.

Methods limitations

The *microclima* package is the best available resolution temperature modelling tool, but it still has important limitations. It uses a relatively simplistic schema for vegetation structure shading effect and does not account for the influence of drought on soil heating (Maclean et al., 2019), this will likely lead to underestimates of temperature in our Mediterranean study area. Moreover, the spatial scaling of our modelling approach may have underestimated the use of microclimate refugia in the case of very small-scale habitat features. Individuals experience their thermal environment at scales from centimetres to few meters (Potter & Woods, 2013), and thus might utilise small, isolated trees or bushes as microclimate refugia not captured by the land cover resolution (100m) (EEA, 2018). The technology needed to obtain such fine-scale vegetation information across a species' distribution is not yet fully available, though increases in LiDAR coverage and decrease of acquisition costs may enable this in the future for relatively large landscape scales (Hancock et al., 2021; Kearney & Porter, 2009).

We focussed on quantifying microclimate refugia in areas where little bustards were present, and thus did not investigate potential refugia availability in the wider landscape. However, we quantified microclimate refugia availability within a 500m buffer, which represents a large area compared to the range used by territorial males and their average distance moved during the breeding season (Silva et al., 2017, see Table S2.2). Moreover, although microclimate refugia use is limited in both seasons, the results show that a quarter of little bustard locations in the breeding season and more than a third in the post-breeding season are in areas where microclimate refugia is available within 500m. Microclimate refugia availability is a fine scale metric that considers the availability of colder sites in the 500m buffer around each GPS location.

Finally, this study focuses on understanding the factors that determine the availability and use of microclimate refugia and does not evaluate whether these microclimate refugia prevent exposure to thermal stress.

Future studies examining microclimate refugia opportunities at the wider landscape scale could be informative in identifying areas where refuge availability may be limiting, particularly if parts of the former range have already become unsuitable for little bustard presence due to the lack of microclimate buffering opportunities.

Finally, we were only able to capture and track male bustards in our study system, and our findings are thus specific to males. Given the reproductive strategy of the species, female decisions on microhabitat selection are likely to differ markedly from those of males during the breeding period, reflecting the constraints imposed by nesting and chick-rearing. During post-breeding, however, little bustards form mixed-sex flocks and thus our male-biased sample may be more representative of the behaviour of both sexes during that period.

Conclusions

We show that tracking data and microclimate modelling tools can yield important insights into the availability and use of microclimate refugia. These results can be used to identify the habitat features that provide microclimate refugia opportunities for populations at the edge of species' ranges or those affected by climate warming and exposure to extreme temperatures. Our results show that the presence of small patches of taller non-herbaceous vegetation, provide microclimate refugia opportunities through the creation of a more heterogeneous thermal landscape (Carroll et al., 2016; Scheffers et al., 2014). Microclimate refugia were available in approximately a quarter of the little bustard locations, suggesting that availability of microclimate refugia may be limited for these grassland birds in some parts of their Iberian range (e.g., Baixo Alentejo, Portugal).

Further research on the contribution of microclimate refugia for species fitness, behaviour and habitat selection is still needed to inform the design and management of breeding and post-breeding areas resilient to climate warming.

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Chapter 2 Supplementary Materials

CORINE Land Cover to MODIS type of habitat conversion

Table S2.1 - Match between CORINE Land Cover and MODIS habitat categories, used to generate the habitat raster to run the *microclima* package

CORINE Land Cover categories	MODIS categories
Agro-forestry areas	Savannas
Complex cultivation patterns	Savannas
Transitional woodland-shrub	Savannas
Annual crops associated with permanent crops	Short grasslands
Land principally occupied by agriculture, with significant areas of natural vegetation	Short grasslands
Natural grasslands	Short grasslands
Non-irrigated arable land	Short grasslands
Pastures	Short grasslands
Permanently irrigated land	Cropland
Rice fields	Cropland
Vineyards	Open shrubland
Sclerophyllous vegetation	Open shrubland
Broad-leaved forest	Evergreen broadleaf forest
Fruit trees and berry plantations	Evergreen broadleaf forest
Olive groves	Evergreen broadleaf forest
Coniferous forest	Evergreen needleleaf forest
Mixed forest	NA
Airports	NA
Construction sites	NA
Discontinuous urban fabric	NA
Industrial or commercial units	NA

Statistics of distance between consecutive points, in an hourly interval, for each season, for each individual per year

Table S2.2 - Basic statistics of distance between consecutive GPS locations (per hour) for each little bustard per year, in each season

	Breeding	**Post-breeding**
Grouping	Ind/year	
Total nº GPS locations	54998	51407
Mean distance (m)	129.75	290.52
Median distance (m)	36.72	31.10
Standard deviation of distance (m)	417.78	2341.01

CORINE Land Cover information

Table S2.3 - CORINE Land Cover categories conversion into four classes of vegetation type (arboreous, herbaceous, shrubby and 'other type of habitats' of land cover), based on their description (EEA 2018)

CORINE Land Cover categories	Vegetation type
Agro-forestry areas	Arboreous
Annual crops associated with permanent crops	Arboreous
Broad-leaved forest	Arboreous
Coniferous forest	Arboreous
Fruit trees and berry plantations	Arboreous
Mixed forest	Arboreous
Olive groves	Arboreous
Beaches, dunes, sands	Herbaceous
Complex cultivation patterns	Herbaceous
Inland marshes	Herbaceous
Land principally occupied by agriculture, with significant areas of natural vegetation	Herbaceous
Natural grasslands	Herbaceous
Non-irrigated arable land	Herbaceous
Pastures	Herbaceous
Permanently irrigated land	Herbaceous
Rice fields	Herbaceous
Salines	Herbaceous
Salt marshes	Herbaceous
Sparsely vegetated areas	Herbaceous
Water bodies	Herbaceous
Water courses	Herbaceous
Construction sites	Other type of habitat
Continuous urban fabric	Other type of habitat
Discontinuous urban fabric	Other type of habitat
Estuaries	Other type of habitat
Industrial or commercial units	Other type of habitat
Intertidal flats	Other type of habitat
Mineral extraction sites	Other type of habitat
Road and rail networks and associated land	Other type of habitat
Sea and ocean	Other type of habitat

CORINE Land Cover categories	Vegetation type
Sport and leisure facilities	Other type of habitat
Airports	Other type of habitat
Sclerophyllous vegetation	Shrubby
Transitional woodland-shrub	Shrubby
Vineyards	Shrubby

After the simplification of CORINE land covers into 4 classes of vegetation type, the degree of change between CORINE 2012 and CORINE 2018, in the 500 meters surrounding of the little bustard GPS location, was calculated. Between 2012 and 2018, 99.64% and 95.62% of CORINE land cover categories remained the same for breeding and post-breeding seasons, respectively (Table S2.4). In the breeding season, the conversion was done from herbaceous to shrubby vegetation and from shrubby to herbaceous vegetation with 0.36% and 0.01%, respectively. In the post-breeding season, occurred more changes, from arboreous to herbaceous vegetation in 0.86% of the areas; from herbaceous to arboreous (3.29%) or to 'other type of habitats' of land cover (0.05%); from shrubby to herbaceous vegetation (0.14%) and from 'other type of habitats' of land cover to herbaceous vegetation (0.04%) (Table S2.4).

Table S2.4 - CORINE Land Cover changes between vegetations classes from 2012 and 2018 maps

CORINE 2018 / CORINE 2012	Breeding season			Post-breeding season			
	Arboreous (%)	Herbaceous (%)	Shrubby (%)	Arboreous (%)	Herbaceous (%)	Shrubby (%)	Other (%)
Arboreous (%)	4.04	0	0	4.55	0.86	0	0
Herbaceous (%)	0	91.78	0.36	3.29	89.08	0	0.05
Shrubby (%)	0	0.01	3.82	0	0.14	0.31	0
Other (%)	-	-	-	0	0.04	0	1.68

Little bustard GPS location information.

In Table S2.5 are presented the details regarding the little bustards GPS points. The number of individuals per year relates with individuals that were followed for more than one year. The data were filter, so GLMM were done considering only the time (hour) period when microclimate refugia was used by the little bustard (see methods section). The percentage of GPS points above 25°C is related with the total number of GPS points. The percentage of GPS points in microclimate refugia above 25°C is related to the total number of GPS points above 25°C.

Table S2.5 - Information related with little bustard GPS locations

	Breeding	Post-breeding
Num. ind. tracked	77	68
Num. years	11 (2009-2019)	
Num. ind/year	103	90
Total num. GPS locations	43 500	49 185
Period of use of microclimate refugia (hour)	6 - 17	7 – 20
GPS points > 25°C	15 271 (35.1%)	31 198 (63.4%)
GPS points > 25°C in microclimate refugia	296 (1.9%)	422 (1.4%)

GLMM summary for predictors of microclimate refugia availability

Table S2.6 – GLMM summary for predictors of microclimate refugia availability, for both breeding and post-breeding seasons

	Breeding				Post-breeding			
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
Intercept	-2.71	0.25	-10.71	< 0.01	-2.73	0.26	-10.74	< 0.01
MCP 50 longitude	**-1.33**	**0.40**	**-3.34**	**< 0.01**	-0.54	0.30	-1.81	0.07
MCP 50 latitude	**1.40**	**0.35**	**4.03**	**< 0.01**	-0.13	0.24	-0.57	0.57
Land use buffer arboreous	**-0.47**	**0.08**	**-5.73**	**< 0.01**	**0.07**	**0.03**	**2.05**	**0.04**
Land use buffer shrubby	**0.40**	**0.07**	**5.85**	**< 0.01**	**0.10**	**0.03**	**3.55**	**< 0.01**
Median Temperature	0.04	0.05	0.86	0.39	**0.10**	**0.03**	**3.61**	**< 0.01**
Std Temp. buffer	**2.10**	**0.08**	**25.85**	**< 0.01**	**2.01**	**0.05**	**40.64**	**< 0.01**
RAC 300m	**3.36**	**0.11**	**31.02**	**< 0.01**	**3.96**	**0.08**	**48.22**	**< 0.01**

GLMM summary for predictors of microclimate refugia use

Table S2.7 – GLMM summary for the predictors of microclimate refugia use, for both breeding and post-breeding seasons

	Breeding				Post-breeding			
	Estimate	Std. Error	z value	p-value	Estimate	Std. Error	z value	p-value
Intercept	-7.91	0.48	-16.56	< 0.01	-9.12	0.50	-18.26	< 0.01
MCP 50 longitude	**-1.17**	**0.54**	**-2.16**	**0.03**	**-1.26**	**0.50**	**-2.54**	**0.01**
MCP 50 latitude	**1.48**	**0.43**	**3.42**	**< 0.01**	0.43	0.36	1.18	0.24
Land use point: arboreous	**5.72**	**0.51**	**11.25**	**< 0.01**	**6.99**	**0.34**	**20.66**	**< 0.01**
Land use point: shrubby	-0.24	0.99	-0.24	0.81	**6.10**	**0.52**	**11.73**	**< 0.01**
Land use buffer arboreous	**-0.82**	**0.23**	**-3.59**	**< 0.01**	**-2.07**	**0.17**	**-12.35**	**< 0.01**
Land use buffer shrubby	0.20	0.20	1.02	0.31	**-0.64**	**0.14**	**-4.41**	**< 0.01**
Active period	-0.52	0.33	-1.57	0.12	**1.09**	**0.21**	**5.13**	**< 0.01**
Julian day	-0.13	0.18	-0.71	0.48	**0.21**	**0.09**	**2.32**	**0.02**
Median temp. buffer	0.20	0.17	1.19	0.24	**0.31**	**0.09**	**3.49**	**< 0.01**
Std Temp. buffer	**0.79**	**0.12**	**6.57**	**< 0.01**	**1.15**	**0.09**	**13.36**	**< 0.01**
RAC 300m	**1.74**	**0.14**	**12.16**	**< 0.01**	**1.05**	**0.07**	**14.24**	**< 0.01**

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— Chapter 3 —

Temperature and microclimate refugia use influence migratory timings of a threatened grassland bird

"The Norwich chapter stands as a flourishing phase – a canvas of incredible learning, painting the vibrant strokes of our journey and providing the inspiration for the chapters that lie ahead."

Temperature and microclimate refugia use influence migratory timings of a threatened grassland bird

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Authors' contributions

RFR, AMAF, JPS and JJG conceived the overall study. JPS was responsible for capturing and tagging the little bustards. RFR prepared the dataset, coded the models, and analysed the data, assisted by JJG and AMAF. RFR wrote the manuscript assisted by AMAF with revisions of JPS, JJG. All authors gave final approval for publication.

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Abstract

Seasonal changes in resource availability are known to influence the migratory behaviour of animals, including both timing and distance. While the influence of environmental cues on migratory behaviour has been widely studied at the population level, it has rarely been examined at the spatial scale at which individuals experience their environment. Here, we test the hypothesis that individuals exposed to similar large-scale environmental cues may vary in migratory behaviour in response to the different microclimate conditions they experience at fine scales.

We combine high-spatial and temporal resolution microclimate and habitat information with GPS tracking data for a partially migratory threatened grassland bird. Data from 47 little bustards (*Tetrax tetrax*; 67 breeding events) tracked between 2009 and 2019 was used to (i) evaluate individual consistency in migratory behaviour (timing and distance) and (ii) assess whether the local environmental characteristics experienced by individuals – and in particular their use of microclimate refugia - influence distance and timing of migration, from and to the breeding sites.

Migratory distance was consistent for birds tracked over multiple years, while the timing of migration showed high variability among individuals. Departures from breeding areas spanned from May to August, with a few birds remaining in their breeding areas. Vegetation greenness (a proxy for food availability) was positively associated with the time birds spent in the breeding area. The best model also included a positive effect of microclimate refugia availability on breeding season length, although an interaction with temperature suggested that this effect did not occur at the highest relative temperatures. The return date to breeding grounds, although spanning from September to April, was not influenced by the environmental conditions or food availability.

Food availability, measured by a vegetation greenness proxy, was associated with later migration at the end of the breeding season. Availability of cooler microclimate refugia may also allow for later departures from the breeding sites in all but the hottest conditions. Management measures that increase microclimate refugia availability and provide foraging resources can thus potentially increase the length of the breeding season for this species.

3.1 Introduction

Migration is a complex behaviour undertaken by billions of organisms annually. These seasonal movements are primarily associated with declines in food availability and deterioration of environmental conditions (Newton, 2010). The decision to migrate, however, may be influenced by internal factors such as experience or physiological condition, or external factors like high temperatures (Mueller et al., 2013; Newton, 2010). Adjusting the timing of migration allows individuals to avoid spatiotemporally unsuitable environments, increasing survival and fitness (Dingle, 2014; Reid et al., 2018).

Migratory species can vary from fully obligate migrants, where all individuals undertake seasonal movements between distinct geographical sites (Dingle, 2014), to partial-migrants where a proportion migrate while others remain resident at their breeding sites (Chapman et al., 2011a; Newton, 2010; Reid et al., 2018). Within a species distribution, environmental variability can affect the frequency of migratory individuals within a population (Linek et al., 2021). Individuals may also perform short-, medium- or long-distance seasonal migrations, to one or several destinations, across environmental gradients (Chapman et al., 2011a; Reid et al., 2018) and sex and age are known to influence the migration strategy individuals adopt (Baert et al., 2018; Martín et al., 2016). Partial migration is more common than previously thought (Chapman et al., 2011b) and likely to be maintained if both migratory behaviours (residency and migration) yield equivalent fitness, or each confers different benefits to individuals (Buchan et al., 2020; Chapman et al., 2011b; Kokko, 2011). This migratory diversity has been associated with greater population-scale resilience to environmental changes in breeding and post-breeding areas (Gilroy et al., 2016).

Changes in environmental conditions can lead to variability in the timing of migration, breeding and even moulting (Gordo, 2007; Tomotani et al., 2018; Zaifman et al., 2017). For example, precipitation and temperature at breeding sites have been shown to influence the departure from the breeding area (i.e. the start of autumn migration) for four trans-Saharan and six intra-European passerine species that migrate through Heligoland, Germany (Haest et al., 2019).

Migratory repeatability – i.e. whether individuals perform similar migrations between years – is a good indicator of the extent to which individual migratory decisions are shaped by responses to environmental cues (Reid et al., 2020). Common terns (*Sterna hirundo*) breeding in northwest Germany, for example, showed high within-individual repeatability in most aspects of their migratory journeys, suggesting a relatively limited impact of environmental cues on their migratory decisions (Kürten et al., 2023). While elk (*Cervus* *elaphus*) in Canada, by contrast, showed low individual repeatability and often changed between resident and migratory strategies (Eggeman et al. 2016). In european shags (*Phalacrocorax aristotelis*), a partially migratory species breeding in Scotland, 64% of the individuals kept their migratory strategy (resident, early or late-migrant), between years (Reid et al., 2020), translating to a relatively high within-individual repeatability. However, like migratory strategy, within-individual repeatability can be influenced by sex and age (Fudickar et al., 2013).

Despite the increasing body of literature on migratory movements of partial migratory species, our understanding of how environmental conditions influence migratory responses is still limited.

The factors that influence between-individual variability in migratory parameters within populations have been examined at broad spatial scales (Gill et al., 2014; Reid et al., 2020; Wilson et al., 2011), contributing to a general understanding of individual responses to environmental variability. However, there is a mismatch between the macro spatial scale most studies use to quantify environmental variation and the fine spatial scale at which individuals experience their environment (Suggitt et al., 2018). Fine-scale heterogeneity in environmental conditions allows for local areas with cooler temperatures than surrounding conditions (hereafter microrefugia); these may provide opportunities for individuals to persist in regions where larger-scale climate conditions become unsuitable (Maclean & Early, 2023; Maclean et al., 2015; Ramos et al., 2023). Potentially, migratory patterns may also be influenced by microrefugia, particularly for species that are highly sensitive to temperatures, but this remains to be shown. Access to microrefugia is an increasing focus of ecological studies (Massimino et al., 2020; Suggitt et al., 2011), as it can increase individuals' fitness and can help predict species responses to environmental change (Maclean & Early, 2023).

Understanding species' responses to microclimate conditions is data-demanding and logistically challenging due to the need to combine animal movement and environmental data. In recent decades, high resolution GPS tracking devices have allowed scientists to study animal movement, behaviour, and habitat use at high spatial and temporal resolution scales (Cagnacci et al., 2010; Kays et al., 2015), but availability of environmental data matching the temporal and spatial resolutions experienced by organisms has been limited (Bütikofer et al., 2020; Potter et al., 2013; Ramos et al., 2023). Here we combine high resolution animal tracking data with newly developed microclimate modelling tools to determine the influence of environmental conditions on individual migratory decisions. We use GPS tracking data of a grassland bird from a long-term study, to i) evaluate individual consistency in migratory timings (of departure and return) and distance travelled, and to ii) evaluate the influence of microclimate refugia, alongside other environmental characteristics, as determinants of variability in migration.

3.2 Methods

Study area and study system

The Iberian Peninsula is simultaneously a global biodiversity hotspot (Hoffman et al., 2016 and one of the world's most vulnerable regions to climate change (IPCC, 2017). The region is expected to suffer from extensive warming and increasing drought frequency in the near future (Jones et al., 2020), which are predicted to lead to species range contractions (IPCC, 2017). Species inhabiting semi-natural grasslands, with flat open areas and low vegetation cover, are particularly exposed to high temperatures throughout the year.

The little bustard, *Tetrax tetrax* (Linnaeus, 1758), is a medium-sized grassland specialist bird classified globally as 'Near Threatened' (BirdLife International, 2021). In the Iberian Peninsula, the species is partially migratory, with migratory individuals performing short- (mean ≈ 20km) to medium-distance (mean ≈ 400km) movements (García de la Morena et al., 2015). Migration takes place at the end of the breeding season (between May and August) when temperatures increase and vegetation starts to dry, limiting trophic resources (Silva et al., 2007). Despite recent severe population declines in both Portugal and Spain due to habitat loss and degradation (García de la Morena et al., 2015; Silva et al., 2018), which may be exacerbated by climate change (Marques et al., 2020; Traba & Morales, 2019), Iberia is still home to the most significant little bustard breeding populations in western Europe.

Satellite GPS tracking data

Between 2009 and 2019, 77 male little bustards were captured and tagged in five breeding areas across the southwestern Iberian Peninsula, in Alentejo (Portugal) and Extremadura (Spain), during the breeding season (April and May). Little bustards breed in an exploded lekking system (Morales et al., 2002), where breeding males defend their territories from other males and show exuberant displaying behaviour to attract visiting females (Morales et al., 2002). Breeding males were captured using a decoy (stuffed female) and snares

(Ponjoan et al., 2010; Ramos et al., 2023). Females, on the other hand, are extremely difficult to capture.

GPS tracking devices, which varied between 2% and 4% ($\bar{x}$ = 3.2%) of the birds' body mass (Kenward, 2000), were deployed using a thoracic harness made of Teflon Ribbon with a weak link to avoid lifelong deployment. Two types of Solar GPS devices were used: Platform Transmitter Terminal (Solar Argos/GPS 30g PTT - Microwave Telemetry), deployed on 19 birds between 2009 and 2011, and 28 Global System for Mobile Communications (GSM) devices (Flyway 25g - Movetech Telemetry), deployed between 2014 and 2019. Transmitters were programmed to record a GPS position every 2 h (PPT) or 10 to 30 min (GSM). Bird trapping and GPS tagging were approved by the Instituto da Conservação da Natureza e das Florestas (Portuguese authority), 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 authority), through the license to José Mª Abad-Gómez.

We only utilised information from birds captured before the 1st of May, which had at least seven days of associated data before departing from the breeding area, leaving 47 birds for analysis. Restricting our sample to birds caught before 1st May also ensures we fully sample the period during which birds are typically more vulnerable to increasing temperatures and food shortages (Gudka et al., 2019; Silva et al., 2015).

Migration timings and distance

The 47 birds provided information for 67 breeding seasons, with 12 and 4 birds being followed during two and three consecutive breeding seasons, respectively. For each bird-season we identified the date of departure from the breeding area, defined as movement away from the centroid of the breeding locations for a minimum period of one month. Birds that continued to use the breeding area throughout the year, even after the breeding season had ended, were referred to as residents (García de la Morena et al., 2015).

For migratory birds, we determined, when possible, the date birds returned to the breeding areas. For some birds, it was not possible to obtain a return date, either because the bird died, or the tracking device failed.

Each bird's daily centroid coordinates were calculated using QGIS version 3.10 (QGIS, 2022), for both breeding and post-breeding seasons. Subsequently, the mean centroid of the breeding season was retrieved for each individual. The total distance travelled by each bird was determined using the cumulative sum of the distance between that mean centroid and the daily post-breeding centroids.

Environmental cues

For the breeding season, environmental variables were collected between the 1st of May and the departure date of each bird. Temperature was modelled at fine spatial scales using the *microclima* (Maclean et al., 2019) and *NicheMapR* (Kearney & Porter, 2017) packages in R version 4.1.0 software (R Core Team, 2016). We generated hourly temperatures modelled at a 30 × 30m resolution calculated at 20cm above the ground (Ramos et al., 2023). This spatial resolution is likely to miss some small microclimate refugia features but is the best possible resolution considering the current land cover data availability (Ramos et al., 2023).

We obtained the hourly temperature for each GPS location and the minimum and median temperature within a 500m buffer of the birds' locations (Ramos et al., 2023). All temperature variables were then averaged by day, to minimize the differences in programming between the tagging devices.

Little bustard breeding season spans from April to June (Silva et al., 2014a), though some individuals remain in the breeding area until August. During this period, temperatures can range between 20 and 45ºC. We quantified temperature exposure for each individual relative to the population average using a Generalised Additive Model (GAM), from the *mgcv* (Wood, 2001) R package, fitting a Gaussian regression smooth to estimate mean daily temperatures of the studied population as a function of Julian date. We summed the residuals of each bird's daily temperature exposure from May 1st until the bird's departure date as an index of each individual's overall exposure to higher or lower temperatures, relative to the studied population within each bird's tracking period (hereafter 'relative temperature exposure').

