The influence of environmental conditions on individual behaviour and population trends of European birds

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Abstract

Global biodiversity is facing multiple interconnected threats due to anthropogenic activity. Changes in land use can cause habitat loss and significant disturbance, which may lead to population declines. Climate change may bring about warming temperatures, as well as an increase in the frequency of extreme weather events. The extent to which different taxa may be affected by these changes will vary, and therefore, successful implementation of conservation action requires an understanding of the factors determining species vulnerability. Individual behavioural responses to current environmental conditions, such as spatiotemporal changes in activity and use of micro-refugia, may provide insights into strategies of coping with extreme weather. In this thesis, I assess the range of climatic conditions species experience within their breeding distributions as well as individual-level behaviour across the temperature gradient, to explore the effects of environmental change on species and individuals, using the little bustard (*Tetrax tetrax*) and the Eurasian kestrel (*Falco tinnunculus*) as model species representing the grassland bird community of Southern Europe, an area already experiencing severe climatic changes. I produce a metric of the climatic niche breadth of 159 European breeding bird species, accounting for range size, and relate this to the species' population trends, to show that for species with similar range sizes, those experiencing a broader range of climatic conditions were less likely to be declining. I provide further evidence of a nuanced relationship between climatic niche breadth and range size and produce a metric that allows for the incorporation of this relationship into species vulnerability assessments. I then compare site usage by little bustards during the warmest part of the year and find that sites were more likely to be used if they were characterised by lower temperatures and greater microclimate refugia availability, but low shrubby cover. This suggests that while shrubs may provide microclimate refugia, too high shrub density may reduce site suitability. Finally, I investigate activity levels and micro-habitat use of Eurasian kestrels, and show that individuals were less active at higher temperatures and used trees as potential micro-refugia. The findings of this thesis highlight the crucial role of understanding individual behavioural responses in the face of extreme weather conditions, as well as the importance of micro-refugia availability for individual persistence under global warming.

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Chapter 1: General introduction

1.1 Global biodiversity trends and main threats

Global biodiversity loss is a major challenge facing humanity (Johnson et al. 2017). Anthropogenic activity has been identified as the main driving factor of these changes, having both direct and indirect effects on biodiversity trends (Tilman et al. 2017, Jaureguiberry et al. 2022). Nevertheless, there is variability across studies in terms of magnitude and even direction of the biodiversity trends (Dornelas et al. 2019, 2023, Finn et al. 2023). These differences may stem from the application of different measurement and estimation approaches or investigating biodiversity changes at different spatiotemporal scales (McGill et al. 2015, Gregory et al. 2023, Johnson et al. 2024, Fletcher et al. 2025). Studies often utilize relatively simple metrics such as species richness, which may fail to capture the nuanced relationships within communities and ecosystems (Fletcher et al. 2025). For example, while the number of species within a community may not change due to equivalent numbers of species lost and gained, phylogenetic or functional diversity could still decline (Voskamp et al. 2022), resulting in a community that is overall less productive or resilient to environmental change and disturbance (Cardinale et al. 2012, Laureto et al. 2015, Voskamp et al. 2017, Stewart et al. 2022).

The variation in trends observed across biomes or taxonomic groups may be a result of a variety of possibly interconnected and interacting threats affecting biodiversity (Howard et al. 2020). Furthermore, factors impacting biodiversity are unlikely to affect species through the same mechanisms and to the same extent, due to differences in species life history traits, ecological niche, or ability to adapt (Van Turnhout et al. 2010, Mason et al. 2019, Rigal et al. 2023). For example, while many bird populations within Europe have suffered significant losses, common and long-distance migrant species, as well as those associated with grassland, farmland, and coastal habitats have been particularly negatively affected (Burns et al. 2021). Estimation of global biodiversity trends has also been limited by data availability and biases, with some areas, biomes, and taxonomic groups being consistently underrepresented (Caldwell et al. 2024, Brodie et al. 2025). Understanding how global environmental change affects species and disentangling the species responses to it, is key to producing conservation guidelines and environmental policy, ensuring the protection of biodiversity.

Land use change

To understand biodiversity responses to environmental change, it is essential to identify the main threats and their impacts. Human activity has led to major changes in land cover, often resulting in significant disturbance and natural habitat loss (Jaureguiberry et al. 2022). Vast proportions of the landscape undergo changes to accommodate anthropogenic activities, including deforestation and conversion of areas into agricultural land or plantations (Giam 2017, Fleiss et al. 2022, Wiebe & Wilcove 2025). The creation and expansion of urban settlements have produced large patches which may be completely uninhabitable to numerous species and contribute to landscape fragmentation (Concepción et al. 2015). The use of materials such as concrete prevents access to soil, reducing resource availability (Fenoglio et al. 2021) and diminishing heat dissipation which contributes to relatively higher temperatures in urban areas (Jambhekar et al. 2025). In rural areas, changes and intensification of agricultural practices have had a disproportionately negative effect on farmland-associated species (Rigal et al. 2023, Busana et al. 2025). Monoculture plantations and cropland reduce habitat heterogeneity, decreasing the availability of food as well as nesting and refugia sites (Yahya et al. 2022, Vujanović et al. 2023). Earlier harvests may overlap with the birds' breeding season causing nest destruction and offspring loss (Gameiro et al. 2024). Furthermore, the overexploitation of natural resources, including overharvesting of terrestrial and marine wildlife has led to major trophic changes and even community collapse (Jaureguiberry et al. 2022).

Changes to land use are also associated with animals encountering infrastructure and being exposed to potentially toxic chemicals. Pesticides, which have been used increasingly frequently, may cause mortality as well as the disruption of processes within organisms (Beringue et al. 2024). The toxic chemicals may also be indirectly ingested, thus spreading across food webs (Wan et al. 2025). Pollutants and waste materials are found across ecosystems and may cause entanglement (Heinze et al. 2025), as well as internal damage or poisoning when potentially toxic materials and substances are ingested (Browne et al. 2015, Murray et al. 2016, Lopes et al. 2021). Collisions with buildings, energy infrastructure, or vehicles are also more likely (Grilo et al. 2021, Gauld et al. 2022, Pay et al. 2025). These disturbances not only cause direct mortality and reduce fitness but may also have behavioural implications (Doherty et al. 2021). Finally, the introduction of non-native, invasive species, both intentional and accidental, may result in population declines or even extinctions of native species, through outcompeting or facilitation of the spread of new pathogens (Tompkins et al. 2003, Clavero et al. 2009, Newsome et al. 2024).

Climate change

Anthropogenic activity has also led to global climate change, which has been identified as one of the largest current threats to biodiversity (Parmesan & Yohe 2003, Intergovernmental Panel On Climate Change [IPCC] 2023) and is now being explicitly considered in IUCN red list reports (Foden et al. 2019, IUCN 2025). Global warming and an increase in the frequency of extreme events can increase the occurrence of thermal stress for organisms (CaraDonna et al. 2017, Alfonso et al. 2021). The increased frequency of extreme weather events will also likely result in higher rates of disturbance to natural systems as well as potential direct harm to individuals, for example through injury due to heavy wind or rainfall, death through exposure, or wildfires (Sun et al. 2019). Heterogeneity and unpredictability of climatic conditions is also expected to increase, which may have a severe effect on animal populations (Vasseur et al. 2014). These increases in the frequency and duration of extreme events can have more detrimental effects on individual survival than an overall, gradual change in conditions (Marcelino et al. 2020).

The implications of environmental changes are likely to vary, with species showing a variety of responses (Prieto-Ramirez et al. 2018, Pollock et al. 2021). Some may gain while others will lose environmental suitability (Stephens et al. 2016), and therefore, understanding how to protect the species most vulnerable to these environmental changes is essential to design effective conservation strategies (Bloomgarden 1995, Scheffers & Pecl 2019, Synes et al. 2020). As the rate of environmental changes is uneven globally, the observed effects and responses may also vary spatially and temporally, where population trends become decoupled (Viana & Chase 2022), highlighting the need for an improved understanding of responses to environmental change at micro-scale (Gunn et al. 2022, Kemppinen et al. 2024). Moreover, identifying threat hotspots and most vulnerable populations requires mapping of the distribution of threats as well as the extent of exposure to environmental change (Buchan et al. 2022, 2023).

1.2 Species-level responses to environmental change

Physiological and morphological responses

Global warming and extreme weather events may cause morphological and physiological responses (Sheridan & Bickford 2011, Ryding et al. 2024). Bergmann's rule predicts that animals inhabiting warmer areas are likely to have a relatively lower body mass than individuals found in colder habitats (Meiri 2011). Smaller individuals may be able to withstand higher temperatures without experiencing extreme thermal stress compared to larger individuals (Buckley 2021). Hence, with global temperature increases, average individual body size within a population or species may decrease, as the frequency of larger individuals is reduced, while smaller ones become more common, which has already been observed in multiple studies (e.g. CaraDonna et al. 2017, Prokosch et al. 2019). However, this trend does not seem to be universal, with studies across taxonomic groups finding high between-group variability, as well as little to no support for this hypothesis (e.g. Gardner et al. 2011, Riemer et al. 2018). Overall, the generally larger species might be more severely affected by global warming than smaller ones (Lefort et al. 2015, Lindmark et al. 2019). Hence, the response to increased global temperatures could also differ between species of different body sizes, where larger individuals could show different strategies to survive in extreme heat compared to smaller animals (Fuller et al. 2016).

Distributional shifts

Species distributions may permanently shift in relation to environmental change (Maclean et al. 2008, Chen et al. 2011, McCaslin & Heath 2020). These changes may occur as a direct response to climate change. For example, as temperatures within areas occupied by the species exceed a tolerable threshold, species might shift their distribution to inhabit areas with less extreme temperatures (Thomas et al. 2006). On the other hand, climate change could affect the species indirectly, through the effect on resource availability, for example, by affecting the activity and distribution of prey species (CaraDonna et al. 2017, McCaslin & Heath 2020). Hence, as a result of range shifts, the distributional overlap between predators and their prey may be reduced (Carroll et al. 2024), and in response, the range of the population or whole species may shift to maintain overlap with resource distribution (Chen et al. 2011).

Environmental change may result in local or global extinctions (Thomas et al. 2004, Pio et al. 2014). Climate change has been identified as a major threat to species persistence, with even those previously assumed to be relatively resilient being at risk depending on the magnitude of changes (Malanoski et al. 2024). Species may disappear from previously occupied areas if conditions there become unsuitable. They may shift their distributions to areas that remain or become suitable (Chen et al. 2011), or if such areas are unavailable, become extinct. These may occur simultaneously with environmental changes, or there may be a delay in response (Gaüzère & Devictor 2021, Haddou et al. 2022), posing a further challenge to predicting threats to and responses at the global level.

Phenological shifts

In order to track seasonality and take advantage of suitable environmental conditions, phenological and life history responses, such as changes in the timing of breeding or migration may occur (Parmesan & Yohe 2003, , Lancaster et al. 2015, CaraDonna et al. 2017). For example, white storks (*Ciconia ciconia*) were found to either delay or advance their arrival at breeding sites depending on temperatures they were exposed to during wintering or migration (Gordo et al. 2013). Bird species were also observed to migrate shorter distances in response to climate change (Visser et al. 2009). Similarly, many species may start to breed earlier in the season, and the duration of breeding may also be reduced (Pearce-Higgins & Green 2014, Halupka & Halupka 2017, Hällfors et al. 2020). However, this phenological shift may not be the same or occur to the same extent across whole communities, resulting in a mismatch between the species and its resource (Visser & Both 2005, CaraDonna et al. 2017, Burgess et al. 2018, Shipley et al. 2020), potentially causing population declines (Both et al. 2006).

Environmental change can also affect biotic interactions, such as competition or predation (Gilman et al. 2010). If a shift in breeding phenology results in competing species breeding at the same time, this may lead to increased intensity of competition during that period (Hällfors et al. 2020). Additionally, declining resource availability, in the form of reduced number of suitable nesting sites or decreasing prey populations, could result in a considerable increase in competition intensity (Mason et al. 2014). As the size of habitable areas decreases, predation intensity in these sites may increase (Gilman et al. 2010). Moreover, parasite infection may amplify the negative effects of global climate change, for example through weakening the individual and reducing their heat tolerance (Hector et al. 2019). Finally, higher temperatures as well as distributional and behavioural changes in pathogen hosts as a result of climate change, may affect disease prevalence (Yon et al. 2019, Prosser et al. 2023).

Responses to environmental change may differ among species and populations (Gardner et al. 2011, Catry et al. 2015, Gillings et al. 2015, Riddell et al. 2021), and even vary depending on life-history strategy and stage (McDermott Long et al. 2017). Individual-level behavioural changes are already occurring in response to altered environmental conditions. These may include the adjustment of large- and small-scale spatiotemporal movement patterns, such as migration, diel activity, or habitat selection (e.g. Harmange et al. 2021, Ruegg et al. 2021, Vignali et al. 2021, Alessandrini et al. 2022). Behavioural responses may occur at population- or individual-levels rather than uniformly across species. This heterogeneity poses a challenge for quantifying the impact of environmental change, as disentangling these mechanisms requires fine-scale individual-level observations which are often limited.

1.3 Population- and individual-level responses to environmental change

Migratory behaviour

Climate change has been shown to have varying effects depending on migratory status, with long-distance migrants being particularly vulnerable (Lees et al. 2022). Long-distance migrants may have broader annual climatic niches (Ruegg et al. 2021) and exhibit greater flexibility in terms of the range of climatic conditions they encounter but are more likely to be affected by phenological mismatches (Lameris et al. 2018, Robertson et al. 2024). Hence, within-species diversity in migratory strategy may allow the species to respond better and make them less susceptible to environmental change (Gilroy et al. 2016).

Environmental change may drive shifts in migratory strategies, in terms of migratory distance and route (Gu et al. 2021). With seasonally changing climatic conditions, individuals may adjust their migratory patterns to track suitable conditions for breeding or wintering (Martínez–Meyer et al. 2004, Zurell et al. 2018, Illán et al. 2022, Yanco et al. 2024). Furthermore, microclimate availability and exposure to extreme weather may also affect individual migratory behaviour. For example, individuals of a partially-migratory bird species, the little bustard (*Tetrax tetrax*) have been shown to remain longer at breeding areas where microclimate refugia were available, unless exposed to particularly high temperatures (Ramos et al. 2023a). Individuals also moved longer distances when little microclimate refugia was available within their breeding areas, to locations with either greater microclimate refugia or those with lower temperatures during the post-breeding season (Ramos et al. 2025).

Temporal activity patterns

Individuals may reduce their activity during periods when conditions are particularly harsh, e.g. during the warmest parts of the day (Franzén et al. 2022). Furthermore, they might shift their diel activity to periods of the day when conditions are suitable, for example, by only foraging during times of day when temperatures are within a tolerable range, or even switching between predominantly diurnal or nocturnal activity (Riddell et al. 2021, Gilbert et al. 2022). However, this may significantly limit the time available for foraging, particularly when foraging outside of daylight hours is impossible (Silva et al. 2015). Furthermore, temporal changes in activity patterns driven by environmental changes may result in mismatches between prey and predator peak activity times, and may lead to reduced foraging success and increased effort, as individuals may need to forage longer to obtain sufficient food (Cunningham et al. 2021). These shifts in temporal activity are likely to result in decreased adult fitness and increased mortality. Reproductive success might also be directly reduced, as the quantity of food that adults are able to supply to juveniles will be limited, causing them to starve (van de Ven et al. 2019, Seress et al. 2020). Furthermore, juvenile and adult mortality could further increase due to greater incidence of exposure to extreme heat as well as cold, e.g. during periods of intense rain and wind (McKechnie & Wolf 2010).

Spatial activity patterns and use of micro-refugia

Site selection may be altered and the frequency of use of a variety of sites may change due to patches becoming unsuitable through land use change or the need to shelter from unfavourable conditions under climate change (Suggitt et al. 2012, Gilbert et al. 2022). Lack of suitable habitat might significantly limit species distributions, in extreme cases leading to local or global extinction (Tellería et al. 2019). As parts of the species distribution become climatically uninhabitable, individuals may retreat to sites with suitable microclimate, known as microclimate refugia (Massimino et al. 2020). This was observed in white-tailed deer, which changed the frequency with which they utilized conifer compared to deciduous forest sites depending on ambient temperature (Gilbert et al. 2022). Similarly, little bustards were shown to utilise microclimate refugia more frequently at higher temperatures (Ramos et al. 2023b). Such refugia areas may possess characteristics which reduce or even eliminate the negative effects of climate change within an individual's home range (Suggitt et al. 2015, Williamson et al. 2021). For example, individuals using forest sites showed a smaller temporal body mass decline than their counterparts utilizing different habitat types (Reiner et al. 2021). Furthermore, north-facing rather than south-facing sites may be selected, as these will be less exposed to sunlight, and therefore, to heat (Suggitt et al. 2011). Microclimate refugia may often be the last stand of rare and endemic species (García et al. 2020). The availability of a broad variety of suitable microclimate sites, may thus be the key to enabling individuals to persist in a changing environment (Suggitt et al. 2018). Hence, identifying the characteristics of these potential refugia sites may be crucial for conservation (Keppel et al. 2012).

The use of fine-scale patches to shelter from unfavourable conditions highlights that individuals are unlikely to be experiencing the landscape in a homogeneous way, but rather utilize a variety of its characteristics at the microhabitat and microclimate scale (Bütikofer et al. 2020). This also means that the effects of environmental change on individuals are likely to operate at a much smaller, microclimate scale (Suggitt et al. 2011, Potter et al. 2013, Maclean et al. 2017, Bramer et al. 2018). To date, this issue has been frequently recognised (e.g. Bütikofer et al. 2020), yet studies looking at the impact of climate change, individual use of environmental space, and responses to climate change at sufficiently fine spatial scales are lacking. A majority of studies informing policy and conservation action identify climate refugia at landscape and global scales (e.g. Warren et al. 2018). Broad macroclimatic scales have been shown to produce inaccuracies, as well as to over- or under-estimate the effects and associated responses or even miss them completely (Stark & Fridley 2022, Maclean & Early 2023). Hence, to obtain a full and detailed picture of population and individual strategies, we need to study microclimate at the intersection of individual and distributional position scale (Suggitt et al. 2011, Huang et al. 2021).

1.4 Differences between populations within species' ranges

Populations at the edge of the species distribution may be differently affected by climate change than those found at the core (Gaston 2003, Oliver et al. 2009). In particular, peripheral suitable habitat availability can be much more limited than toward the core of the range, thus, these populations may be more susceptible to habitat loss and other adverse effects of changes in climatic factors (Cianfrani et al. 2018, Orme et al. 2019).

Furthermore, both the habitat, and therefore, the populations occupying it, can be considerably more fragmented at the edge than at the core of the species distribution (Gaston 2003).

Microclimate refugia might become of crucial importance to populations and individuals at range edge (e.g. García et al. 2020). Habitat specificity has been shown to increase at the edge of species distributions (e.g. Oliver et al. 2009). The frequency of use of microclimate refugia is likely to also be higher in peripheral populations, as conditions become increasing suboptimal going from the distribution core to edge (Gaston 2003). Furthermore, the behavioural strategies might become more prominent or differ from those utilized by individuals occupying the central parts of the species distribution (e.g. Eccard et al. 2023).

1.5 Ecological niches and environmental change

Variation in ecological niches may differentiate the effects of environmental change on species (Smeraldo et al. 2021). The ecological niche describes the range of conditions that the species experiences and can be defined across multiple dimensions (Ingram et al. 2018). Specialist species in terms of habitat or diet may be more severely affected than generalist species, as these species may show lower flexibility in their response to climate change (Roberts et al. 2011, Pearce-Higgins et al. 2015, Rödder et al. 2021). On the other hand, ecological specialisation may become more common and widespread as a result of climate change, for example, as has been observed for two generalist species of coral reef damselfish, which became more closely associated with a specific habitat type as water temperatures increased (Matis et al. 2018).

The niche characteristics may vary within a species: between populations or even individuals (Bolnick et al. 2003, Schirmer et al. 2020). This niche diversity could be key for species persistence under environmental change. The degree of specialisation, and therefore, the response to environmental change within a species, can vary depending on the position within the distribution. Individual dietary niche may be narrower towards the edge of their species distribution as the availability of their favoured resource becomes more and more limited, or even absent (Juškaitis et al. 2015). Severely limited or fragmented habitat as well as extreme climatic conditions can also be a driving force for individual specialisation on more energetically profitable resources, for example larger prey items, in order to persist in the challenging environment of the species range edge (Zalewski 2005). On the other hand, peripheral populations may become more generalised to maximise their use of the limited but still available resources (Shively et al. 2018). Finally, some studies have found no differences in the degree of specialisation across the species range (e.g. Appel et al. 2018), which highlights the diversity of strategies and challenges encountered throughout global biodiversity.

The characteristics of the climatic niche of a species may predict how it responds to environmental change. Experiencing and tolerating a wide range of climatic conditions, i.e. having a broader climatic niche, may be linked to greater resilience to climate change (e.g. Ruegg et al. 2021). This is frequently linked with the size of the species' distribution, as a relatively small area may provide a lower opportunity for encountering diversity in climatic conditions. This link between distribution size and vulnerability to climate change has been previously shown (Vincent et al. 2020), however, common and widespread species have also displayed disproportionate declines (Inger et al. 2015, Daskalova et al. 2020), suggesting that the size of the species distribution may be an insufficient approximation of the range of climatic conditions experience. These declines of widespread species may be because while there is a positive correlation between spatial and climatic breadth (Dallas & Kramer 2022), this relationship is likely more nuanced. The most frequently occurring climates have been found to occupy a relatively low proportion of the total global climatic space, and therefore, a species with a seemingly large distribution may still have a relatively narrow climatic niche (Rodrigues & Botero 2025). Furthermore, species with large distributions but narrow climatic niches may be relatively more susceptible to climate change as any change in climatic conditions across the range will quickly fall outside of the suitable range, causing distribution-wide declines. Finally, any currently drawn inference on the relationship between climatic niches and the effect of environmental change may be limited as the observed niche is the realised rather than the fundamental climatic niche of the species, and therefore, with changes in climate, the realised climatic niches of species may also shift (Chevalier et al. 2024).

Incorporating the significant between-individual variability and disentangling the fine-scale individual-environment relationships are essential for designing effective management strategies and conservation action that will maximise the chances of the persistence of the highest proportion of global biodiversity. Hence, it is of paramount importance to continue improving our understanding of the mechanisms driving species and individual vulnerability to environmental change, as well as identifying the behavioural responses which are likely to be key for survival of individuals as climate changes and extreme weather events become more frequent. This requires both fine-scale environmental data as well as individual-level observations. With technological advances, and particularly, the development of GPS tracking devise, it is possible to observe individual behaviour at previously impossible scales (López-López 2016) and link this behavioural to the macro- and micro-scale environmental conditions the individuals are experiencing.