For each little bustard GPS location, the availability of microclimate refugia was defined as the presence of areas with minimum temperatures at least 0.5ºC cooler than the median temperature within 500m surrounding each GPS location (Ramos et al., 2023). We then calculated the percentage of GPS locations with available microclimate refugia (1) throughout each bird's breeding season.

Satellite-derived Normalized Vegetation Index (NDVI) is a measure of vegetation greenness and biomass (Pettorelli et al., 2005). Since little bustards feed mainly on green plants, NDVI can be used as predictor of food availability (Pettorelli et al., 2005). We obtained NDVI values for all little bustard GPS locations using 8-day composite 250m spatial resolution MODIS (Moderate Resolution Imaging Spectroradiometer) images (Vermote, 2015) (product MOD09Q1). We used Google Earth Engine (Didan, 2015; Gorelick et al., 2017), to retrieve the NDVI value of the closest date to each GPS fix. We evaluated the information retrieved to ensure all images were of good enough quality to be used in the study (Didan, 2015). NDVI was calculated as the difference between the near infra-red (NIR) and the red (R) reflectance values over the sum of the two (Huete et al., 2002):

$$NDVI = \frac{NIR - R}{NIR + R}$$

As with relative temperature exposure, we quantified the NDVI experienced by each individual relative to the population average by fitting a GAM to model daily NDVI for each individual as a smoothed function of Julian day. We then summed the residuals for each individual as an index of its relative NDVI with respect to the studied population during each individual's tracking period (hereafter designated as relative NDVI).

The post-breeding period began on the day each bird completed the migration (i.e. reached the post-breeding area) and ended on 15th of September. In this period of the annual cycle the species is exposed to the highest temperatures and to food shortages (Silva et al., 2007). For each little bustards GPS location during post-breeding period the same three environmental variables were calculated: relative temperature exposure, the percentage of available microclimate refugia and relative NDVI, following the method used for the breeding season.

Statistical analysis

Repeatability (R) is commonly evaluated as the intra-class correlation coefficient (ICC) which reflects the degree of consistency of each individual's behaviour or response (Nakagawa et al., 2010). R varies between 0 and 1, where 0 indicates the same degree of variation in the individual's repeated behaviour as the variation in the population, and 1 indicates a strong reliability on the individual behaviour or response (Liljequist et al., 2019; Sokal & Rohlf, 1995).

We estimated the repeatability of migratory timing (departure and return dates from and to the breeding area) and distance travelled using Generalized Linear Mixed Models (GLMM) and parametric bootstrapping with 1,000 iterations, to estimate the associated uncertainty. All migratory and resident birds were used in the analysis, with the individual ID used as grouping factor and the breeding population as a random effect. The consistency analysis was carried out using the rpt function from the *rptR* package (Stoffel et al., 2017).

We fitted Linear Mixed-effects Models (LMM) from the *lme4* package (Bates et al., 2015) to analyse the influence of ecological variables (percentage of microclimate refugia availability, relative temperature exposure and relative NDVI) on migratory departure dates, with individual ID as a random factor.

Unlike departure dates, which were broadly normally distributed, return dates were strongly bimodal (Figure S3.1). We therefore converted the return dates to a binary variable (pre- and post-November 30th) (García de la Morena et al., 2015) and fitted a Generalized Linear Mixed Model (GLMM) (Bolker et al., 2009) with a binomial error distribution and a logit-link function (Zuur et al., 2009) to examine the effects of climatic variables on the probability of early or late return.

The return date model included the climatic and relative NDVI (as a proxy for food availability) variables for both the preceding breeding and the post-breeding seasons (until 15th of September) to account for potential seasonal carry-over effects. The influence of ecological variables on migratory timing was assessed using only migratory birds (i.e., excluding resident individuals). We did not analyse environmental correlates of distance travelled between breeding and post-breeding sites, as the consistency analysis showed that individuals did not vary significantly in migration distance between years, indicating that migration distances are unlikely to be influenced by short-term environmental conditions (see Results section).

Model selection for migratory timings was carried out using the *MuMIn* (Barton & Barton, 2015) R package. All models within ΔAICc < 2 of the top model were considered plausible and thus presented separately (Akaike's Information Criterion corrected for small sample size) (Burnham & Anderson, 2002; Grueber et al., 2011).

For the return date model, due to the low sample size (Harrel, 2001), we limited the number of variables included in each model to three, and tested all three-way combinations of all variables.

To evaluate potential spatial autocorrelation, we used spline correlogram plots with 95% pointwise confidence intervals calculated using 500 bootstrap resamples (Dormann et al., 2007; Rhodes et al., 2009). These spline correlograms were run using model residuals, after any spatial autocorrelation explained by the explanatory variables had been accounted for

(Dormann et al., 2007; Rhodes et al., 2009). Spline correlograms were produced using the *ncf* R package (Bjornstad & Bjornstad, 2016).

We tested for multicollinearity between variables, aiming for $-0.7 > r < 0.7$ and a variance inflation factor (VIF) smaller than 3 (Zuur et al., 2009). All models and summary statistics were run in the R version 4.1.0 (R Core Team, 2016).

3.3 Results

Migration timing and patterns

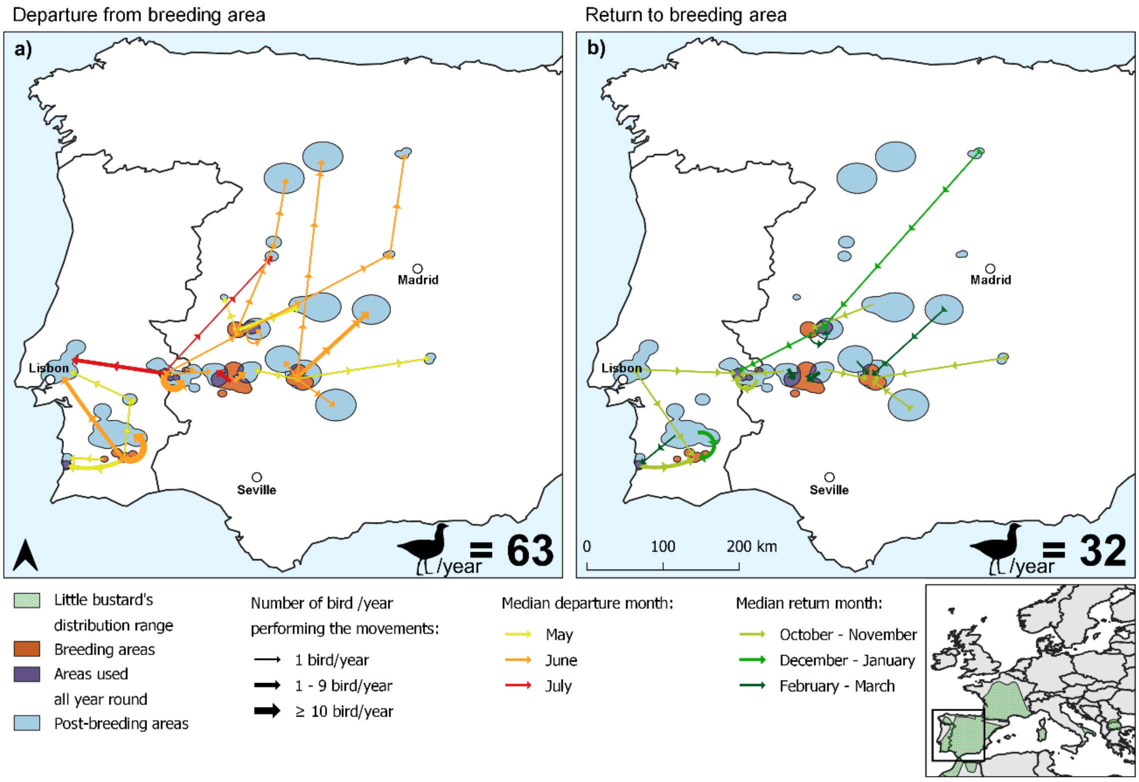

Figure 3.1 – Migration movements of little bustards from breeding (orange) to post-breeding (blue) areas, revealed from GPS tracking data obtained in the Iberia Peninsula. a) All 63 breeding to post-breeding movements; b) All 32 post-breeding to breeding movements. The areas used all year round are represented in purple. The arrows represent the movements to and from post-breeding areas, each colour representing a different month. The little bustard's distribution range (BirdLife International, 2021) is represented in green on the inset map.

Of the 67 post-breeding movement events, 63 departed the breeding area between the 10th of May and the 22nd of August, with most birds leaving their breeding grounds during June (median = 20th June ± 23 days) (Figure 3.1). One bird switched from migration to residency, remaining in the post-breeding area in the second year (southwestern area, Figure 3.1). The remaining three individuals/years adopted a resident strategy, remaining in the same area throughout the year (moving less than 1.5 km from the breeding area).

The distance travelled varied greatly between birds, with movements ranging from 4 to 421 km, and with some birds using more than one post-breeding area (Figure 3.1). Some of the breeding areas were also used as post-breeding areas, either by resident birds, birds with short migratory movements, or birds that moved from other breeding areas (shown in purple in Figure 3.1).

Out of the 63 migratory events, we were able to collect 32 return migratory movements. Contrary to the departure movement, the return migration was usually direct between the post-breeding and breeding areas. These movements occurred across an extended period of the year, between the 24th of September and 25th of April, with most return movements occurring between October and November (median = 29th November ± 68 days) (Figure 3.1).

Individual migratory consistency

Individuals showed significant repeatability between years in the distance travelled between breeding and post-breeding areas (R = 0.64, Figure 3.2 a) and d), Figure S3.2), suggesting that individuals are unlikely to vary their migration distance in response to environmental conditions. However, dates of departure from and to the breeding area did not show significant repeatability between years (R = 0.35 and R = 0.17, respectively, Figure 3.2 b) - d), Figure S3.2), suggesting that migration timings could vary with respect to environmental conditions experienced by individuals.

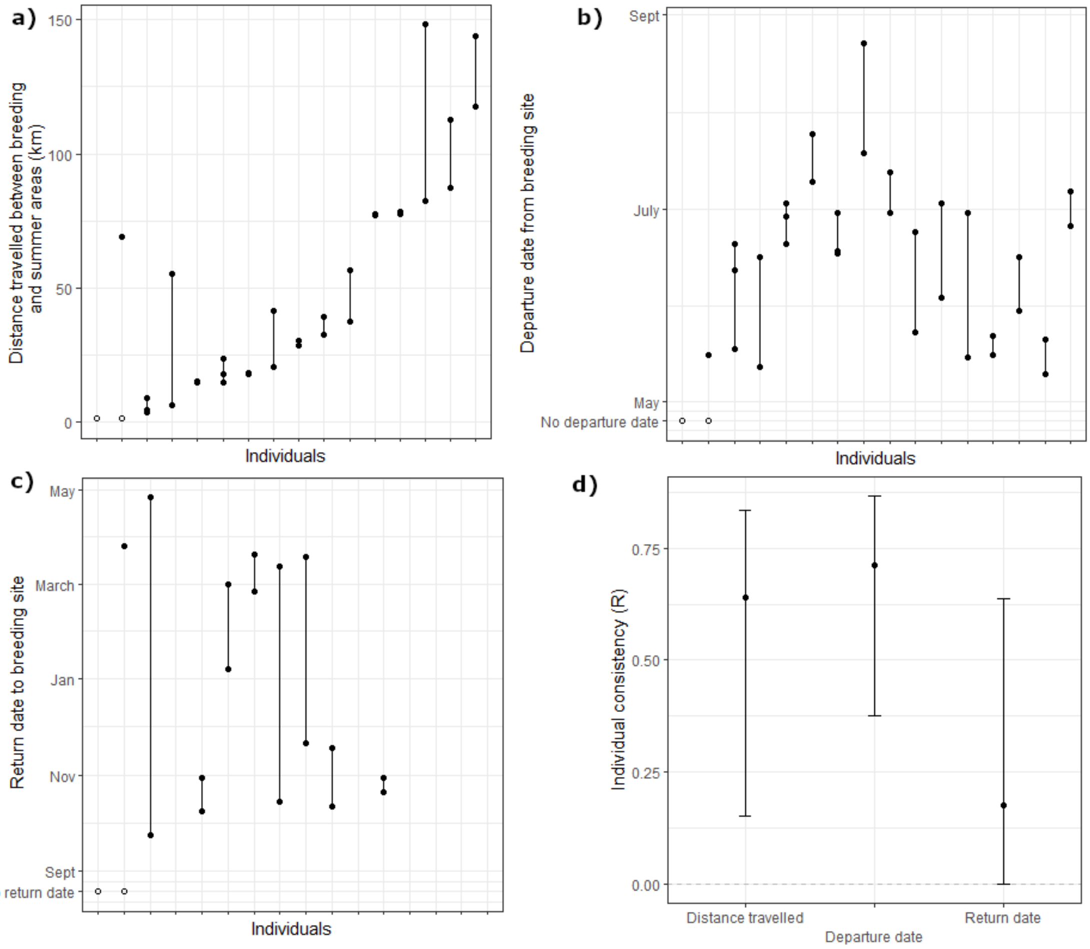

Figure 3.2 – Values of three phenological behaviours, a) distance travelled, b) departure date and c) return date, during multiple years of male little bustards (n = 36 birds). Values for the same individual are linked by vertical lines. Resident birds are shown as white dots, with no departure or return dates. d) Individual consistency (R) of the three migratory related variables showing the total population level variance, explained by consistent, repeated individual behaviour. Estimated repeatability does not differ significantly from zero, where the 95% CI bar overlaps with R = 0 (grey dotted horizontal line).

Departure date in relation to climatic conditions

The top model explaining variation in individual departure dates included effects of the percentage of available microclimate refugia, relative temperature exposure and their interaction, and relative NDVI. There was some support for the positive effect of percentage of available microclimate refugia during the breeding season on departure date as it was retained in the top model set, although the coefficient was not significant (F = 8.51, p = 0.131). There was strong support for a significant positive relation between departure date and relative NDVI (F = 15.82, p = 0.003, Figure 3.3 and Figure 3.4a)). There was also some support for a marginally significant interaction between available microclimate refugia and relative temperature exposure, such that the positive effect of microclimate refugia on departure date is reduced at higher temperature exposure levels (F = 21.07, p = 0.099, Figure 3.3 and Figure 3.4b)).

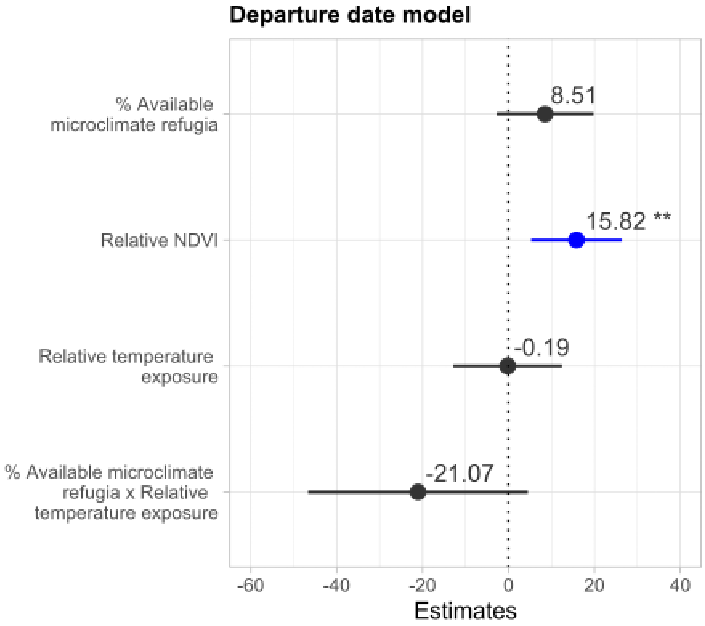

Figure 3.3 – GLMM results for the predictors of departure date from the breeding areas. Variable significancy is shown: ** p < 0.01; * 0.01 < p < 0.05; others, p > 0.05. Positive effects are shown in blue, negative effects in red and not significant effects in black.

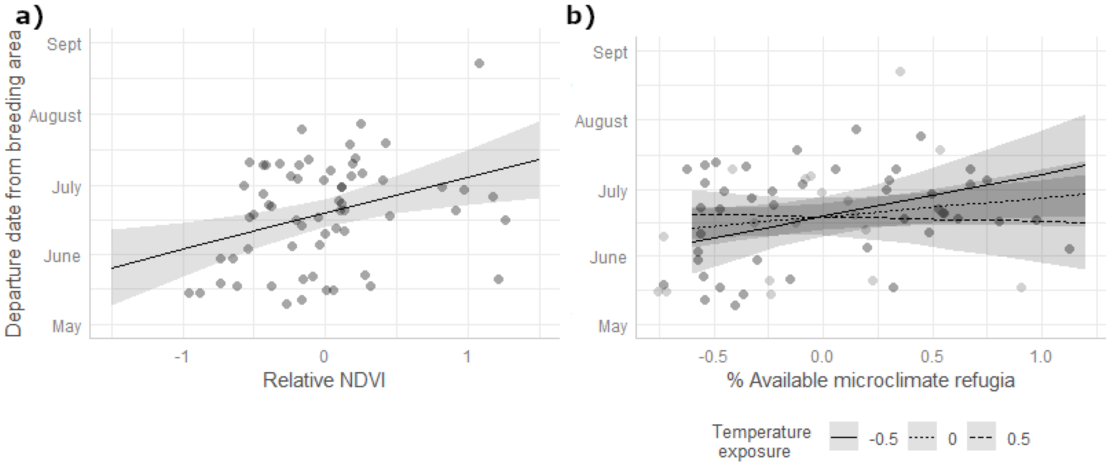

Figure 3.4 – Relationship between the breeding area departure date and a) relative NDVI and b) the interaction between the percentage of microclimate refugia and temperature exposure.

Return date in relation to climatic conditions

Neither the relative temperature, microclimate refugia, nor NDVI during the breeding or post-breeding seasons showed any significant relationship with variation in individual return dates, with the null model being identified as the most parsimonious model (Table S3.1).

3.4 Discussion

Our results show that the migratory timing of male little bustards is influenced by environmental variables measured at the fine spatiotemporal scales experienced by individuals. While the distance travelled after the breeding season was consistent from one year to the next within individuals and is thus likely to be strongly influenced by site fidelity (Alonso et al., 2020), the departure date varied with food availability (as indicated by relative NDVI). Interestingly, we also found some support that birds inhabiting sites with greater refugia availability also left their breeding sites later, though this effect was statistically uncertain and reduced when individuals were exposed to the highest temperatures. Return dates to the breeding area were highly variable; we could not detect any relationship with environmental cues during the breeding or post-breeding seasons, suggesting other factors may influence the timing of pre-breeding movements.

Migration timing and patterns

Partial migration in the Iberian Peninsula's little bustard population has previously been shown to be associated with resource depletion in the breeding sites and extreme temperatures during post-breeding (García de la Morena et al., 2015; Silva et al., 2007). We found a high degree of variability in timing of little bustards' post-breeding movements, with birds moving to the post-breeding areas between May and the end of August, with most movements occurring during June. This extended migration period has previously been associated to the different migratory strategies within the Iberian population (García de la Morena et al., 2015). Our tracked birds mainly moved north, or to coastal or higher-altitude areas. In these areas, individuals may encounter lower temperatures and higher food availability than the breeding sites during the non-breeding period (García de la Morena et al., 2015; Silva et al., 2007).

Residents, while in low numbers (only three birds, followed for four seasons in total), were detected at multiple breeding populations. Iberian little bustards were historically described as resident/sedentary birds (Cramp & Simmons, 1980), but this is now thought to be a less frequent strategy (García de la Morena et al., 2015). Most little bustards are short to medium-distance migratory birds and their behaviour is most likely a genetic trait (Villers et al., 2010), even though other non-genetic factors, such as environmental conditions and individual fitness, may influence this behaviour (Pulido, 2007). One bird in our study shifted from a migratory to resident behaviour over the course of the two years of tracking. This bird remained in its first tracked post-breeding area for the subsequent breeding and post-breeding seasons. As previously shown, species with greater variability in their migratory strategies tend to be more resilient to environmental change. Hence, partial-migration can potentially increase species resilience and adaptation to changing environments (Gilroy et al., 2016). The return dates varied greatly over a period of seven months, with birds returning to the breeding sites between the end of summer (September) and the start of the breeding season (April).

Individual migratory consistency

Like other bustard species, male little bustards show high breeding site fidelity and post-breeding site fidelity (Alonso et al., 2020; Burnside et al., 2017). If no major habitat changes occur, there is a high probability of birds using the same breeding and post-breeding sites over multiple years (García de la Morena et al., 2015) as shown by the high repeatability of distances travelled between breeding and post-breeding sites found in this study. Post-breeding sites are likely to be selected during the bird's first migratory attempt (Burnside et al., 2017). Understanding the environmental cues that influence the first migration is thus likely to be critical in determining the drivers of variation in migration distance. Juvenile tracking is, therefore, an important priority for future studies.

While most of our tracked birds showed high consistency in the distance travelled, some individuals changed post-breeding sites between years (Figure 3.2a)). We hypothesise that these differences could reflect changes in habitat between years or extreme climatic events, such as drought years, which may lead birds to relocate to areas with higher post-breeding productivity. Changes could also relate to the age of the individual, with older, more experienced birds having more consistent migratory routes (McKinnin et al., 2014; Newton, 2010; van Wijk et al., 2016). Additional multi-year tracking is needed to test these hypotheses.

The timing of migration of different migratory bird species has previously shown to be associated with climate variables measured at coarse scales, including temperature, precipitation, and wind (Haest et al., 2019). In our study, both the departure and return dates to breeding areas showed lower within- than between-individual consistency, suggesting a potential influence of environmental factors on these dates.

Departure date in relation to environmental conditions

We also found some support that males within areas with greater availability of microclimate refugia were more likely to leave their breeding grounds later, although this effect was only marginally significant. Microclimate refugia occur in areas with greater heterogeneous thermal landscapes, promoted by the existence of small patches of non-herbaceous vegetation (trees and shrubs) (Carroll et al., 2016; Ramos et al., 2023; Scheffers et al., 2014). The interaction between refugia availability and temperature, which was marginally significant ($p = 0.099$), suggested that individuals exposed to very high relative temperatures may depart from the breeding area earlier, regardless of the availability of microclimate refugia. This is possibly related to a thermal limit, above which the available microclimate refugia within the region can no longer buffer individuals against thermal stress. Nevertheless, the positive effect (although not significant) of microclimate refugia availability at medium and lower temperature exposure levels suggests the potential importance of microclimate refugia in prolonging the breeding season in this species.

Temperatures experienced by individuals, although included in the model, had no significant linear effect ($F = -0.19$) in influencing their departure date from breeding areas. However, previous studies showed that temperature can be a critical factor in movement phenology (Gordo, 2007; Tomotani et al., 2018; Zaifman et al., 2017). Additionally, little bustards are known to reduce their activity at temperatures above 25°C (Silva et al., 2015). We hypothesise that this lack of significant effect of temperature may be due to exposure to high temperatures throughout the breeding season, expected due to recent warming (see Chapter 1). Exposure to high temperatures may affect the breeding and feeding behaviour hence may not be as strongly associated with the timing of movement.

We found a positive influence of relative NDVI on post-breeding departure dates. NDVI is considered a good proxy for assessing food availability for this herbivorous species (Pettorelli et al., 2005), and food availability is known to be a key determinant of habitat quality for grassland birds (Alonso et al., 2001; Limiñana et al., 2008; Silva et al., 2007). Additionally, NDVI is correlated to precipitation and temperature (Hao et al., 2012), two climatic variables known to influence migration timings (Haest et al., 2019). In the Iberian Peninsula, NDVI peaks during April/May and decreases steeply between the end of May and June, as the ambient temperature increases (Marcelino et al., 2020). As a result, areas with higher NDVI levels later in the breeding season are likely to support breeding for a longer period of time.