1.6 Study areas and study species

This thesis aims to investigate the impact of environmental conditions at population and individual levels. First, I quantify the realised climatic niche of 159 breeding bird species within Europe, then focus on two case study species (Eurasian kestrel *Falco tinnunculus* and little bustard *Tetrax tetrax*) to examine the characteristics of sites used and activity patterns during a season when individuals are likely to experience the highest temperatures across their annual cycle. The species were studied in three regions within the Iberian Peninsula (Portugal and Spain) where monitored populations of the species persist: Alentejo (Portugal), Extremadura, and Andalusia (Spain).

The climate within the Iberian Peninsula is characterised by dry, warm summers and wet but mild winters, with the area already having been exposed to global warming in recent decades. The predominant habitat type within the study areas are semi-natural grasslands, composed of low herbaceous vegetation cover with small areas of shrub and sparse trees, and some wetland areas in Andalusia (Doñana National Park). These grasslands have been formed through agricultural activity, and therefore, are susceptible to changes in management strategies. The habitat has undergone significant transformation in recent decades, with cereal fields now changed to areas for livestock grazing, as well as the type of crop grown also having changed, including increasing creation of olive groves and vineyards.

The little bustard and Eurasian kestrel represent the grassland avian community within the semi-natural grasslands of the Iberian Peninsula and are suitable study systems because of their differing ecological characteristics, and particularly the differences in foraging behaviour between the two species – the little bustard is a ground foraging bird, and the kestrel is an aerial predator. Hence, not only are their behavioural responses to high temperatures likely to be different, the characteristics of sites used as micro-refugia as well as more generally their refugia requirements may also differ. In particular, the types of landscape feature that may create the refugia used by either species is likely to be different. As the little bustard is a ground forager, the aspect of foraging areas may also play an important role for this species – shaded, north-facing slopes may be a key source of shelter from exposure to high temperatures during the day. In contrast, Eurasian kestrels do not spend almost any time on the ground, and therefore, the aspect may not be as important, however, they may instead rely on wall cavities or trees as refugia, both features which the little bustard is unlikely to utilise. Furthermore, both species are resident within the Iberian Peninsula and exhibit variability in the small-scale movement strategies that the individuals within these populations adopt (García-Silveira et al. 2022; Ramos et al. 2023a). These differences are hypothesized to be a response to seasonal changes in food availability as well as exposure to particularly high temperatures and varied micro-refugia availability (García-Silveira et al. 2022; Ramos et al. 2023a; Coutinho Soares et al. 2025).

The little bustard populations within the Iberian Peninsula have faced dramatic declines in recent years, with a decrease of 77% being recorded in the last two decades (Silva et al. 2023). These decreases have been attributed to landscape transformation, in particular the intensification of agricultural practices (Silva et al. 2024). As a result, the distribution of the little bustard populations has become restricted to areas with remaining semi-natural grasslands, which are becoming climatically unsuitable. Hence, understanding site usage patterns, especially under ongoing habitat and climate changes, is of key importance to designing conservation action for this and other grassland species within the Iberian Peninsula.

The Eurasian kestrel is a species that is widespread across Europe, with Iberia falling at the warm edge of the species' range and indeed its climatic niche. Hence, individuals occupying these areas are likely to be exposed to particularly high temperatures in relation to other parts of the kestrel's European range, providing an ideal case study for understanding individual behavioural responses to high temperatures.

Little bustard

The global distribution of the little bustard can be separated into the eastern range, with breeding populations in southern parts of Russia, Ukraine, Kazakhstan, and China, and the western populations within the Iberian Peninsula, as well as parts of France and Morocco (Morales and Bretagnolle 2022). This species utilizes open habitats such as grasslands, scrublands, steppe, and agricultural areas (Silva et al. 2004). Individuals forage on the ground and adults are almost strictly herbivorous, with their diet being dominated by legumes and grasses, but will also consume arthropods especially in the chick-feeding period (Bretagnolle et al. 2022).

The breeding season within the western populations starts in March or April and can last until early July (Bretagnolle et al. 2022). During the breeding season, males establish loosely spaced aggregations to display in order to attract females, which are referred to as an exploded lekking system. The little bustard nests on the ground within herbaceous vegetation to shelter the nest from adverse weather as well as potential predators (Mañosa et al. 2022). Only females provide care to the young, therefore, males may move to non-breeding areas earlier than females. The eastern populations are fully migratory, as are populations within France (Morales et al. 2022). However, individuals breeding within Portugal and Spain display more varied migratory strategies, where some individuals may be resident, while others undertake short- to medium-distance post-breeding movements, to areas within the North of the Iberian Peninsula (García de la Morena et al., 2015; Coutinho Soares et al. 2025).

While globally it has been classified as ‘Near Threatened’ (IUCN 2025), the populations within the Iberian Peninsula have undergone dramatic declines in recent decades and have been classified as ‘Vulnerable’ within Europe (IUCN 2025).

The little bustard data used in Chapter 3 of this thesis was collected between 2009-2019, by the Steppe Birds MOVE group (based at CIBIO/BIOPOLIS/University of Porto; PI: João Paulo Silva). Trapping occurred at known lekking sites in breeding areas within Alentejo, Portugal (Castro Verde, Vila Fernando) and Extremadura, Spain (Llanos de Caceres, Merida, Campina Sur/La Serena) regions. Males were attracted to the trapping site using a stuffed decoy of a female and trapped using snares. The GPS tracking devices (Platform Transmitter Terminal (PTT) Solar Argos/ GPS 30g from Microwave Telemetry; Global System for Mobile Communications (GSM) Flyway 38g from Movetech Telemetry) were attached with a Teflon Ribbon thoracic harness. The weight of the device was on average 3.2% of the individuals’ body weight (Ramos 2024). Tracking data processing, including microclimate modelling has been carried out by Rita F. Ramos (Ramos 2024), and I have performed further processing to produce the final data used for analyses.

All captures and handling of little bustards, and deployment of GPS tracking devices were performed under license and in accordance with relevant guidelines and regulations. Licences were issued by 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.

Eurasian kestrel

The Eurasian kestrel is widely distributed throughout Europe and parts of Asia and Africa. Kestrels breeding in eastern and northern Europe migrate to sub-Saharan Africa (BirdLife International 2021). Populations within south-western Europe are mostly resident, however, studies show that individuals from these populations may also perform short- to long-distance movements (e.g. García-Silveira et al. 2022). The kestrel is found in open habitats, predominantly in farmland, as well as in urban areas (Shrubb 1993; Riegert et al. 2009).

Kestrels feed on rodents (*Mus*, *Apodemus*, and *Microtus* spp.), small birds, and insects (Casagrande et al. 2008; Orihuela-Torres et al. 2017). While they also hunt from perches, kestrels exhibit a characteristic foraging behaviour, flying between patches and hovering in the air when prey is detected (Shrubb 1993; Village 2010). The breeding season starts between April and May and can last until late July. Eurasian kestrels may use different structures for nesting, commonly occupying wall cavities, nest boxes, or abandoned nests of other species. Males and females share parental care, with females predominately incubating from laying and within the first two weeks after hatching (Costantini and Dell'Omo 2020).

The Eurasian kestrel has been classified as 'Least concern', however, populations in Europe have been declining, with loss of habitat due to changes and intensification of agricultural practices and increased use of rodenticides being the main identified drivers behind the negative trend (BirdLife International 2021).

Eurasian kestrel trapping was carried out in three areas were breeding populations are monitored: the Castro Verde Special Protection Area (SPA) in Portugal, and areas in Doñana National Park and around Seville in Andalusia, Spain. Adult individuals were captured near breeding sites using bow-net traps or within nest boxes. The tracking devices were attached to the back of the animal using a Teflon ribbon harness. The weight of the device did not exceed 4% of the individual's body mass.

In Portugal, 15 devices were deployed. LoRa GPS tracking devices were used (≤6.5g; UEA IP device). I programmed and tested these devices, and they were assembled within custom-made 3D printed housings and tested at UEA by me and other members of the research group. The tracking data were collected by me, Aldina Franco, and Inês Catry, and I have carried out all data processing.

In Spain, 58 devices were deployed. The following device models were used: Axy-Trek (4g; TechnoSmart, Italy), UVA-BITS (7g; University of Amsterdam, The Netherlands), Pathtrack nanofix GEO+RF (4.7g) and MINI loggers (5g; INTERREX Poland). These data were collected through the MERCURIO-SUMHAL project (EBD-CSIC, PI: Javier Bustamante) and are available on Movebank (ID: 2970193504). Additional data on breeding timings were compiled from camera trap footage by David Ramón-Martínez.

Permissions to trap and deploy devices on Eurasian kestrels were obtained from ICNF (PT; permits 84/2021, 92/2023, 104/2024), Consejería de Sostenibilidad y Medio Ambiente, and Consejería de Agricultura Pesca y Desarrollo Rural, Junta de Andalucía (ES; Dirección General de Gestión del Medio Natural, DGMN 02/02/2018, DGMN 10/08/2018, DGMN 11/120/2021 and DGMN 28/07/2023 and Dirección General de la Producción Agrícola y Ganadera DGPAG 14/05/2018/086 and DGPAG 29/01/2024/015).

1.7 Thesis structure

This thesis investigates the range of climatic conditions experienced by species within their geographic distributions and explores differences in individual habitat use and activity in response to high temperatures, with the aim to improve our understanding of how species, populations, and individuals may be affected by and respond to global climate change. To achieve these aims, in Chapter 2, I determine the realised climatic niche breadths of multiple European breeding birds and relate these to the species' long-term population trends. In Chapters 3 and 4, I use two species, the little bustard (*Tetrax tetrax*) and the Eurasian kestrel (*Falco tinnunculus*), as case studies to investigate habitat use and behaviour across the temperature gradient. In particular, I use GPS tracking data to gain insight into differences between sites used during the warmest part of the year, and assess the utilisation and usage frequency of potential micro-refugia sites.

Widespread species are often assumed to be overall resilient to environmental change, as broad geographic range is frequently equated with experiencing, and therefore, being able to withstand, a broad range of climatic conditions. However, recent studies have shown significant declines in common and widespread species (Inger et al. 2015). In **Chapter 2** I quantify the range of climatic conditions experienced by 159 bird species within their European breeding distributions by calculating a metric of their realised climatic niche breadth accounting for distribution area. I relate this metric to long-term population trends of these species to investigate whether for a given distribution area, the species with a broader climatic niche are less likely to be declining. This chapter is published in the *Journal of Biogeography*.

Individuals move to escape unfavourable conditions or lack of resources. This is a challenge for the design and management of protected areas, as these are static in space, and if conditions are seasonally unsuitable, the focal species may move outside existing protected areas, exposing them to more threats. In **Chapter 3** I use GPS tracking data of 47 little bustards to compare the post-breeding conditions at used and non-used sites, and predict site suitability changes under three warming scenarios. This chapter is published in *Biological Conservation*.

Individuals may employ a variety of behaviours to withstand exposure to high temperatures. They may reduce activity at times characterised by particularly warm weather and may utilise habitat features, known as micro-refugia, that shelter them from the heat. With global warming, the frequency and intensity of extreme weather events such as heatwaves will increase, and therefore, understanding these behavioural responses as well as ensuring the availability of micro-refugia will be paramount to individual persistence. In **Chapter 4** I use GPS tracking data of 48 Eurasian kestrels in Portugal and Spain to explore activity patterns across the temperature gradient and investigate the use of trees as potential micro-refugia to prevent exposure to high temperatures. This chapter will be submitted to the *Journal of Animal Ecology*.

In **Chapter 5**, I present the general conclusions and insights from the empirical chapters, discuss the broader context and implications of the findings presented in this thesis in terms of conservation in the face of global environmental change, as well as directions for future research.

Each chapter of this thesis is written as a standalone publication, with the relevant references and supporting information directly following the main text.

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European breeding bird declines associated with narrower climatic niches

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ABSTRACT

Aim

Anthropogenic climate change has increasingly been identified as a major threat to global biodiversity. However, the extent of this threat is likely to be uneven across species, due to differences in life histories or exposure to environmental change. The range of climatic conditions a species experiences across its range extent, known as the realised climatic niche, may be an indicator of species resilience to climate change. Species with large range extents, occurring across diverse climatic conditions, are expected to be less affected by climate change due to lower physiological constraints and tolerance to a wider range of climates. However, this may not be the case if local populations are adapted to specific environmental conditions. In this study, we investigate whether the extent of the species' realised climatic niche, also known as the climatic niche breadth, is linked to their long-term population trends.

Location

Europe

Taxon

Birds

Methods

We extract climate data across the breeding-only and resident ranges of 159 European bird species and use an ordination method to produce a representation of the species climatic niches. We then relate the niche breadth of each species to their range area, and incorporate this relationship, along with the species' diet, main habitat type, migratory status, and average body mass, to investigate their relationship with the species long-term population trend.

Results

Species with small range areas showed larger variation in climatic niche breadth than species with larger ranges. For species with similar range areas, those with broader climatic tolerance were less likely to be declining than those with narrow climatic niches.

Main conclusions

These findings can help us understand the threats associated with climate change and allow for rapid assessment of the importance of climatic factors on population trends, providing an invaluable tool for targeting habitat conservation.

Keywords: climatic tolerance, European breeding birds, population declines, population trends, realised climatic niche, species ranges,

2.1 Introduction

In the face of the global biodiversity and climatic crises, understanding the drivers of species population trends is of key importance to revert or slow biodiversity declines (Poiani et al. 2011). Climate has been shown to be a major influence, impacting population dynamics and spatial distributions of many species (Parmesan & Yohe 2003, Spooner et al. 2018, Intergovernmental Panel On Climate Change (IPCC 2023). Species responses to climate change, including phenological and behavioural changes, can vary with factors such as body mass, diet type, migratory strategy, or main type of habitat used, with some groups being more affected than others (Gordo et al. 2013, Rushing et al. 2020, Martay et al. 2023). For example, long-distance migratory species have suffered stronger populations declines than either short-distance migrants or resident species (Lees et al. 2022), with climate-driven phenological changes resulting in mismatches between the peak of food abundance and migrant arrival identified as one of the causes for these declines (Both et al. 2006, Jones & Cresswell 2010, Lameris et al. 2018). Many species are experiencing changes in climatic suitability across their ranges as a result of climate change, particularly within breeding sites (Howard et al. 2020, Martay et al. 2023). Many areas currently occupied may become unsuitable in the near future, causing species distributions to shrink due to local extinctions, or shift towards new areas with suitable conditions (Huntley et al. 2008, Chen et al. 2011, McCaslin & Heath 2020). This is possible because populations can grow faster in areas with high climatic suitability and may be limited in areas with less suitable conditions, with consequences for population trends and long-term persistence (Ruegg et al. 2021). These lines of evidence suggest that species with narrower climatic niches, i.e. the range of climatic conditions that species tolerate and in which populations are able to persist, may be more vulnerable to the impacts of environmental change, although this prediction has seldom been tested at large spatial scales.

Species' range area has been shown to be a good predictor of responses to climate change (Schwartz et al. 2006), as well as declines in abundance (Collen et al. 2011) and vulnerability to habitat loss (Staude et al. 2020). While species distributions are determined by the interplay of a range of factors, species occupying smaller areas are more likely to have more specific climatic requirements compared to widespread species (Pigot et al. 2010, Graham et al. 2010, Freeman et al. 2022). Furthermore, the scale at which a species' distributional or phenological shifts occur, triggering any potential mismatches with resources, may only affect a relatively smaller proportion of a large range compared to that of narrowly distributed species. Hence, based on climate conditions alone, species with larger range areas would be expected to tolerate and thrive in a wider range of conditions and be relatively more resilient to changes in climate (Schwartz et al. 2006, Ohlemüller et al. 2008). However, many widespread species have been facing population declines (Elliott et al. 2010, Burns et al. 2021) which, among other factors, have been attributed to climate change (Howard et al. 2020, Buchan et al. 2023).

One possible reason for the recent climate-related declines of widespread species is that the extent of and variation in climatic conditions are uneven across geographic space, with some conditions being more widespread than others (Huntley et al. 2016). Hence, while the two may generally be correlated (Dallas & Kramer 2022), a large area occupied is not necessarily synonymous with a large range of climatic conditions, indicating that range area alone may not always be a sufficient predictor of the impacts of climate change on species (Ficetola et al. 2020). New hypotheses are therefore needed to help explain why some common wide-ranging species are currently facing sharp declines in abundance (Gaston & Fuller 2008, Gregory et al. 2019, 2023). In turn, biodiversity conservation planning needs to consider the level of exposure to climate change, and species' ability to tolerate and adapt to changing climatic conditions, and the extent to which these can be predicted from trait-related susceptibilities (Foden et al. 2013).

Species' climatic niche breadth can help predict responses to climate change (Herrera et al. 2018). Numerous studies have investigated the role of climate change as a driver of population declines (e.g. Jiguet et al. 2007, 2010a; Tayleur et al. 2016), however, only temperature metrics have been used to define the climatic niche, which may lead to the omission of important across-species variability and produce an incomplete characterisation of the species' climatic niche (but see Ruegg et al. (2021) and Hällfors et al. (2024)). Furthermore, while the size of the species' range is usually considered in these studies, it is considered separately to the climatic niche. While range size is likely to be correlated with climatic niche breadth, this relationship is unlikely to be ubiquitous and species with similar range sizes may be exposed to different variability in climatic conditions. Disentangling the relationship between range size and climatic niche breath could, therefore, provide important insights into species responses to climatic conditions and help explain the large variability in population trends. We aim to present a more complete view of the realised climatic niche while explicitly incorporating the effects of range size.

Birds are a well-studied taxon with high-quality population and distribution data available across broad spatial scales (e.g. Gregory et al. 2005, Ding et al. 2024). Due to this, they have been commonly used as indicator species in biodiversity assessments (Gregory et al. 2019, Fraixedas et al. 2020). The Pan-European Common Bird Monitoring Scheme (PECMBS) collates data from long-term population surveys carried out by regional schemes across Europe, allowing species population trends to be monitored over time (Gregory et al. 2005, Brlík et al. 2021). At the same time, wide-scale declines among bird species breeding in Europe have been observed (Burns et al. 2021). The wealth of data collected as well as the challenges faced by this taxonomic group make them an excellent taxon for testing hypotheses on climatic niche breadths.

Here, we aim to investigate whether the extent of the climatic niche breadth influences the long-term population trends of breeding birds in Europe. We account for range size, species traits such as migration strategy, main habitat type occupied, diet type, and mass, as well as species' tolerance to human-modified environments. We predict that for two species with a similar breeding range size, the species with a narrower climatic niche breadth will be more likely to be declining.

2.2 Methods

Species distributions and population trend data

This study included distribution data for all bird species that have breeding or resident ranges in Europe and for which population trend data is available. The species' breeding and resident ranges were obtained from BirdLife International (2020). These have been collated and updated up to the year 2020. For each species, we obtained the slope of the population trend calculated over the years 1980-2019 from the PECBMS dataset which includes 170 species (Gregory et al. 2005, Brlík et al. 2021). Our final dataset included 159 species. The common pheasant (*Phasianus colchicus*) was removed due to it being a non-native species frequently released into the wild for hunting purposes. A further ten species were removed as only a 10-year population trend was available for them (the minimum number of years over which a long-term trend was calculated was 22, median = 39; Supporting information). The long-term European population trends of the species considered in our study varied between 0.91 and 1.07, with values of 1 suggest that the population is stable, values above 1 indicate a population increase, and values below 1 – a decreasing population trend.

Realised climatic niche breadth

The study extent was limited to the geographic extent of Europe, bound at longitudes from -24.33 to 59.00° and latitudes between 34.92 and 75.00°. To represent the climatic conditions within the study extent, we used the 19 bioclim variables, averaged over the years 1970-2000 from WorldClim2 at 5-arcminute resolution (Supporting information; Fick & Hijmans 2017). This 30-year climate norm period was considered the most appropriate to characterise the climate over the years in which the bird species population trends were calculated (Supporting information).

To obtain the climatic data within each species' European breeding distribution, the WorldClim2 rasters, containing the 19 bioclim variables, were cropped to match the species distribution polygons (obtained from BirdLife International (2020)), then the points and associated values of each of the variables were extracted. This approach assumes the current bird distributions have, on average, remained constant over the 30 years covered by the climate information used in this study.

To construct the species' climatic niches, we followed the framework outlined by Broennimann et al. (2012). The scaled and centred 19 bioclim variables were transformed through principal component analysis (PCA-env) using the *ade4* package (Dray & Dufour 2007). The PCA was carried out with climatic data for the entire study extent, therefore, constraining the climatic niche within the range of climatic conditions available across the geographic extent of Europe (Broennimann et al. 2012). The number of principal components (axes) was set to two, as these cumulatively explained over 70% (73.47%) of the variance in the data (Supporting information). These new orthogonal axes represent the climatic niche of each species using dimensions created as a combination of climatic variables (Broennimann et al. 2012).

The principal component scores corresponding to data points within each species' breeding and resident distribution were used to produce a hypervolume representing the species climatic niche (Blonder et al. 2014). This was repeated separately for each of the species. The hypervolume was constructed using the support vector machine algorithm with default parameters from the package *hypervolume* (Blonder et al. 2018, 2023; Supporting information). The volume of the shape obtained was then taken as a measure of the breadth of the realised climatic niche. As we only use two dimensions, the metric representing the realised climatic niche is the area of the resulting shape, however, for clarity we refer to this as the volume.

Niche breadth and population trend relationship

The range of climatic conditions experienced by species, and thus the breadth of their climatic niche, has been shown to be correlated with the area of the species' range (Ficetola et al. 2020). The larger the area occupied, the more likely it is to encompass a broader variety of climatic conditions. We produced an index of climatic niche breadth to range area by dividing the species' realised niche breadth (i.e., the climate niche volume) by the species' breeding-only and resident area (within the study extent). An increasing value of this index indicates a broad climatic niche breadth relative to the range area, while a low value suggest that the climate niche of that species is relatively narrow for the area of its range. This niche breath/range area index was then related to the species long-term population trends in Europe (PECBMS). An alternative approach would be to obtain the residuals of the relationship between the niche breadth and species range size. However, due to the non-linear relationship between the niche breadth and range area, as well as unequal residual variances across the range of fitted values (heteroscedasticity), this approach was considered unsuitable (Supporting information).

Across the 159 breeding bird species, the long-term population trend was available for a different number of years, ranging between 40 and 22 years. For each species, we calculated the proportion of the maximum number of years, for which the trend was produced. Hence, records for species for which the population trend was calculated over the full 40 years received a value of 1, while others were assigned a proportionally lower number. This enabled us to give more weight to the species that had a population trend estimated over a longer period, which may capture responses to climate change across broader temporal scales.

Furthermore, depending on species life histories, (e.g. habitat associations, migratory strategy), the breeding climatic niche obtained may represent a different proportion of the species' entire niche. For example, the overall realised climatic niches of migratory species with large wintering areas outside of Europe, and therefore, the climatic variability these species encounter, may be underrepresented in this study. This is also linked with population trends, as factors outside of the extent of this study may have a strong impact on migratory species (Howard et al. 2020). Thus, to account for these differences across species, we included a weight in our model, calculated as an average of two proportions: (1) the proportion of the total species distribution area falling within the study extent, and (2) the proportion of years over which the species population trend was calculated.

We classified each species' diet type as feeding mainly on invertebrates ('Invertebrate'), plants and/or their seeds ('Plant/Seed'), vertebrates or through scavenging ('VertScav'), or omnivorous ('Omnivore') following the EltonTraits 1.0 dataset (Wilman et al. 2016). Moreover, migration strategy may also influence vulnerability to environmental change (Samplonius et al. 2018), and this study includes both migrant and resident species. Thus, we categorised the migration strategy of each bird species as resident, partial or full migrant, following Gilroy et al. (2016). We also included natural logarithm-transformed body mass of each species, obtained from the EltonTraits 1.0 dataset (Wilman et al. 2016). Body mass is also a good proxy for species longevity, as the rate of any change will be different for species with a slower generational turnover (which also tend to be larger overall). While our species list includes multiple avian groupings, we have not accounted for phylogenetic relationships as similar studies looking at population trends, as well as climatic niches and range areas, have not identified a significant association with these (Koleček et al. 2014, Kambach et al. 2019). Finally, while evidence of the importance of niche position and the latitudinal gradient in climate has been previously demonstrated (e.g. Jiguet et al. 2010b; Dallas & Kramer 2022), we have not included this in our analysis because any summary metric of the species' range is unlikely to be adequate for species with disjunct distributions.

Habitat disturbance and loss were also identified as a key threat to bird populations, and different habitat types are likely to be affected to varying extents (Gregory et al. 2019). Hence, we included the main habitat type utilised by each species (farmland, forest, wetland, shrub, and other) as a variable in the full model. This data was obtained from the PECBMS dataset, which included three habitat categories: forest, farmland, and other. For all species that had their main habitat type classified as other, we used the dataset *Life-history characteristics of European birds* (Storchová & Hořák 2018) and Birds of the Western Palearctic (Cramp 1977-1994) to further subdivide this category into shrub, wetland, and other.

We have also accounted for the anthropogenic transformations of the landscape which are a key factor affecting population dynamics and trends (Buchan et al. 2022), and therefore, produced a variable representing the tolerance of a given species to human-modified habitats. This was done by first determining whether each species can be found in farmland, urban areas, plantation forests, or grazed areas during its breeding season. This data was obtained from Buchan et al. (2022) and completed for the missing species following Birds of the Western Palearctic (Cramp 1977-1994). The tolerance to human-modified habitats was then calculated as a sum of how many of these habitats is the species found in during the breeding season. This produced a category ranging between 1 and 4, where four means that the species is found in all these habitats, while one indicates that the species will be found in only one of these modified habitats in the breeding season.

To investigate the relationship between the species niche breadth/area index and their long-term population trends within our study area, we fitted a linear model with the weighed long-term slope of the population trend (from PECBMS) as the response variable and as explanatory variables, the niche breadth/area index (natural logarithm-transformed), the level of tolerance to human modified environments (0=low tolerance to 4=high tolerance), and the following species traits: main diet type (factor with four levels: Invertebrate, Plant/Seed, Vert/Scav, Omnivore), migration strategy (factor with three levels: resident, partial migrant, full migrant), average species body mass (natural-log transformed), main habitat type (factor with five levels: farmland, forest, wetland, shrub, and other).

All possible subsets model selection and model averaging was then carried out using the 'dredge' function from the *MuMIn* package (Bartoń 2023). Selection was done based on model AICc and models were considered equally parsimonious when within ΔAICc < 2 (Burnham & Anderson 2002). The adjusted criterion (AICc) was used due to a relatively low sample size (N = 159) resulting in a data to estimated model parameter ratio being <40 (Burnham & Anderson 2002). Marginal means were calculated and post-hoc covariate level comparisons were carried out based on the full model average and with average values of remaining covariates using the package *emmeans* (Lenth et al. 2024). All data preparation and analyses were carried out in R v4.2.1 (R Core Team 2022).

2.3 Results

European climatic niche

The distribution of the 159 species included in this study was plotted in geographic space, showing that a maximum of 121 species co-occur in central Europe (Fig.2.1a). Within the species included in this study, 58 species had a decreasing population trend (slope < 0.99), populations of 68 species were stable (0.99 ≤ slope ≤ 1.01), and 33 species were increasing (slope > 1.01). Among species with smaller distribution areas (< 2,500,000 km^2), 7 species are declining, 12 are stable, and 12 have increasing population trends. Out of the 31 species with medium-sized distributions (2,500,000 ≤ distribution area ≤ 5,000,000 km^2), 14 are declining, 12 are stable, and only 5 are increasing. Similarly, for the 97 species with large distributions (> 5,000,000 km^2), 37 species are declining, 44 have stable trends, and 16 are increasing.

The realised climatic niche breath given by the first two principal components cumulatively explained 73.47% of the variance within the dataset, with the individual principal components one (PC1) and two (PC2) explaining 42.06 and 31.41% of the variance, respectively. Both temperature- and precipitation-related variables contributed to the principal components (Supporting information). PC1 was composed of mainly precipitation variables, as well as variables relating to temperature seasonality, while PC2 included temperature averages, extremes, and temperature variability (Supporting information). The resulting representation of the realised climatic niches of the 159 species was nested, with a maximum niche overlap of 152 species (Fig.2.1b). We found a strong positive relationship between the realised climatic niche and the range size (Fig.2.1c), however, species with small range areas showed larger variation in climatic niche breadth than species with larger range areas.

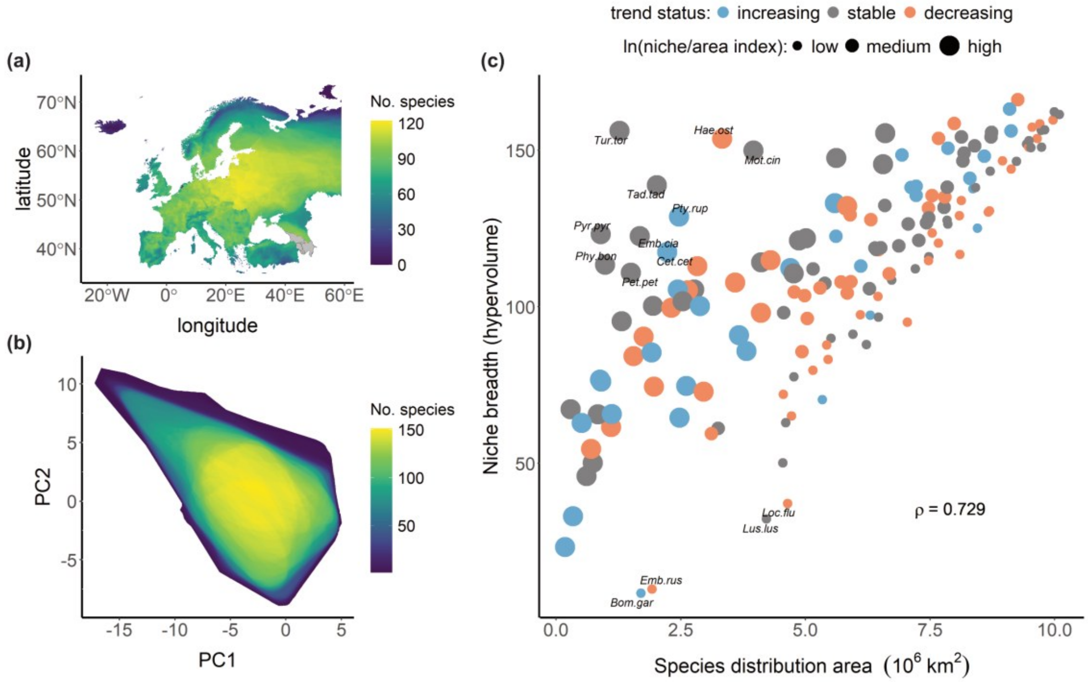

Figure 2.1. Distribution and overlap of species ranges within the study extent (a); the overlap of estimated hypervolumes representing the realised climatic niche of the focal species across the breeding and resident parts of their ranges within Europe (b); and the relationship between the realised climatic niche breadth (area of the hypervolume) and the range area (c), with the Spearman's correlation coefficient (ρ), and the colours indicating the species status according to the PECBMS long-term population trend: increasing (blue; slope < 1.01), stable (grey, 0.99 ≤ slope ≥ 1.01), and decreasing (red, slope < 0.99), and size showing the value of the natural logarithm of the niche to area index for each species, grouped based on quantiles, where values below -11.01 are classified as 'low' (33rd quantile), between -11.01 and -10.72 as 'medium', and above -10.72 as 'high' (67th quantile); Abbreviated species names are given for those species with a particularly broad niche for their range area (i.e. those with niche breadth of over 100 and area below 2.5×10^6 km^2 or niche breadth over 145

and area below 5.0 × 10^6 km^2) or those with a very narrow niche breadth for their range area (1.0 × 10^6 < area < 5.0 × 10^6 km^2 and niche breadth < 50). Species range maps from BirdLife International (2020).

Climatic niche breadth and long-term population trends

The climatic niche breadth to range area index was a good predictor of bird population declines across Europe, together with species traits and tolerance to human-modified environments. The model selection procedure indicated six equally parsimonious models (Table 2.1). The niche breadth to range area index, tolerance to human-modified environments, and habitat type were included in all six top models. Diet was retained in three models, migration strategy in two, and body mass in one of the six models (Table 2.1).

Table 2.1. Results of model selection for models explaining the long-term population trends. 1 = ln(index), 2 = habitat type, 3 = tolerance to human-modified environments, 4 = diet, 5 = ln(mass), 6 = migratory strategy.

Variables	df	logLik	AICc	ΔAICc	Weight
1234	11	413.29	-802.78	0.00	0.27
123	8	409.61	-802.26	0.52	0.21
1236	10	411.46	-801.43	1.35	0.14
12346	13	414.96	-801.41	1.37	0.14
1235	9	410.23	-801.26	1.52	0.13
12345	12	413.53	-800.92	1.86	0.11

From the outcome of the full model average, species with a narrower realised climatic niche for a given area (low index values) were more likely to be declining compared to those with a relatively broader niche, which were more likely to be increasing (high index values; Table 2.2, Fig.2.2). Farmland species are experiencing greater population declines compared to species associated with other habitat types (Fig.2.2; Supporting information) and species able to tolerate a greater number of human-modified environments were less likely to be declining (Table 2.2, Fig.2.2).

We found similar population trends across the five diet type groups considered here (Table 2.2; Fig.2.2; Supporting information). Moreover, full and partial migrants, and resident species did not differ in their respective rate or direction of population change (Table 2.2,

Fig.2.2; Supporting information). Finally, populations were equally likely to decline or increase irrespective of body size (Table 2.2).

Table 2.2. Full average model parameter estimates based on six linear models identified as equally parsimonious in all-possible-subsets model selection procedure, explaining the variation in the species long-term population trend as a function of index of realised climatic niche breadth to range area (ln transformed), main habitat (reference = wetland), level of tolerance to human-modified environments (Tol; 0-4), diet type (reference = VertScav), body mass (ln transformed), and migration strategy (reference = resident). The adjusted R^2 of global model was 0.250. Lines in bold indicate statistically significant effects at alpha level 0.05.

Parameter	Estimate	Std. Error	Adj. SE	z-value	p-value
Intercept	**1.105**	**0.031**	**0.031**	**35.945**	**<0.001**
Ln(niche breadth/area)	**0.010**	**0.003**	**0.003**	**3.744**	**<0.001**
Habitat(Wetland:Farm)	**-0.020**	**0.005**	**0.005**	**3.956**	**<0.001**
Habitat(Wetland:Forest)	0.001	0.005	0.005	0.137	0.891
Habitat(Wetland:Other)	0.000	0.005	0.005	0.062	0.950
Habitat(Wetland:Shrub)	-0.004	0.006	0.006	0.549	0.583
Tol. to human env.	**0.004**	**0.002**	**0.002**	**2.704**	**0.007**
Diet(VertScav:Invert)	-0.005	0.007	0.007	0.749	0.454
Diet(VertScav:Omniv)	-0.003	0.006	0.006	0.556	0.578
Diet(VertScav:Plant)	-0.008	0.009	0.009	0.875	0.381
Ln(body mass)	0.000	0.001	0.001	0.336	0.737
Mig(Resident:Long)	0.000	0.003	0.003	0.121	0.904
Mig(Resident:Partial)	0.002	0.004	0.004	0.485	0.628

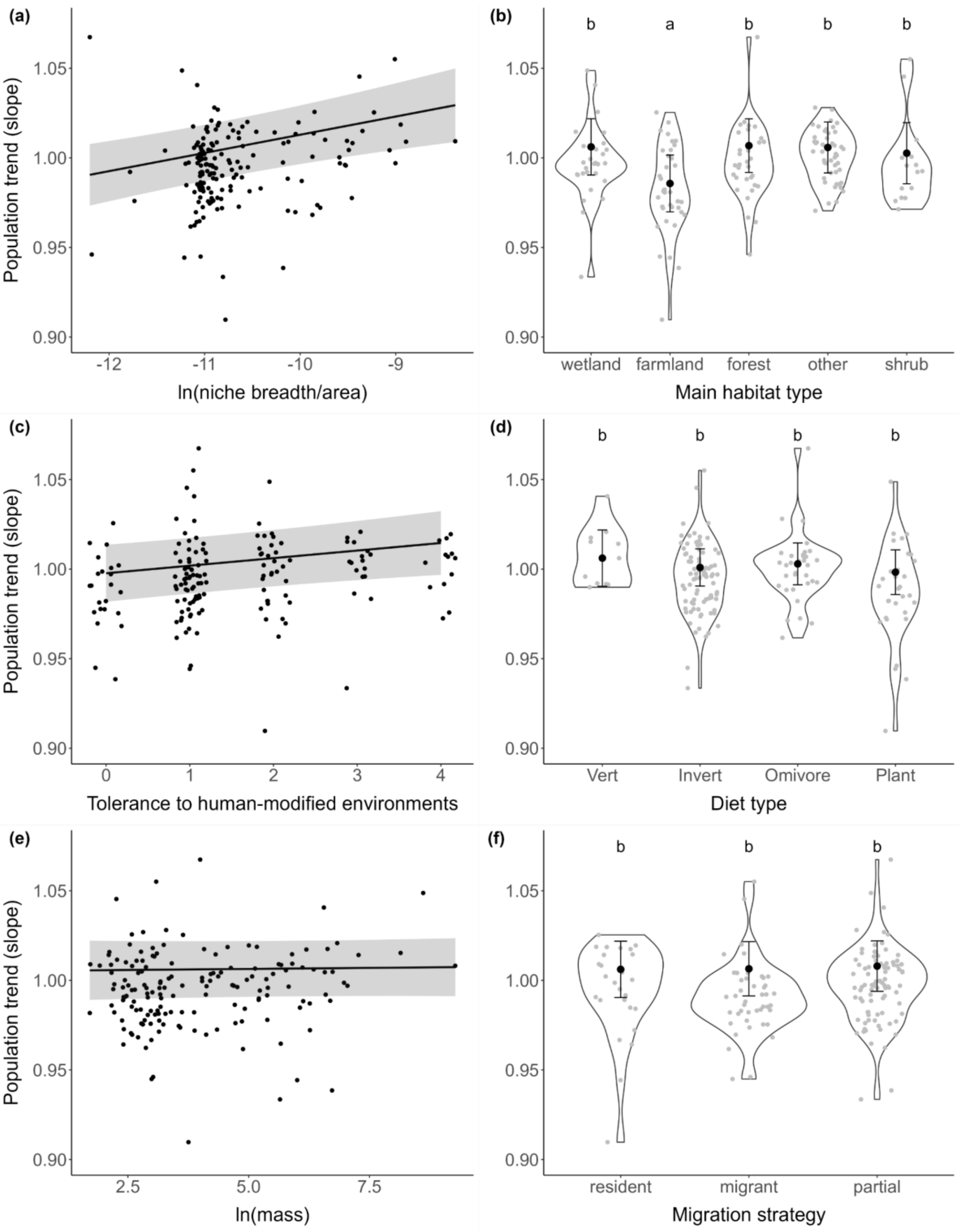

Figure 2.2. Full-average model predictions from linear model of the long-term population trends across species (from PECBMS) in relation to index of niche breadth to range size (area; a), main habitat type used by species (farmland, forest, other, shrub, and wetland; b), level of tolerance to human modified environments (0 = no tolerance, 4 = able to tolerate all human-modified

environments; c), diet type (invertebrate, omnivore, plant/seed, vertebrate/fish/scavenging; d), natural logarithm-transformed body mass (non-significant effect, Table 2; e), and migration strategy (migrant, partial, resident; f). Predictions for each variable were calculated using average values of the remaining continuous predictors, for tolerance to human-modified environments a value of 2, and for the following levels of categorical variables: migration status = resident, diet = VertScav, habitat = wetland. Shaded area and error bars show 95% confidence intervals. Black (in (a), (c), and (e)) and grey points show the raw data distribution.

2.4 Discussion

Faced with the challenges of the global biodiversity crisis and climate change, the rapid assessment of species vulnerability to environmental change has become of paramount importance to address the challenges associated with species conservation. While previous research has focused on population trends and the size of species' ranges to prioritise conservation action (Myers et al. 2000), this study shows that variation in climatic conditions (i.e. realised niche breadth) within a species range can provide greater nuance in understanding species resilience to factors that affect their population trends. In particular, we show that the climatic niche breadth to range area index can help predict which species may be more vulnerable to population declines. We find that for species occupying a similar area of geographic space, those with broader climatic niches, and therefore, possibly higher climatic tolerances, are more likely to be increasing compared to species with relatively narrower climatic niches.

Our study highlights the considerable variability across species in the relationship between niche breadth and range area. This is particularly true for species with relatively small and medium-range areas, as these species in our study had both very narrow and very broad climatic niches. A similar relationship has been found in a multi-taxa study carried out across North and South America, showing both a clear general trend while also highlighting idiosyncratic results between species (Dallas & Kramer 2022), and providing further evidence that climatic niche breadth should not be treated as synonymous with distributional size. Moreover, while rare species are frequently thought to be the most prone to population declines (Vincent et al. 2020), rarity has previously been found not be an important variable explaining species population trends (Daskalova et al. 2020). A possible reason for this could be that small-ranged species are commonly focal species for conservation actions, and therefore, targeted management may potentially buffer or delay the negative effects of environmental change (Gaget et al. 2024). This, combined with our results, highlights that using range size alone may oversimplify our understanding of species environmental tolerance, and the climatic niche to range area index is likely a useful tool in anticipating the effects of climate change.

The drivers behind species with broader niches being more likely to have increasing population trends are likely multifaceted and complex. Species with broader climatic niches, i.e. those experiencing a wider range of climatic conditions are likely to have broader physiological limits, enabling them to adapt and persist in areas with greater climatic variability (e.g. Jiguet et al. 2006). This in turn could mean that changes in climatic conditions may be less likely to extend past their physiological thresholds, making the species with a broader climatic niche more resilient, and therefore, less likely to experience population declines (Carrera et al. 2022). Furthermore, the effects of climate change are likely to vary spatially (e.g. Antão et al. 2022), hence, species with broader climatic niches may also be better able to sustain populations across their current range, while species with narrow climatic niches may be more vulnerable to local extinctions, and disappear from parts of their range, therefore experiencing greater population declines (Grinder & Wiens 2023).

The links between climatic exposure and climate resilience have been previously investigated at local scales, for example willow flycatcher (*Empidonax traillii*) populations in North America with relatively narrower climatic niches are declining more rapidly than populations with broader niches (Ruegg et al. 2021). Similarly, the level of vulnerability to climate change has also been shown to vary depending on the extent to which species or populations have encountered climatic changes regardless of whether the species possessed characteristics classified as particularly under threat (Bailey et al. 2022). Moreover, populations exposed to higher levels of climatic variability may be better able to respond to environmental extremes as shown in damselflies (*Ischnura elegans*), where individuals from populations experiencing greater climatic variability were faster at recovering from exposure to extreme cold compared to populations inhabiting less climatically heterogeneous areas (Lancaster et al. 2015). Finally, climatic niches, and particularly a relatively narrow range of temperature tolerances, have been associated with the occurrence of northward distributional shifts during the last 20 years, across over 80 bird species in Finland (Hällfors et al. 2024). Our findings complement these studies with larger-scale evidence across a wider species pool, further emphasising the importance of climatic niches for understanding population trends.

As expected, species that occur in human-modified habitats were less likely to be declining. Species associated with more natural habitats, by contrast, are more vulnerable to habitat disturbance, fragmentation, and loss (Matuoka et al. 2020, Storch et al. 2023), the effects of which may be amplified by climate change (Khelifa et al. 2022). There are trade-offs to using human-disturbed sites, as proximity to humans might reduce predation intensity or increase food availability but induce high levels of disturbance within such habitats and have a detrimental effect on individual performance (Reynolds et al. 2019). Hence, with increasing urbanisation and heightened levels of anthropogenic disturbances to natural environments over the last several decades, it is unsurprising that species able to utilise human-modified habitats are showing growing population trends.

While the population trends were relatively similar across species associated with most habitat types, farmland species were more likely to be declining, which has also been described by recent research (Lees et al. 2022, Storch et al. 2023). This negative trend has been attributed to particularly high levels of disturbance due to the increasing intensity of agricultural activities (Donald et al. 2001, Rigal et al. 2023). Furthermore, the highly detrimental impact of land use change on bird species may be intensified by climate change (Srinivasan & Wilcove 2021), highlighting the complexity of the impacts of global environmental change on species population trends.

We found no overall effect of diet type on long-term population trends. All diet groups were expected to have similar trend slopes. Previous studies looking at population trends within Europe found a negative population trend in species feeding on seeds as well as on invertebrates (Bowler et al. 2019). Similarly, within the island bird species in Panama, insectivorous species were shown to be most prone to extinction (Curtis et al. 2021). The lack of any significant difference observed in our study might be due to diet and habitat being linked and therefore, the effect of diet may have been diluted by the presence of habitat type within the model (Bowler et al. 2019). Indeed, the extent of declines in insectivorous species varied across different farmland habitat types and has been linked to increased levels of disturbance and agricultural activity (Reif & Hanzelka 2020).