Although not included in this analysis, other studies have pointed to wind as a crucial factor in determining migration timings, alongside precipitation and temperature (Haest et al., 2019). Since most individuals migrate short distances at low altitudes (Alonso et al., 2020) and have an active flapping flight, the use of wind is likely less relevant for this species, while precipitation is a rare event during Mediterranean summers.

Return date in relation to climatic conditions

Despite the high variability of return dates in our study (Figure 3.2 b) and d)), we found no relationship between return dates and any of the environmental variables considered. Although return dates range from September to April, male little bustards do not start displaying until late March/April (Mañosa et al., 2022), suggesting that factors unrelated to the timing of breeding influence the return dates. It is possible that the lack of significant relationships was due to low sample size or lack of information about other variables, such as grazing regimes, vegetation height, and land cover type, that greatly affect little bustards' post-breeding habitat selection (Santangeli et al., 2012; Silva et al., 2007). Moreover, disturbance (human and livestock) can force the birds to change areas, including returning to the breeding site earlier (Tarjuelo et al., 2015). Much attention has been given to the effects of climate change on return (pre-breeding) migration, mainly for long-distance migrants (Gallinat et al., 2015; Jenni & Kéry, 2003), and less attention is given to climatic features influencing post-breeding migration. Our findings suggest that in this species, climate variables (particularly temperature) are more important in determining the timing of departure from breeding area (autumn migration) than the return (winter/spring migration) dates.

Conservation implications

Understanding how different migratory strategies are maintained in a population is crucial, especially for declining species where the presence of diverse movement strategies can help promote resilience to environmental change (Gilroy et al., 2016). Additionally, exploring the influence that microclimate has in maintaining these strategies can be particularly relevant when designing conservation measures to enhance the availability of climate refugia across landscapes.

Microrefugia are widely recognised for potentially playing a critical role in promoting resilience to climate change, buffering individuals from detrimental environmental conditions, by providing shelter from elevated temperatures, and reducing the energetic costs of thermoregulation (du Plessis et al., 2012; Scheffers et al., 2014). Our study is the first to suggest that microclimate refugia could also extend the breeding season length in a migratory species, suggesting positive impacts on breeding success may occur, by allowing males to stay longer at the lekking areas.

Our results, therefore, potentially could have important potential implications for the design of climate-adaptive conservation measures. With increasing temperatures and lower annual precipitation (IPCC, 2017), vegetation in our study region is likely to dry sooner and faster in the future, while temperature exposure will increase. These conditions can lead male little bustards to leave the breeding site early, shortening the breeding period. Provision of habitat features that ensure microclimate refugia (i.e. shrubby herbaceous scattered patches) could increase the availability of areas where birds can thermoregulate at lower metabolic cost during the warmest hours of the day, potentially enabling them to extend their breeding season long enough to maintain viable breeding populations (Suggitt et al., 2018).

This study shows climate may play a significant role in determining the end of the breeding season of male little bustards and provides some evidence for how management can potentially extend it, by creating microclimate refugia. This would, ultimately, keep the breeding areas suitable for longer and could play an important role within vulnerable ecosystems to climate change (IPCC, 2017).

Although this study focuses on males' migratory behaviour, our findings likely extend to females, despite having a more restricted post-breeding migratory behaviour, since they singly raise the chicks and carry out late migratory movements (Silva et al., 2014b). Prolonged stays at the breeding grounds can potentially make them vulnerable to high temperatures and low food availability during the hottest period of the year. Thus, microclimate refugia can potentially, be critically important for females and chicks. Return migration occurs when birds are flocking, and the movements of tagged males are representative of the movements of many individuals. Future studies examining female migratory responses to climate are urgently needed.

Conclusion

We show that distance travelled varies little within individuals, probably due to their breeding and post-breeding site fidelity, but the timings of migratory movements can vary markedly from year to year. Departure timing from the breeding area was strongly affected by NDVI (a proxy for food availability), and potentially also by microclimate refugia availability, as this variable was included in the best model. Our findings suggest the potential importance of fine-scale habitat features that can act as microclimate refugia, in this case effectively prolonging the stay at breeding grounds in all but the hottest conditions. In our study region, microclimate refugia occur in areas with small patches of non-herbaceous vegetation (trees and shrubs) (Carroll et al., 2016; Ramos et al., 2023; Scheffers et al., 2014). Thus, while the presence of open grassland habitat is a critical requirement for little bustards, the existence of small and scattered patches of trees and shrubs may play an increasingly important role in determining habitat quality for this species in a warming world.

Acknowledgments

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Chapter 3 Supplementary Materials

Return dates distribution

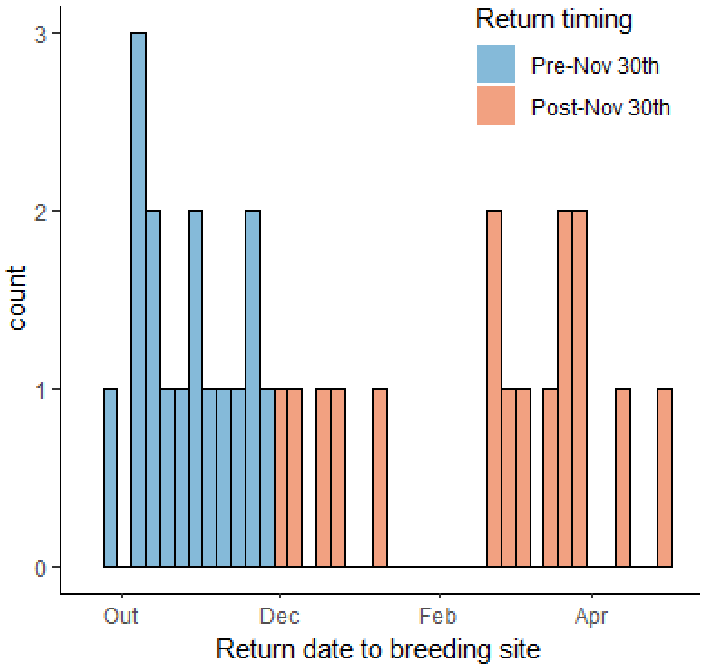

Figure S3.1 – Histogram for the return dates of little bustards to the breeding site (i.e. pre-breeding migration), colour-coded as the binary variable (pre- and post-November 30th) (García La Morena et al., 2015)

Individual migratory consistency

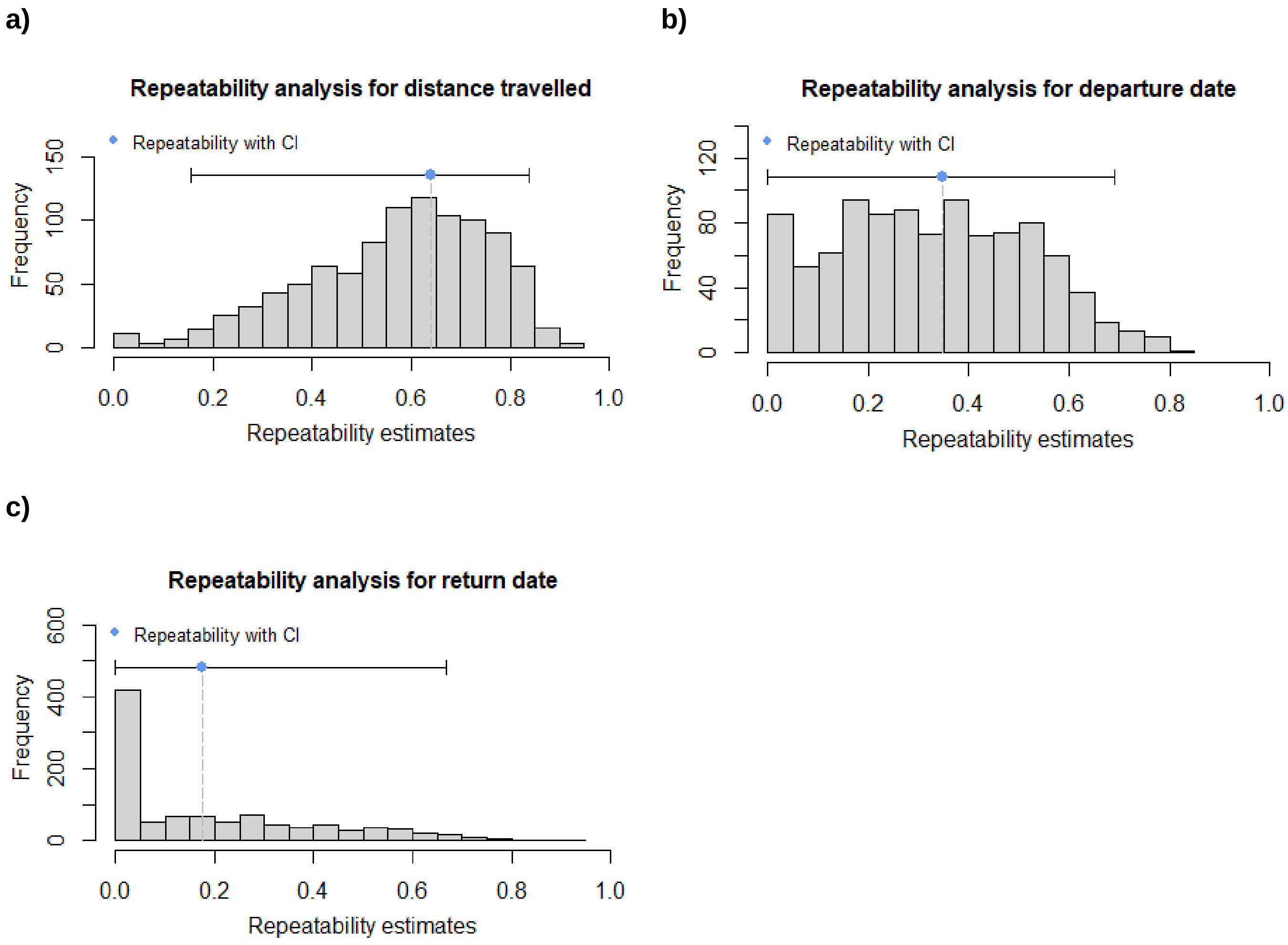

Figure S3.2 – Plots of the distribution of the parametric bootstrap samples, point estimate and the limits of the confidence interval for a) distance travelled; b) departure date and c) return date between the breeding and post-breeding areas

GLMM summary for the candidate models from MuMin for the predictors of return date

Table S3.1 - GLMM summary for the top Δ AICc < 2 predictors of return date to the breeding areas. Due to the low sample size, two distinct models were runed, using the temperature, microclimate refugia availability and NDVI conditions during the breeding season (breeding variables) and using the same variables during the post-breeding season (post-breeding variables). In all cases the null model was selected, and being the most parsimonious one, we can not explain the variables responsible for the return dates to the breeding area

Model	Variables					AICc	Δ AICc
	Intercept	*Microclimate refugia availability*	*Relative temp. exposure*	*Interaction term: microclimate refugia availability vs. relative temperature exposure*	*NDVI*		
Using breeding variables							
1	0.012					48.60	-
2	0.007				-0.623	50.46	1.86
Using post-breeding variables							
1	0.012					48.60	-
2	0.012				0.896	49.83	1.23
3	0.012		0.594			50.50	1.90

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— Chapter 4—

Microclimate refugia availability predicts migratory strategy and individual niches

In Porto, I found a new crew breaking new ground for shark conservation –
a journey where every effort counts, except liking dolphins."

Microclimate refugia availability predicts migratory strategy and individual niches

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Authors' contributions

RFR, AMAF and JPS conceived the overall study. JPS was responsible for capturing and tagging the little bustards. RFR prepared the dataset, coded the models, and analysed the data, assisted by KZ, JJG and AMAF. RFR and KZ wrote the manuscript assisted by AMAF with revisions from JPS, JJG. All authors gave final approval for publication.

Abstract

The characterisation of species' environmental niches can help predict responses to global environmental change and identify areas that change in suitability as conditions change. However, environmental niches, i.e. the full range of conditions a species experiences, have frequently been described at coarse spatial and temporal scales, not accounting for individual variability and constraints. Within species ranges and even within populations, individuals may vary in their ability to access microclimate refugia or may adopt different movement strategies to avoid exposure to unsuitable conditions. This individual variability is poorly understood but could help us understand species capacity to adjust to changes in climate.

We used an 11-year satellite tracking dataset and high-resolution remotely sensed habitat and climate information to investigate the environmental niche of the endangered little bustard (*Tetrax tetrax*) at the warm edge of its distribution, in southern Europe, during both breeding and post-breeding seasons. Our study aimed to determine if local conditions experienced by individuals during the breeding season can be used to predict different movement strategies. Furthermore, we examined if distance travelled influenced the level of dissimilarity between seasonal niches.

The environmental niche was characterized along a gradient of temperature and microclimate refugia availability. Our results revealed that individuals occupying breeding areas with low microclimate refugia availability were more likely to move longer distances after breeding. Furthermore, migratory individuals maintained similar niches across seasons, whereas resident and short-distance migrants predominantly displayed a "niche switching" strategy.

Temperature and microclimate refugia availability during the breeding season can help predict individual differences in migratory behaviour of little bustards and their niche tracking/switching behaviour. Global warming and subsequent declines in microclimate refugia availability may force this species to move earlier and longer distances after breeding. This information can help design conservation strategies resilient to climate change for little bustards and other endangered grassland bird species.

4.1 Introduction

The species' ecological niche can have multiple interconnected dimensions (Soberón, 2007), such as the dietary niche which relates to the range of food items consumed, or the environmental niche that describes the climatic and habitat conditions which the species utilizes and is able to withstand (Ingram et al., 2018). In addition to these, a myriad of biotic interactions, such as competition, predation, or prey and food item availability, limit species distributions to a fraction of the fundamental niche - the realised niche (Hutchinson, 1978). While the species niche describes the range of conditions where a species can occur, the extent of any given niche dimension may vary between individuals and across populations due to individual variability in physiological, biological and behavioural traits (Soberón, 2007). Some individuals may be niche specialists, having a narrow niche relative to their population or species, while others may be generalists with relatively broad niches (Bolnick et al., 2003). The occurrence of both specialized and generalist individuals within populations is a source of species diversity (Araújo et al., 2011; Carlson et al., 2021) that confers an evolutionary advantage since such species may be better able to adjust to environmental changes (Bolnick et al., 2007). Understanding the underlying factors limiting individual variability can aid the design of target conservation measures aiming to help species adapt to the current fast rate of environmental change.

Species and individual niches may also vary throughout the annual cycle induced by seasonal differences in environmental conditions (Cohen & Jetz, 2023; Winger et al., 2018), especially at higher latitudes. Through migration, individuals can either maintain their environmental niche throughout the year, by moving between areas with similar environmental characteristics, a phenomenon referred to as "niche tracking" (Gomez et al., 2016), or undergo a complete niche change, known as "niche switching" (Ponti et al., 2020). These seasonal niches play a crucial role in individual fitness and survival, with the breeding season often being the most critical period (Harrison et al., 2011) when individuals may require access to specific habitats, food resources or social conditions (Ponti et al., 2020). In the post-breeding period individuals can be more mobile, utilizing different combinations of environmental conditions, and therefore have broader niches (Suárez-Seoane et al., 2008). The movement strategies that enable niche tracking or switching can also vary between individuals within populations and species (Fandos et al., 2020; Illán et al., 2022).

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

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

In this study, we analyse movement data from 47 little bustards (*Tetrax tetrax*), satellite tracked over 11 years, in five southern European breeding populations and characterise individual and population environmental niches across the breeding and post-breeding seasons. We also determine the micro-scale environmental factors (e.g. temperature, microclimate refugia and food availability) that may influence individual migratory distances and subsequent niche switching/tracking strategies for this partially migratory species.

4.2 Methods

Study site and target species

The Iberian Peninsula is simultaneously a global biodiversity hotspot and one of the world's most vulnerable regions to climate change (Pörtner et al., 2022). The region is expected to suffer from extensive warming and increasing drought frequency in the near future (Jones et al., 2020), which is expected to cause habitat changes, species range contractions or even (local) extinctions

(Pörtner et al., 2022). Conditions are particularly rough in flat and open areas with low vegetation cover, such as semi-natural grasslands, where species are exposed to high temperatures throughout the year. Within the Iberian Peninsula, semi-natural grasslands are one of the most climate change sensitive habitats, due to their ecological characteristics and dependency on human management through agricultural activities and livestock grazing (Emanuelsson, 2008).

Semi-natural grasslands in Iberia are crucial for grassland birds, including several endangered species that use this habitat mainly during the breeding period. Among those species, the little bustard, *Tetrax tetrax* (Linnaeus, 1758), is a medium-sized grassland specialist bird classified as 'Near Threatened' (BirdLife International, 2021). Recent studies indicate a severe decline in little bustard breeding numbers in the Iberian Peninsula (Silva et al., 2024), which used to be a stronghold of this species' western distribution (García de la Morena, 2018; Silva et al., 2018). The main Iberian breeding populations are predominantly concentrated in the Extremadura, Castilla La Mancha (Spain), and Alentejo (Portugal) regions (Equipa Atlas, 2008; García de la Morena et al., 2018), all of which are affected by elevated temperatures and vulnerable to climate change (Pörtner et al., 2022; Ramos et al., 2023a).

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

Previous studies, at a relatively coarse scale, described the little bustard's niche emphasising the importance of temperature range and annual rainfall (Delgado et al., 2011; Suárez-Seoane et al., 2008). Moreover, this species is known to decrease their activity patterns at temperatures above 25°C (Silva et al., 2015) and to search for microclimate refugia sites during the warmer parts of the year (Ramos et al., 2023a).

Tracking and location data

Between 2009 and 2019, 47 male little bustards were captured and tagged in five distinct breeding areas across the southwest Iberian Peninsula, in Alentejo (Portugal) and Extremadura (Spain) during the breeding season (April and May). Breeding males were attracted by a stuffed female acting as a decoy and trapped with snares (Ponjoan et al., 2010; Ramos et al., 2023a). GPS tracking devices varying between 2% and 4% ($\bar{x}$ = 3.2%) of the birds' mass (Kenward, 2000), were deployed using a thoracic harness made of Ribbon Teflon with a weak link to avoid lifelong deployment. Two types of Solar GPS devices were used. Platform Transmitter Terminal (Solar Argos/GPS 30g PTT – Microwave Telemetry) devices were deployed on 19 birds between 2009 and 2011, and Global System for Mobile Communications (GSM) devices (Flyway 38g – Movetech Telemetry) were deployed on 28 birds between 2014 and 2019. Transmitters were programmed to record a GPS position every 2 hours (PTT) or 10 to 30 minutes (GSM).

Bird trapping and the deployment of GPS devices were approved by the 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.

We only included in the analysis birds captured before the 1st of May, and with at least seven days of data prior to the departure from the breeding areas. This threshold was defined to reduce the influence of the tagging date, which can vary greatly between individuals, and influence the characterisation of the breeding season. Subsequently, the departure from the breeding area was identified for each bird, movement to non-breeding areas was considered to occur if individuals did not return to the breeding area for a minimum period of 30 days. Birds that extended their usage of the breeding area during the whole year were considered residents, since they used the breeding area after the breeding season was over (i.e., in June/July) (Jiguet & Bretagnolle, 2001).

We defined the breeding season as the period between the 1st of May and the date of departure from the breeding area, and the post-breeding season as the period between the 15th of July (or the exact individual arrival date at the post-breeding area, if later) and the 15th of September. The post-breeding period corresponds to the hottest period of the year when exposure to extreme heat is highest and food shortages occur (Silva et al., 2007). There was no overlap between breeding and post-breeding periods across all birds.

Environmental data

We collected micro-scale environmental data for all little bustard GPS locations. Hourly temperatures were extracted using the *microclima* (Maclean et al., 2019) and *NicheMapR* (Kearney & Porter, 2017) packages in R version 4.1.0 software (R Core Team, 2016). Each little bustard GPS location was then associated with the corresponding hourly temperatures modelled at a 30 x 30m resolution at 20cm above ground (Ramos et al., 2023a). Furthermore, we calculated various temperature metrics, including the minimum, maximum, mean, median, and standard deviation, within a 500m buffer surrounding each GPS location data. Subsequently, we assessed the temperature difference between GPS location and the corresponding median of the buffer, as well as the difference between the minimum temperatures and the median within the buffer. These two variables enabled us to determine use and availability of microclimate refugia, respectively (Ramos et al., 2023a):

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

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

Negative values of both variables indicate microclimate refugia use and availability, since it translates in point temperatures cooler that the median of the buffer (Ramos et al., 2023a).

Normalized Difference Vegetation Index (NDVI) information was extracted for all little bustard GPS locations from MODIS satellite at a 250 m resolution and 8-day interval, using the Google Earth Engine (Didan, 2015; Gorelick et al., 2017; Figure 4.1c) and d)). We evaluated the information retrieved to ensure all images had good enough quality to be used in the study (Didan, 2015). Satellite-derived NDVI is a measure of vegetation greenness and biomass, used widely to examine patterns of vegetation productivity and biodiversity distribution at large spatial and temporal scales (Pettorelli et al., 2005). As little bustards feed mainly on green plants, NDVI is broadly used as predictor of food availability (Pettorelli et al., 2005). Moreover, precipitation acts as a stimulus for vegetation growth, and therefore is highly correlated with NDVI (Li et al., 2019; Schultz & Halpert, 1993). Thus, NDVI is both a good indicator of precipitation patterns in the previous months and a proxy of food availability, which is a key determinant of little bustard movements and space use (Pettorelli et al., 2005; Ramos et al., 2023b).

Temperatures above 25°C are known to significantly reduce little bustards' activity (Silva et al., 2015) and may influence the timing of movement (Ramos et al., 2023b). The proportion of locations collected when temperatures exceeded this threshold varied greatly during the breeding periods across the five-breeding populations and ranged between 30.5% in Llanos de Caceres and 55.3% in Castro Verde (Figure 4.1a)). During the post-breeding period, this proportion increased in all sites with temperatures reaching above 25°C at more than 50% of the sites, and the greatest differences in this proportion between seasons being in Llanos de Caceres, Merida and Vila Fernando (Figure 4.1b)).

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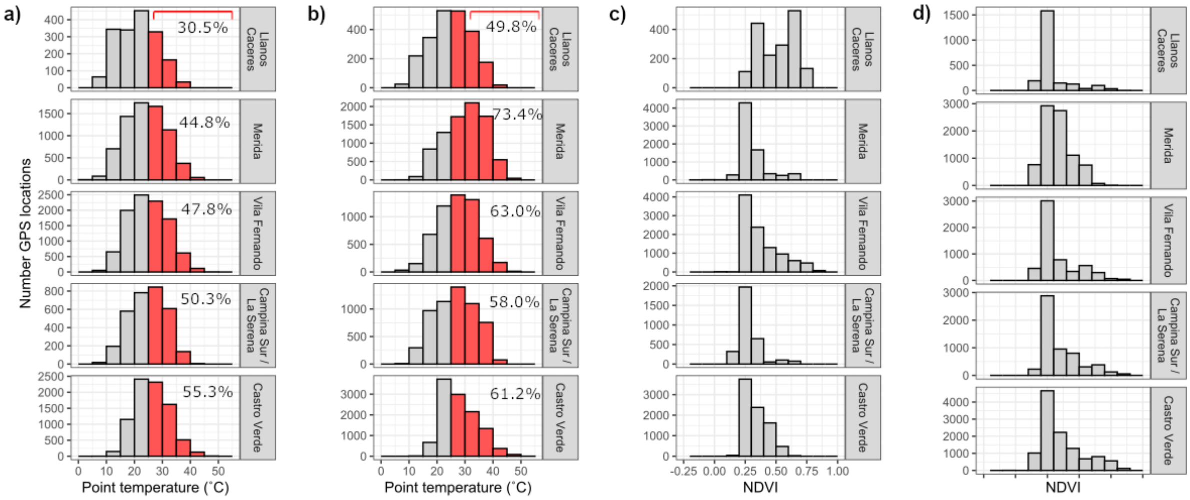

Figure 4.1 – The distribution of the micro-scale (30m) temperatures at the GPS locations obtained in each population for the a) breeding and b) post-breeding periods, showing temperature above (red) and bellow (grey) 25°C; NDVI values at GPS locations for c) breeding and d) post-breeding populations.