Population trends were similar across the three migratory strategies: resident, partial and full migrants. This result differed from previous studies that highlighted considerable declines in migratory species populations (e.g. Gilroy et al. 2016, Howard et al. 2020, Vickery et al. 2023). The discrepancy between the findings of these studies and our results may stem from these studies focusing exclusively on migratory species (Howard et al. 2020, Vickery et al. 2023) or considering a different and greater number of species (Gilroy et al. 2016). Furthermore, the factors driving population changes of migratory species have been shown to differ between breeding and wintering parts of their range (Howard et al. 2020) and trends varied even within the migratory species group depending on the location of wintering grounds (Vickery et al. 2023). Coupled with our relatively broad classification of migratory strategy, this variability may explain why the differences in population trends between full and partial migrants and resident species have not been captured here.

We did not find any difference in population trend in relation to species body size. This was unexpected, as generation turnover is generally faster in smaller-bodied species, and therefore, changes may be more noticeable in those populations. Furthermore, the effects of climate change have been frequently shown to differ depending on either lifespan or body size (e.g. Mason et al. 2019, Storch et al. 2023, Gregory et al. 2023). This is true not only when considering the overall population trend but, e.g. in breeding and nesting success, where as temperatures increase, offspring production in species with relatively larger body sizes was expected to decrease. In contrast, the opposite was predicted to be true for smaller species (Halupka et al. 2023).

This study treated bird species ranges in Europe as static distributions and there was a temporal mismatch between the climate and species distribution data used here. The historical annual average climate data used in this study covered the years 1970-2000, while the species distribution data was collated from 1980 to the year 2020. We adopted this simplified approach because this temporal mismatch is unlikely to affect the results at the spatial scale this study was conducted, and due to the speed at which bird species respond to climate chance (Pearce-Higgins & Green 2014). The events potentially impacting population trends, such as climate change or disturbances, tend to occur or progress rapidly, while species responses may not always be instantaneous (Menéndez et al. 2006). Furthermore, species respond to extremes rather than to changes in mean climate, but the effect of extremes is better captured by long-term population trends and changes in distribution.

Our definition of the realised climatic niche and the inferences that can be made need to be approached with caution. The metric obtained provides the range of conditions a species experiences, i.e. it exists within such combinations of climatic conditions and can maintain viable populations. However, the spatial locations where a species is found are determined by a variety of interacting variables, including biotic and abiotic interactions, and thus the fundamental niche may be broader than the realised niche (Hutchinson 1953). If these biotic interactions change, which could occur due to the speed at which different species respond to climate changes (Parmesan & Yohe 2003), the realised climatic niche breath may also change, hence the hypervolume that characterises the species climatic niche may be different in the presence of new species interactions.

2.5 Conclusions

This study highlights the importance of understanding the level of exposure to climatic variability when assessing vulnerability to population declines. We show that for a given distribution area, species with a broader climatic niche are less likely to be declining than species within narrower climatic conditions. In agreement with previous studies, we found that species associated with farmland habitats were more likely to be declining, while those able to tolerate human-modified environments were expected to have an increasing population trend.

However, changes in climatic conditions within the extent of this study, as well as shifts in species distributions across the temporal scale considered here, were not included in the models, presenting a static view of the exposure to climatic variability based on average variable values. This approach is largely useful for multi-species large-scale overviews such as this study, however, caution should be taken if our results were to be used for planning specific conservation action, as in that case, a more dynamic approach to modelling species niches may be more appropriate.

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Chapter 2 Supporting information

Data sources

We used extant ranges of the 159 bird species included in the study (see Table S2.2 for rationale) and clipped them to the spatial extent of Europe (between longitudes from -24.33 to 59.00° and latitudes 34.92 and 75.00°). We used species distribution polygons from BirdLife International and not the data from the European Breeding Bird Atlas (EBBA), as while it overlaps temporally with the climate data used in this study (see below for details), the gridded atlas data are less suitable for representing the full species' extent over longer time periods due to being highly dependent on temporal changes in species distributions. The ranges were then used to extract climate data for each species from the 19 bioclimatic variable layers, containing averages for the period 1970-2000 at a 5-arcminute resolution (Table S2.1). The species considered in this study include those present in the study area throughout the year, as well as species wintering outside of Europe, however, we use averages of year-round conditions to characterise the climatic niche. This was done to, firstly, allow niche comparisons across species, as metrics summarising ranges of conditions, which were obtained for different periods (e.g. different number of months) are not equivalent but defining a period when species are present may not be straightforward in all cases. Secondly, species dynamics are likely driven not only by direct effects of the conditions they encounter, but also indirectly, through environmental impacts on their resources. Hence, considering the conditions year-round is the most appropriate representation of how the climate may impact these areas.

The extracted climatic variables are scaled and centred, then transformed using principal component analysis (PCA) to produce the species' climatic niches. Two principal components were retained as they cumulatively contained over 70% of variance of the non-transformed data. The principal component scores were used to construct the hypervolume representing each species' realised climatic niche. The area (volume) of that two-dimensional hypervolume was taken as the niche breadth, and used with species traits (body mass, main diet type, main habitat type, migratory status, and tolerance of human modified environments (calculated as the sum of the number of human-modified environments used by each species)) to explain long-term population trends (Table S2.1).

Table S2.1. List of datasets and their respective sources.

Data type	Dataset name	Reference
Climate data	Bioclimatic variables, WorldClim2 1970-2000	Fick, S.E. & R.J. Hijmans, 2017. https://www.worldclim.org/
Species distributions	Bird species distribution maps of the world	BirdLife International and Handbook of the Birds of the World (2020) Bird species distribution maps of the world. Version 2020.1. Available at http://datazone.birdlife.org/species/requestdis. European Bird Census Council (EBCC); www.ebcc.info
Realised climatic niche breadth	-	See Table S2.4
Population trends	Pan-European Common Bird Monitoring Scheme European species trends and indices (December 6, 2021)	European Bird Census Council (EBCC)/BirdLife/Royal Society for the Protection of Birds (RSPB)/Czech Society for Ornithology (CSO); Gregory et al. 2005, Brlík et al. 2021 https://pecbms.info/trends-of-common-birds-in-europe-2021-update/
Body mass	EltonTraits 1.0	Wilman et al. 2016 https://doi.org/10.6084/m9.figshare.c.3306933.v1
Main diet type	EltonTraits 1.0	Wilman et al. 2016 https://doi.org/10.6084/m9.figshare.c.3306933.v1
Main habitat type	Pan-European Common Bird Monitoring Scheme European species trends and indices (December 6, 2021)	European Bird Census Council (EBCC)/BirdLife/Royal Society for the Protection of Birds (RSPB)/Czech Society for Ornithology (CSO); Gregory et al. 2005, Brlík et al. 2021 https://pecbms.info/trends-of-common-birds-in-europe-2021-update/
	Life-history characteristics of European birds	Storchová & Hořák 2018 https://doi.org/10.5061/dryad.n6k3n
	Birds of the Western Palearctic: Handbook of the Birds of Europe, the Middle East and North Africa	Cramp 1977-1994
Migratory status	-	Gilroy et al. 2016 https://doi.org/10.1111/ele.12569
Use of human-modified environments	-	Buchan et al. 2022 https://doi.org/10.1111/geb.13551
	Birds of the Western Palearctic: Handbook of the Birds of Europe, the Middle East and North Africa	Cramp 1977-1994

Species list

Out of a total of 170 species available in the Pan-European Common Bird Monitoring Scheme (PECBMS; Gregory et al. 2005, Brlík et al. 2021) dataset, this study used the long-term population trends for 159 species (Table S2.2). Ten species were removed because there were no long-term trends available for them, and one species, *Phasianus colchicus* was removed because it is a non-native species that is frequently released, and therefore, its population trends are likely driven by different factors than for most other bird species. The minimum number of years over which the long-term trend was calculated for the species considered was 22.

Table S2.2. List of species available in the PECBMS data set (published December 2021), whether species was included in the study as well as the reason for exclusion.

Scientific name	Common name	Incl.	Reason
Acanthis flammea	Common redpoll	Yes	-
Accipiter nisus	Eurasian sparrowhawk	Yes	-
Acrocephalus arundinaceus	Great reed warbler	Yes	-
Acrocephalus palustris	Marsh warbler	Yes	-
Acrocephalus schoenobaenus	Sedge warbler	Yes	-
Acrocephalus scirpaceus	Eurasian reed warbler	Yes	-
Actitis hypoleucos	Common sandpiper	Yes	-
Aegithalos caudatus	Long-tailed tit	Yes	-
Alauda arvensis	Eurasian skylark	Yes	-
Alcedo atthis	Common kingfisher	Yes	-
Alectoris rufa	Red-legged partridge	Yes	-
Anas platyrhynchos	Mallard	Yes	-
Anthus campestris	Tawny pipit	Yes	-
Anthus pratensis	Meadow pipit	Yes	-
Anthus trivialis	Tree pipit	Yes	-
Apus apus	Common swift	Yes	-
Ardea cinerea	Grey heron	Yes	-
Bombycilla garrulus	Bohemian waxwing	Yes	-
Bonasa bonasia	Hazel grouse	Yes	-
Bubulcus ibis	Cattle egret	Yes	-
Burhinus oedicnemus	Eurasian stone-curlew	Yes	-
Buteo buteo	Common buzzard	Yes	-
Calandrella brachydactyla	Greater short-toed lark	Yes	-
Calcarius lapponicus	Lapland longspur	No	no long-term slope
Carduelis carduelis	European goldfinch	Yes	-
Carduelis citrinella	Citril finch	No	no long-term slope
Carpodacus erythrinus	Common rosefinch	Yes	-
Cecropis daurica	Red-rumped swallow	Yes	-
Certhia brachydactyla	Short-toed treecreeper	Yes	-
Certhia familiaris	Eurasian treecreeper	Yes	-

Cettia cetti	Cetti's warbler	Yes	-
Chloris chloris	European greenfinch	Yes	-
Ciconia ciconia	White stork	Yes	-
Circus aeruginosus	Marsh harrier	Yes	-
Cisticola juncidis	Zitting cisticola	Yes	-
Clamator glandarius	Great spotted cuckoo	Yes	-
Coccothraustes coccothraustes	Hawfinch	Yes	-
Columba oenas	Stock dove	Yes	-
Columba palumbus	Wood pigeon	Yes	-
Corvus corax	Common raven	Yes	-
Corvus corone	Carrion crow	Yes	-
Corvus frugilegus	Rook	Yes	-
Corvus monedula	Jackdaw	Yes	-
Cuculus canorus	Common cuckoo	Yes	-
Cyanecula svecica	Bluethroat	Yes	-
Cyanistes caeruleus	Eurasian blue tit	Yes	-
Cyanopica cyanus	Azure-winged magpie	Yes	-
Cygnus olor	Mute swan	Yes	-
Delichon urbicum	House martin	Yes	-
Dendrocopos major	Great spotted woodpecker	Yes	-
Dendrocopos syriacus	Syrian woodpecker	No	no long-term slope
Dryobates minor	Lesser spotted woodpecker	Yes	-
Dryocopus martius	Black woodpecker	Yes	-
Egretta garzetta	Little egret	No	no long-term slope
Emberiza calandra	Corn bunting	Yes	-
Emberiza cia	Rock bunting	Yes	-
Emberiza cirlus	Cirl bunting	Yes	-
Emberiza citrinella	Yellowhammer	Yes	-
Emberiza hortulana	Ortolan bunting	Yes	-
Emberiza melanocephala	Black-headed bunting	No	no long-term slope
Emberiza rustica	Rustic bunting	Yes	-
Emberiza schoeniclus	Reed bunting	Yes	-
Erithacus rubecula	European robin	Yes	-
Falco tinnunculus	Common kestrel	Yes	-
Ficedula albicollis	Collared flycatcher	Yes	-
Ficedula hypoleuca	European pied flycatcher	Yes	-
Fringilla coelebs	European chaffinch	Yes	-
Fringilla montifringilla	Brambling	Yes	-
Fulica atra	Eurasian coot	Yes	-
Galerida cristata	Crested lark	Yes	-
Galerida theklae	Thekla's lark	Yes	-
Gallinago gallinago	Common snipe	Yes	-
Gallinula chloropus	Common moorhen	Yes	-
Garrulus glandarius	Eurasian jay	Yes	-
Grus grus	Common crane	Yes	-
Haematopus ostralegus	Eurasian oystercatcher	Yes	-
Hippolais icterina	Icterine warbler	Yes	-
Hippolais polyglotta	Melodious warbler	Yes	-
Hirundo rustica	Barn swallow	Yes	-

Iduna pallida	Olivaceous Warbler	No	no long-term slope
Jynx torquilla	Eurasian wryneck	Yes	-
Lanius collurio	Red-backed shrike	Yes	-
Lanius minor	Lesser grey shrike	No	no long-term slope
Lanius senator	Woodchat shrike	Yes	-
Larus ridibundus	Black-headed gull	Yes	-
Leiopicus medius	Middle spotted woodpecker	Yes	-
Limosa limosa	Black-tailed godwit	Yes	-
Linaria cannabina	Common linnet	Yes	-
Locustella fluviatilis	River warbler	Yes	-
Locustella naevia	Grasshopper warbler	Yes	-
Lophophanes cristatus	Crested tit	Yes	-
Lullula arborea	Woodlark	Yes	-
Luscinia luscinia	Thrush nightingale	Yes	-
Luscinia megarhynchos	Common nightingale	Yes	-
Lyrurus tetrix	Black grouse	Yes	-
Melanocorypha calandra	Calandra lark	Yes	-
Merops apiaster	European bee-eater	Yes	-
Motacilla alba	White wagtail	Yes	-
Motacilla cinerea	Grey wagtail	Yes	-
Motacilla flava	Western Yellow Wagtail	Yes	-
Muscicapa striata	Spotted flycatcher	Yes	-
Nucifraga caryocatactes	Northern nutcracker	Yes	-
Numenius arquata	Eurasian curlew	Yes	-
Numenius phaeopus	Eurasian whimbrel	Yes	-
Oenanthe cypriaca	Cyprus wheatear	No	no long-term slope
Oenanthe hispanica	Western black-eared wheatear	Yes	-
Oenanthe oenanthe	Northern wheatear	Yes	-
Oriolus oriolus	Golden oriole	Yes	-
Parus major	Great tit	Yes	-
Passer domesticus	House sparrow	Yes	-
Passer montanus	Tree sparrow	Yes	-
Perdix perdix	Grey partridge	Yes	-
Periparus ater	Coal tit	Yes	-
Petronia petronia	Rock sparrow	Yes	-
Phasianus colchicus	Common pheasant	No	non-native, released species
Phoenicurus ochruros	Black redstart	Yes	-
Phoenicurus phoenicurus	Common redstart	Yes	-
Phylloscopus bonelli	Western Bonelli's warbler	Yes	-
Phylloscopus collybita	Common chiffchaff	Yes	-
Phylloscopus sibilatrix	Wood warbler	Yes	-
Phylloscopus trochilus	Willow warbler	Yes	-
Pica pica	Eurasian magpie	Yes	-
Picus canus	Grey-headed woodpecker	Yes	-
Picus viridis	Green woodpecker	Yes	-
Pluvialis apricaria	European golden plover	Yes	-
Podiceps cristatus	Great crested grebe	Yes	-
Poecile montanus	Willow tit	Yes	-
Poecile palustris	Marsh tit	Yes	-

Prunella modularis	Dunnock	Yes	-
Ptyonoprogne rupestris	Eurasian crag martin	Yes	-
Pyrrhocorax pyrrhocorax	Red-billed chough	Yes	-
Pyrrhula pyrrhula	Eurasian bullfinch	Yes	-
Regulus ignicapilla	Common firecrest	Yes	-
Regulus regulus	Goldcrest	Yes	-
Saxicola rubetra	Whinchat	Yes	-
Saxicola torquatus	Stonechat	Yes	-
Serinus serinus	European serin	Yes	-
Sitta europaea	Eurasian nuthatch	Yes	-
Spinus spinus	Eurasian siskin	Yes	-
Streptopelia decaocto	Eurasian collared dove	Yes	-
Streptopelia turtur	Turtle dove	Yes	-
Sturnus unicolor	Spotless starling	Yes	-
Sturnus vulgaris	Common starling	Yes	-
Sylvia atricapilla	Eurasian blackcap	Yes	-
Sylvia borin	Garden warbler	Yes	-
Sylvia cantillans	Eastern subalpine warbler	Yes	-
Sylvia communis	Common whitethroat	Yes	-
Sylvia curruca	Lesser whitethroat	Yes	-
Sylvia hortensis	Western Orphean warbler	Yes	-
Sylvia melanocephala	Sardinian warbler	Yes	-
Sylvia melanothorax	Cyprus warbler	No	no long-term slope
Sylvia nisoria	Barred warbler	Yes	-
Sylvia undata	Dartford warbler	Yes	-
Tachybaptus ruficollis	Little grebe	Yes	-
Tadorna tadorna	Common shelduck	Yes	-
Tetrax tetrax	Little bustard	Yes	-
Tringa erythropus	Spotted redshank	No	no long-term slope
Tringa glareola	Wood sandpiper	Yes	-
Tringa nebularia	Common greenshank	Yes	-
Tringa ochropus	Gren sandpiper	Yes	-
Tringa totanus	Common redshank	Yes	-
Troglodytes troglodytes	Eurasian wren	Yes	-
Turdus iliacus	Redwing	Yes	-
Turdus merula	Common blackbird	Yes	-
Turdus philomelos	Song thrush	Yes	-
Turdus pilaris	Fieldfare	Yes	-
Turdus torquatus	Ring ouzel	Yes	-
Turdus viscivorus	Mistle thrush	Yes	-
Upupa epops	Eurasian hoopoe	Yes	-
Vanellus vanellus	Lapwing	Yes	-

Defining the species climatic niche using PCA-env and hypervolume

The species realised climatic niche for the 159 species included in this study was characterised using 19 bioclim variables, encompassing both temperature and precipitation variables, averaged across the period 1970-2000. To define the niche, we used the PCA-env method defined by Broennimann et al. (2012). The list of bioclim variables and their contributions to each principal component are listed below (Table S2.3).

The main contributing variables to PC1 included precipitation (bio19, bio12, bio13, bio16, bio6, bio11, bio17, bio14, bio9) and temperature seasonality (bio3, bio4, bio7), while PC2 was mainly composed by temperature average variables, as well as those relating to temperature extremes and ranges (Fig.S2.1).

Table S2.3. Variable contributions to principal components. Climate data from obtained from Worldclim (Fick & Hijmans 2017)

Variable name	code	PC1	PC2
mean annual air temperature	bio1	-0.186	-0.332
mean diurnal air temperature range	bio2	0.079	-0.290
isothermality	bio3	-0.249	-0.229
temperature seasonality	bio4	0.309	0.039
mean daily maximum air temperature of the warmest month	bio5	0.017	-0.366
mean daily minimum air temperature of the coldest month	bio6	-0.275	-0.228
annual range of air temperature	bio7	0.303	-0.013
mean daily mean air temperatures of the wettest quarter	bio8	0.167	-0.105
mean daily mean air temperatures of the driest quarter	bio9	-0.225	-0.275
mean daily mean air temperatures of the warmest quarter	bio10	-0.026	-0.363
mean daily mean air temperatures of the coldest quarter	bio11	-0.265	-0.254
annual precipitation amount	bio12	-0.299	0.169
precipitation amount of the wettest month	bio13	-0.284	0.121
precipitation amount of the driest month	bio14	-0.244	0.232
precipitation seasonality	bio15	0.016	-0.161
mean monthly precipitation amount of the wettest quarter	bio16	-0.287	0.129
mean monthly precipitation amount of the driest quarter	bio17	-0.258	0.219
mean monthly precipitation amount of the warmest quarter	bio18	-0.097	0.306
mean monthly precipitation amount of the coldest quarter	bio19	-0.310	0.045

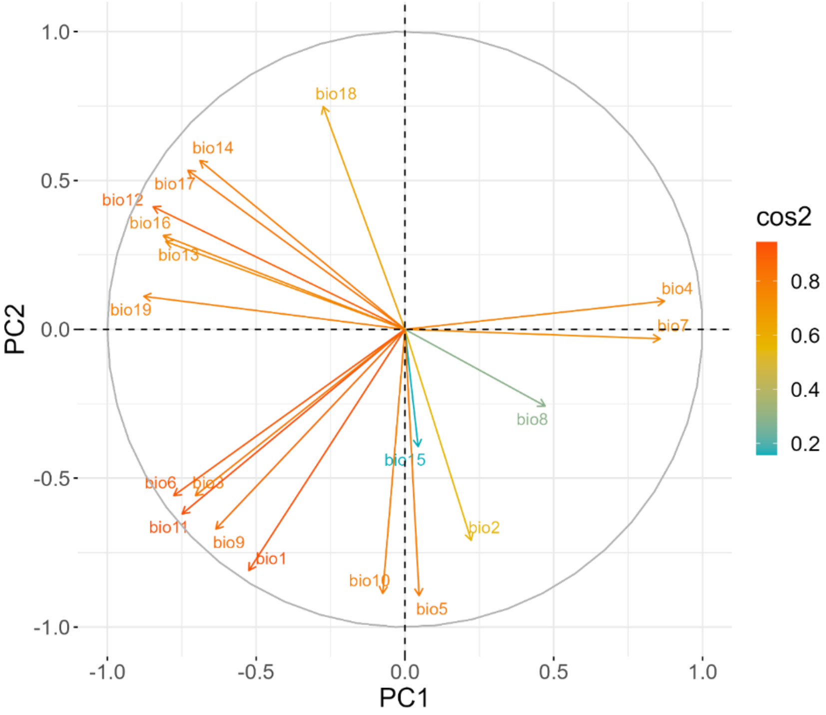

Figure S2.1. Variable contributions to principal component one (PC1) and two (PC2). The colour gradient shows the quality of representation of each variable by the principal components (cos2), where high values mean good representation and low mean poor representation.

We use the principal component scores across the two axes to construct the two-dimensional species climatic niche hypervolume using the support vector machine algorithm with default parameters from the package *hypervolume* (Blonder et al. 2018, 2023). This method was selected as it is less susceptible to extreme values and outliers, allowing for the full range of climatic variability to be represented (Blonder et al. 2018). Furthermore, random points are produced around each point within the data to construct the hypervolume boundaries, therefore, maintaining a relatively similar sampling effort for each of the species considered, regardless of initial sample size (Blonder et al. 2014, 2018).

Species data used in the analysis of long-term population trends

For each species, the realised climatic niche breadth within the study area was calculated (Table S2.4). To account for species differences in range sizes we also calculated the area of the species range falling within the study extent. This range size was divided by the niche breadth to produce the range size to niche breadth index, which was natural logarithm-transformed and used in the model explaining long-term population trends. To account for the across-species variability resulting from parts of some species' ranges falling outside of the study extent, we calculated the proportion of the total species range that was within the study extent. Secondly, the population trends were not calculated over the same number of years for all species, so the proportion of years used to produce each species' trend out of the maximum 40 years was also calculated, where a value of 1 means that the species trend was calculated over 40 years. These two proportions were combined by obtaining their average and used as weights in the linear model (Table S2.4). The full model explaining the slope of the long-term trend of each species contained the following variables: niche breadth to range size index (natural logarithm transformed), diet type, habitat type, body mass (natural logarithm transformed), migration status, level of tolerance to human-modified environments.

Table S2.4. The climatic niche breadth to range size index (Index) and species traits used to model species long-term population trends, and the proportion of species range within the study extent (Prop. area), the proportion of years (out of 40) over which the population trend was calculated (Prop. yrs), as well as the average of these proportions (Combined weights) which was used as a weight in the model. The slope of the long-term population trend for each species for the period 1980-2019 was obtained from the Pan-European Common Bird Monitoring Scheme dataset (PECBMS; European Bird Census Council (EBCC)/BirdLife/Royal Society for the Protection of Birds (RSPB)/Czech Society for Ornithology (CSO); Gregory et al. 2005, Brlík et al. 2021; available at https://pecbms.info/trends-of-common-birds-in-europe-2021-update/). Diet type and body mass were obtained from the EltonTraits 1.0 dataset (Wilman et al. 2016), migratory status from Gilroy et al. (2016). The main habitat type for each species was classified following the PECBMS, "Life-history characteristics of European birds" (Storchová & Hořák 2018) datasets, and The Handbook of Birds of the Western Palearctic (Cramp 1977-1994). The tolerance to human-modified environments (Tol.) was calculated by summing the number of human-modified environments (out of cropland, grazing, urban, and forest habitats) each species was present in, obtained from Buchan et al. (2022) and The Birds of the Western Palearctic (Cramp 1977-1994).

Scientific name	Population trend	Prop. years	Prop. area	Combined weights	Diet type	Body mass	Migratory status	Habitat type	Habitat type source	Tol.	Niche breadth	Index
Tachybaptus ruficollis	1.007	0.744	0.13	0.437	Invertebrate	169.43	partial	wetland	Storchová and Hořák 2018	0	121.228	0.0000249

Podiceps cristatus	0.992	0.744	0.22	0.482	VertFishScav	730.96	partial	wetland	Storchová and Hořák 2018	1	108.553	0.0000161
Bubulcus ibis	1.009	0.538	0.005	0.272	Invertebrate	365.95	partial	farmland	PECBMS	2	67.277	0.0002300
Ardea cinerea	1.014	1	0.108	0.554	VertFishScav	1443	partial	wetland	Storchová and Hořák 2018	1	133.143	0.0000238
Ciconia ciconia	1.015	1	0.193	0.597	VertFishScav	3445.8	partial	farmland	PECBMS	3	85.891	0.0000225
Cygnus olor	1.008	1	0.453	0.726	PlantSeed	10682.04	partial	wetland	Storchová and Hořák 2018	3	105.545	0.0000381
Tadorna tadorna	0.997	0.718	0.18	0.449	Invertebrate	1146.83	partial	wetland	Storchová and Hořák 2018	1	138.891	0.0000688
Anas platyrhynchos	1.005	1	0.204	0.602	Omnivore	843.42	partial	wetland	Storchová and Hořák 2018	3	151.992	0.0000161
Circus aeruginosus	1.041	1	0.211	0.606	VertFishScav	704.07	partial	wetland	Storchová and Hořák 2018	1	97.333	0.0000155
Accipiter nisus	0.996	1	0.233	0.616	VertFishScav	220.79	partial	forest	PECBMS	1	151.385	0.0000180
Buteo buteo	1.018	1	0.395	0.698	VertFishScav	759.1	partial	other	PECBMS	3	125.102	0.0000148
Falco tinnunculus	0.99	1	0.173	0.587	VertFishScav	183.21	partial	farmland	PECBMS	4	153.789	0.0000159
Bonasa bonasia	0.985	1	0.301	0.651	PlantSeed	429	resident	forest	PECBMS	1	65.137	0.0000138
Lyrurus tetrix	0.999	0.59	0.326	0.458	PlantSeed	1068.66	resident	other	PECBMS	0	98.088	0.0000215
Alectoris rufa	0.972	0.538	0.993	0.766	PlantSeed	527.86	resident	farmland	PECBMS	2	61.599	0.0000560
Perdix perdix	0.944	1	0.55	0.775	PlantSeed	405.3	resident	farmland	PECBMS	1	95.081	0.0000135
Gallinula chloropus	0.996	1	0.191	0.595	Omnivore	339.63	partial	wetland	Cramp 1977-1994	1	126.816	0.0000171
Fulica atra	1.005	1	0.172	0.586	PlantSeed	717.12	partial	wetland	Storchová and Hořák 2018	1	119.43	0.0000174
Grus grus	1.049	0.897	0.257	0.577	PlantSeed	5499.99	partial	wetland	Storchová and Hořák 2018	2	70.335	0.0000132
Tetrax tetrax	0.939	0.538	0.3	0.419	PlantSeed	833.45	partial	farmland	PECBMS	0	74.501	0.0000380

Haematopus ostralegus	0.987	1	0.278	0.639	Invertebrate	526	partial	wetland	Storchová and Hořák 2018	0	153.692	0.0000462
Burhinus oedicnemus	0.988	0.538	0.139	0.339	Omnivore	459	partial	farmland	PECBMS	2	105.288	0.0000399
Pluvialis apricaria	1.001	0.974	0.44	0.707	Invertebrate	214	partial	shrub	Storchová and Hořák 2018	0	100.293	0.0000516
Vanellus vanellus	0.978	1	0.336	0.668	Invertebrate	218.37	partial	farmland	PECBMS	2	129.112	0.0000160
Gallinago gallinago	0.976	1	0.143	0.572	Invertebrate	112.94	partial	wetland	Cramp 1977-1994	1	118.218	0.0000183
Limosa limosa	0.965	0.897	0.192	0.545	Invertebrate	288.37	partial	farmland	PECBMS	1	72.072	0.0000158
Numenius phaeopus	1.015	0.897	0.17	0.534	Invertebrate	364.57	migrant	wetland	Cramp 1977-1994	0	74.774	0.0000287
Numenius arquata	0.989	1	0.248	0.624	Omnivore	802.99	partial	other	PECBMS	1	108.027	0.0000183
Tringa totanus	0.977	1	0.202	0.601	Invertebrate	129	partial	wetland	Cramp 1977-1994	1	158.55	0.0000199
Tringa nebularia	0.994	0.538	0.071	0.305	Invertebrate	187	migrant	wetland	Cramp 1977-1994	1	61.132	0.0000188
Tringa ochropus	1.004	1	0.104	0.552	Invertebrate	71.4	migrant	forest	PECBMS	1	50.176	0.0000110
Tringa glareola	0.997	1	0.099	0.549	Invertebrate	62.05	migrant	wetland	Cramp 1977-1994	1	63.019	0.0000137
Actitis hypoleucos	0.982	1	0.126	0.563	Omnivore	48	migrant	wetland	Storchová and Hořák 2018	0	153.768	0.0000200
Larus ridibundus	0.934	0.744	0.142	0.443	Invertebrate	284	partial	wetland	Storchová and Hořák 2018	3	127.804	0.0000202
Columba oenas	1.009	1	0.747	0.874	PlantSeed	290.79	partial	forest	PECBMS	4	112.155	0.0000156
Columba palumbus	1.017	1	0.736	0.868	PlantSeed	490	partial	other	PECBMS	4	156.176	0.0000171
Streptopelia decaocto	1.019	1	0.369	0.684	PlantSeed	148.96	resident	other	PECBMS	4	138.13	0.0000194
Streptopelia turtur	0.962	1	0.366	0.683	Omnivore	132	migrant	farmland	PECBMS	1	116.773	0.0000144
Clamator glandarius	1	0.538	0.053	0.296	Invertebrate	143	resident	other	PECBMS	3	50.13	0.0000684

Cuculus canorus	0.986	1	0.199	0.6	Invertebrate	111.36	migrant	other	PECBMS	3	159.666	0.0000160
Apus apus	0.997	1	0.283	0.642	Invertebrate	37.6	migrant	other	PECBMS	4	150.972	0.0000155
Alcedo atthis	0.991	0.718	0.228	0.473	VertFishScav	31.09	partial	wetland	Storchová and Hořák 2018	0	118.309	0.0000184
Merops apiaster	1.001	0.769	0.311	0.54	Invertebrate	56.6	migrant	other	PECBMS	2	114.225	0.0000278
Upupa epops	1	0.769	0.121	0.445	Invertebrate	66.93	partial	farmland	PECBMS	1	118.741	0.0000186
Jynx torquilla	0.975	1	0.248	0.624	Invertebrate	34.96	partial	other	PECBMS	1	131.48	0.0000176
Picus canus	0.984	0.769	0.416	0.593	Invertebrate	137	resident	forest	PECBMS	1	104.69	0.0000219
Picus viridis	1.019	1	0.938	0.969	Invertebrate	176	resident	other	PECBMS	2	122.486	0.0000218
Dryocopus martius	1.006	1	0.329	0.665	Invertebrate	321	resident	forest	PECBMS	1	96.668	0.0000150
Dendrocopos major	1.014	1	0.352	0.676	Omnivore	74.94	resident	other	PECBMS	2	148.048	0.0000172
Leiopicus medius	1.017	0.769	0.924	0.847	Invertebrate	59	resident	forest	PECBMS	1	90.906	0.0000248
Dryobates minor	0.967	1	0.438	0.719	Invertebrate	19.8	resident	forest	PECBMS	1	133.939	0.0000165
Melanocorypha calandra	0.97	0.538	0.366	0.452	Omnivore	61.6	partial	farmland	PECBMS	2	99.694	0.0000432
Calandrella brachydactyla	1.013	0.538	0.149	0.344	Invertebrate	21.06	partial	farmland	PECBMS	2	105.564	0.0000433
Galerida cristata	0.91	0.949	0.204	0.577	PlantSeed	42.68	resident	farmland	PECBMS	2	103.538	0.0000208
Galerida theklae	1.025	0.538	0.148	0.343	Invertebrate	38.17	resident	farmland	PECBMS	2	33.12	0.0000983
Lullula arborea	1.028	1	0.795	0.898	Omnivore	26.9	partial	other	PECBMS	1	112.974	0.0000185
Alauda arvensis	0.982	1	0.273	0.636	PlantSeed	37.31	partial	farmland	PECBMS	2	150.986	0.0000159
Ptyonoprogne rupestris	1.014	0.538	0.191	0.365	Invertebrate	20.4	partial	other	PECBMS	0	128.801	0.0000523
Hirundo rustica	0.996	1	0.104	0.552	Invertebrate	17.91	partial	farmland	PECBMS	3	156.386	0.0000161
Cecropis daurica	1.015	0.538	0.041	0.29	Invertebrate	22.2	migrant	other	PECBMS	3	76.749	0.0000871
Delichon urbicum	0.983	1	0.296	0.648	Invertebrate	14.5	migrant	other	PECBMS	3	158.476	0.0000163
Anthus campestris	0.981	0.718	0.219	0.468	Invertebrate	23	migrant	farmland	PECBMS	0	114.929	0.0000267
Anthus trivialis	0.978	1	0.272	0.636	Invertebrate	23.33	migrant	forest	PECBMS	1	135.504	0.0000180

Anthus pratensis	0.981	1	0.52	0.76	Invertebrate	18.4	partial	farmland	PECBMS	2	104.415	0.0000179
Motacilla flava	0.962	1	0.22	0.61	Invertebrate	17.68	partial	farmland	PECBMS	2	130.258	0.0000150
Motacilla cinerea	0.997	1	0.12	0.56	Invertebrate	17.15	partial	wetland	Cramp 1977-1994	0	149.928	0.0000379
Motacilla alba	0.999	1	0.168	0.584	Invertebrate	23.93	partial	wetland	Cramp 1977-1994	3	162.258	0.0000162
Bombycilla garrulus	1.067	0.795	0.053	0.424	Omnivore	54.41	partial	forest	PECBMS	1	8.556	0.0000050
Troglodytes troglodytes	1.011	1	0.382	0.691	Invertebrate	9.74	partial	other	PECBMS	2	148.438	0.0000214
Prunella modularis	0.993	1	0.699	0.849	Omnivore	20.24	partial	other	PECBMS	2	145.543	0.0000222
Erithacus rubecula	1.007	1	0.656	0.828	Omnivore	17.7	partial	other	PECBMS	2	143.291	0.0000165
Luscinia luscinia	0.992	1	0.491	0.746	Invertebrate	23.8	migrant	shrub	Cramp 1977-1994	1	32.273	0.0000077
Luscinia megarhynchos	0.983	1	0.312	0.656	Invertebrate	19.6	migrant	shrub	Cramp 1977-1994	1	107.768	0.0000300
Cyanecula svecica	0.978	0.59	0.152	0.371	Invertebrate	17.23	partial	shrub	Cramp 1977-1994	0	96.213	0.0000191
Phoenicurus ochruros	1.011	0.949	0.188	0.568	Invertebrate	16.5	partial	other	PECBMS	1	112.38	0.0000239
Phoenicurus phoenicurus	1.011	1	0.404	0.702	Invertebrate	14.59	partial	forest	PECBMS	1	137.709	0.0000165
Saxicola rubetra	0.975	1	0.42	0.71	Invertebrate	16.6	migrant	farmland	PECBMS	0	120.336	0.0000157
Saxicola torquatus	0.995	0.769	0.131	0.45	Invertebrate	14.09	partial	farmland	PECBMS	1	147.576	0.0000263
Oenanthe oenanthe	0.975	1	0.236	0.618	Invertebrate	25.39	migrant	other	PECBMS	1	166.163	0.0000179
Oenanthe hispanica	0.968	0.538	0.242	0.39	Invertebrate	15.04	migrant	farmland	PECBMS	0	90.483	0.0000516
Turdus torquatus	0.997	0.538	0.373	0.456	Omnivore	109	partial	other	PECBMS	2	156.238	0.0001230
Turdus merula	1.007	1	0.571	0.786	Omnivore	102.73	partial	other	PECBMS	4	149.046	0.0000182
Turdus pilaris	0.997	1	0.305	0.653	Invertebrate	106	partial	other	PECBMS	1	87.985	0.0000141
Turdus philomelos	1.004	1	0.474	0.737	Omnivore	67.74	partial	other	PECBMS	3	138.137	0.0000164

Turdus iliacus	0.992	1	0.292	0.646	Omnivore	61.2	migrant	other	PECBMS	1	77.646	0.0000163
Turdus viscivorus	0.996	1	0.503	0.751	Omnivore	117.37	partial	forest	PECBMS	2	131.69	0.0000169
Cettia cetti	1.026	0.769	0.382	0.576	Invertebrate	13.22	partial	wetland	Cramp 1977-1994	0	117.485	0.0000528
Cisticola juncidis	1.008	0.538	0.044	0.291	Invertebrate	6.81	resident	other	PECBMS	2	65.653	0.0000785
Locustella naevia	0.97	1	0.649	0.824	Invertebrate	13.3	migrant	wetland	Cramp 1977-1994	0	83.161	0.0000153
Locustella fluviatilis	0.976	0.949	0.696	0.822	Invertebrate	16.1	migrant	shrub	Cramp 1977-1994	0	37.193	0.0000080
Acrocephalus schoenobaenus	0.991	1	0.251	0.626	Invertebrate	11.83	migrant	wetland	Cramp 1977-1994	1	126.443	0.0000179
Acrocephalus palustris	0.991	1	0.668	0.834	Invertebrate	11.5	migrant	wetland	Cramp 1977-1994	0	89.925	0.0000163
Acrocephalus scirpaceus	0.997	1	0.226	0.613	Invertebrate	12.3	partial	wetland	Storchová and Hořák 2018	0	112.081	0.0000218
Acrocephalus arundinaceus	1.002	0.949	0.242	0.595	Invertebrate	30	migrant	wetland	Storchová and Hořák 2018	0	107.467	0.0000199
Hippolais icterina	0.985	1	0.459	0.729	Invertebrate	13.2	migrant	other	PECBMS	1	87.798	0.0000162
Hippolais polyglotta	0.996	0.769	0.334	0.552	Invertebrate	11	migrant	shrub	Cramp 1977-1994	1	95.364	0.0000726
Sylvia undata	0.978	0.538	0.493	0.516	Invertebrate	10.8	partial	shrub	Storchová and Hořák 2018	0	54.602	0.0000779
Sylvia cantillans	1.045	0.769	0.183	0.476	Invertebrate	9.6	migrant	shrub	Cramp 1977-1994	1	76.13	0.0000844
Sylvia melanocephala	1.01	0.769	0.264	0.517	Omnivore	11.7	partial	shrub	Storchová and Hořák 2018	3	65.785	0.0000589
Sylvia hortensis	1.055	0.769	0.193	0.481	Invertebrate	21.9	migrant	shrub	Cramp 1977-1994	1	62.874	0.0001223
Sylvia nisoria	0.983	0.949	0.466	0.707	Invertebrate	22.5	migrant	shrub	Storchová and Hořák 2018	1	85.669	0.0000174

Sylvia curruca	1	1	0.251	0.626	Invertebrate	11.44	migrant	shrub	Storchová and Hořák 2018	1	115.99	0.0000155
Sylvia communis	1.004	1	0.375	0.688	Invertebrate	15.1	migrant	farmland	PECBMS	3	155.701	0.0000178
Sylvia borin	0.993	1	0.363	0.681	Omnivore	18.2	migrant	shrub	Cramp 1977-1994	1	128.374	0.0000172
Sylvia atricapilla	1.027	1	0.584	0.792	Omnivore	16.7	partial	other	PECBMS	1	150.636	0.0000192
Phylloscopus bonelli	1.004	0.769	0.302	0.536	Invertebrate	8.69	migrant	forest	PECBMS	1	113.461	0.0001157
Phylloscopus sibilatrix	0.982	1	0.497	0.749	Invertebrate	9.2	migrant	forest	PECBMS	1	97.478	0.0000160
Phylloscopus collybita	1.016	1	0.329	0.664	Invertebrate	8.3	partial	forest	PECBMS	1	135.558	0.0000188
Phylloscopus trochilus	0.986	1	0.229	0.615	Invertebrate	8.7	migrant	other	PECBMS	1	110.515	0.0000165
Regulus regulus	0.982	1	0.347	0.673	Invertebrate	5.54	partial	forest	PECBMS	1	129.32	0.0000219
Regulus ignicapilla	1.009	0.949	0.638	0.793	Invertebrate	5.6	partial	forest	PECBMS	1	101.771	0.0000401
Muscicapa striata	0.984	1	0.32	0.66	Invertebrate	15.9	migrant	other	PECBMS	1	143.979	0.0000158
Ficedula albicollis	1.02	0.949	0.681	0.815	Invertebrate	12.69	migrant	forest	PECBMS	1	64.607	0.0000261
Ficedula hypoleuca	0.988	1	0.525	0.763	Invertebrate	13.79	migrant	forest	PECBMS	1	107.905	0.0000189
Aegithalos caudatus	1.009	1	0.441	0.721	Invertebrate	8.6	partial	other	PECBMS	2	154.225	0.0000190
Poecile palustris	0.991	1	0.525	0.762	Omnivore	11.14	resident	forest	PECBMS	0	110.692	0.0000233
Poecile montanus	0.964	1	0.351	0.676	Invertebrate	11.1	resident	forest	PECBMS	1	114.724	0.0000154
Lophophanes cristatus	0.989	1	0.985	0.993	Invertebrate	11.04	resident	forest	PECBMS	1	132.209	0.0000227
Periparus ater	0.998	1	0.297	0.649	Omnivore	9.2	partial	forest	PECBMS	2	155.48	0.0000236
Cyanistes caeruleus	1.008	1	0.93	0.965	Omnivore	13.3	partial	other	Storchová and Hořák 2018	4	146.571	0.0000180

Parus major	1.005	1	0.291	0.646	Omnivore	16.25	partial	other	Storchová and Hořák 2018	2	153.05	0.0000161
Sitta europaea	1.018	1	0.335	0.667	Invertebrate	20.37	resident	forest	PECBMS	2	138.468	0.0000192
Certhia familiaris	0.995	1	0.409	0.705	Invertebrate	9	resident	forest	PECBMS	1	118.85	0.0000183
Certhia brachydactyla	1.014	0.949	0.901	0.925	Invertebrate	8.2	resident	forest	PECBMS	1	100.219	0.0000348
Oriolus oriolus	1.002	0.949	0.372	0.66	Omnivore	79	migrant	other	Storchová and Hořák 2018	1	121.181	0.0000167
Lanius collurio	1.001	1	0.392	0.696	Invertebrate	28.44	migrant	farmland	PECBMS	1	126.463	0.0000161
Lanius senator	0.974	0.538	0.16	0.349	Invertebrate	35.97	migrant	farmland	PECBMS	1	84.297	0.0000543
Garrulus glandarius	1.002	1	0.474	0.737	Omnivore	159.46	resident	forest	PECBMS	2	146.47	0.0000159
Cyanopica cyanus	1.019	0.538	0.999	0.769	Invertebrate	95.91	resident	forest	PECBMS	2	23.269	0.0001299
Pica pica	0.992	1	0.307	0.654	VertFishScav	217.48	resident	other	PECBMS	4	156.512	0.0000160
Nucifraga caryocatactes	0.989	0.949	0.191	0.57	PlantSeed	182.51	resident	forest	PECBMS	1	72.918	0.0000247
Pyrrhocorax pyrrhocorax	1.009	0.538	0.069	0.304	Omnivore	276.68	resident	other	PECBMS	1	123.204	0.0001375
Corvus monedula	1.004	1	0.515	0.757	Omnivore	246	partial	other	PECBMS	4	127.632	0.0000163
Corvus frugilegus	1.007	1	0.257	0.628	Omnivore	452.1	partial	farmland	PECBMS	3	91.282	0.0000153
Corvus corone	1.006	1	0.296	0.648	VertFishScav	570	partial	other	PECBMS	4	161.411	0.0000160
Corvus corax	1.021	1	0.174	0.587	VertFishScav	927.97	partial	other	PECBMS	3	163.123	0.0000179
Sturnus vulgaris	0.972	1	0.222	0.611	Omnivore	77.14	partial	farmland	PECBMS	4	146.656	0.0000164
Sturnus unicolor	1.004	0.538	0.737	0.638	Omnivore	83.66	resident	farmland	PECBMS	2	45.969	0.0000755
Passer domesticus	0.981	1	0.149	0.574	PlantSeed	26.51	partial	other	PECBMS	2	157.406	0.0000165
Passer montanus	0.981	1	0.22	0.61	PlantSeed	21.39	partial	farmland	PECBMS	1	130.617	0.0000150
Petronia petronia	1.01	0.538	0.184	0.361	Omnivore	30.2	partial	farmland	PECBMS	1	110.885	0.0000741
Fringilla coelebs	0.999	1	0.563	0.781	Invertebrate	23.81	partial	other	PECBMS	2	150.873	0.0000159

Fringilla montifringilla	0.971	1	0.125	0.562	Omnivore	23.19	partial	shrub	Cramp 1977-1994	1	59.482	0.0000191
Serinus serinus	0.973	0.949	0.799	0.874	PlantSeed	11.2	partial	farmland	PECBMS	1	98.08	0.0000239
Chloris chloris	0.996	1	0.765	0.883	PlantSeed	26	partial	other	PECBMS	3	154.192	0.0000177
Carduelis carduelis	1.016	1	0.534	0.767	PlantSeed	16	partial	other	PECBMS	4	141.031	0.0000170
Spinus spinus	0.995	1	0.321	0.661	PlantSeed	13.24	partial	forest	PECBMS	2	121.912	0.0000243
Linaria cannabina	0.976	1	0.574	0.787	PlantSeed	19.53	partial	farmland	PECBMS	4	135.059	0.0000173
Acanthis flammea	0.97	1	0.068	0.534	PlantSeed	13	partial	other	PECBMS	1	113.022	0.0000399
Carpodacus erythrinus	0.985	1	0.181	0.591	PlantSeed	23.97	migrant	other	PECBMS	2	79.7	0.0000155
Pyrrhula pyrrhula	0.99	1	0.27	0.635	PlantSeed	24.26	partial	forest	PECBMS	1	132.369	0.0000201
Coccothraustes coccothraustes	1	1	0.409	0.704	PlantSeed	56.63	partial	forest	PECBMS	1	105.735	0.0000168
Emberiza citrinella	0.982	1	0.459	0.729	PlantSeed	29.7	partial	farmland	PECBMS	2	123.617	0.0000164
Emberiza cirlus	1.02	0.769	0.866	0.818	PlantSeed	25.6	partial	farmland	PECBMS	2	85.387	0.0000446
Emberiza cia	0.996	0.538	0.291	0.415	PlantSeed	23.43	partial	shrub	Storchová and Hořák 2018	1	122.582	0.0000732
Emberiza hortulana	0.945	1	0.592	0.796	Invertebrate	19.9	migrant	farmland	PECBMS	0	103.31	0.0000160
Emberiza rustica	0.946	1	0.145	0.572	PlantSeed	20.54	migrant	forest	PECBMS	1	9.863	0.0000051
Emberiza schoeniclus	0.99	1	0.266	0.633	PlantSeed	18.4	partial	wetland	Cramp 1977-1994	1	138.174	0.0000176
Emberiza calandra	0.972	1	0.626	0.813	PlantSeed	48.5	partial	farmland	PECBMS	2	106.011	0.0000200

Table S2.5. Habitat type category conversions from the "Life-history characteristics of European birds" (Storchová & Hořák 2018) dataset.