Micro-climate and environmental niche

The fine-scale environmental niche used by little bustard was characterised with the Principal Component Analysis (PCA-occ) outlined by Broennimann et al. (2012). This method transforms the correlated environmental variables into independent principal components, generating a multi-dimensional shape, representing the environmental niche. The number of dimensions considered was determined by the number of principal components cumulatively explaining over 70% of the variance within the initial dataset. The PCA-occ was calculated using the *ade4* package (Dray & Dufour, 2007) and the *ecospat* (Broennimann et al., 2014) R packages with the environmental variables outline above for all little bustard's GPS location data included in this study.

The environmental space utilized by little bustards in different parts of the range and annual cycle, as well as differences among individuals, was determined using the 99.5% kernel (to eliminate outliers) and the package *adehabitatHR* (Calenge, 2006). The PCA scores were extracted for each individual, population, and season. We then carried out a kernel overlap analysis comparing individuals, populations, and seasons, using QGIS version 3.10 (QGIS, 2022). Finally, we determined, for each individual, the percentage of the fine-scale used environmental niche occupied per season, for each given year.

Statistical analysis

The coordinates of the daily centroid were calculated for each bird, across the breeding and the post-breeding seasons, using QGIS version 3.10 (QGIS, 2022). The distance travelled to the post-breeding areas was calculated as the Euclidean distance between the breeding centroid and the consecutive daily centroids until the arrival date at the post-breeding area (Ramos et al., 2023b). The dissimilarity value between breeding and post-breeding used environmental niche was given by the distance, in the PCA matrix, between the breeding and post-breeding centroids, for each individual.

We fitted two Linear Mixed-effects Models (LMM) using the *lme4* package (Bates et al., 2015), the first to analyse the influence of the individual breeding niche on the distance travelled and the second to examine the effect of individual used niche, as well as, the distance travelled on the dissimilarity between seasonal niches. In both models, we used the year and the breeding population as random factors. The individual used environmental niche was included in the models either as scores along each of the PCA axis considered or as the percentage of each individual used niche. Since little bustard age is difficult to estimate, for birds with multiple years of data, we only included the latest year in the model. Adult birds tend to have a strong site fidelity in both breeding and post-breeding seasons (Alonso et al., 2020; García de La Morena et al., 2015), which can be derived from a learning process while they are immature birds, as documented in other bustard species (Burnside et al., 2017; Newton, 2010), hence, by using the most recent year of data, we maximize the chance of representing individual's migratory decisions during adulthood.

4.3 Results

During the 11-year study, we captured and deployed GPS tracking devices on 47 male little bustards in five different populations. We collected more than 30,000 GPS locations in both breeding and post-breeding seasons, which we used to build the fine scale used environmental niche. The little bustards used areas at breeding sites varied between 36,123 ha, in Vila Fernando and 162,547 ha, in Merida (Figure 4.2, Table 4.1). The distance travelled to the post-breeding sites varied greatly between individuals, with movements ranging from 1 to 421km (median = 36km) and with some birds using more than one post-breeding area (Figure 4.2).

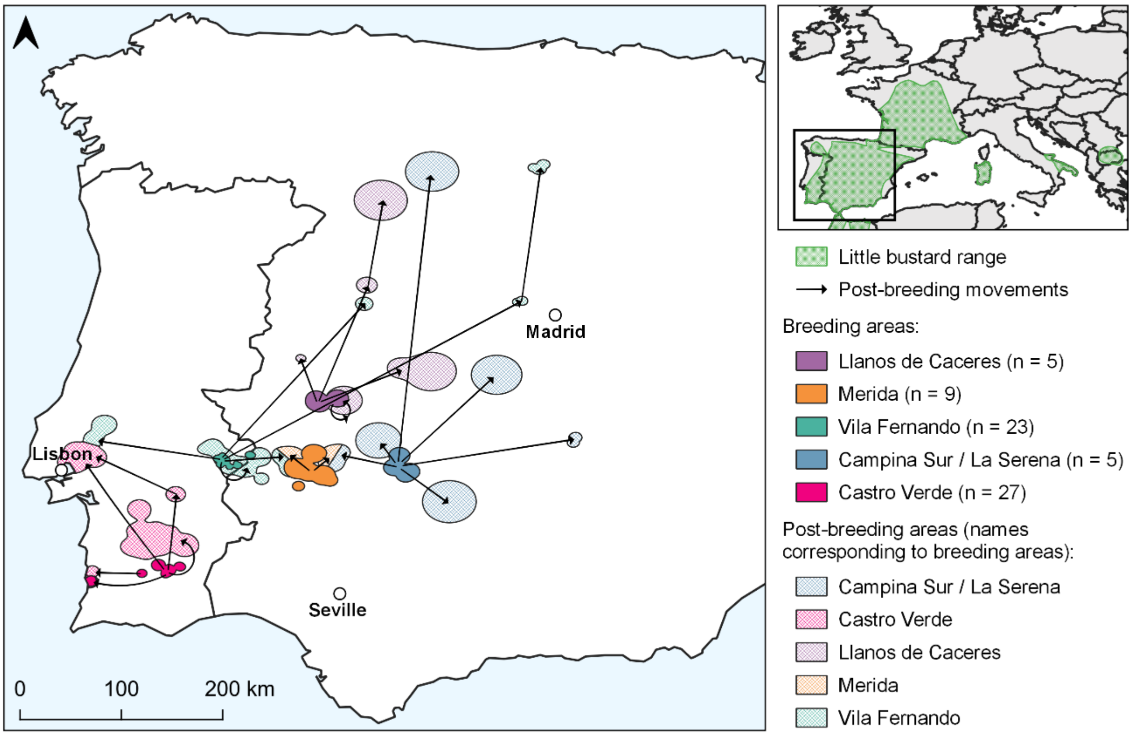

Figure 4.2 - Migratory movements of 47 male little bustards from breeding (full) to post-breeding (transparent) areas in the Iberian Peninsula obtained from GPS tracking data. Each breeding population is represented in a different colour. The arrows represent the movements to post-breeding areas. The little bustard's range (BirdLife International, 2021) is represented in green in the inset map.

Fine-scale used environmental niche

The little bustard environmental niche was defined by the first two PCA axes, capturing 76.59% of the variation in the environmental data (58.09% within the first and 18.50% within the second component, Figure 4.3a)). The first axis was strongly and positively associated with temperature (point temperature, mean temperature, median temperature, minimum temperature, and maximum temperature). The variance along the second axis reflected the microclimate refugia availability, with a strong positive value associated with the temperature standard deviation and a negative association with the positive values of the difference between minimum and median temperatures (reflecting microclimate refugia availability associated with the positive side of the second axis; Figure S4.1).

The breeding season niche represented 85.34% of the total fine scale used environmental niche, while post-breeding represented 90.93% (Figure 4.3b). The post-breeding niche overlapped in 89.39% with the breeding niche (Figure 4.3b)). In relation to breeding, during the post-breeding season there was a shift towards hotter niches with more microclimate refugia availability.

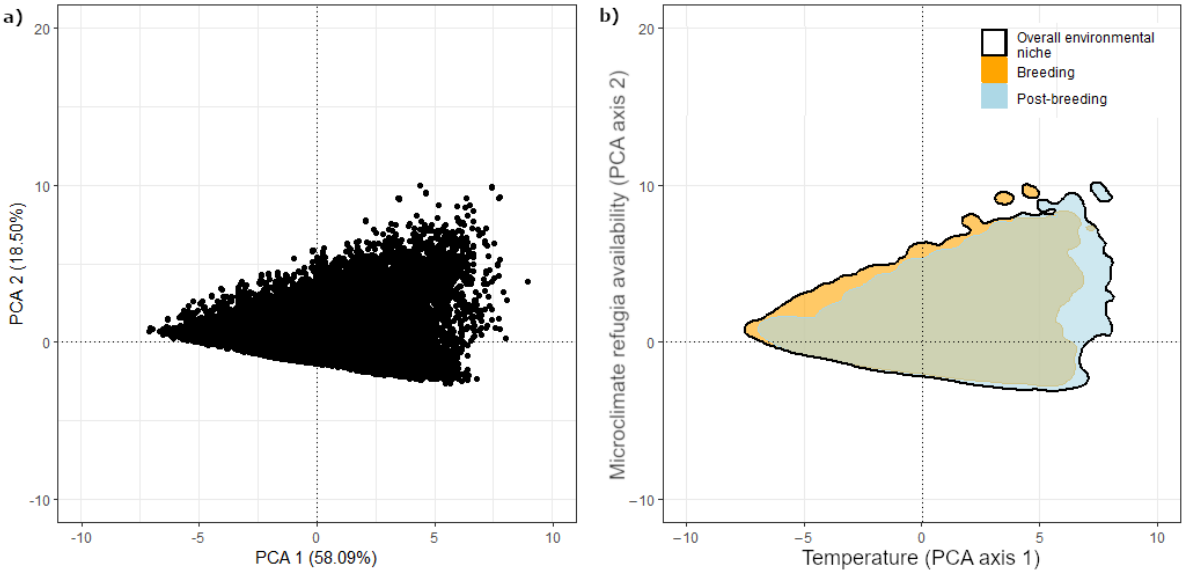

Figure 4.3 – a) Environmental experienced niche of the little bustard based on occurrences in Iberian Peninsula; b) Environmental experienced niche in each season, breeding (orange) and post-breeding (blue)

Out of the five breeding areas (Figure 4.2), three had a breeding niche smaller than 50% of the overall used niche (Campina Sur / La Serena, Castro Verde and Llanos de Caceres) (Table 4.1, Figure S4.3). The two other breeding population (Merida and Vila Fernando) had a wide breeding niche, representing more than 95% of the season's used niche (Table 4.1, Figure 4.3). Some populations had a relatively small number of tracked individuals and such a low sample size could be insufficient to adequately represent the entire breeding population's niche size. To test whether this is the case, we randomly selected five individuals from populations with larger sample sizes (Merida, Vila Fernando and Castro Verde) and repeated the analyses to produce the breeding niche using just these five individuals. We did not find any major differences in the breeding population niche sizes when using five random individuals only compared to including all individuals, suggesting that five tracked individuals per population provide a representable sample of the breeding population (detailed results presented in Figure S4.4).

Table 4.1 - General spatial (used areas, number of individuals per year, and GPS locations) and fine scale used environmental niche (breeding and post-breeding seasons overlap) information for each breeding population. [a] Numbers in relation to the overall breeding season niche. [b] Percentage of overlap with the season's overall used niche.

Capture site	**Breeding used area** (ha)	**Num. ind./year**[a]	**Num. GPS locations**[a]	**Breeding season overlap**[b]	**Post-breeding season overlap**[b]
Llanos de Caceres	77,846	5	1,728	39.94	37.91
Merida	162,547	9	7,197	98.08	96.68
Vila Fernando	36,123	23	9,931	99.05	93.98
Campina Sur / La Serena	91,923	5	3,170	48.60	38.20
Castro Verde	57,996	27	8,296	46.67	78.88

For most breeding populations, the used niche remained similar throughout the year, despite the post-breeding movements performed by the individuals (Figure 4.4). The majority of populations maintained a similar percentage of niche occupied in relation to the season's used niche, except Castro Verde, for which the environmental used niche increased from 46.67% in the breeding to 78.88% in the post-breeding season (Table 4.1, Figure S4.3), with the expansion being toward areas with more microclimate refugia availability (Figure 4.4b)).

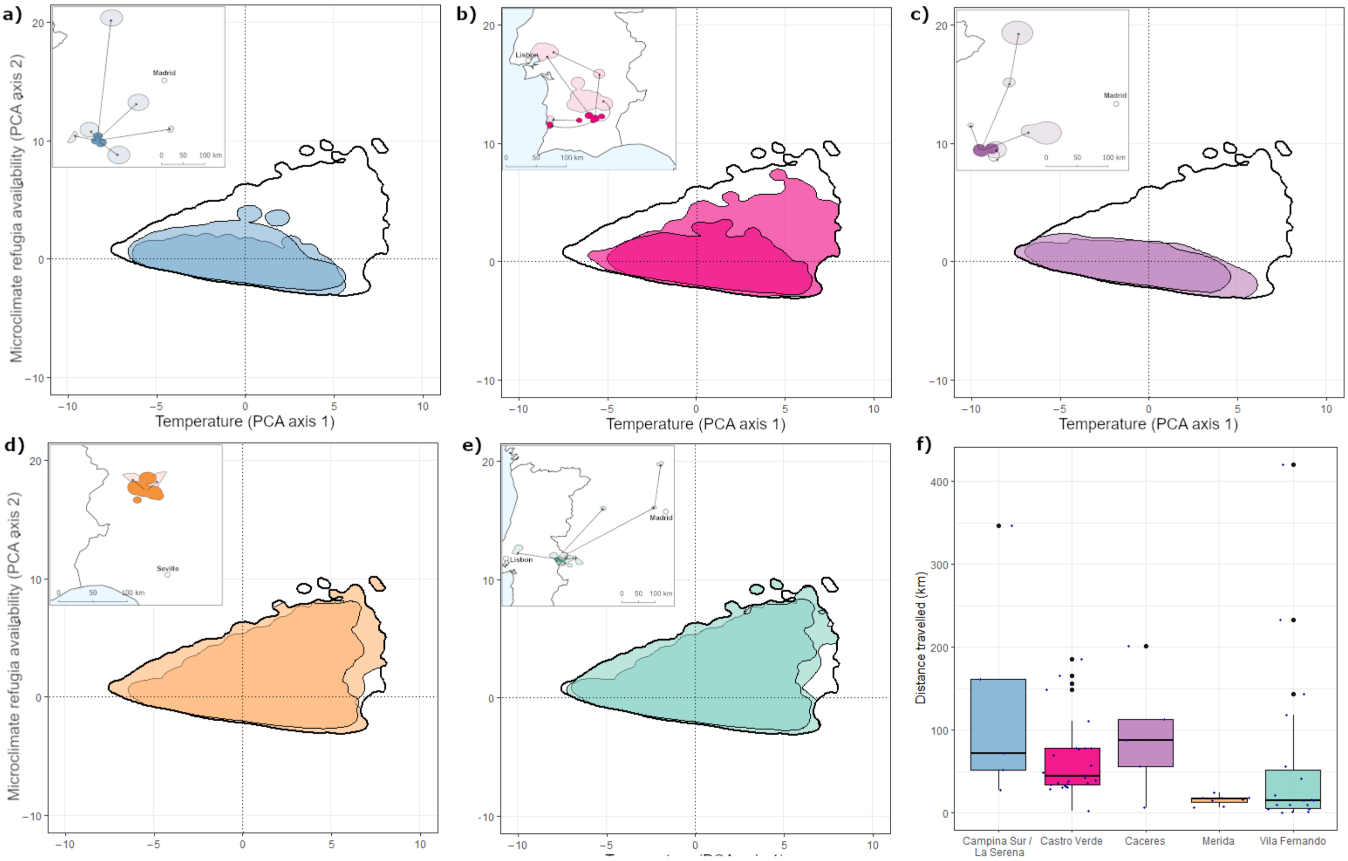

Figure 4.4 - Breeding and post-breeding used environmental niche for each breeding population with information of the post-breeding movements (inset map), and the distances travelled (f). From top left to bottom right: Campina Sur / La Serena, Castro Verde, Llanos de Caceres, Merida, and Vila Fernando.

Distance travelled and niche dissimilarity in relation to the breeding environmental niche characteristics

Distance travelled was negatively associated with microclimate refugia availability (the PC2; F = -0.723, p < 0.001), while there was no significant association with temperature (PC1; F = -0.276, p = 0.1; Figure 4.5, Table S4.1). Dissimilarity between seasons was higher as the distance travelled in the post-breeding migration decreased (F = -44.511, p = 0.025) (Figure 4.6).

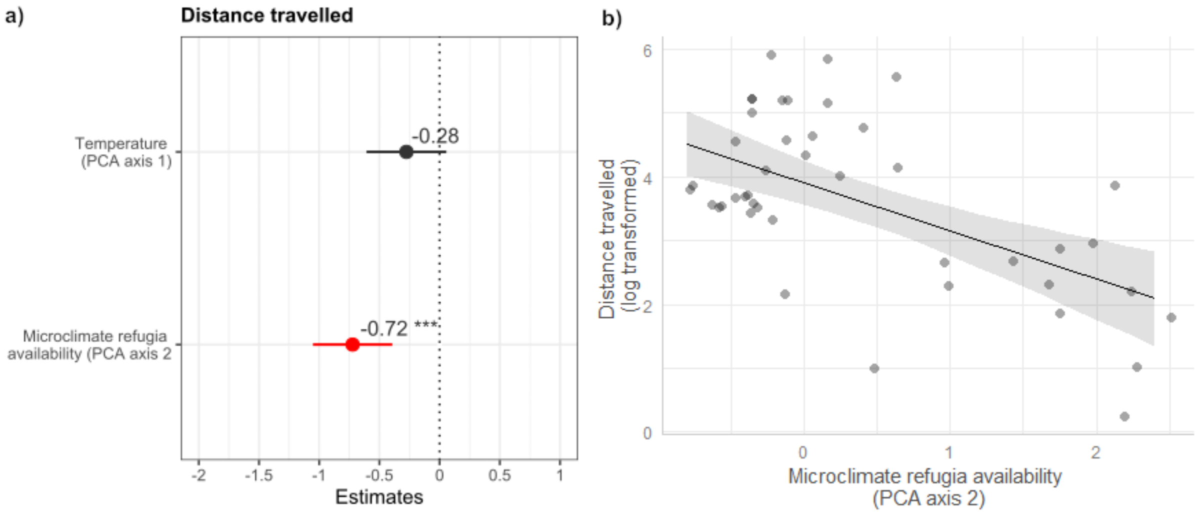

Figure 4.5 - Coefficient estimates from LMM explaining the a) individual migratory distance travelled using environmental niche dimensions (temperature and microclimate refugia availability and b) the distance travelled in the post-breeding migration in relation to microclimate refugia availability (PC2).

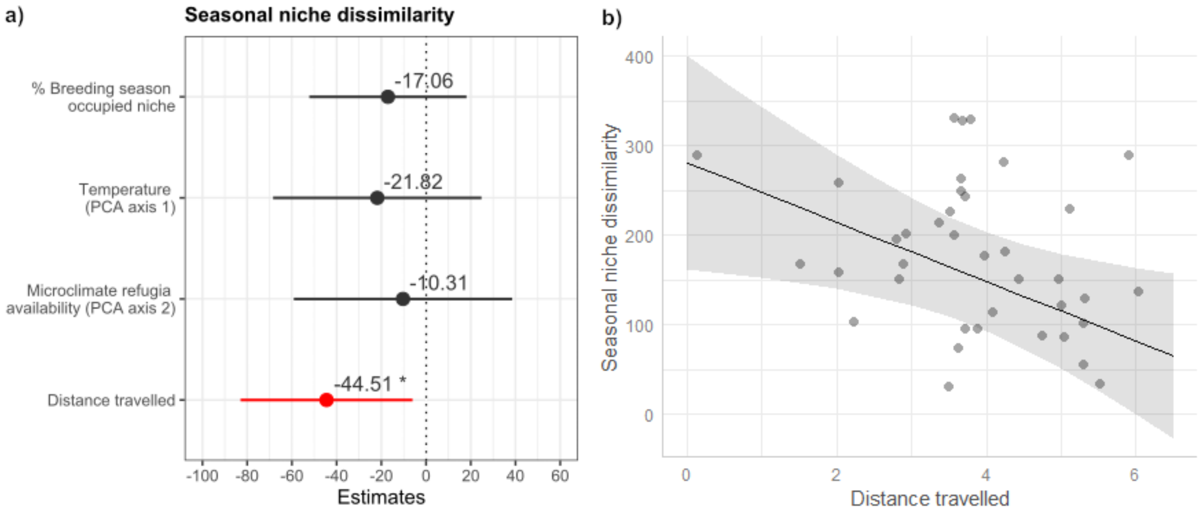

Figure 4.6 - a) Coefficient estimates from LMM for the effect of niche characteristics and migratory distance travelled on the dissimilarity between the seasonal niches. Covariate significance is shown: *** $p < 0.01$; * $0.01 < p < 0.05$; none/otherwise, $p > 0.05$. b) Dissimilarity between the seasonal niches in relation to the distance travelled in the post-breeding migration.

4.4 Discussion

Our study, utilizing a robust dataset of 11 years of tracking data with more than 30,000 GPS locations, primarily focused in understanding of the environmental niche of an endangered grassland bird specialist. We found that the little bustard environmental niche within the Iberian Peninsula is defined by gradients of temperature and microclimate refugia availability. Moreover, while there was a significant overlap of the seasonal niches at the species level, some differences in the extent of seasonal niche overlap were detected across populations. At the individual level, we observed a negative relationship between migratory strategy and microclimate refugia availability during the breeding season, whereby individuals with less refugia available within their breeding sites tend to move longer distances. Additionally, migratory strategy was also negatively related to niche dissimilarity between seasons, as birds that performed longer movements maintained a similar fine-scale used environmental niche between the breeding and post-breeding seasons.

Our study highlights temperature as the most important environmental variable in defining the niche of the little bustard, explaining more than half of the variation within the data. This finding is consistent with previous studies that have identified temperature as a critical factor in determining the macro-scale environmental niches of species, including that of the little bustard (Delgado et al., 2011; Fandos & Telleria, 2020; Ponti et al., 2020). Temperature is a well-known driver and limiting factor at both species- and individual-levels, frequently shown to have direct effects on individuals through thermal stress, as well as affecting them indirectly, by reducing food availability (Breed et al., 2013; Chen et al., 2011; Hao et al., 2012; Rastogi, 2007). Furthermore, extreme temperatures have also been linked to changes in individual breeding and migratory behaviour (Tomotani et al., 2018).

Microclimate refugia was the second most important variable defining the environmental niche. Although little bustards occasionally use microclimate refugia (Ramos et al., 2023a), these areas may become crucial during the post-breeding season when temperatures increase, and food becomes scarce (Silva et al., 2007). Areas of microclimate refugia availability can provide necessary shelter from high temperatures for both little bustards, as well as for arthropods, which can be a food source for the species, especially in drier habitats (González del Portillo et al., 2021; Jiguet, 2002; Suggitt et al., 2018). Given that little bustards show reduced activity levels when temperatures are above 25°C and can experience temperatures of up to 40°C during the post-breeding season in the Iberian Peninsula (Ramos et al., 2023a; Silva et al., 2015), it is unsurprising that microclimate refugia, along with temperature, are crucial in defining the fine-scale environmental niche of the species.

The importance of NDVI in the niche definition of migratory species has been highlighted in previous studies (Fandos et al., 2020; Somveille et al., 2019), and it has also been identified as the main determinant of little bustards' post-breeding migratory timings (Ramos et al., 2023b). In this study, NDVI had a relatively low contribution, being associated to the first principal component only (Figure S4.1 and Figure S4.2). NDVI may be particularly relevant during the post-breeding season, which is known to be a period of food shortage (Silva et al., 2015; Somveille et al., 2019).

Hence, we may have not observed this effect here as the post-breeding season represents only half of the study dataset. Moreover, during the breeding season, male little bustards can complement their plant-based diet with large carabids and beetles (Suarez-Seoane et al., 2008), which may help explain the low importance of NDVI in the PCA environmental space.

The individual and population environmental niches varied mainly in the second PCA axis, that relates with microclimate refugia availability. Microclimate refugia were relatively limited for three breeding populations (Castro Verde, Caceres and Campina Sur/La Serena), particularly during the breeding season, a trend that continued into the post-breeding season for Caceres and Campina Sur/La Serena populations. Furthermore, the breeding population of Castro Verde extended the environmental niche towards areas with more microclimate refugia availability in the post-breeding season, suggesting a niche-switching strategy (Martínez-Meyer et al., 2004; Nakazawa et al., 2004). On the other hand, both the Merida and Vila Fernando populations had broad environmental niches with relatively more microclimate refugia available throughout the year, and individuals from these breeding populations performed, on average, the shortest post-breeding movements (Figure 4.4f)). During the breeding season, male little bustards are more restricted to lekking areas, which are characterized by open sites that allow birds to be seen by conspecifics but also expose them to elevated temperatures (Silva et al., 2015; Silva et al., 2017). Castro Verde is one of the warmest areas within the little bustard's range in the Iberian Peninsula and has had the highest temperature anomaly, reaching 2°C during the breeding season, over the past 30 years (Ramos et al., 2023a). Hence, individuals from this breeding population may shift their seasonal niches to include greater refugia availability, as this shelter from the extreme heat within the area may be necessary to maintain fitness and for their survival. As for little bustards from Merida and Vila Fernando, since their breeding niche is broad enough in both PCA axis (temperature and microclimate refugia availability), it may allow them to cope with increasing temperatures throughout summer (the post-breeding season), and thus, individuals have in general a niche tracking strategy remaining closer to their breeding areas.

The availability of microclimate refugia during the breeding season was negatively associated with the migratory strategy of male little bustards, with longer distance migrants encountering less microclimate refugia availability. Migration can have a potentially detrimental effect on fitness due to the high energetic cost and the hazards involved (Dingle, 2014; Wikelski et al., 2003), which needs to be balanced with the benefits of higher food availability and better environmental conditions at new sites (Fandos & Telleria, 2020; Somveille et al., 2019). Although microclimate refugia availability is dynamic over time, areas with low availability during the breeding season are likely to remain so during post-breeding and may also be exposed to higher temperatures (Ramos et al., 2023a). Therefore, migration may be the most advantageous strategy for birds experiencing low microclimate refugia availability during their breeding season, as it may enable them to switch niches.

Similarly, migratory behaviour was also a predictor of seasonal dissimilarity in the used environmental niche. While previous studies have focused on niche dissimilarity at the species level by comparing long-distance migrants to resident birds (Cohen & Jetz, 2023; Gomez et al., 2016; Ponti et al., 2020), this study analysed the distance travelled across a gradient of resident, short-, medium-, and long-distance migrants to show a diversity of niche switching and tracking strategies within and across populations (Somveille et al., 2019). Individuals that travel longer distances are usually niche trackers, a behaviour already documented at the species level for multiple species (Fandos & Tellería, 2020; Somveille et al., 2019). Short-distance migrants and residents, being mostly niche switchers, can be exposed to harsh conditions during the warmest period of the year, the post-breeding season (Fandos & Tellería, 2020). Thus, remaining stationary requires a higher tolerance to sub-optimal conditions and may involve behavioural and physiological changes to cope with unfavourable conditions (Cohen & Jetz, 2023). Nonetheless, these are also the individuals with higher microclimate refugia availability during the breeding season and may use their micro-scale environment more efficiently than birds with less microclimate refugia available. Moreover, remaining closer to the breeding sites can be advantageous, as it removes the additional physiological strain of movement which could otherwise have a negative effect on individual fitness during the subsequent breeding season.

While little bustards exhibit high site fidelity during both breeding and post-breeding seasons, and migratory behaviour is likely a genetic trait (Alonso et al., 2020; Burnside et al., 2017; Villers et al., 2010), in partially migratory species migration is known to be plastic (Pulido, 2007; Salewski & Bruderer, 2007). As such, individuals may adapt their migratory strategy to continue tracking their environmental niche or adjust it in response to environmental shifts between the breeding and post-breeding seasons, which may enable behavioural responses to climatic variability and help little bustards adapt to ongoing climate change.

Our results suggest that migratory distance can determine whether individuals track or switch environmental niches with longer distance migrants being mostly niche trackers, while residents and short distance migrants usually switching their niches. However, other factors such as niche breadth or breeding latitude are known to influence seasonal niche strategy at the species level (Gomez et al., 2016) and should be considered in future studies. We demonstrated that temperature is the main factor influencing the fine scale used environmental niche of male little bustards. Complementary to this, we found that microclimate refugia availability, particularly during the breeding season, plays a key role in driving niche switching and can help predict individual movement strategies, which to our knowledge, has not been demonstrated before.

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Chapter 4 Supplementary Materials

Little bustard environmental niche characterization

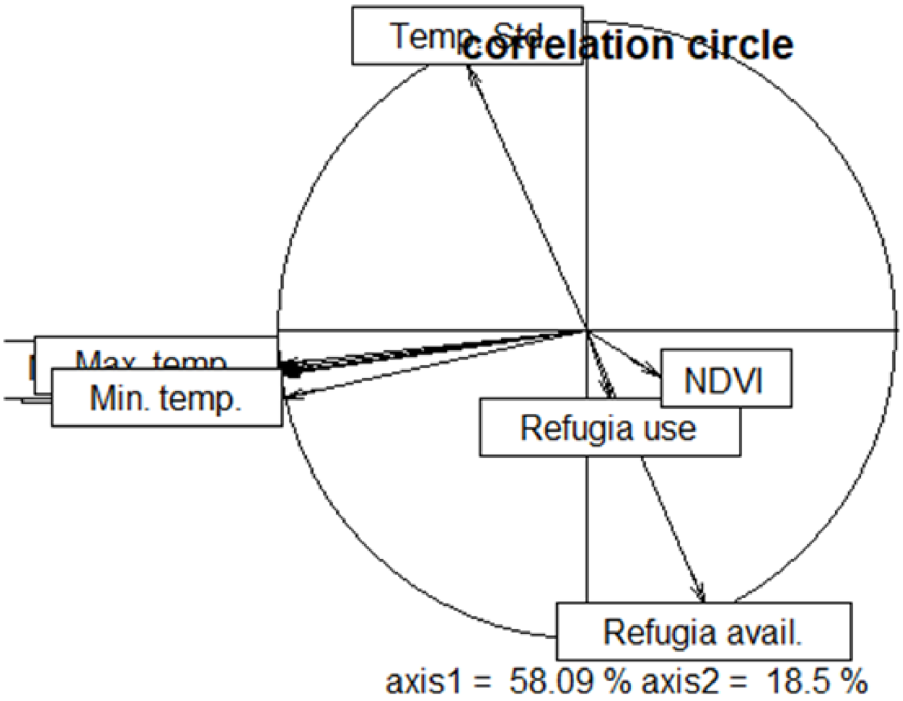

Figure S4.1 – Correlation circle showing the contribution of the different variables to the two main axis of the PCA, which describe the little bustard's environmental niche

Where negative values of Refugia Use and Refugia Availability variables indicate microclimate refugia use and availability, since it translates in point temperatures cooler that the median of the buffer (Ramos et al., 2023a). Hence, the positive side of Axis 2 represent areas of refugia use and refugia availability, and with higher temperature standard deviation within the buffer.

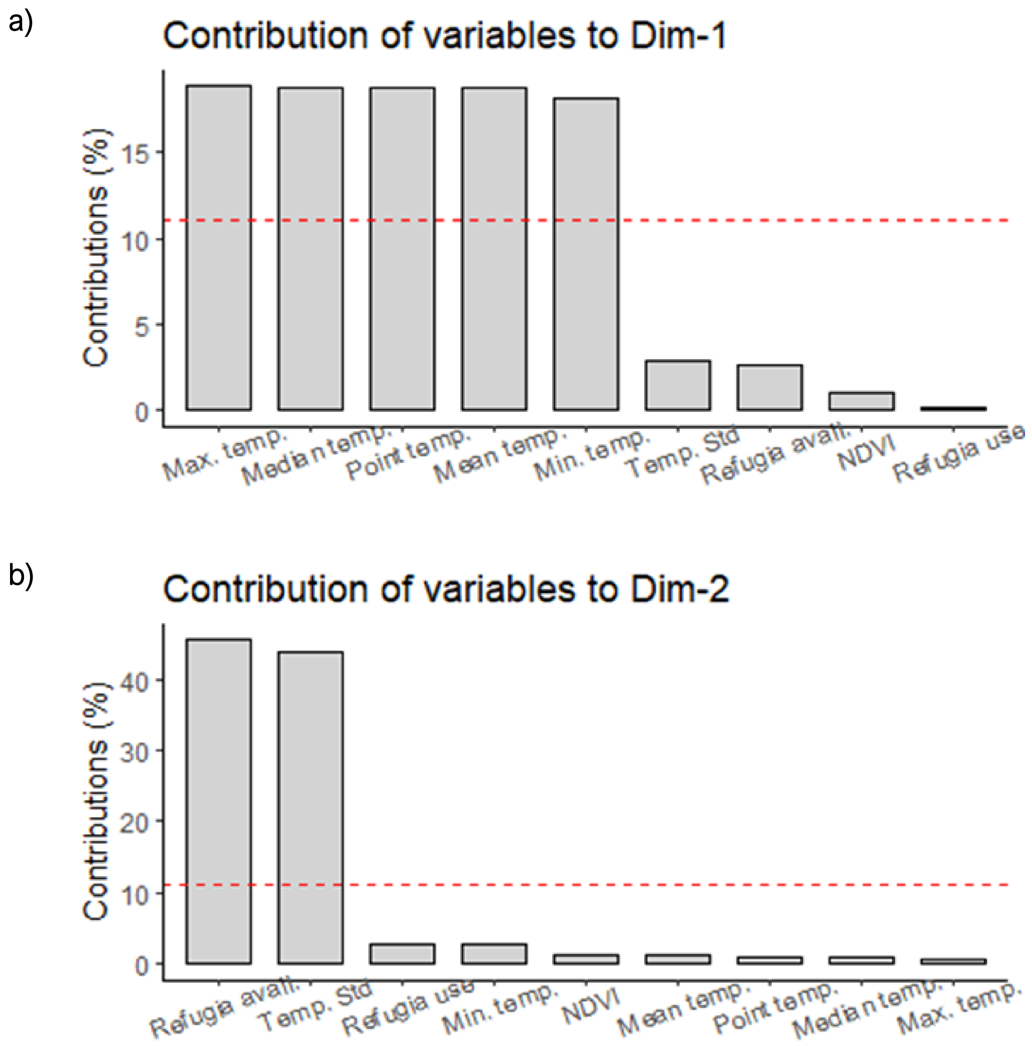

Figure S4.2 – PCA-env results a) Individual contribution of each environmental variable to the first PCA axis. b) Individual contribution of each environmental variable to the second PCA axis.

Environmental experienced niche for the five breeding areas

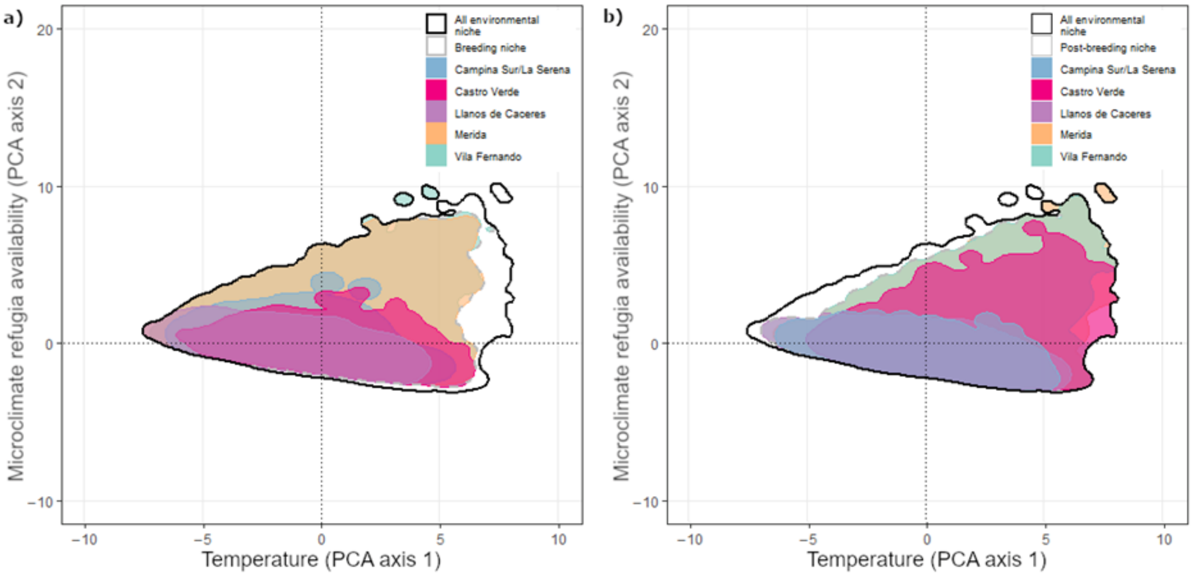

Figure S4.3 – Environmental experienced niche of each breeding population during a) breeding and b) post-breeding seasons

Test of breeding population niche size based on number of individuals

Two of the five breeding populations have few individuals tagged. Nonetheless, the breeding used area of those two populations were the second and third biggest areas. However, the fact that the breeding niche was smaller than 50% of the overall used niche raised the question if such small sample size would be representative of the population.

To address that question we used the breeding populations with more individuals (Castro Verde: 26 individuals, Vila Fernando: 23 individuals and Merida: 9 individuals) and calculated the seasonal niche size based in a random combination of five individuals (out of the total per breeding site). We run this analysis for all possible combinations of 5 individuals within each breeding populations for each season, up to a maximum of 10.000 combinations, due to memory and processing limitations.

The results obtained are presented in Figure S4.4, where the dark blue rhombuses represent the seasonal niche size obtained running the analysis for all the individuals in each population. Since the rhombuses are within the boxplot ranges in the upper quadrant, we do not expect that the results obtained for the two smaller populations (Llanos de Caceres and Campina Sur/La Serena) are underrepresented.

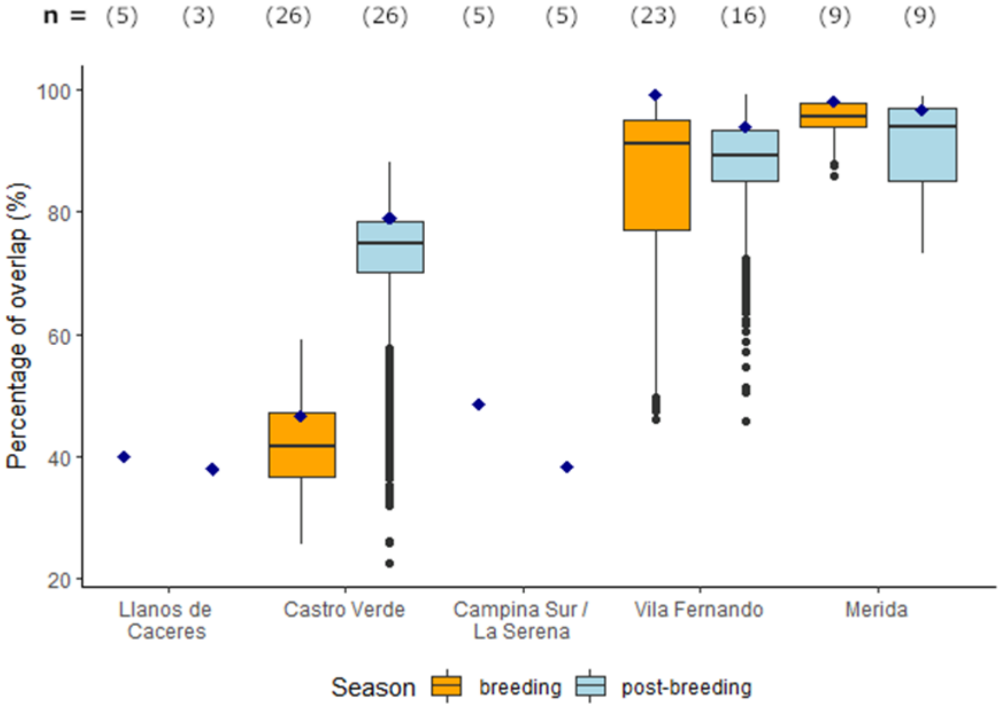

Figure S4.4 – Variation of seasonal niche size using five individuals per breeding area. Orange and light-blue boxplots represent the breeding and post-breeding seasons, respectively. Dark blue rhombuses represent the seasonal niche size obtained when using all the individuals of each breeding area (percentages showed in the manuscript).

Information of distance travelled and Environmental experienced niche

Table S4.1 - Individual information of distance travelled and environmental experienced niche in the breeding season

Breeding population	Year	Individual ID	Post-breeding distances travelled (km)	Breeding				
				Pop/year (season niche)	*Ind/year (pop/year)*	*% occupied niche*	*Num. GPS points*	*Used area (ha)*
Campina Sur / La Serena	2015	Boot7	27.04	34.86	100.00	34.86	904	46.75
		Boot8	347.08		97.55	34.01	1027	35.39
	2019	Cabeza_1	161.64	48.55	67.06	32.56	195	207.87
		Cabeza_2	71.18		61.92	30.06	337	610.17
		Cabeza_3	52.00		100.00	48.55	707	275.00
Castro Verde	2009	PTT_91469_1	165.77	32.47	98.31	31.92	108	237.51
		PTT_91470_1	77.17		100.00	32.47	84	298.95
		PTT_91473_1	111.12		100.00	32.47	114	73.24
		PTT_91481_1	56.85		99.54	32.32	199	31.83
	2010	PTT_91469_2	28.75	35.13	100.00	35.13	360	62.49
		PTT_91470_1	77.74		100.00	35.13	355	142.15
		PTT_91471_2	39.39		82.38	28.94	133	68.51
		PTT_91475_2	33.56		99.72	35.03	312	141.60
		PTT_91481_1	37.54		100.00	35.13	354	476.09
	2011	PTT_91469_2	30.52	34.14	100.00	34.14	436	64.87
		PTT_91470_2	69.30		90.46	30.88	95	4.55
		PTT_91471_2	32.46		99.97	34.13	312	47.83
		PTT_91473_3	30.12		100.00	34.14	418	111.15
		PTT_91475_3	35.38		78.38	26.76	238	90.90
		PTT_91476_4	77.68		90.19	30.79	96	642.48

		PTT_91478_5	31.40		100.00	34.14	355	140.84
		PTT_91482_2	148.75		99.73	34.05	465	278.08
	2012	PTT_91470_2	1.66	36.57	62.38	22.81	730	569.44
		PTT_91476_4	78.34		99.79	36.49	126	82.72
	2015	Acc7	155.86	44.42	100.00	44.42	155	270.08
	2017	LB_01_pt	48.02	39.49	100.00	39.49	222	4.86
	2019	lb_pt_2	185.56	30.89	95.00	29.34	199	1069.08
		lb_pt_3	45.57		89.49	27.64	708	41.37
		lb_pt_4	42.19		82.29	25.42	652	180.64
		lb_pt_5	34.64		84.58	26.13	677	41.65
		lb_pt_6	35.46		92.68	28.63	393	96.07
Llanos Caceres	2015	Acc4	201.27	34.20	100.00	34.20	253	135.98
		Boot4	55.40		99.90	34.17	220	213.88
		Boot5	112.61		100.00	34.20	193	3.00
	2016	Boot4	6.43	36.75	99.47	36.56	767	23.49
		Boot5	87.37		79.54	29.23	295	18.20
Merida	2015	Boot3	18.00	98.96	100.00	98.96	544	724.79
	2016	Boot3	23.90	94.25	100.00	94.25	1108	6607.78
	2017	Boot3	15.01	93.56	94.97	88.85	404	632.81
		LB_09_sp	-		72.82	68.13	789	38.86
		LB_11_sp	6.12		74.66	69.85	620	4.97
		LB_12_sp	7.61		86.95	81.35	1397	95.03
	2018	LB_09_sp	18.10	77.00	63.59	48.97	914	29.00
		LB_Mirandilla	15.58		99.64	76.72	628	913.74
	2019	LB_09_sp	18.32	69.63	100.00	69.63	793	937.92
	2009	PTT_91471_1	232.79	87.31	64.75	56.53	371	52.35

Vila Fernando		PTT_91472	9.16		93.89	81.98	288	955.85
		PTT_91475_1	14.78		65.86	57.50	270	80.89
		PTT_91479	55.76		56.87	49.65	265	23.16
		PTT_91480	15.40		58.98	51.49	300	1152.61
		PTT_91482_1	1.36		100.00	87.31	729	655.25
	2010	PTT_91479	-	96.56	82.32	79.49	458	13429.45
		PTT_91480	-		58.58	56.56	373	240.07
		PTT_91482_1	1.59		100.00	96.56	720	439.49
	2011	PTT_91480	14.99	52.32	100.00	52.32	351	202.07
	2012	PTT_91480	-	53.22	100.00	53.22	360	25.80
	2015	LB-1	3.86	90.89	54.48	49.52	71	211.69
		Acc10	-		60.95	55.40	183	136.86
		Acc11	20.80		80.67	73.32	330	93.52
		Acc13	143.83		55.56	50.50	130	147.53
		Acc14	-		54.67	49.69	164	31.61
		Acc8	0.30		98.64	89.65	1571	82.17
		Boot6	9.66		70.32	63.92	1243	308.15
	2016	LB-1	9.25	95.83	50.32	48.22	325	71.63
		Acc11	41.29		100.00	95.83	709	151.48
		Acc13	117.58		46.42	44.49	207	547.26
	2017	LB-1	4.41	67.80	95.56	64.79	265	371.64
		LB_16_pt	420.63		61.80	41.90	248	157.98

— Chapter 5 —

Movement strategies of an endangered grassland bird in response to environmental variability

"Embrace 'Leve-Leve' as the way to thrive on the little lost island in the heart of the
Gulf of Guinea – a beacon of inspiration and resilience,
illuminating the path towards the end of the journey."

Movement strategies of an endangered grassland bird in response to environmental variability

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Authors’ contributions

RFR, JPS and NQ conceived the overall study. JPS was responsible for capturing and tagging the little bustards. RFR prepared the dataset, coded the models, and analysed the data, assisted by FV and NQ. RFR wrote the manuscript assisted by FV, JPS with revisions of AMAF and NQ. All authors contributed critically to the drafts and gave final approval for publication.

Abstract

Understanding species' movement patterns, and the factors influencing them, is vital for comprehending how they respond to environmental changes. This study focuses on the little bustard (*Tetrax tetrax*), a grassland specialist bird susceptible to threats posed by climate and environmental change. To investigate its within season foraging movement strategies, we used high-resolution GPS tracking devices and integrated remote sensing optical (MODIS) and radar (PALSAR) data to assess environmental factors.

The study found that little bustard movements were dominated by patterns associated with sparsely and randomly distributed resources (i.e., Lévy flights), while a quarter of the movements displayed mixed characteristics and were classified as “Mixed Brownian”. This Mixed Brownian movements are probably associated with the breeding behaviour of the species (i.e., lekking system) which contrasts with the more mobile foraging behaviour. Lévy flights were influenced by environmental factors, which varied between each season. During the breeding season, a strong positive response was found for areas with higher moisture levels in soil and vegetation. Diversely, in the post-breeding season, optimal search patterns were related to more productive areas, related with greater food availability and areas distant from roads. In the winter season, Lévy-like movements were positively associated to areas with higher moisture levels similar to breeding areas, and for organic carbon content. Overall, optimal search patterns were associated with areas of greater food availability.

The study's results provide valuable insights into how environmental factors, mostly inferred from satellite data (i.e., multispectral and radar images) may affect little bustard movement strategies throughout the year. These findings emphasize the need to maintain patches of heterogeneous habitats to ensure food availability and promote optimal search strategies. By tailoring conservation efforts to promote optimal search strategies, we can help preserve both the little bustard and its grassland ecosystems, in the face of environmental challenges.