Original habitat type category	Converted habitat type category
Shrub	Shrub
Tundra	
Reed	Wetland
Swamps	
Freshwater	
Marine	
Savanna	Other
Grassland	
Mountain meadows	
Desert	
Woodland	
Rocks	
Human settlements	

Incorporating the niche breadth and range area relationship

The climatic niche breadth and range size of a species are likely to be highly correlated. To account for this, as well as to be able to compare species with similar range sizes, we produce an index by dividing the niche breadth by the range size. Species with a large value of this index have a relatively broad climatic niche compared to their range size, while a small value means that a species has a narrow climatic niche in relation to the area it occupies. This index, however, should not be interpreted as niche breadth per unit of range size, as this would imply that climatic variability is homogeneous across space, but rather as a proportion of niche breadth to range size, allowing for the comparison of climatic niche breadths across species with differing range sizes.

An alternative approach to accounting for the correlation between niche breadth and range size would be to regress one against the other and obtain the residuals of this relationship. However, we have not done so for various reasons. Firstly, the relationship between niche breadth and range size was non-linear and upon inspection of model residuals, we found evidence of uneven error variance (heteroscedasticity; Fig.S2.2). As this violates the assumptions of the linear model, we do not believe that the residuals from this model would be a sufficiently reliable metric to be used in further analyses.

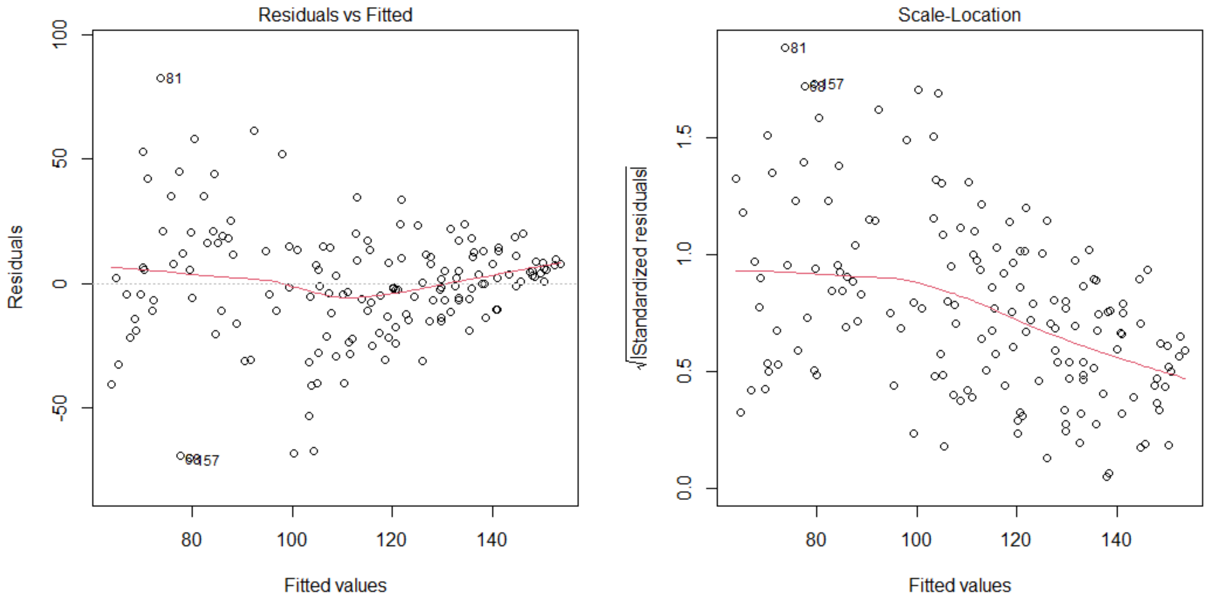

Figure S2.2. Model residuals and the square-root of standardized residuals against fitted values from linear model (LM) of the relationship between species climatic niche breadth and species range size.

Post-hoc factor level effects and contrasts for habitat type, diet, and migratory status

The estimated marginal mean effects of the main habitat type, diet, and migratory status have been calculated based on the full model average across the top six most parsimonious models, i.e. those within ΔAICc < 2. The post-hoc contrasts have identified a significant difference only between levels of habitat type, with farmland-associated species being more likely to face population declines than any other bird group (Table S2.6, Fig.S2.3).

Table S2.6. Post-hoc estimated marginal mean effects (emmean) and pair-wise comparisons (contrasts) for each level of three categorical variables, from full model average. Means and contrasts for each level calculated using values averaged across levels of the remaining levels.

Main habitat type					
Means					
Level	emmean	SE	df	lower.CL	upper.CL
wetland	1.001	0.004	147	0.992	1.009
farmland	0.980	0.004	147	0.973	0.988
forest	1.002	0.004	147	0.995	1.008
other	1.000	0.003	147	0.994	1.007
shrub	0.997	0.005	147	0.987	1.008
Contrast					
Levels	estimate	SE	df	t.ratio	p.value
wetland-farmland	0.020	0.005	147	3.987	0.001
wetland-forest	-0.001	0.005	147	-0.138	1.000
wetland-other	0.000	0.005	147	0.063	1.000
wetland-shrub	0.004	0.006	147	0.553	0.981
farmland-forest	-0.021	0.005	147	-4.632	0.000
farmland-other	-0.020	0.004	147	-4.631	0.000
farmland-shrub	-0.017	0.006	147	-2.770	0.049
forest-other	0.001	0.004	147	0.231	0.999
forest-shrub	0.004	0.006	147	0.699	0.956
other-shrub	0.003	0.006	147	0.527	0.985
Diet					
Means					
Level	emmean	SE	df	lower.CL	upper.CL
VertFishScav	1.000	0.007	147	0.987	1.013
Invertebrate	0.995	0.002	147	0.991	0.999
Omnivore	0.997	0.003	147	0.990	1.003
PlantSeed	0.992	0.004	147	0.985	1.000
Contrast					
Levels	estimate	SE	df	t.ratio	p.value
VertFishScav-Invertebrate	0.005	0.007	147	0.752	0.876
VertFishScav-Omnivore	0.003	0.006	147	0.559	0.944
VertFishScav-PlantSeed	0.008	0.009	147	0.877	0.817
Invertebrate-Omnivore	-0.002	0.003	147	-0.568	0.942
Invertebrate-PlantSeed	0.003	0.004	147	0.674	0.907
Omnivore-PlantSeed	0.005	0.006	147	0.836	0.837
Migratory status					

Means

Level	emmean	SE	df	lower.CL	upper.CL
resident	0.995	0.003	147	0.989	1.002
migrant	0.996	0.003	147	0.990	1.001
partial	0.997	0.002	147	0.992	1.002

Contrast

Levels	estimate	SE	df	t.ratio	p.value
resident-migrant	0.000	0.003	147	-0.122	0.992
resident-partial	-0.002	0.004	147	-0.486	0.878
migrant-partial	-0.001	0.003	147	-0.474	0.884

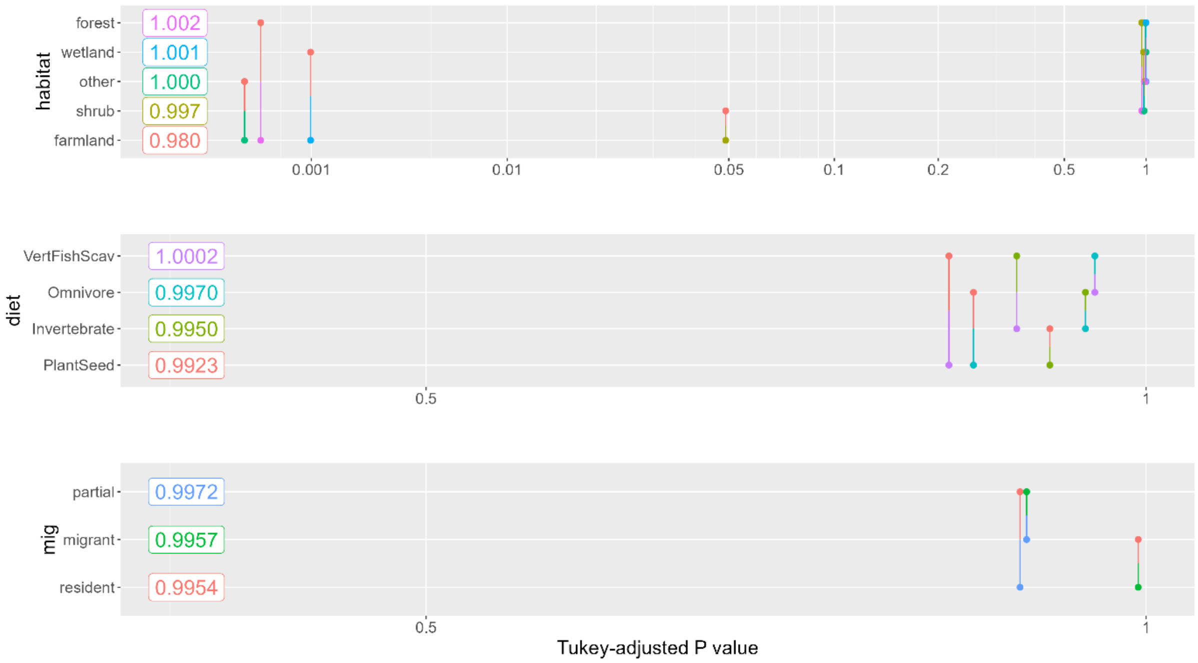

Figure S2.3. Pairwise p-value plots of the estimated marginal means across levels of habitat (top), diet (middle), and migration status (mig; bottom) variables based on the full model average.

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

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K.Z.: conceptualization, methodology, data curation, formal analysis, visualization, writing – original draft, review and editing; R.F.R.: conceptualization, methodology, data curation, writing – review and editing; I.C.: funding acquisition, supervision, writing – review and editing; J.J.G.: funding acquisition, methodology, supervision, writing – review and editing; J.P.S.: funding acquisition, resources, supervision, writing - review and editing; A.M.A.F.: conceptualization, funding acquisition, methodology, supervision, writing – review and editing.

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ABSTRACT

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

Keywords: farmland and grassland birds, microclimate refugia, site usage, GPS tracking data, little bustard

3.1 Introduction

Protected areas (PAs) are a cornerstone of biodiversity conservation and key to protecting endangered species. These areas may shield species from the negative effects of anthropogenic activities (e.g. hunting and land-use change; Buchan et al., 2023) as well as promote population recovery and increase (Wauchope et al., 2022). Through the widespread and pervasive impact of habitat degradation, PAs often become patches of fragmented natural or semi-natural habitats in otherwise inhospitable landscapes (Brennan et al., 2022; Ward et al., 2020), producing isolated populations of species they were designated to protect (Méndez et al., 2011; Santiago-Ramos & Feria-

Toribio, 2021). Furthermore, as local conditions become seasonally unfavourable, individuals may move to new areas and return once conditions improve (Cohen & Jetz, 2023; Zurell et al., 2018). However, such movements pose challenges for species conservation within static protected areas, as individuals may be forced to move outside of these areas in order to find sites with suitable conditions (Pérez-Granados et al., 2025; Santiago-Ramos & Feria-Toribio, 2021). Furthermore, the recent fast speed of climate change (IPCC, 2023) can render previously occupied distribution areas climatically unsuitable, driving a shift in species distributions (Chen et al., 2011) through movement, local extinctions, and population declines (Pearce-Higgins & Green, 2014). Thus, the effective management of protected areas for species conservations needs to consider not only the prevention of habitat loss and elimination of threat exposure, but also individual seasonal movement patterns and distributional shifts in response to climate change (Garden et al., 2015; Pérez-Granados et al., 2025; Thomas et al., 2012).

Some habitat characteristics may provide shelter from the negative effects of climate warming by providing small-scale refuge from extreme conditions and allowing sites to be utilized when the surrounding landscape has become inhospitable (Ramos et al., 2023a; Suggitt et al., 2018). These microclimate refugia may take the form of habitat patches, such as wetland and forest areas, shielded cliff edges, or individual habitat features like rock structures or vegetation (García et al., 2020; Williamson et al., 2021). They can be used as nesting sites, or for resting during foraging, and provide shelter from high temperatures (Ramos et al., 2023a). The presence of microclimate refugia has been shown to improve individual survival in areas particularly exposed to high temperatures (Lima et al., 2016). Furthermore, refugia are expected to be crucial landscape features for allowing population persistence despite global warming (Stark & Fridley, 2022; Suggitt et al., 2018). This has been shown across different bird species, populations of which have already been negatively affected by rising temperatures. For example, bird populations in areas with microclimate refugia were less likely to be declining (Kim et al., 2022). Thus, microclimate availability can be a key buffer against elevated temperatures and play an important role in the management of protected areas to increase their resilience to climate change (Jones et al., 2023).

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

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

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

3.2 Methods

Study species and tracking data

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

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

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

The little bustard breeding season starts in April and ends, on average, in June. The post-breeding (summer) season in this study includes the months of July, August, and September (15th July - 15th September; Ramos et al., 2023a). This is the period corresponding to peak temperatures within the Iberian Peninsula. To increase consistency between individuals the data acquisition for the breeding period only included tracking data from the 1st of May, as the timings of tag deployment could occur throughout April.

To determine whether a GPS location obtained during breeding was also used in the post-breeding season, we produced a circular buffer, with a radius of 500 meters, around each GPS location and examined the buffer overlap between breeding (i.e. any GPS location collected from any individual during the breeding season) and post-breeding (i.e. any GPS location collected from an individual during the post-breeding season) locations across all birds. Hence, in this study a location (also referred to as site or area) is defined as the GPS location and the corresponding 500m buffer around it. If a breeding location buffer overlapped at least 50% with a post-breeding location buffer, this would be classified as used in both the breeding and post-breeding seasons. Otherwise, the breeding location would be assigned as used by individuals in this study exclusively in the breeding season (hereafter referred to as 'non-used in post-breeding' or 'non-used') and the post-breeding location would be classed as used by focal individuals in the post-breeding season only (hereafter referred to as 'used in post-breeding' or 'used'). Due to the relatively low number of locations used in both seasons (N = 1,253 out of 85,759 GPS locations), and as the aim of this study was to investigate the conditions at used and non-used sites during the post-breeding season, the locations used in both breeding and post-breeding and those used in the post-breeding only were combined for the purpose of analysis and are referred to as 'used' in this study.

The distribution of the GPS locations obtained and whether they are used or non-used in the post-breeding season is shown in Fig.3.1.

Environmental data

To characterise the microclimatic conditions at each site we first obtained hourly microclimate temperatures at a 30 m resolution and 20 cm above ground using the fully automated microclimate modelling procedure from the *microclima* package (Maclean et al., 2019). To generate these temperatures, the microclimate model used National Centers for Environmental Prediction climate reanalysis data (NCEP) (Kanamitsu et al., 2002; Kemp et al., 2012), and accounted for terrain characteristics through a digital elevation model from Amazon Web Services (AWS) and habitat type. Temperature was extracted at the GPS location and in each 30m cell within a 500 m buffer around the GPS location. Microclimate refugia availability was defined as the difference between the minimum and median temperature available within the buffer of each GPS location. A more negative value represented a larger difference between the minimum and median temperature within the buffer, and therefore, a greater availability of microclimate refugia. To characterise the micro-scale habitat at each site we used CORINE land cover maps at 100m resolution for reference years 2012 and 2018 (European Environment Agency. European Union's Copernicus Land Monitoring Service). All land use types were simplified into one of the four categories: arboreous, herbaceous, shrubby, or other habitat. To ensure that these land use datasets are sufficient to represent the habitat across the study period we compared the proportion of land use change between the 2012 and 2018 datasets across the four habitat categories (herbaceous, shrubby, arboreous, other habitat) in a 500m buffer around all GPS locations collected. We found that the overall number of locations with a change in habitat cover proportion was low, with a change in shrubby cover occurring at 3.30% (N = 2,871; 80.21% increase and 19.79% decrease in shrubby cover), change in herbaceous at 6.65% (N = 5,757; 18.84% increase and 81.16% decrease in herbaceous cover), and change in proportion of arboreous cover within 4.59% (N = 3,987; 73.86% increase and 26.14% decrease in arboreous cover) of all buffers. This relatively low number of sites at which the proportion of habitat cover changed suggest that the two datasets are sufficient to represent the habitat cover within our study area during this period. For data collected between 2009 – 2014 we used the 2012 dataset, and for data collected in 2015 – 2019 we used the 2018 land use dataset. We extracted the proportion of each habitat type category within a 500m buffer around each GPS location. The proportion was arcsine square-root transformed due to large skew towards extreme ends of the proportion range (i.e. large number of near-zero or near-one values). Site usage decisions may be in part driven by the availability of resources such as food. Hence, we included the Normalized Vegetation Index (NDVI) for every GPS location as an approximation of food availability (Pettorelli et al., 2005; Ramos et al., 2023b). Little bustards feed predominantly on green plants, as well as on arthropods (Bretagnolle et al. 2022), therefore, NDVI provides a direct (i.e. indicating the presence of green plants) and indirect (i.e. indicating presence of patch characteristics favourable for arthropods) approximation of food availability at each location. To calculate NDVI we extracted near infra-red (NIR) and red (R) reflectance values at each GPS location from an 8-day average Moderate Resolution Imagining Spectroradiometer (MODIS) surface reflectance images at a 250m resolution using Google Earth Engine (Didan, 2015; Gorelick et al., 2017). The NDVI at each location was calculated as the difference between the near infra-red and red reflectance (NIR – R) divided by the sum of near infra-red and red reflectance (NIR + R; Huete et al. 2002). Full details of producing the dataset are available in Ramos et al. (2023a) and Ramos et al. (2023b).