5.1 Introduction

Movement is a fundamental aspect shaping animals' ecology and behaviour, with a substantial body of research focusing on species migration (Joly et al., 2019; Newton, 2010; Stern & Friedlaender, 2018). Daily movements, including foraging, seeking shelter from predators, avoiding unsuitable environmental conditions and interaction with other individuals, are critical for species' survival (Bernich et al., 2022; Nathan et al., 2008; Ramos et al., 2023a). The complexity of these movements arises from a combination of innate instincts, plasticity, learned behaviours, and the interplay with environmental factors (Gill et al., 2014; Knudsen et al., 2011; Ramos et al., 2023b), resulting in the movement ecology discipline as one tendentially requiring an interdisciplinary approach. On such issue, understanding species' movement patterns and what influences them is vital for comprehending species ecology, particularly within a context of environmental changes (Parmesan, 2006; Pörtner et al., 2022).

To better understand species' movements, behaviour, and habitat use over the past few decades, researchers have widely adopted high-resolution GPS tracking devices, which enable precise spatial and temporal data collection (Cagnacci et al., 2010; Kays et al., 2015). Moreover, continuous advancements in satellite remote sensing, notably the massive growth in public Earth observation satellite data from multiple sensors, may provide unprecedented landscape information that can be matched with the data from tracking devices over large areas (Coops & Wulder, 2019; Schulte to Bühne & Pettorelli, 2017). By integrating data from various remote sensing sources captured at different temporal and spatial scales we can gain deeper insights into the environmental variation that affects species distribution and their movement strategies (Crispim-Mendes et al., 2024; Wilmers et al., 2015).

When looking at movement strategies and resource availability, optimal foraging theory suggests that when information is limited, individuals should adopt a specialized random walk known as Lévy flight (Viswanathan et al., 2011). Lévy flights are highly efficient and increase the probability of encounters with sparsely and randomly distributed resources (Focardi & Cecere, 2014). Conversely, when resources are abundant or predictable, a Brownian motion is the most effective movement strategy (Humphries et al., 2010; Sims et al., 2012). Brownian motions are characterized by steps of similar and constant length, with random turning angles, resulting in an irregular search pattern (Turchin, 1996). Lévy flights, on the other hand, entail a search pattern comprising many small steps interspersed with longer relocation steps, drawn from a probability distribution with a power-law tail (Pareto-Lévy distribution) (Viswanathan et al., 1999).

Although previous studies with terrestrial organisms have identified Lévy flights during foraging, they were controversial due to the use of debated statistical methods (Edwards et al., 2007;

Edwards, 2011; Sims et al., 2007). However, recent studies, using state-of-the-art statistical frameworks, have shown Lévy flights in a broad range of marine species (Hays et al., 2012; Humphries et al., 2012; Sims et al., 2012). The present study aims to advance knowledge in this research area for terrestrial species, by coupling an advanced Lévy-related statistical approach with readily available remotely sensed data, we used an iconic and endangered grassland bird specialist as a case study.

The little bustard, *Tetrax tetrax* (Linnaeus, 1758), is a medium-sized grassland specialist bird classified as 'Near Threatened' (BirdLife International, 2021), inhabiting the Iberian Peninsula, which serves as the species stronghold within Western Europe. Despite ongoing conservation efforts, breeding numbers in the region have been declining (Morales & Bretagnolle, 2022; Silva et al., 2018; Traba et al., 2022). The species faces severe threats from climate change, which has been leading to shorter breeding seasons, with reduced display activity (Gudka et al., 2019; Ramos et al., 2023b; Silva et al., 2015) and limiting microclimate refugia availability (Ramos et al., 2023a). Moreover, increasing drought and heat wave frequencies in this Mediterranean ecosystem further constrain feeding resources, especially during the post-breeding period (Pörtner et al., 2022; Ramos et al., 2023b; Silva et al., 2007). Additionally, migratory individuals are at higher risk of colliding with power lines and experiencing greater human disturbance outside protected areas (Gameiro et al., 2020; Marques et al., 2020; Traba & Morales, 2019). This highlights the importance of better understanding this species' year-round movement strategies in Iberia and what influences them, in order to develop efficient conservation and management actions.

This study aims to investigate the foraging movement strategies of the little bustard. This species feeds mainly on green plants, which are not consistently available throughout the species' annual cycle (Silva et al., 2007), making the optimal foraging theory highly relevant. Leveraging long-term tracking data and fine-scale remote sensing information, our research seeks to i) investigate whether little bustards exhibit Lévy flights or Brownian motions in each month ii) compare movement strategies across each phenological season (breeding, post-breeding, and winter); iii) unravel the effect of environmental factors on little bustards' movement patterns on each season. To achieve this, we used movement data from 38 GPS-tagged little bustards tracked between 2017 and 2022 in the Iberian Peninsula.

5.2 Methods

Study area and study system

The Iberian Peninsula is simultaneously a global biodiversity hotspot and one of the world's most vulnerable regions to climate change (Pörtner et al., 2022). The region is expected to suffer from extensive warming and increasing drought frequency in the near future (Jones et al., 2020), which will likely lead to habitat change and species contractions (Pörtner et al., 2022). The semi-natural grasslands, open areas, and low vegetation cover, which are found in this region are particularly exposed to high temperatures throughout the year, making them vulnerable to climate change.

Little bustards were captured and tagged across the southwestern Iberian Peninsula, in Alentejo (Portugal) and Extremadura (Spain), during the breeding season (April and May). Little bustards breed in an exploded lekking system (Morales et al., 2001), where breeding males defend their territories from other males and show exuberant displaying behaviour to attract visiting females (Morales et al., 2001). Birds were captured in the males lekking area using a decoy (stuffed female) and snares (Ponjoan et al., 2010; Ramos et al., 2023a).

Birds were equipped with GPS/GSM loggers, weighing between 15 and 25g, from three suppliers, Movetech Telemetry ("Flyway-23"), E-obs (25g), and Ornitela (models "OrniTrack-15", -20 and -25). The devices were attached with a thoracic harness made of Ribbon Teflon with a weak link composed of cotton thread that degrades over time, to avoid lifelong deployment, weighing less than 3% of the bird's body mass (Kenward, 2000). Transmitters were programmed to record a GPS position every 10, 20, or 30 minutes, depending on the model. This study was carried out in agreement with the Portuguese and Spanish authority recommendations. Licenses to deploy the loggers were granted by Instituto da Conservação da Natureza e das Florestas (Portuguese authority) and Consejería de Medio Ambiente y Rural, Políticas Agrarias y Territorio, Junta de Extremadura (Spanish authority).

Data preparation

We filtered the GPS dataset to include one location per wake-up (every 10-, 20- or 30-minutes dependent on the device). The dataset was then subdivided per month and subsequent filtering was applied, to retain only the bird/month data - hereby called movements - which had complete months (see subsection on "MLE analysis" for more details). Since Maximum Likelihood Estimation (MLE; Clauset et al., 2009) (see subsection on "MLE analysis" for more details) needs constant time intervals between GPS locations, we interpolated missing data for all movements, depending on the transmission schedule. We then kept only those with less than 20% of interpolated data for the daytime of little bustards' movement. We excluded night-time data from the interpolation cut-off since the transmission schedules of the GPS tags did not include the collection of points between 9 pm and 5 am. Moreover, the aim of the study focused on day habitat use, so night points were less relevant.

Remote sensing indices and data pre-processing

For each GPS locations within the monthly movements were associated with dynamic remote sensing information from optical and radar public satellites given useful inferences on vegetation biophysical conditions and structure (Schulte to Bühne & Pettorelli, 2017). Pre-processing steps were performed to filter out problematic pixels (e.g., clouds) from the acquired time series, and to match time series indices with the movement data. Such operations were finalized via the GEE_xtract framework (Valerio et al., 2024), utilizing the Google Earth Engine (GEE) cloud computing platform (Gorelick et al., 2017).

MODIS (EOS AM-1) was selected as optical scientific research satellite, in particular the level-2 reflectance "MOD09GQ" associated product. From multispectral imageries, the Normalized Difference Vegetation Index (NDVI; Huete et al., 2002) and the Modified Soil-Adjusted Vegetation Index 2 (MSAVI2; Richardson et al., 1977) were calculated. Both indices can infer attributes like photosynthetic active radiation in low productive regions (e.g. grasslands) and in semi-arid environments (Leprieur et al., 2000; Paruelo et al., 1997) (Table 5.1). Within GEE, the Gross Primary Productivity (GPP) was also considered using the “MOD17A2H.061” product, which describes the amount of CO2 fixed by plants through photosynthesis per unit time (Sims et al., 2006), as well as the land surface temperature (LST) under the “MOD11A1.061” product, which reflects the radiometric temperature emitted from land (Wan, 2008) (Table 5.1). The mean precipitation (P_Mean) and temperature (T_Mean) were considered as climatic-related indices, utilizing the “E-OBS” dataset from the Copernicus Climate Change Service (Cornes et al., 2018), and the daily temperature range bioclimatic product (Bio2) from the WorldClim project (Fick & Hijmans, 2017) (Table 5.1). As radar satellites, the multi-temporal ALOS/PALSAR and PALSAR2 were selected, using the L-band “dual-polarization” (HV and HH; Table 5.1) Synthetic Aperture Radar (SAR) to infer vegetation structure and soil moisture conditions (Hill et al., 1999; McNairn et al., 2009).

Other more conventional and static products considered: “topographic indices”, such as altitude (Dem), slope, topographic roughness index (TRI) and topographic wetness index (TWI), all derived by the NASADEM Global Digital Elevation Model (Crippen et al., 2016); “anthropogenic indices”, such as distance to power lines and distance to roads, derived from the OpenStreetMap products (http://download.geofabrik.de/) (Table 5.1); finally, “soil indices”, such as bulk density (BD), organic carbon density (OCD), pH and sand content (SD), all retrieved from the SoilGrids project (Poggio et al., 2021) (Table 5.1).

The remote sensing data for each GPS location was then averaged per month to align with the MLE analysis output.

Table 5.1- Remote sensing indices used as explanatory variables to model the exponent of Lévy flights.

Variable name	Variable abbreviation	Scale (Temporal/Spatial)	Satellite/Mission/ Project	Variable Group	Description
Modified Soil-Adjusted Vegetation Index 2	MSAVI2	Daily/250m	MODIS (MOD09GQ)	Spectral indices	Relative measure of chlorophyll content, indicated specifically for bare areas.
Normalized Difference Vegetation Index	NDVI				Relative measure of chlorophyll content, where areas with higher NDVI values typically exhibit increased vegetation cover.
Mean daily precipitation	P_Mean	Daily/ ~ 30km	Copernicus (E-OBS)	Climatic indices	Amount of rain that falls in a place within a 24-hour period.
Mean daily temperature	T_Mean				Temperature calculated from the highest and lowest values recorded within a 24-hour period.
Gross primary production	GPP	8 days/500m	MODIS (MOD17A2H)	Satellite-based models	Total amount of carbon, that plants in an ecosystem convert through photosynthesis.
Land surface temperature	LST	Daily/1km	MODIS (MOD11A1)	Thermal infrared	Temperature of the Earth's ground surface inferred by remote sensing instruments.
Horizontal transmitter-horizontal receiver	HH	Annual/25m	PASLSAR (ALOS PALSAR 1&2)	Dual polarization	Horizontal-horizontal (HH) polarization in radar remote sensing, particularly sensitive to moisture, hence useful for inferring soil moisture content.
Horizontal transmitter-vertical receiver	HV				Horizontal-vertical (HV) polarization ratio in radar remote sensing, in turn sensitive to the volume scattering effects caused by vegetation. Useful for inferring their vertical structure.
Distances to power lines	Euc_PL	250m	OpenStreetMap	Anthropogenic indices	Proximity to major electrical transmission lines.
Distances to roads	Euc_Roads				Proximity to major roads.

Daily temperature range	Bio2	1000m	WorldClim (V. 2)	Climatic indices	Difference between the highest and lowest temperatures recorded.
Altitude	Dem	30m	NASADEM	Topographic indices	Altitude above sea level.
Slope	Slope				Measure of steepness or inclination of a land surface.
Topographic roughness index	TRI				Ruggedness or variability of terrain.
Topographic wetness index	TWI				Estimation of the potential for water accumulation or saturation.
Bulk density	BD	250m	Soil-Grids	Soil indices	Measurement of the mass of sediment per unit volume, hence considering the solid particles.
Organic carbon density	OCD				Quantification of the amount of organic carbon stored per unit volume of soil.
pH	pH				Measurement of acidity or alkalinity of the soil solution.
Sand content	SC				Proportion of sand particles in the soil.

MLE analysis

According to the Lévy flight foraging (LFF) hypothesis, animals should adopt a Lévy flight pattern while foraging, maximizing resource encounter probabilities (Viswanathan et al., 2011). The LFF hypothesis operates within truncated power-law values between 1 and 3, representing destructive search ($\mu \rightarrow 1$, if resources are consumed and not available for subsequent searches), optimal search ($\mu \approx 2$, for sparsely distributed resources in revisitable areas), and optimal resource exploitation ($\mu \rightarrow 3$, for predictable and widely distributed resources) (Humphries et al., 2012).

For each movement, parameters for Exponential (Brownian movements) and Truncated Pareto (TP; Lévy flights) distributions were estimated using Maximum Likelihood Estimation (MLE; Clauset et al., 2009). The paired competing distribution (exponential or TP) was compared using log-likelihoods and Akaike Information Criteria (AIC) weights. The decision tree based on the method proposed by Humphries et al. (2012) (Figure S5.1) was used to obtain the best-fitted distribution for each movement. The decision tree considers each distribution's competing AIC and the alternative, favouring the first in both TP and exponential distributions. It evaluated the goodness of fit (GOF) between the two distributions. It also evaluated whether the TP distribution had an exponent within the Lévy range ($1 < \mu < 3$) and if the orders of magnitude (OOM) were bigger than 1.5. From the above criteria, the datasets were categorized as i) TP, where AIC supported TP and either AIC or GOF rejected the exponential, the exponent fell in the Lévy range ($1 < \mu \leq 3$) and the fit spanned at least 1.5 OOM; ii) exponential, where AIC or GOF supported exponential and AIC or GOF rejected the competing TP; iii) Mixed Brownian, where none of the above applied or where the TP fit was supported by AIC and GOF but fell outside the Lévy range or had less than 1.5 OOM (Humphries et al., 2012).

For the MLE analysis to identify the different distributions (Exponential or Truncated Pareto) a minimum number of GPS points is needed to obtain robust and statistically sound results (Clauset et al., 2009). For that reason, and given the time interval between GPS locations, the month was used as the time resolution unit for all analyses.

After obtaining the classification for each movement (from the MLE analysis), we tested if different GPS fix intervals affected the MLE analysis result. We used the 10-minute GPS tags and ran the MLE analysis at 10, 20, and 30-minute schedules, comparing the results with a Wilcoxson paired test. The test confirmed that no significant differences occurred between the three-time schedules, indicating that the results of all GPS tag types were comparable and could be included in the final models (see Table S5.1 for detailed information).

Statistical analysis

After retrieving the remote sensing variables per month and obtaining the monthly category from the MLE analysis, the months were merged into three distinct seasons: breeding, which comprises the months of April and May for all birds, plus June specifically for those that did not migrate and remained in the breeding area (Silva et al., 2014); post-breeding, including the months from July through September, which represent the period of the species' annual cycle when it is exposed to the highest temperatures and food shortages (Silva et al., 2007); and, winter, comprising the months between November and February, when little bustards gather in flocks, and food availability is expected to be higher (García de La Morena et al., 2015).

For movements categorized as Truncated Pareto (TP), and prior to the multivariate analysis, we used Univariate Generalized Linear Models (GLMs) to identify the most relevant variables within our pool of remote sensing variables, retaining all variables with a p-value lower than 0.2. For all movements classified as Lévy flights, we then applied Linear Mixed-effects Models (LMM), using the *lme4* package (Bates et al., 2015), to analyse the influence of environmental conditions on the Lévy exponent for all three seasons. In all models, we used the year and the individual ID as random factors. A backward elimination approach, based on AIC, was applied to each model to identify the most relevant variables for each season. All models and summary statistics were executed using the R version 4.1.0 (R Core Team, 2016).

5.3 Results

We ran the MLE analysis for 326 months of tracking data, from 38 little bustards. Lévy flights occurred in 251 (77%) of the monthly movements, while no month fitted a Brownian (exponential) movement. However, a significant proportion of the trajectories (23%) were not fitted by either distribution and we classified them as "Mixed Brownian" (Figure 5.1).

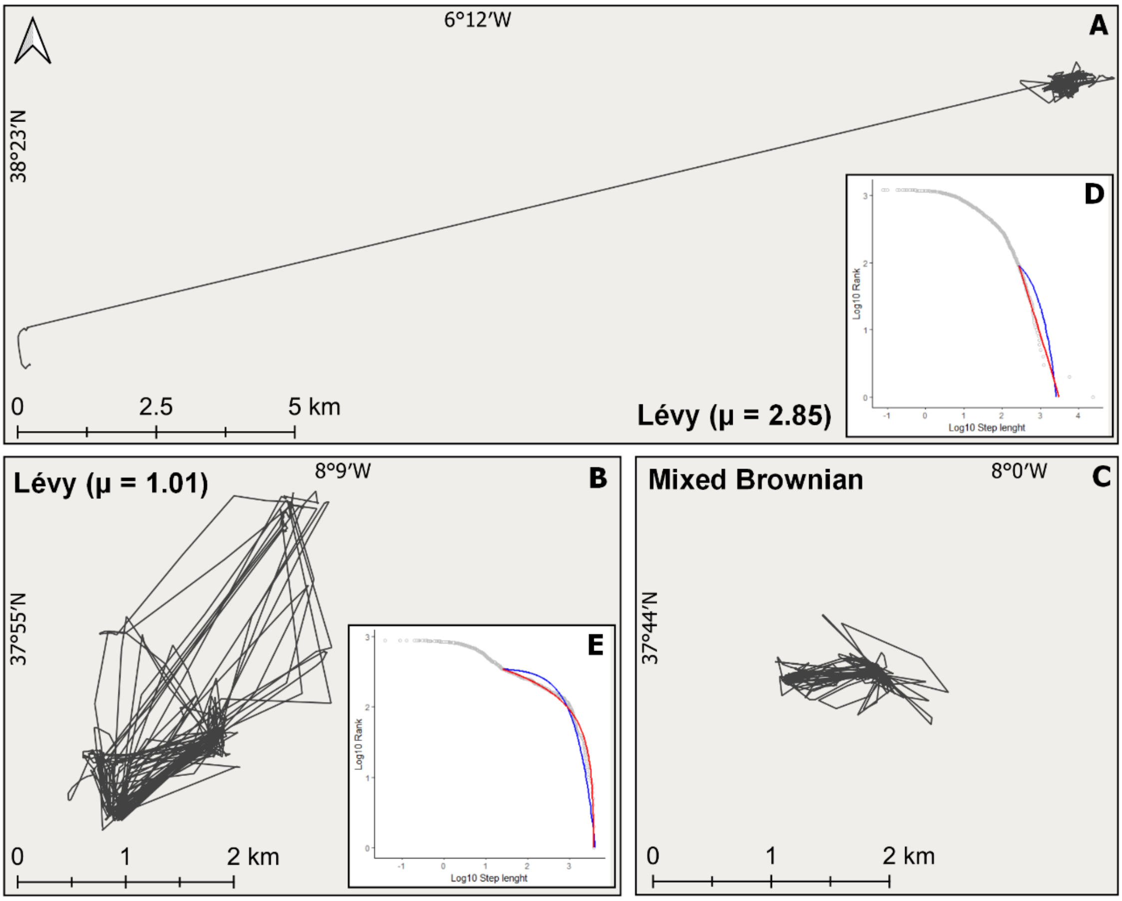

Figure 5.1 – GPS tracking of little bustards showing A) a monthly movement of Usagre-04 (May 2022), exhibiting a Lévy flight (μ = 2.85; B) a monthly movement of PT-06-2019 (September 2019), exhibiting a Lévy flight (μ = 1.01) and C) a monthly movement of PT-05-2019 (May 2019) classified as Mixed Brownian movement. Examples of MLE parameter fitting and wAIC model selection showing truncated Lévy best fits for D) Usagre-04 (May 2022) and E) PT-06-2019 (September 2019): showing observed step lengths; red lines, best-fit Lévy flight; blue lines, best-fit Brownian Movement.

Mixed movements were detected in all seasons but were more common during the breeding season (≈ 50%) and less frequent in winter (≈ 8%) (Figure 5.2). For the 251 Lévy flight movements, nearly half occurred during post-breeding (48.6%), although with a lower Lévy exponent ($\bar{\mu}$ = 1.44 ± 0.23) compared to the other seasons (Figure 5.2). The highest mean Lévy exponent was recorded during the breeding season ($\bar{\mu}$= 1.65 ± 0.40), despite representing only 21.1% of the total Lévy flights identified across seasons (Figure 5.2).

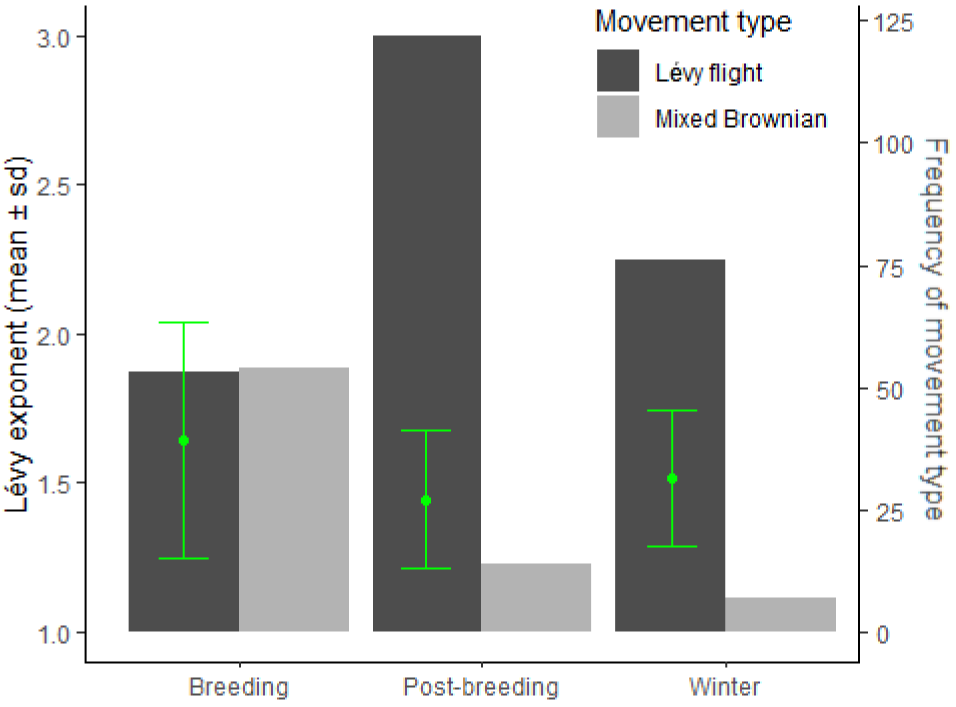

Figure 5.2 – Frequencies of movement types in different seasons (breeding, post-breeding, and winter) (y2 axis), with mean and standard deviation of the Lévy exponent per season, for the Lévy flight movements (y1 axis).

The Lévy exponent for the breeding season was positively associated with HH (F = 0.112, p = 0.001), which was the only variable retained in the model (Figure 5.3).

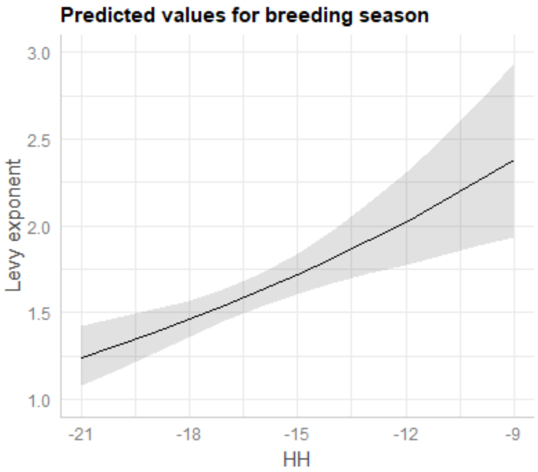

Figure 5.3 - Relationship between the breeding Lévy exponent and horizontal transmitter-horizontal receiver (HH).

For the post-breeding season, the model retained four variables (Figure 5.4). Lévy exponent was positively associated with Gross Primary Production (GPP; F = 0.061, $p < 0.001$) and Distance to roads (Euc_Roads; F = 0.051, p = 0.003) and negatively associated with Topographic Wetness Index (TWI; F = -0.050, p = 0.003) (Figure 5.4 and 5.5). The final model also retained Mean temperature, despite being only marginally significant (T_Mean; F = 0.024, p = 0.076).

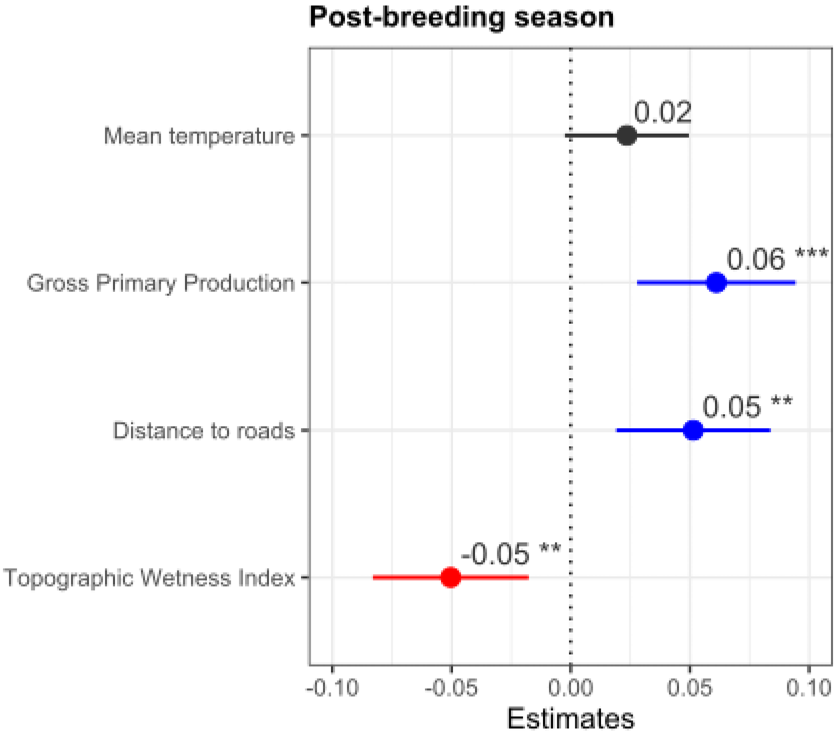

Figure 5.4 - GLMM results for the predictors of Lévy exponent, for post-breeding season. Variable significancy is shown: *** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$; others, $p > 0.05$. Positive effects are shown in blue, negative effects in red, and non-significant effects in black.

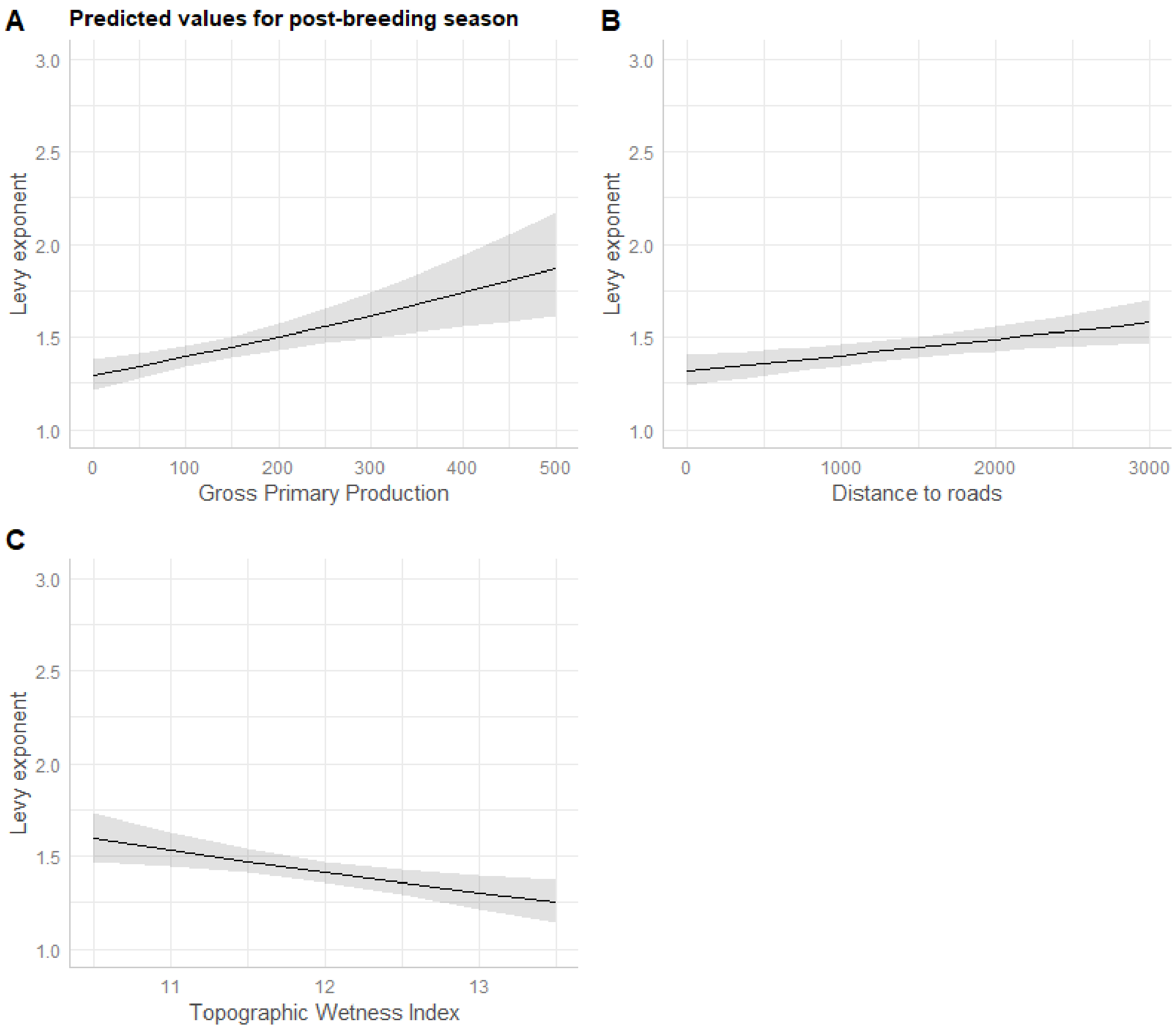

Figure 5.5 - Relationship between the post-breeding Lévy exponent and A) Gross Primary Production (GPP); B) Distance to roads (Euc_Roads); C. Topographic Wetness Index (TWI).

For the winter season, the model retained five variables (Figure 5.6). Lévy exponent was positively associated with HH (F = 0.04, p = 0.033) and Carbon density (OCD; F = 0.07, p = 0.003) (Figure 5.6 and 5.7). The final model also retained three non-significant variables (Figure 5.6).

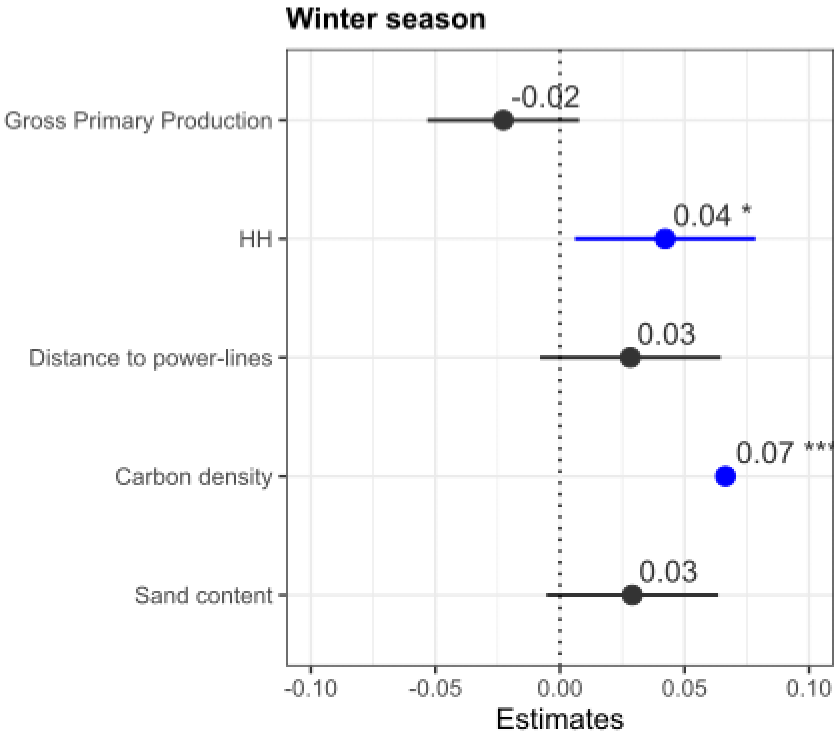

Figure 5.6 - GLMM results for the predictors of Lévy exponent, for the winter season. Variable significancy is shown: *** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$; others, $p > 0.05$. Positive effects are shown in blue, negative effects in red, and no significant effects in black.

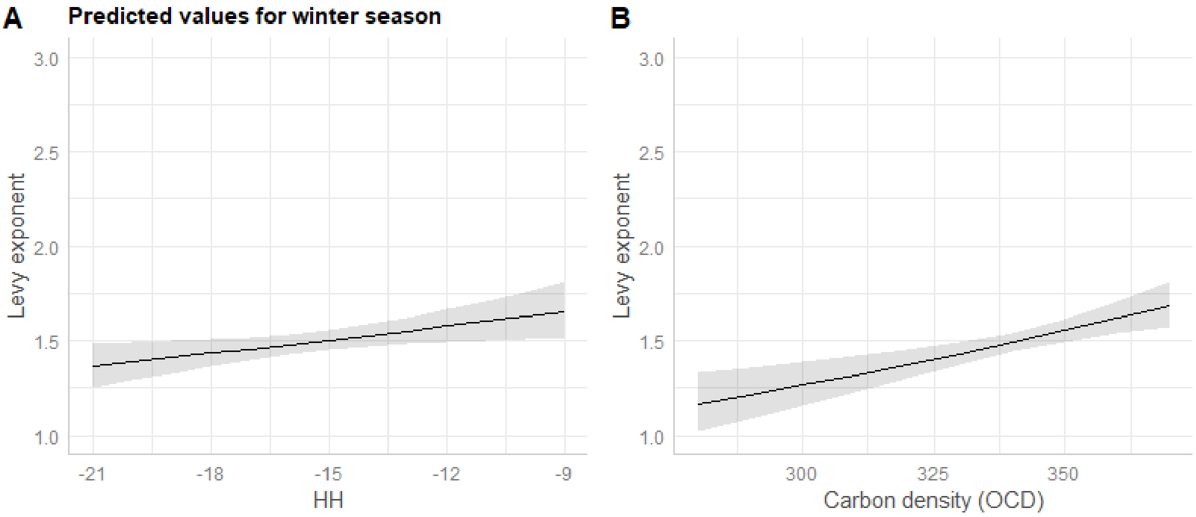

Figure 5.7 - Relationship between the winter Lévy exponent and A) Horizontal transmitter-horizontal receiver (HH); B) Carbon density (OCD).

5.4 Discussion

Understanding species movement strategies, particularly in threatened and mobile taxa is crucial to implement effective conservation measures. In the past, the classification of Lévy flights and

Brownian motions in terrestrial species sparked controversy, primarily stemming from the utilization of suboptimal analytical approaches. In this study, we took advantage of the combination of high-quality data from tracking devices and remote sensing satellites, through innovative analyses, to investigate the movement strategies of a threatened grassland bird throughout the year. More specifically, our research improved the understanding of how various environmental factors influence the year-round movement patterns of little bustards.

Our study primarily identified Lévy flights as the dominant movement pattern, with a smaller fraction of movements categorized as Mixed Brownian movements. Lévy flights are typically associated with sparsely and randomly distributed resources and involve a series of small steps connected by longer relocations, which usually relate with larger-scale movements (Humphries et al., 2010; Humphries et al., 2012). Brownian movements, on the other hand, are related to abundant and predictable resources, since resources are highly available it is not necessary to perform long-distance movements and spatial scale is usually narrower than Lévy flights (Sims et al., 2012). While we did not detect pure Brownian movements, we identified Mixed Brownian movements, those that do not fit any of the distributions (Lévy or Brownian) (Humphries et al., 2012), in approximately a quarter of all movements. This high proportion is likely due to the temporal scale of our data analysis, which captured diverse movement patterns within a single month, making the movement too complex to detect the specific movement pattern. Previous research on marine predators found similar high proportions of Lévy flights, when compared to Brownian or Mixed Brownian movements (Humphries et al., 2010). In their study, Humphries et al. (2010) found that shark species exhibit a higher proportion of Lévy flights in off-shelf and stratified areas of the northeast Atlantic and Central eastern Pacific, respectively. These areas correspond to less productive areas when compared with frontal/shelf areas, which tend to promote Brownian-type movement. Little bustards of the Iberia Peninsula inhabit semi-natural grasslands, open areas with low vegetation cover maintained by agricultural activity and livestock grazing, highly dependent on human management (Emanuelsson, 2008). Food availability is also influenced by the Mediterranean climate characterized by mild or cold wet winters and hot, dry summers, with a three-month dry period that dries the vegetation. It is also a vulnerable region to climate change (Pörtner et al., 2022), which limits the species' habitat quality and availability of feeding resources throughout the year, particularly during the summer (post-breeding season). These habitat characteristics alter food availability in irregular patterns and can help explain the high proportion of Lévy flights when compared with Mixed Brownian movements.

The proportion of Lévy flights varied significantly between seasons, with nearly half occurring during the post-breeding season and only 21.1% during the breeding season. During the breeding season movements were evenly distributed between Lévy flights and Mixed Brownian movements. The high proportion of Mixed Brownian movements when compared with other seasons may be related to the species' breeding behaviour. Little bustards breed in an exploded lekking system, which is characterized by males defending small and clustered areas that are visited by females with the only purpose of mating (Morales et al., 2001). This lekking areas are usually composed of a territorial male, in the centre of the lek, and several floater males, which can visit different lekking areas (Silva et al., 2017). Thus, movements by male little bustards may be heavily dictated by their breeding strategies (territorial vs floater males). Consequently, the Mixed Brownian movements may represent tracks having both Lévy and Brownian features, which are expected considering males' lekking behaviour and changes in foraging movements throughout the month.

Lévy movements displayed varying exponents between seasons, despite all being lower than the theoretical optimal search ($\mu \approx 2$), where food resources are distributed in revisitable areas and may be only temporarily depleted (Bartumeus & Catalan, 2009; Viswanathan et al., 2011). Breeding season showed the higher mean Lévy exponent ($\bar{\mu}$ = 1.65), while the post-breeding and winter seasons showed lower means ($\bar{\mu}$ = 1.44 and $\bar{\mu}$ = 1.52, respectively). These patterns agree with resource availability, with the breeding season having the highest resource levels (Bravo et al., 2017; Bretagnolle et al., 2022) and post-breeding being a period of food scarcity (Silva et al., 2007), where birds perform movements towards areas with greater food availability (e.g. irrigation plots), carrying out in occasions ballistic-like movements, lower than the optimal Lévy search. However, despite the differences, none of the seasons exhibited destructive search patterns ($\mu \rightarrow 1$), where resources are not available for subsequent visits (Santos et al., 2004; Sims et al., 2012). Variability of the Lévy exponent was also higher during the breeding period, which was expected considering the season particularities. As stated before, the breeding season has higher food availability, but depletes rapidly once temperatures increase at the end of May (Bretagnolle et al., 2022; Silva et al., 2007). This seasonal variability and the singularities of little bustards' breeding behaviour can contribute to a higher variation of Lévy movements within the same season (that spans from April to June).

For movements identified as Lévy flights, we modelled the exponent (μ) in relation to the environmental and climatic remote sensed variables. During the breeding season, only the variable HH (PALSAR - Horizontal transmitting, horizontal receiving signal) emerged as statistically significant. The positive response for backscatter values in HH polarization can be interpreted as a tendency towards more irregular areas (surface roughness) with higher levels of moisture and vegetation (e.g., crops; Aubert et al., 2011; Fontanelli et al., 2022; Hill et al., 1999). Since little bustards feed mainly on green plants, areas with higher humidity in the ground likely reflect areas with greater biomass and thus higher food availability (Silva et al., 2007). Therefore, higher HH indices are associated with Lévy exponents between the optimal Lévy search and optimal exploitation of resources ($2 < \mu < 3$) (Humphries et al., 2012). Nonetheless, the breeding season is when male little bustards are more constrained due to breeding behaviour (Silva et al., 2017). This explains why only dynamic remote sensing data at high resolution (25m) exerted a significant effect on explaining such types of short movements, while other indices derived by sensors with moderate resolution (i.e., MODIS; 250m) were inconsistent.

In contrast, the post-breeding season featured four retained variables in the final model, with three of them having statistical significance. This season aligns with the European summer (July to September), being characterized by constant food scarcity (Silva et al., 2007) and promoting little bustards' movements towards sub-optimal areas (Silva et al., 2007; Silva et al., 2015). Higher Gross Primary Production (GPP) and increased distance from roads were associated with movement patterns that approximated optimal Lévy searches. GPP is an overall indicator of dynamic green biomass (Sims et al., 2006), providing high-temporal resolution data (8 days) of feeding resources. This is relevant because food availability in the Mediterranean region changes dramatically over the summer owing to high temperatures and low precipitation rates (Pörtner et al., 2022). Here, it is possible that the GPP represented sources of food supply in areas subjected to rapid fluctuations in environmental conditions. This is corroborated by the lack of support for the HH index, which can also be used to infer biomass attributes (Fontanelli et al., 2022), though it was derived from a sensor with annual site revisitation, hence less able to capture intra-year vegetation dynamics (e.g., phenology). Besides, road density was previously pointed as a disturbance factor influencing little bustards' distribution (Silva et al., 2023), hence, higher distances to roads will likely translate in better quality areas, with lower disturbance promoting non-ballistic movements.

Additionally, the model revealed a negative association between movement strategies and the Topographic Wetness Index (TWI), contrary to our initial expectations. While resources tend to be more abundant in areas with higher water availability (Hill et al., 1999) which is consistent with the obtained values, however, exceptionally high values TWI may be associated with areas featuring excessive water content. Such conditions can render the habitat unsuitable for grassland birds, potentially leading to permanent flooding. This could explain the observed negative trend in our model.

In the winter, which typically has increased resources available, when compared with breeding and post-breeding seasons, we noted a positive relationship between Lévy exponents and HH. This relationship was more pronounced during the breeding season, indicating movements shifting from optimal search strategies to optimal resource exploitation ($2 < \mu < 3$), with Lévy exponents closer to optimal search during winter. Such a less strong response may be explained by the fact that towards the end of the winter within the Mediterranean region, vegetation is already well developed, and, thus, little bustards' food should be widely available (Bravo et al., 2017). However, in recent decades, temperature increases and changes in precipitation patterns, and drought frequency have been altering this pattern (Pörtner et al., 2022; Ramos et al., 2023a). Thus, this may help explain why, although food is usually available throughout the landscape, the variable is still significant and included in the model. Furthermore, we identified a positive relation between winter Lévy exponent and organic carbon density, which is in turn considered an indicator of soil quality (Aguilera et al., 2018), suggesting areas of greater productivity and consequently higher food availability.

The dichotomy between the selection of static and dynamic variables for model retention among seasons underscores the importance of real-time resource availability data during periods of food scarcity, such as the post-breeding season. In contrast, during seasons with higher resource availability, more static variables (e.g., HH) suffice to elucidate little bustards' movement strategies.

Challenges and opportunities

The use of the entire month to assess movement strategies, although informative, lacks detail and did not always allow for a representative information about individual behaviour. Future studies, using tracking data with accelerometer, should be planned to obtain detailed information across the month and compare it with the current information. However, despite the challenge of lack of detail within each month, we were able to build a temporal representative dataset, which included year-round information from five different years (2017-2022).

Additionally, while we corroborated the utility of integrating radar-derived information associated with wildlife habitat characteristics (Valerio et al., 2023), advantages in utilizing optical-derived information emerged only during specific seasons (e.g., GPP). This is likely because we employed variables with a gradient from moderate to high resolution of both temporal and spatial scales (Table 5.1). However, to broaden the scope of the results, a balanced compromise between spatial and temporal resolution indexes should be considered in the future, such as from the Sentinel missions, for both optical and radar data given the high resolution (10m) and moderate site revisitation (6 days) from the sensors.

Another limitation relates with the coarse resolution of the climatic-related variables. It is known that fine scale environmental variation can exceed that found at coarse scales (Maclean et al., 2017; Suggitt et al., 2018). Moreover, previous studies showed the importance of microclimate refugia for little bustards exposed to high temperatures and in determining migratory timings (Ramos et al., 2023a; Ramos et al., 2023b). These findings highlight the need for the use of fine-scale climate-related variables, but those are still being developed to cover species entire ranges and at high-frequency time-series.

Conservation and management implications

Understanding the intricacies of animal movement patterns and the factors influencing them holds paramount importance for effective conservation measures. Little bustards, like many other species, are susceptible to threats associated with extensive movements to fulfil their physiological needs, including food, breeding habitat, and shelter from unsuitable environmental conditions (Silva et al., 2023).

Our study, using the little bustard as a model species, identifies key environmental characteristics that shaped movement strategies across the species' annual cycle. Inadequate habitats potentiate ballistic-like search patterns ($\mu \rightarrow 1$), which occur when food resources are consumed and not available for subsequent searches (Humphries et al., 2012). This can force birds to travel further distances to search for new feeding areas, which may increase collision risks with power lines (Marques et al., 2020). It can also be related with concentrated food resources with low vegetation cover, inadequate for breeding and resting (e.g., pivots) (Alonso et al., 2020; Silva et al., 2007). Although little bustards are grassland specialist birds, this habitat lacks the necessary food requirements year-round, especially during post-breeding, a season of food shortage (Silva et al., 2007).

Conservation efforts should focus on promoting areas with higher productivity, that benefit optimal search strategies ($\mu \approx 2$) and prevent ballistic-like movements. Management actions should conserve areas that provide higher levels of food availability during breeding and winter seasons, identified by high level of soil moisture and soil productivity ensuring movements closer to optimal Lévy searches, and reducing the need for extensive travel. For the post-breeding season, conservation action should concentrate in providing food availability further away from human infrastructures which would likely prevent ballistic movements related to greater energy expenditure.

Our findings emphasize the importance of coupling high-quality telemetry and remote sensing data in tailoring conservation strategies that account for the dynamic interplay between movement and environmental patterns, ultimately ensuring little bustard and grassland ecosystems preservation.

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Chapter 5 Supplementary Materials

MLE analysis decision tree

The following decision tree is an adaptation of the decision tree presented by Humphries et al. (2012) and it was used to create the R code to obtain the best-fitted distribution between Exponential and Truncated Pareto to classify each movement.