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

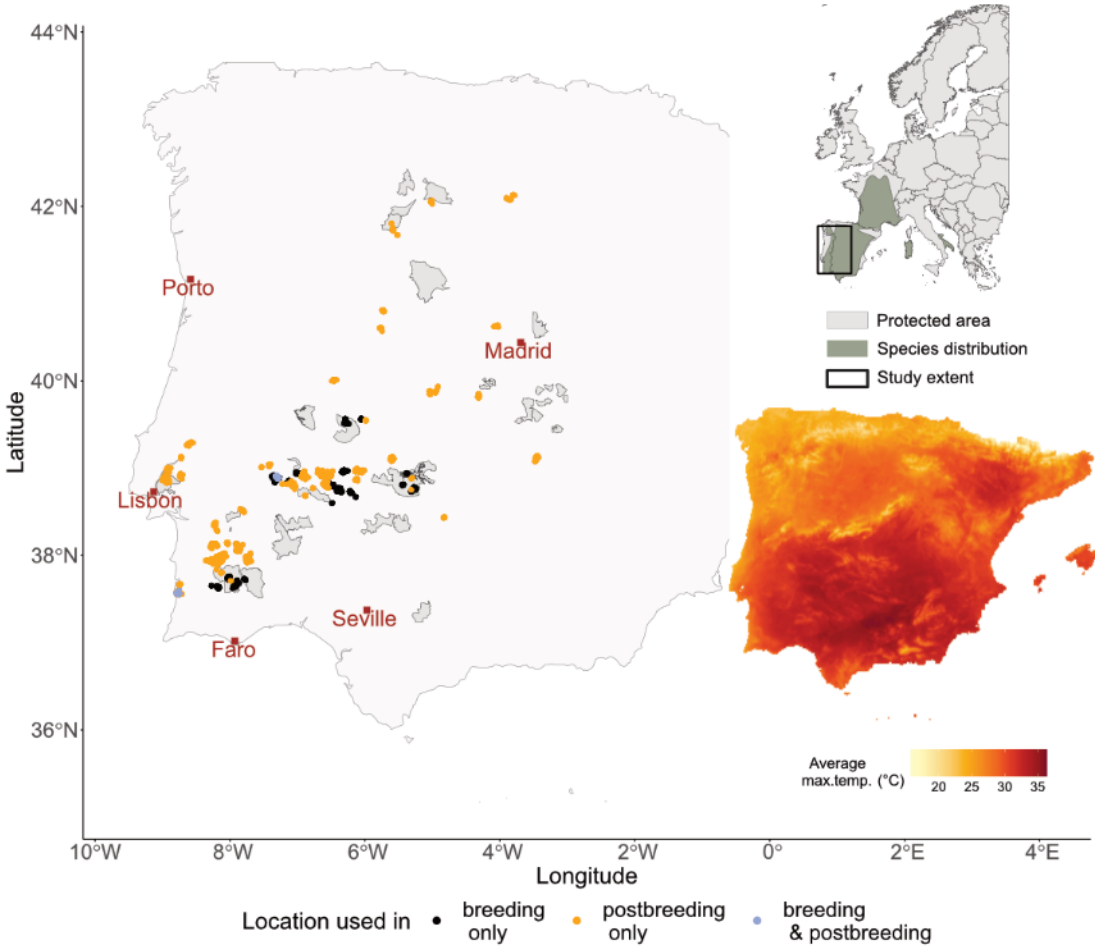

Figure 3.1. Little bustard GPS locations collected from 47 individuals between years 2009-2019, the little bustard range within Europe (top right; shaded area; BirdLife International 2020), and the average maximum monthly temperature for July – September 2009-2019 for the Iberian Peninsula (bottom right; produced using the CRU-TS 4.06 dataset downscaled with WorldClim 2.1 (Fick & Hijmans, 2017; Harris et al., 2020). Black points show locations used in the breeding season only (N = 53,158) 63% of these are within protected areas (PAs), in orange are the locations occupied only in the post-breeding season (N = 31,348) 4.4% within PAs, and in blue those used in both breeding and post-breeding (N = 1,253) 61.2% within SPAs. The darker grey areas show the selected protected areas with agro-steppe habitat used by little bustards based on Gameiro et al. (2020), using data obtained from European Environmental Agency (EEA). Vector data for mapping were obtained from *rnaturalearth* (Massicotte et al., 2023).

Statistical analyses

The GPS location data are largely clustered, and the dataset includes spatial overlap due to the individuals remaining in or returning to roughly the same place for long periods. Locations in close proximity have partially overlapping 500 m buffers, resulting in highly similar values for the environmental variables of interest. This poses a problem as high spatial autocorrelation and pseudoreplication violate the model assumptions. Furthermore, some sites may be over-represented due to varying sample size across individuals as a result of the different data collection schedules for different devices (10-120 minutes). Hence, the data was spatially thinned, to randomly retain only locations with a minimum distance of 500m between them, therefore, preventing the same location from being included in the dataset more than once, and ensuring all observations used to fit the model are independent. The study area was sub-divided using a 0.5° resolution 12x12 square grid (144 cells, approximately 40 km^2 each) and within each grid cell, the locations were thinned to a minimum distance of 500 m using the 'thin' function from the *spThin* package (Aiello-Lammens et al., 2015). The procedure was repeated 20 times to ensure the largest possible sample size retained, and we ensured that the resulting sample size was unaffected if the number of repeats was greater than this. The full dataset contained 85,759 data locations, the thinned datasets had approximately 1.3% of the data (N = 1,140). Thinning was carried out separately for the GPS locations that were abandoned and used after breeding to prevent loss of data due to proximity between them. To avoid a biased subsample being used for analysis, the thinning procedure was further randomised. Out of the 20 subsets generated through the thinning procedure, only those with the maximum sample size were retained. Then, for each of the 144 grid cells, one dataset was randomly selected, producing an overall dataset that was further cleaned using *CoordinateCleaner* (Zizka et al., 2019) to check for invalid coordinates, and then used for modelling (details described below). This procedure was repeated 100 times to minimise the likelihood of a biased sample being selected. The model coefficients for the 100 models were stored, and model averaging was carried out using the 'model.avg' function from the *MuMIn* package (Bartoń, 2023) with equal weights given to each model, to produce the average model coefficients. The output is presented in Supporting information. As the variability in model coefficients produced by the 100 models was low, to simplify the modelling and prediction process, a single thinned dataset was randomly selected out of the 100 repetitions of the thinning procedure and used in subsequent analysis, the results of which are presented below.

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

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

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

3.3. Results

The final dataset consisted of 1,140 location records obtained from 47 tracked little bustards between 2009 and 2019, of which 754 were used, and 386 were abandoned in the post-breeding season. The probability of a location being used by little bustards in the post-breeding season decreased with increasing temperatures, but little bustards were more likely to use locations with higher NDVI and greater microclimate refugia availability (Table 3.1, Fig.3.2a-c). Site usage probability was significantly higher in locations with low shrubby cover and exhibited a steep decline with increasing shrub density (Fig.3.2d). In contrast, the proportion of arboreous cover did not significantly affect site usage during the post-breeding season (Table 3.1).

Table 3.1. Parameter estimates from a generalized linear model (GLM) explaining the probability of site usage by little bustards during the post-breeding season as a function of temperature, microclimate refugia availability (difference between the minimum and median temperature within 500m buffer), the proportion of arboreous and shrubby cover within 500 m buffer around the GPS location (arcsine square-root transformed), NDVI, and time (in minutes) since the warmest hour of the day.

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

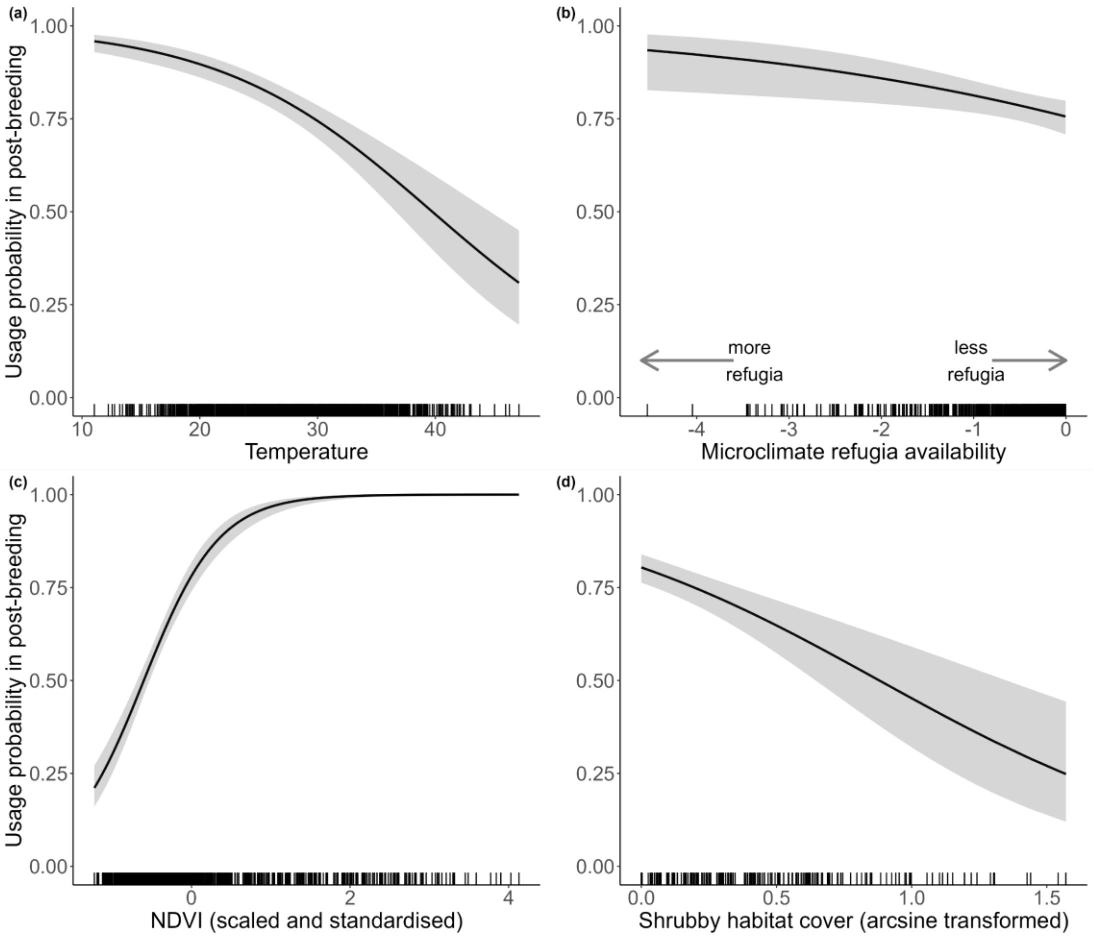

Figure 3.2. Model predictions from generalized linear model (GLM) of current site usage probability in the summer (post-breeding season) by the little bustards in relation to temperature at point (a), microclimate refugia availability (calculated as the difference between the minimum and median temperatures within a 500-m buffer; b), NDVI (c), and the proportion of shrubby cover within 500-m buffer around GPS location (d). Shaded areas represent the 95% confidence intervals and rug shows raw data distribution.

From all locations used in the post-breeding season, only approximately 6.6% locations (pre-thinned sample size, 2,144 out of 32,601) fall within PAs (Fig.3.3). Out of these, 9.3% (157) would lose suitability if temperatures increased by 1.5°C, 11.5% (247) with a 2.7°C temperature increase, and 14.4% (309) locations would be lost if the temperature was increased by 3.6°C.

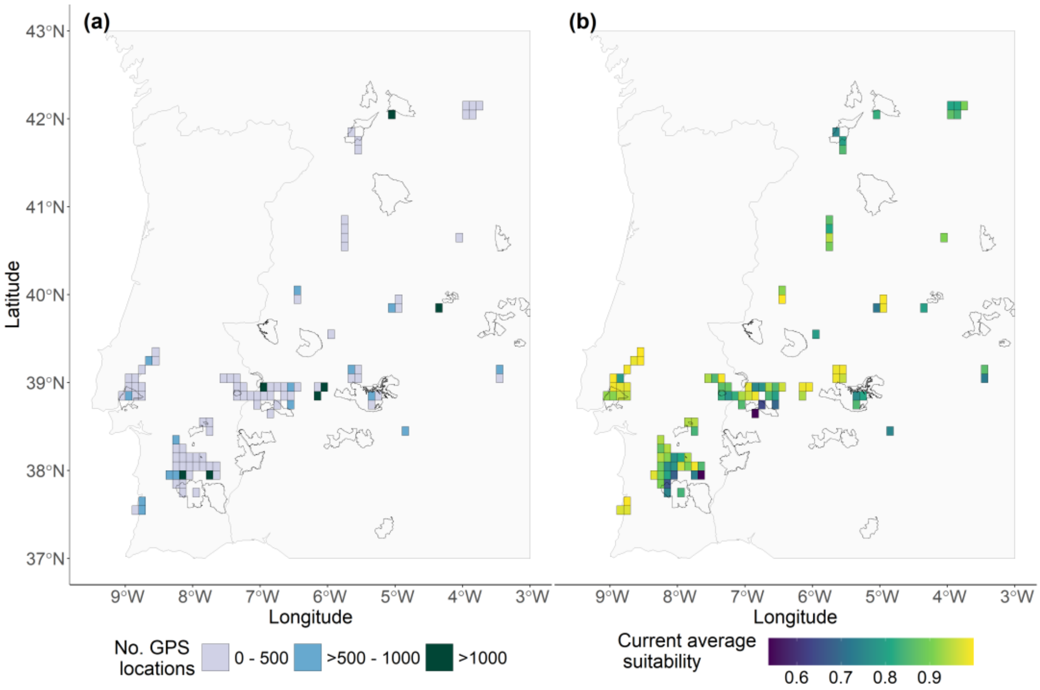

Figure 3.3. The number of GPS locations used in the post-breeding season within each grid cell (cell resolution = 0.1°; N = 32,601; a), and current (2009-2019) average suitability during the post-breeding season within each grid cell as predicted by the generalized linear model using current site characteristics (b).

The predicted number of sites used decreased for all warming scenarios: at 1.5°C temperature increase approximately 9.3% (3,017) locations were expected to be lost, 11.2% (3,665) lost at 2.7°C, and 12.8% (4,172) locations lost with a 3.6°C temperature increase. When GPS locations were combined into a grid (0.1°resolution), some spatial differences were observed. Across all temperature increase scenarios, over two-thirds (70.3 – 77.23%) of grid cells were predicted to have up to 10% declines in the number of suitable locations. However, some grid cells were predicted to experience major losses in suitability, with a 65.6% decline in the predicted number of suitable locations when the temperature was increased by 1.5°C, 75.0% with an increase of 2.7°C, and 78.1% loss predicted when point temperatures were increased by 3.6°C (Fig.3.4). Losses of more than 50% of used locations were predicted in approximately 4% of the grid cells in all temperature increase scenarios.

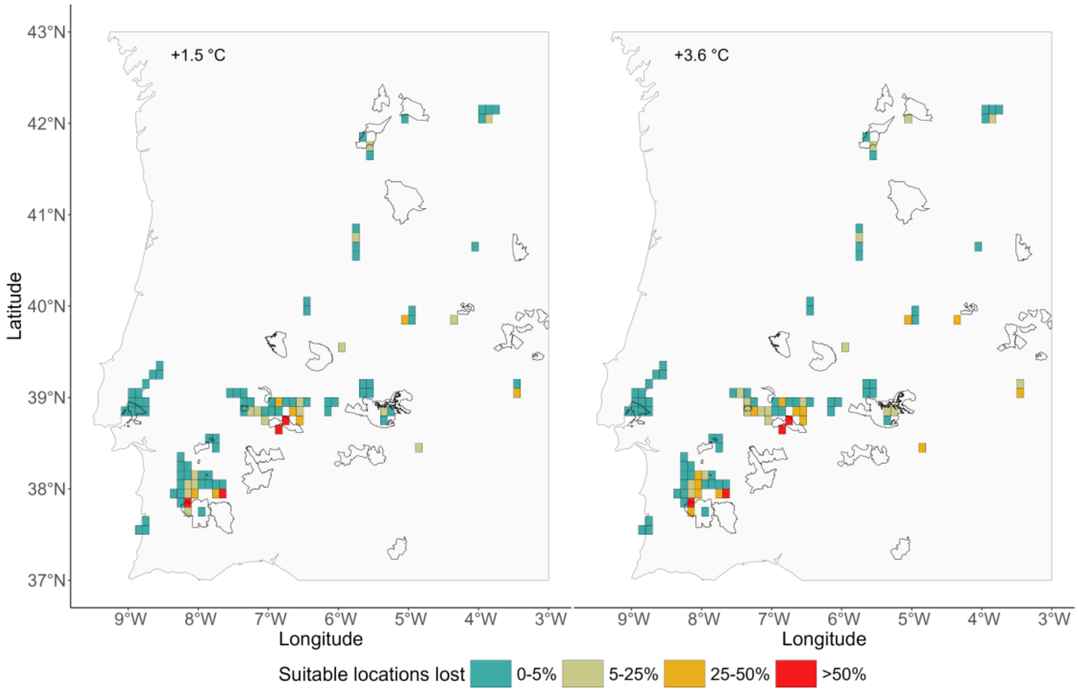

Figure 3.4. The proportion of locations that become unsuitable for little bustards with a 1.5°C or 3.6°C temperature increase within each grid cell (resolution = 0.1°), predicted from the generalized linear model. Predicted site usage determined using a probability cut-off of 0.6. Within PAs, 3.5% of sites are predicted to become unsuitable with an average warming of 1.5°C, while with a 3.6°C temperature increase this loss in suitability is expected to be 10.6%.

3.4 Discussion

Conservation efforts of grassland birds in Europe, including the little bustard, have led to the designation of a network of Special Protection Areas (SPAs), which were designed for the protection of the species during the breeding season but not during other phenological stages. Protected areas, and particularly SPAs, have been shown to increase rare species abundance and the likelihood of them colonising these areas (Barnes et al., 2023). Our study shows that these grassland SPAs indeed protect a large proportion of the little bustard breeding occurrences, however, in the post-breeding season, only approximately 6.6% of the recorded locations fell within the protected areas. The sites used in the post-breeding season were characterised by lower temperatures, higher availability of microclimate refugia, and increased NDVI, but reduced shrub cover. Furthermore, predictions from our model show consistent declines in post-breeding site suitability across all future temperature increase scenarios, highlighting that parts of the little bustard distribution which are already characterised by relatively low suitability, such as central and southern parts of the

Iberian Peninsula, will continue to decline in suitability due to increasing temperatures. Consequently, this reduction in site suitability may induce little bustards to move earlier to find cooler conditions (Ramos et al., 2023b).

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

Refugia availability within the grassland habitats of the Iberian Peninsula can be linked to isolated patches of shrub and trees in otherwise open habitats, and it has been shown that little bustards tend to select sites with these habitat features (Ramos et al., 2023a). At the same time, usage of sites with a higher proportion of herbaceous vegetation cover is also crucial, as these are where food availability may be highest. After the breeding season, in the summer months, food availability is greatly reduced within the SPAs, which is likely one of the major reasons for little bustards moving away from these areas during the post-breeding migration (Crispim-Mendes et al., 2024; Silva et al., 2023). This introduces a trade-off and explains the negative relationship between site usage and shrubby cover we find in this study. Use of shrubs as microclimate refugia has previously been shown (e.g. Shelef & Groner 2011; Ruth et al. 2020), and the availability of scarce shrubby patches providing refugia will likely increase in importance with global warming. Furthermore, microclimate refugia availability has been shown to increase with increasing shrubby cover (Ramos et al. 2023a). However, sites with high shrubby cover during the post-breeding season tend to be drier, possibly abandoned fields, which may provide abundant microclimate refugia but limited food sources. Hence, while the presence of scattered shrubby patches that do not significantly disrupt the open habitats may generally be beneficial for little bustards, by significantly increasing microclimate refugia availability (Ramos et al., 2023a), a high proportion of them within the habitat may make the patch less favourable for the species.

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

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

The Iberian Peninsula has already experienced changes related to global warming, and these are expected to continue in the next decades (IPCC, 2023). In addition to thermal strain on individuals, increasing temperatures, particularly earlier in the year, may result in vegetation drying out sooner, which may limit food availability. Furthermore, the threat may not be solely linked with year-to-year warming, but also with the increase in the occurrence of extreme events, such as droughts or heatwaves (Marcelino et al., 2020; Maresh Nelson et al., 2024). These more short-term events have been shown to have a particularly negative impact on grassland birds (Maresh Nelson et al., 2024). Based on our predictions, areas which are already experiencing more extreme temperatures, will continue to "deteriorate" in the future. This is particularly true for the centre and southwest part of the species' distribution range in Iberia, which coincides with important little bustard breeding sites within its Iberian range – Alentejo (Portugal) and Extremadura (Spain). Hence, habitat management to provide microclimate refugia will likely be key for enabling species, such as the little bustard, to survive these now unavoidable warming temperatures and increasingly frequent extreme events. The availability of fine-scale GPS tracking data allows us to identify which locations are used by the little bustards, and in combination with micro-scale environmental characteristics, we are able to determine the features of the habitats used. Furthermore, while breeding areas are relatively well protected, this is not the case for the sites used in the post-breeding season. However, during this time individuals are exposed to particularly high temperatures, which are likely to increase with global warming. Hence, the post-breeding areas that offer microclimate refugia shielding individuals from the heat urgently need to be protected to aid species conservation and prevent further rapid declines of the little bustard within the Iberian Peninsula.

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

3.5 Conclusions

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

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this paper was carried out on the High-Performance Computing Cluster supported by the Research and Specialist Computing Support service at the University of East Anglia. This study was prepared using a number of publicly available datasets. Land use information was obtained from the European Union's Copernicus Land Monitoring Service information (2012: https://doi.org/10.2909/a84ae124-c5c5-4577-8e10-511bfe55cc0d and2018: https://doi.org/10.2909/960998c1-1870-4e82-8051-6485205ebbac; 2012-2018 land cover change https://doi.org/10.2909/5654b422-af84-4115-ac3c-5d7dea540ebb), digital elevation model (DEM) from Amazon Web Services (Terrain Tiles - Registry of Open Data on AWS https://registry.opendata.aws/terrain-tiles/), little bustard species distribution polygons from BirdLife International (Handbook of the Birds of the World. Bird species distribution maps of the world. Version 2021.1. Available at http://datazone.birdlife.org/species/requestdis), and polygons of protected areas were obtained from EEA Natura 2000 (Available at: https://www.eea.europa.eu/en/datahub/datahubitem-view/6fc8ad2d-195d-40f4-bdec-576e7d1268e4).

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Chapter 3: Supporting information

Tracking data

Table S3.1. Number of individuals tracked (Individuals), number of individuals that were tracked in previous year(s) (Prev.), number of days over which data were collected (Days), and number of GPS locations collected (N), in breeding and post-breeding of each year of the study.

Year	Breeding				Post-breeding			
	Individuals	Prev.	Days	N	Individuals	Prev.	Days	N
2009	10	0	98	5513	10	0	121	6329
2010	6	3	105	4281	6	3	112	4529
2011	9	3	110	6506	9	3	119	6275
2012	3	3	105	2296	2	2	48	1088
2015	12	0	105	22467	12	0	113	16350
2016	6	6	144	15927	6	6	88	2063
2017	8	2	101	14597	8	2	102	10343
2018	3	1	119	7961	3	1	78	3417
2019	10	2	103	20304	10	2	122	15224

Accounting for diurnal temperature variation

The range of possible temperatures will differ throughout the day, however, our analysis requires the comparison of locations "observed" at different times of the day. To do so, we include a temporal component in the model. Including time of day was not reasonably possible, as we do not include the full 24 hours, rather only "day" i.e. when the little bustard is likely to be active (not roosting sites) and when temperatures may be higher, therefore, microclimate refugia may be utilized. Hence, we find the warmest part of the day by producing the average temperature derived at each of the GPS locations for each of the hours included in our dataset, combined across the abandoned (BR only) and used (PB) locations (Fig.S3.1). Then for each data point, we calculate the absolute difference in minutes from the hour at which it was recorded to the warmest hour of the day and include this as a variable in the model.