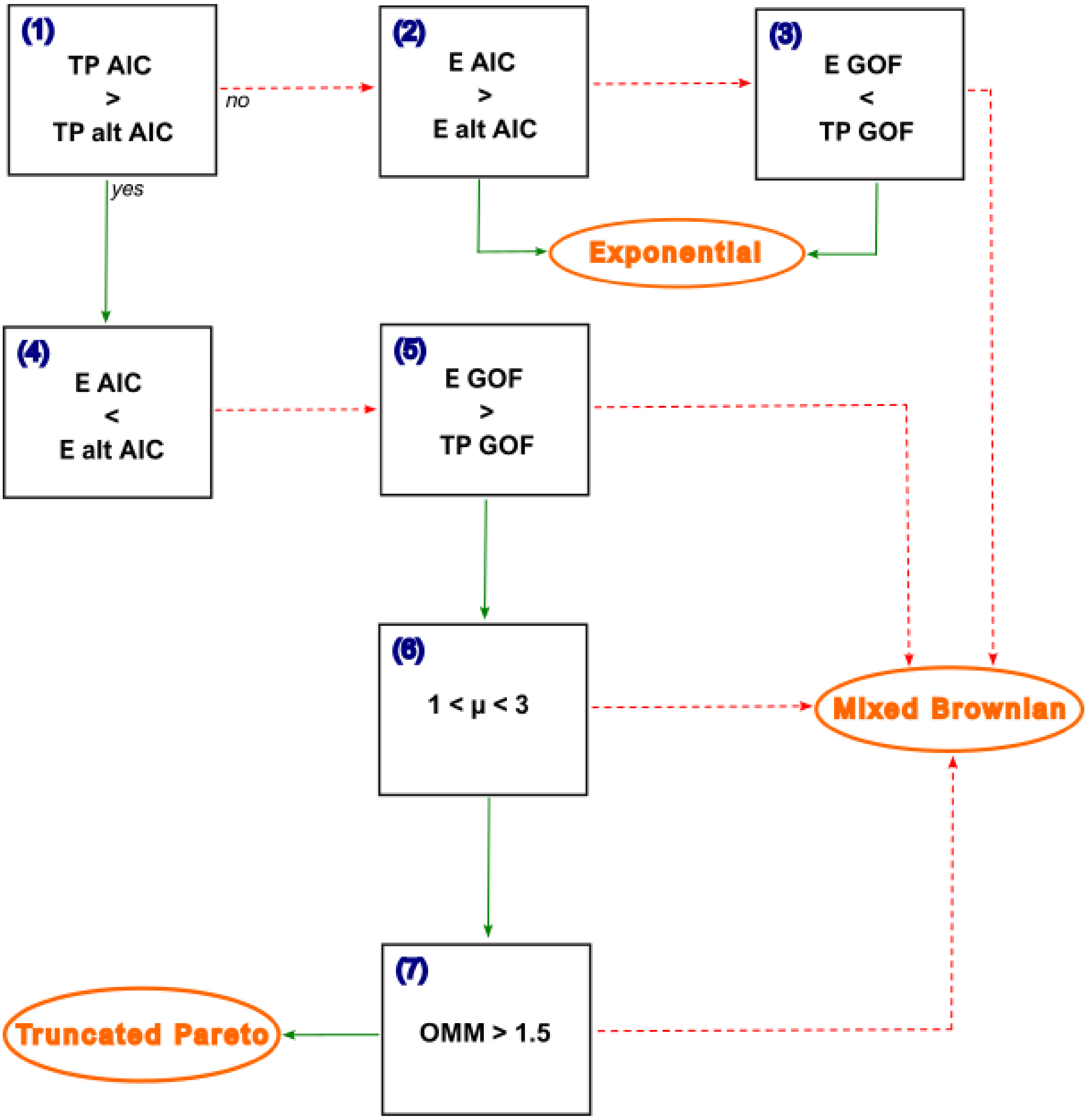

Figure S5.1 - Decision tree, as presented by Humphries et al., 2012 for model selection. The process starts at square (1) and green lines should be followed in case of a positive response and red dashed lines for negative responses. The decision is concluded when one of the orange circles is reached: Exponential, Mixed Brownian or Truncated Pareto.

Comparison of MLE analysis results between different scheduling tracking devices

Since the tracking devices had three different schedules (10, 20, and 30-minutes), before running the Linear Mixed-Models, we tested whether different schedules affected the MLE analysis results. We used the 10-minutes GPS devices and interpolated the data to obtain tracks for the same individual/month for 10-, 20- and 30-minutes intervals and ran the MLE analysis. We then compared the results obtained for the Lévy exponent for each individual/month with a Wilcoxson paired test (Table S5.1). The p-values obtained support the decision of maintaining the MLE analysis and compare the results between the three different scheduled devices, since the Lévy exponent obtained is similar between the three.

Table S5.1 – Wilcoxson paired test for the comparison between 10-, 20- and 30-minutes schedules for the 10-minute tracking devices.

Interpolation timing 1	Interpolation timing 2	Wilcoxson paired test *(p-value)*
10 min	20 min	p = 0.58
10 min	30 min	p = 0.23
20 min	30 min	p = 0.70

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— Chapter 6 —

General Conclusions

"Mozambique opens doors to endless opportunities, guiding us
towards a future filled with inspiration and growth."

General conclusions

6.1 Summary of thesis findings

Ecological studies on species' response to environmental and climatic change are essential for identifying management measures aimed at ensuring a favourable conservation status. In the Iberian Peninsula (e.g. the study area), temperatures have already increased by 2°C over the last three decades, particularly during the spring (e.g. the breeding season) (Figure 2.1). Many species are being impacted by climate and other human-induced environmental changes and some are suffering dramatic population declines. Particularly, grassland birds are declining across Europe, conditioned by specific habitat requirements prone to be impacted by increasing temperatures and human disturbance (Silva et al., 2023; Silva et al., 2024), combined with the lack of conservation measures that account for the fine-scale environmental variation which can buffer species against these changes. Recognizing the urgency to investigate the effects of environmental changes at the scale species experience it, this thesis introduces a novel methodology for determining use and availability of microclimate refugia (Chapter 2), exploring the importance in the species ecology and behaviour in subsequent chapters (Chapters 3 and 4).

My findings indicate that, at the scale of approximately 30 meters (Chapter 2), most little bustards inhabit areas devoid of microclimate refugia opportunities. Notably, their utilisation of microclimate refugia increases in frequency at higher ambient temperatures, despite the overall low utilization of refugia, suggesting an active search for cooler habitats during periods with elevated temperatures. Ultimately, I found that a mixed landscape, featuring a grassland matrix interspersed with small tree and shrub patches, creates a heterogeneous thermal landscape which, I hypothesise, may be beneficial for little bustards during both breeding and post-breeding seasons.

My research shows consistent post-breeding migration distances among birds tracked over multiple years, likely attributed to their fidelity to breeding and post-breeding areas. In contrast, migration timing exhibits considerable variation among individuals and between years, ranging from May to August (Figure 3.1). The departure timing from breeding areas is strongly influenced by Normalized Difference Vegetation Index (NDVI), a variable that was used as a proxy for food availability. I also found a potential influence of microclimate refugia availability, particularly in low and intermediate temperatures (Chapter 3). Additionally, this PhD reveals little bustards are partial migrants showing diverse migration strategies, with migrant and resident birds in the same populations, showing a dynamic response to environmental cues, mainly food availability and temperature.

I explored the fine-scale environmental niche of little bustards, and identified a gradient characterized by temperature and microclimate refugia availability. Some populations exhibit niches with low microclimate refugia availability (Figure 4.4), and individuals occupying those are more likely to migrate longer distances to post-breeding areas. My analysis suggests that migratory birds covering longer distances predominantly adopt a "niche tracking" strategy, while residents and short-distance migratory birds favour a "niche switching" strategy, linked to increased microclimate refugia availability.

In Chapter 5, I broaden the focus to a larger spatial scale, examining within-season foraging movements. I found that the studied populations did not exhibit movements characteristic of use of abundant and predictable resources. Instead, movements were often linked to sparsely and randomly distributed resources, with a quarter of the movements displaying mixed characteristics, especially during the breeding season (Figure 5.2), probably due to the species lekking breeding behaviour (Morales et al., 2001). My exploration of environmental information derived from high-resolution remote sensing data revealed that patterns associated with optimal foraging movements, are mostly related with soil moisture during breeding and winter seasons, and vegetation productivity, and distance from roads during the post-breeding season, emphasising the importance of land use that potentiate food availability and decrease disturbance.

Overall, my research underscores the significance of examining environmental variability at the scale individuals experience their habitat. Leveraging freely available software, remote sensing data, and high-resolution tracking devices, I advanced scientific knowledge on the adaptive strategies of an endangered species to a changing environment. These findings can help design future conservation measures, offering insights for creating resilient habitats that support the persistence of grassland species under current climatic change.

6.2 Broader context

Using technology in ecology

The technological advancements of recent decades have ushered in a significant increase in data generation, particularly in the realm of movement data (Kay et al., 2015). Tracking devices now offer movement information with high spatial and temporal resolution, along with exceptional accuracy (Acacio et al., 2022; Cagnacci et al., 2010). This progress enables a profound understanding of animals' behaviour and movement ecology. Alongside, the proliferation of earth observation satellite data, collected from multiple sensors, facilitates the alignment of landscape information with tracking device data (Coops & Wulder, 2019; Wilmers et al., 2015). This synergy creates opportunities to seamlessly integrate both coarse and fine-scale environmental information into species ecological studies. Moreover, the computational power required to process large volumes of data is becoming increasingly accessible at lower costs. Despite these growing opportunities to incorporate fine-scale and high-resolution data into ecological studies, it remains an underutilized practice. By harnessing the full potential of existing technology and capitalizing on ongoing developments, scientists can investigate animal movement and responses to environmental change at the scales which individuals experience their environment (Bütikofer et al., 2020; Zellweger et al., 2019). This integration of fine and coarse scale information will deepen the knowledge about species behaviour and response to environmental change which can contribute to more integrated and effective conservation measures specially when considering climate resilient habitats.

Implication in a global warming perspective

Global warming, primarily driven by human-induced changes in ecosystems, has emerged as a critical factor profoundly influencing species ecology and its conservation efforts. The well-established impact of rising temperatures influences species range shifts, as well as behavioural and physiological changes (Chen et al., 2011; Fuller et al., 2010; Jiguet et al., 2007).

Despite numerous studies predicting alarming distribution changes under future climate change scenarios (Eichenberg et al., 2021; Hastings et al., 2020; Soroye et al., 2020; Vasiliev & Greenwood, 2021), there is a growing risk of accelerated extinctions if effective conservation measures are not promptly implemented. Notwithstanding, microrefugia have been identified as key contributors to fine-scale environmental variation experienced by individuals in their habitats (Maclean & Early, 2023). These microrefugia create areas significantly cooler than their surroundings, often exceeding the variation observed at a broader scale (Maclean & Early, 2023; Massimino et al., 2020; Suggitt et al., 2011). Additionally, grasslands are characterized by open habitats with short vegetation that provide little shade to buffer species against elevated temperatures (Ribeiro et al., 2016; Traba et al., 2022), exposing species to insolation and forcing them to adopt extreme physiological and behavioural thermoregulation strategies (Rastogi, 2007; Silva et al., 2015; Whittow, 1986). Regrettably, many studies still overlook this fine-scale environmental variation in their distribution analyses, potentially leading to an overestimation of the importance of broad environmental changes (Maclean & Early, 2023).

In this thesis, I showed the importance of looking at the fine-scale environmental variation to better understand species ecology and behaviour and made surprising discoveries. Among the populations studied in this thesis, Castro Verde (Alentejo, Portugal) stands out as a population exposed to high temperatures and with few refugia opportunities, illustrating the importance of looking at fine-scale environmental variation. Identified as one of the warmest and most vulnerable area to climate change of the study sites, individuals here make intermediate use of microclimate refugia during both breeding and post-breeding seasons (Figure 2.3). It is the only population where all individuals undertake post-breeding movements, some to areas with high human disturbance, like the Tagus estuary, making use of irrigated fields (Figure 3.1). Despite being a breeding population with limited microclimate refugia availability during the breeding season, it is the only one where, as a population, individuals adopt a niche-switching strategy, moving to areas with higher microclimate refugia availability during the post-breeding season (Figure 4.4). These trends underscore the importance of providing microclimate refugia, particularly in the breeding areas. Moreover, Castro Verde is not only the most important breeding area of grassland birds in Portugal, but it also encompasses the country's wider grassland areas, where numerous conservation actions have been implemented (Equipa Atlas, 2008; Moreira et al., 2007).

When compared to other populations (e.g. Mérida, in Extremadura, Spain), individuals in Castro Verde not only lack microclimate refugia opportunities but also move longer distances towards areas that offer better conditions (e.g. more food, milder temperatures or with more microclimate refugia available, Chapters 2 and 3). This fact supports the idea that local environmental variation can help species persist under current global warming (Stark & Fridley, 2022; Suggitt et al., 2018), making the incorporation of fine-scale environmental in species distribution models and future projections essential (Lembrechts et al., 2019). Furthermore, by providing microclimate refugia in the species breeding ranges, individuals may mitigate detrimental movements between breeding, post-breeding, and wintering areas. This nuanced understanding underscores the essential role of microrefugia in shaping species responses to global warming and informs targeted conservation strategies.

Broader applicability

While the findings presented in this thesis centre around a specific species, the methodologies and key discoveries have broader applicability to other grassland bird species. The impact of climate change on species ecology has garnered considerable attention, yet species distribution models often lack the fine-scale information provided by tracking devices and various remote sensing sources. This thesis highlights that little bustards actively seek cooler sites in their immediate surroundings, particularly during warmer periods of the day and year (Chapter 2). Furthermore, my research demonstrates that microclimate refugia availability during the breeding season not only plays a crucial role in shaping post-breeding movement strategies but also defines the environmental niche experienced during both breeding and post-breeding seasons (Chapters 3 and 4).

On a broader scale, I have identified the environmental features that promote the existence of microclimate refugia, specifically, patches of shrubby and arboreal vegetation within the herbaceous landscape characteristic of grasslands (Chapter 2). These insights hold significant potential for grassland species conservation, as the alarming decline of biodiversity emphasise the urgency of implementing effective conservation measures (Pörtner et al., 2022; WWF, 2022).

Grassland species in Europe, facing rapid and severe declines primarily due to human activities and climate change, are particularly vulnerable. Changes in agricultural policies, increased habitat fragmentation (e.g., power lines) (Faria et al., 2016; Marques et al., 2020), as well as decrease precipitation and higher temperatures, lead to increased aridity and more frequent drought events, all contribute to this alarming trend (Figure 2.1; Pörtner et al., 2022). This thesis reveals the critical role of fine scale refugia in sheltering grassland species from rising temperatures (Chapter 3 and Chapter 4). It highlights the need to provide areas with high food availability within or close to the breeding areas (Chapter 2 and Chapter 5) to avoid long-distance displacements of individual, which poses high risks during migration and at post-breeding and wintering sites. Additionally, having high quality habitats with food available benefits the maintenance of the current lekking areas of the species (Silva et al., 2017).

Little bustards, among other grassland birds are a species with priority status in Europe under the European Union's Birds Directive (79/409/EEC). To enforce that, Special Protected Areas (SPA's) have been designated in the most crucial grassland areas in the Iberian Peninsula to protect the breeding habitats of grassland birds (79/409/EEC). However, the presence of individuals both inside and outside these SPAs with varying protection and conservation measures, coupled with the partial migratory nature of little bustards, means that SPA's only cover a portion of their annual range. The protection of the species should involve a more comprehensive protected area network, with proper and active management. This need for re-thinking the management done within SPAs is evident in the last three censuses for the species (2006, 2016, and 2022), showing significant declines in the Portuguese population over the past 15 years (Silva et al., 2018; Silva et al., 2023), despite high breeding densities at the start of the century, especially in Alentejo, Portugal (Silva et al., 2010).

Despite scientific evidence calling for action over the past 18 years, effective conservation measures to halt little bustards' declines remain inefficient (Silva et al., 2024). The lack of collaboration between different sectors of the society, such as research institutions (academia), non-governmental organizations (NGOs), and local authorities, contribute to this problem. A multisectoral approach leveraging collaborative efforts could capitalize on the strengths of each sector to implement integrated and effective conservation actions. This collaborative vision is often lacking, with different sectors working independently with the resources they have. Utilizing the evidence-based knowledge of academia, policy makers and governmental environmental agencies could drive conservation measures, monitored and supported by NGOs working in the field.

A key component of implementing this vision is modifying the current Common Agricultural Policy (CAP) from a subsidized livestock production to a balanced livestock and cereal production. Achieving these transitions requires close collaboration between environmental and agricultural government agencies (Silva et al., 2024). Based on the results of my research, habitat suitability can be improved by allowing for more scattered patches of shrubs and trees in the predominantly herbaceous landscape characteristic of grassland areas. This not only provides microclimate refugia areas for many grassland species but can also potentiate feeding resources (Jiguet, 2002; Suggitt et al., 2018). These measures could aid little bustards' conservation by sheltering individuals from unsuitable conditions (e.g. increasing temperatures and heatwaves) while maintaining the necessary habitat conditions in current breeding areas. This is crucial given the species' breeding site fidelity and the challenge of restoring historical breeding sites once they are lost (Silva et al., 2017). Furthermore, as demonstrated in Chapter 2, there is evidence of a noteworthy temperature increase during the little bustards' breeding season in the Iberian Peninsula over the past 30 years, with some regions experiencing an increase of 2°C in maximum temperature.

The approaches and results outlined in this thesis are not only applicable to other grassland species but can also be extended to a wider range of taxa and ecosystems grappling with the impacts of climate change. This research underscores the importance of integrating fine-scale environmental information into conservation strategies to enhance the adaptability and resilience of various species and ecosystems.

6.3 Future studies and implications

The "unmeasured" importance of microclimate refugia

Throughout this thesis I have underscored the potential importance of microclimate refugia for the study species. However, a crucial question remains: "Do little bustards make decisions regarding how and where to move based on the absence of microclimate refugia at the breeding sites?". Recognizing this gap in knowledge, the team is actively addressing this question by investigating the variations between breeding sites abandoned during the post-breeding season and those utilized during this period (Zalewska et al., *in prep*). The post-breeding season is a recognized period of vulnerability for little bustards, characterized by exposure to extreme temperatures and food shortages (Silva et al., 2015; Somveille et al., 2019). Exploring the reasons behind little bustards abandoning their breeding areas will not only enhance our understanding but also contribute to the development of tailored conservation measures aimed at sustaining viable breeding populations, particularly in light of the current temperature increases in these sites (Figure 2.1).

Despite that missing puzzle piece, my research showed the importance of microclimate refugia across various facets of little bustards' phenology, notably influencing their movement strategies (Chapter 3) and defining their environmental niche (Chapter 4). Moreover, these hold substantial potential for broader application to other species, particularly endangered grassland birds protected under national and international conventions (Moreira et al., 2005; Silva et al., 2024). The insights gained from my study can inform conservation efforts and contribute to the preservation of these vulnerable species in the face of environmental changes.

Physiology

A key aspect towards understanding the importance of microclimate refugia in buffering species against detrimental environmental conditions relates to species physiology. Despite the research available regarding endotherms physiology and the thermoregulation mechanisms different taxa adopt to maintain their body temperature (Rastogi, 2007; Rezende & Bacigalupe, 2015; Ruben, 1995), much remains to be understood about species thermic thresholds and the consequences of increasing temperatures for thermoregulation. In order for body temperature to remain relatively stable, endotherms evolved efficient thermoregulatory mechanisms, both physical and chemical (Rastogi et al., 2007). In the case of birds, they also adopted some behavioural strategies such as holding their wings away from the body, reducing their activities to a minimal to reduce metabolic heat production and ultimately moving to shady areas to reduce heat gain (McKechnie

& Wolf, 2019; Rastogi et al., 2007). For the little bustard, research have shown a decrease in activity levels in temperatures above 25°C (Silva et al., 2015), however, it is unlikely that this is the species critical thermal limit.

Although previous studies have investigated the approximate normothermic and maximum thermic limit of some small vertebrates (McKechnie & Wolf, 2019), the thermic tolerances of most species is still unknown. Moreover, it is crucial to understand the implications of increasing temperatures on species physiology and potential implications on their distributions, as some regions of the globe could become unsuitable for endotherms (Rezende & Bacigalupe, 2015).

Technological advancements

Technological advancements in wildlife research have revolutionized our ability to acquire detailed, accurate, and real-time information about species ecology and their daily decision-making processes. The current state of technology enables the tracking of animal migrations and the study of behaviour with unprecedented detail and accuracy, all while minimizing disturbance (Cagnacci et al., 2010; Kays et al., 2015,). Additionally, ongoing improvements in remote-sensing technology enhance the quality, utility, and volume of information generated, facilitating the integration of data from tracking devices and environmental information at large spatial scales with fine-scale resolution (Bütikofer et al., 2020; Valerio et al., 2020). The continuous development of computer power, processing capacity, and storage has reached a point where scientists can harness the incredible amount of information provided by movement ecology technology.

However, like all scientific endeavours, there is still much to be accomplished and ongoing improvements are constant. Throughout this thesis, I have highlighted certain limitations in my findings that would benefit from the technology advancements. Specially, obtaining fine-scale vegetation composition information is crucial for creating realistic vegetation cover layers, which can then be inputted in the microclimate models (Maclean et al., 2019).

Light Detection and Ranging (LiDAR) technology can accurately map vegetation cover at high spatial resolution, covering large areas and providing the necessary data to study microclimate refugia use in detail (Hancock et al., 2021). This technology can correct the underestimation of microclimate refugia use by detecting isolated trees, a habitat element utilized by little bustards during warmer periods of the day, often missed when using CORINE Land Cover maps (Korpela et al., 2010; Silva, *personal observations*; Chapter 2).

Furthermore, with the continuous generation of data from tracking devices and remote sensing satellites, research institutions must provide High-Performance Computing Clusters to facilitate the processing and analysis of this vast amount of information. The availability of a cluster within the Research and Specialist Computing Support service at the University of East Anglia was instrumental in making this thesis possible. It allowed for the generation of hourly ground-level temperature data over an 11-year period and the analysis of data presented in all chapters. The integration of cutting-edge technology, from tracking devices to remote sensing and high-performance computing, has significantly advanced the understanding of wildlife ecology and environmental responses.

Conservation of grassland species

This thesis provided important and timely insights about fine-scale environmental variation in grassland areas of the Iberian Peninsula. I showed the importance of considering microclimate refugia opportunities for little bustards' behaviour and movement strategies (Chapters 2-4). The potential of this thesis findings for the conservation of little bustards and other grassland species is unquestionable. However, much work remains to be done in order to implement the collaborative approach mentioned before. The next steps in this process would be to assess microclimate availability in current grassland areas of the Iberian Peninsula and identify those that could benefit from microclimate management. These areas would ideally benefit a wide variety of species and serve as a pilot to implement fine-scale habitat management in SPAs policies in the future.

Additionally, changes in land use are a pertinent and crucial subject that remains to be addressed and linked with microclimate refugia. Over the last decades, European grasslands have been facing unprecedented declines, primarily attributed to shifts in land use practices such as traditional agricultural abandonment, transition from extensive sheep farming to beef-cattle farming and intensified grazing (Faria & Morales, 2020; Schils et al., 2022; Tóth et al., 2018). These land use changes have been responsible for declines in grassland biodiversity, especially affecting bird communities (Báldi et al., 2005; Reino et al., 2010; Silva et al., 2024; Török et al., 2018).

Despite the existence of SPAs dedicated to preserve grassland species under the Birds Directive (79/409/EEC), there has been a significant loss of grassland area both inside and outside protected areas in recent decades (Gameiro et al., 2020). Recognizing the urgency of the situation, combined by potential exacerbation due to climate change and rising temperatures, it is imperative to promptly implement conservation measures to mitigate further land use changes and facilitate the recovery of European grasslands. Only through such actions can we allocate the necessary focus to the role of microclimate refugia within these ecological systems.

In conclusion, this thesis provides crucial evidence of the importance of fine-scale environmental variation in the species habitats and why it should be considered when planning species conservation, especially in building resilient habitats under current climate change. Hopefully, this research will inspire researchers to consider environmental variation at the scale individuals experience it, leveraging current available technology. Moreover, the aspiration is to establish a multisectoral working group that will effectively aim to preserve grassland species in the near future.

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