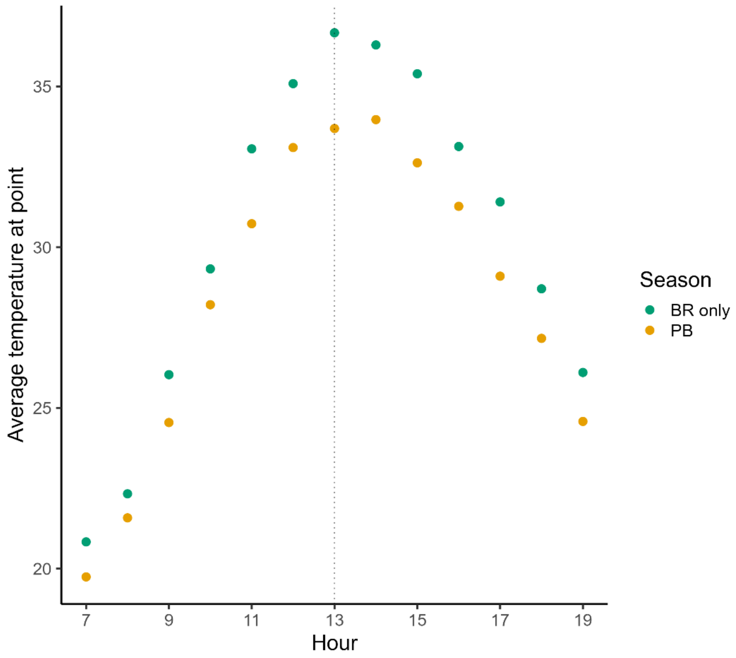

Figure S3.1. Average temperature at point across all abandoned (breeding-only) and used (post-breeding only and resident) locations at all hours of day retained in the model dataset. Dotted line is at hour 13:00.

Protected Areas

Table S3.2. List of protected areas included selected based on Gameiro et al., (2020). The site type indicates the designation type, with sites of type A being designated under the Birds Directive, sites of type B under the Habitats Directive, and sites of type C under both the Birds and the Habitats Directives (data obtained from the European Environmenta Agency).

Site code	Site name	Country	Site type
PTCON0035	Alvito/Cuba	PT	B
PTZPE0043	Campo Maior	PT	A
PTZPE0055	Évora	PT	A
PTZPE0010	Estuário do Tejo	PT	A
PTZPE0046	Castro Verde	PT	A
PTZPE0047	Vale do Guadiana	PT	A
PTCON0009	Estuário do Tejo	PT	B
PTZPE0053	Vila Fernando	PT	A
PTZPE0045	Mourão/Moura/Barrancos	PT	A
ES0000004	Lagunas de Villafáfila	ES	A
ES0000207	Penillanuras-Campos Sur	ES	A
ES0000194	Oteros-Campos	ES	A
ES0000204	Tierra de Campiñas	ES	A
ES0000139	Estepas cerealistas de los ríos Jarama y Henares	ES	A
ES0000369	Llanos de Alcantara y Brozas	ES	C
ES0000398	Llanos y Complejo Lagunar de la Albuera	ES	A
ES0000071	Llanos de Cáceres y Sierra de Fuentes	ES	A
ES0000170	Área esteparia de La Mancha norte	ES	A
ES4310004	Dehesas de Jerez	ES	C
ES6180017	Campiñas de Sevilla	ES	A
ES0000367	La Serena y Sierras Periféricas	ES	A
ES0000435	Área esteparia de la margen derecha del río Guadarrama	ES	A
ES4140036	La Nava-Campos Norte	ES	A
ES6130017	Alto Guadiato	ES	A
ES0000325	Campiña sur – Embalse de Arroyo Conejos	ES	A

Table S3.3. Raw (pre-thinning) sample size of breeding only, post-breeding only, and points used in breeding and post-breeding falling within and outside of protected areas (PA).

Point category	Outside PA	Inside PA	Total
Breeding only	19,673 (37.01%)	33,485 (62.99%)	53,158
Post-breeding only	29,977 (95.63%)	1,371 (4.37%)	31,348
Breeding and post-breeding	486 (38.79%)	767 (61.21%)	1,253

Temperature and refugia availability

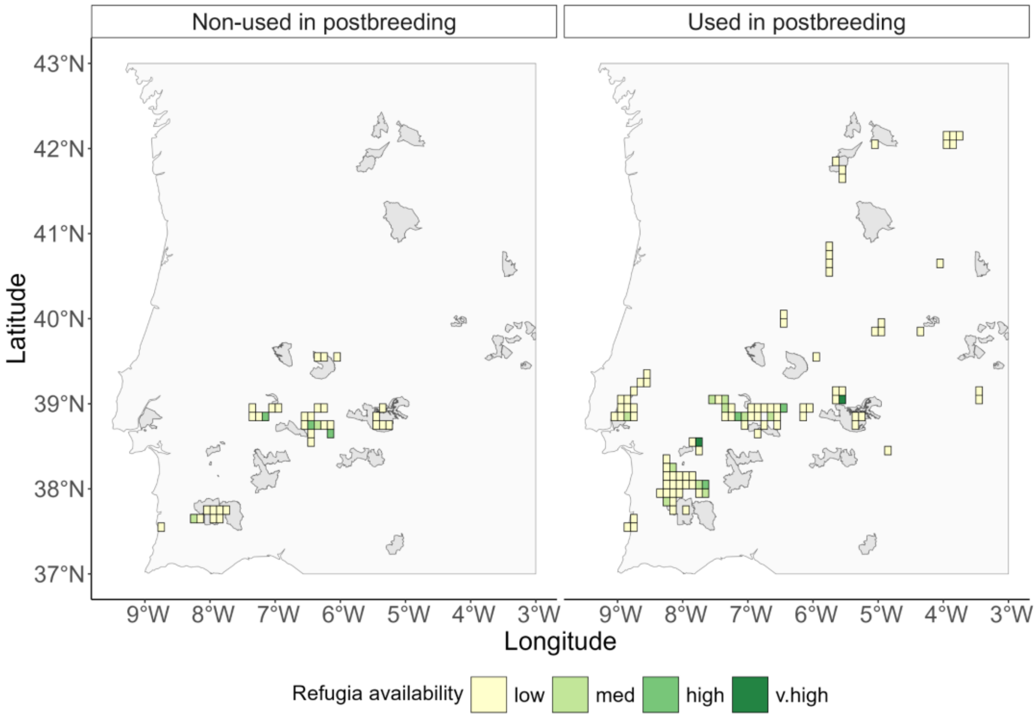

Figure S3.2. Microclimate refugia availability within non-used and used grids during the post-breeding. The darker grey areas show the Special Protected Areas (SPAs) using data obtained from European Environmental Agency (EEA). Vector data for mapping were obtained from *rnaturalearth* (Massicotte et al. 2023).

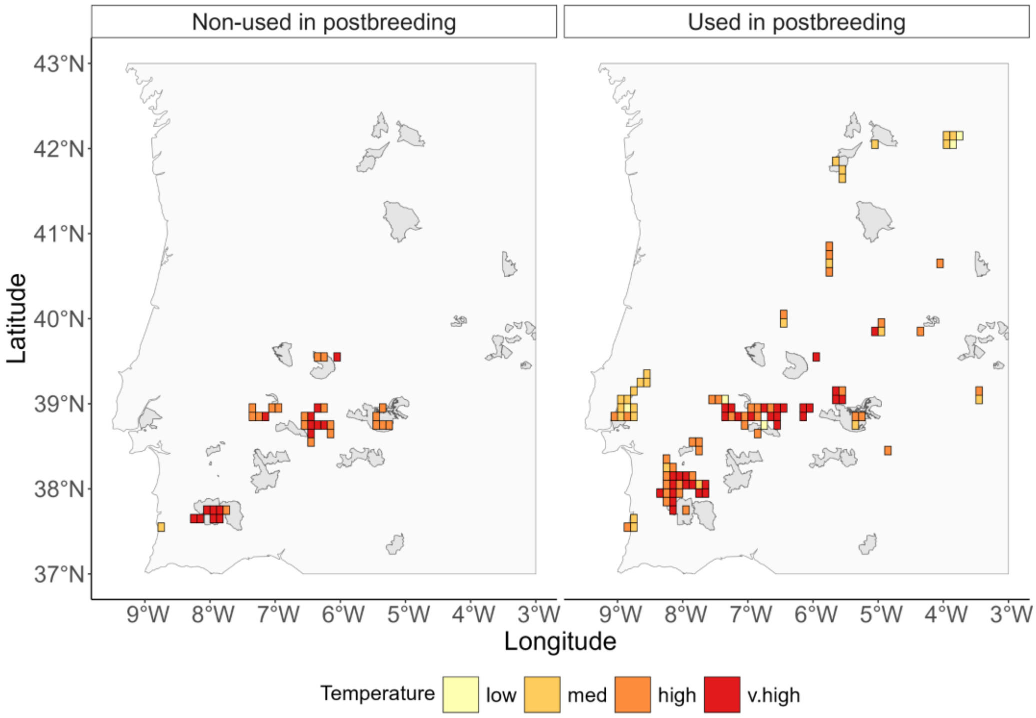

Figure S3.3. Microclimate temperature within non-used and used grids during the post-breeding. The darker grey areas show the Special Protected Areas (SPAs) using data obtained from European Environmental Agency (EEA). Vector data for mapping were obtained from *rnaturalearth* (Massicotte et al. 2023).

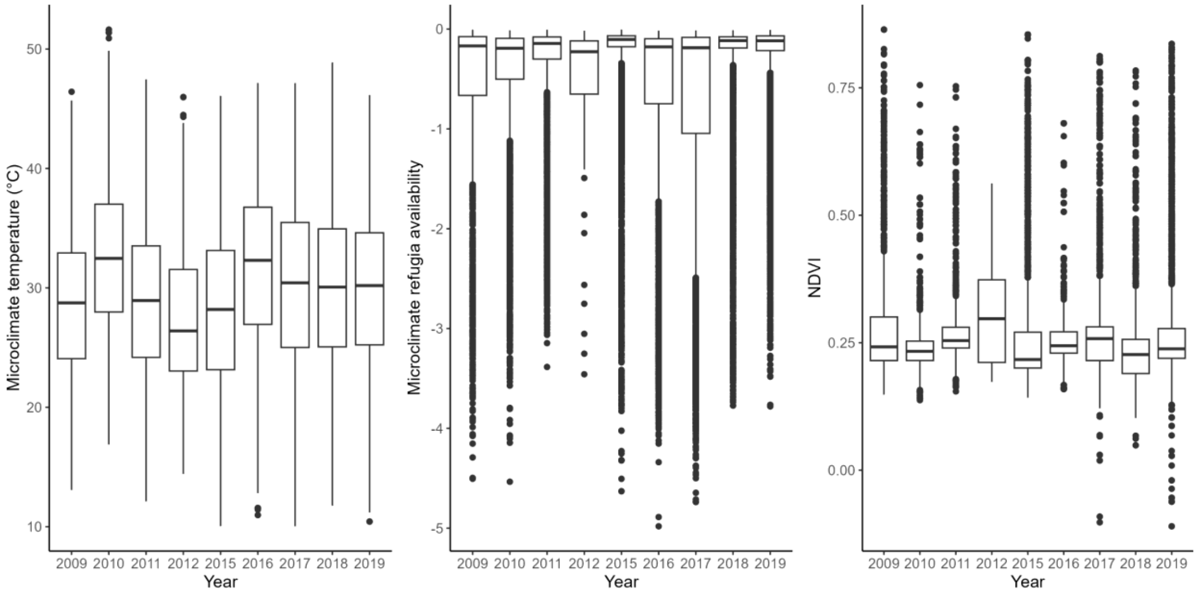

Figure S3.4. Annual range of microclimate temperature, refugia availability, and NDVI across all sites within the study area.

Spatial auto-correlation and thinning

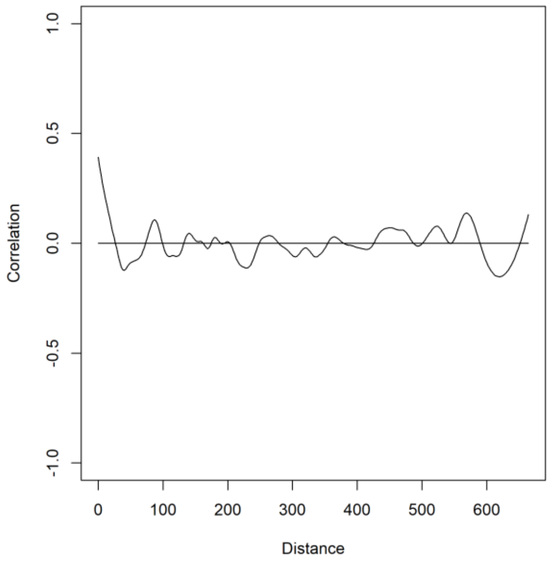

Figure S3.5. Correlogram of residuals from example GLM.

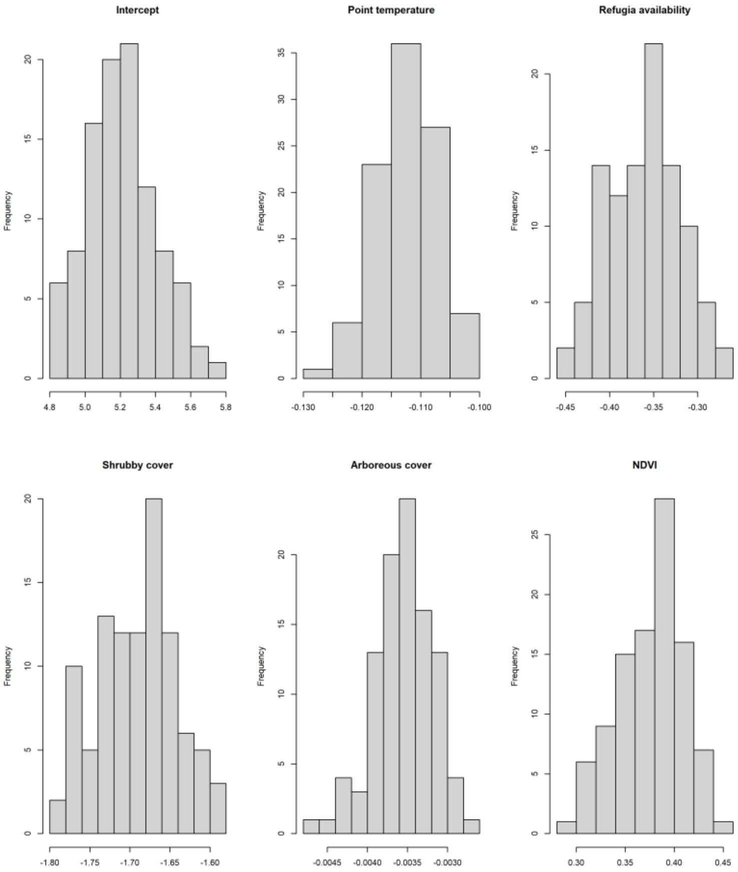

Figure S3.6. Variation in parameter estimates across 100 repeats of a Generalized Linear Model (GLM) explaining the probability of site usage.

Table S3.4. Full model average from 100 repeats of a Generalized Linear Model (GLM) explaining the probability of site usage.

Parameter	Estimate	Std. Error	Adjusted SE	z value	p value
Intercept	5.210	0.616	0.616	8.456	<0.001
Temperature at point	-0.112	0.016	0.016	7.044	<0.001
Microclimate refugia availability	-0.361	0.138	0.138	2.605	0.009
Shrubby cover (arcsine)	-1.691	0.309	0.309	5.472	<0.001
Time since warmest part of day	-0.004	0.001	0.001	3.821	0.000
Arboreous cover (arcsine)	0.376	0.230	0.230	1.631	0.103
NDVI (scaled and standardised)	2.137	0.200	0.200	10.673	<0.001

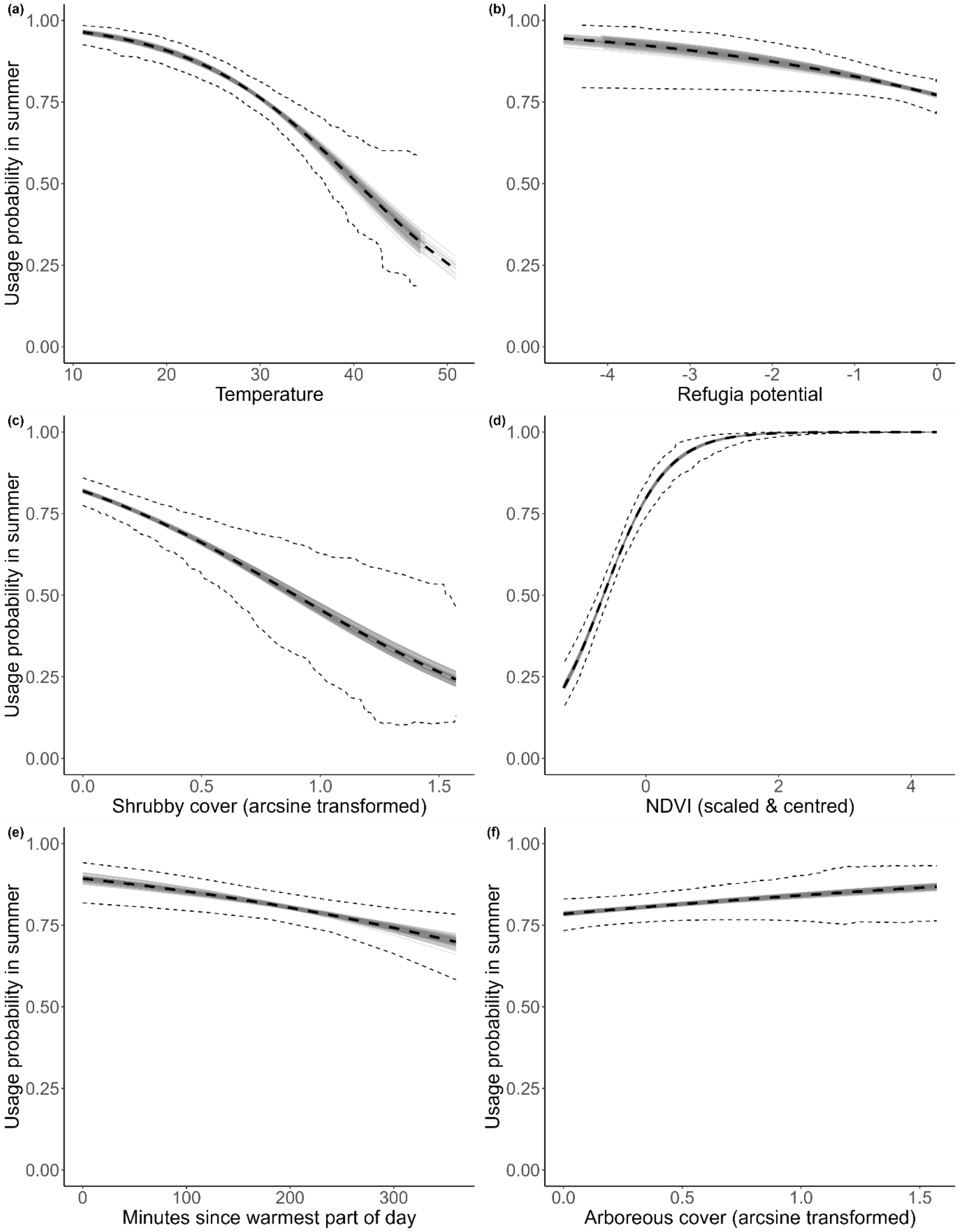

Figure S3.7. Full average model predictions from generalized linear model.

Predicting from model

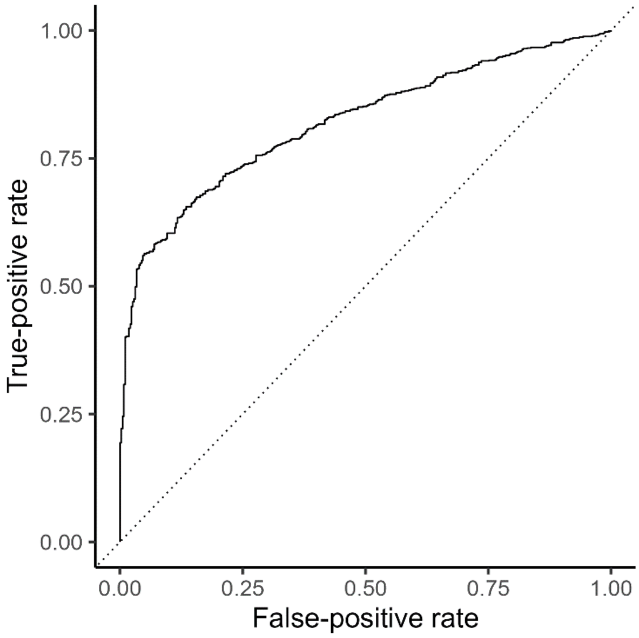

Figure S3.8. ROC curve for generalized linear model fitted to example thinned dataset. AUC = 0.8193.

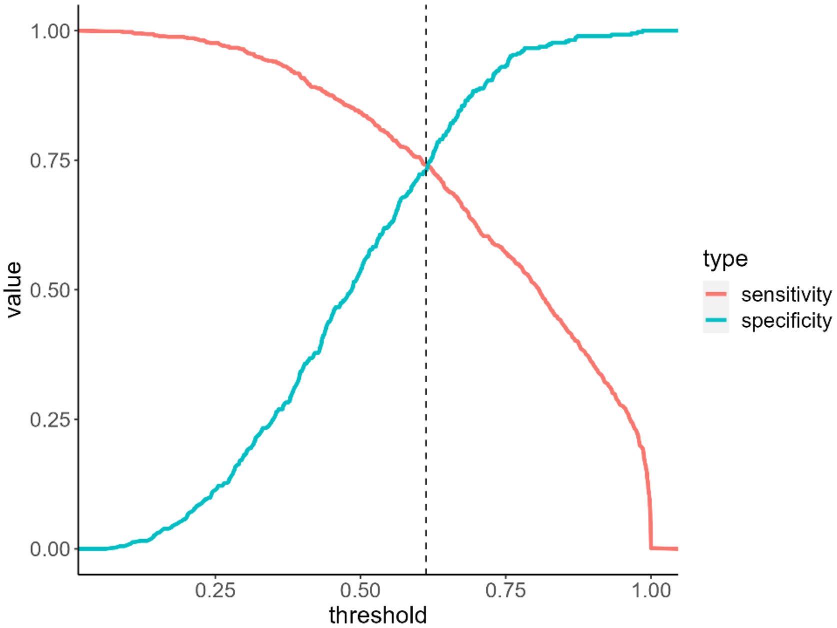

Figure S3.9. Specificity and sensitivity threshold curves. The dotted line shows a threshold value of 0.613 (extracted from the plot).

Table S3.5. Total number of currently suitable points outside PAs = 30,457, and inside PAs = 2,144.

Point location	Remain suitable	Become unsuitable	% become unsuitable
+1.5°C			
Outside PAs	29,882	575	1.89
Inside PAs	2,068	76	3.54
+2.7°C			
Outside PAs	29,324	1133	3.72
Inside PAs	1,978	166	7.74
+3.6°C			
Outside PAs	28,879	1,578	5.18
Inside PAs	1,916	228	10.60

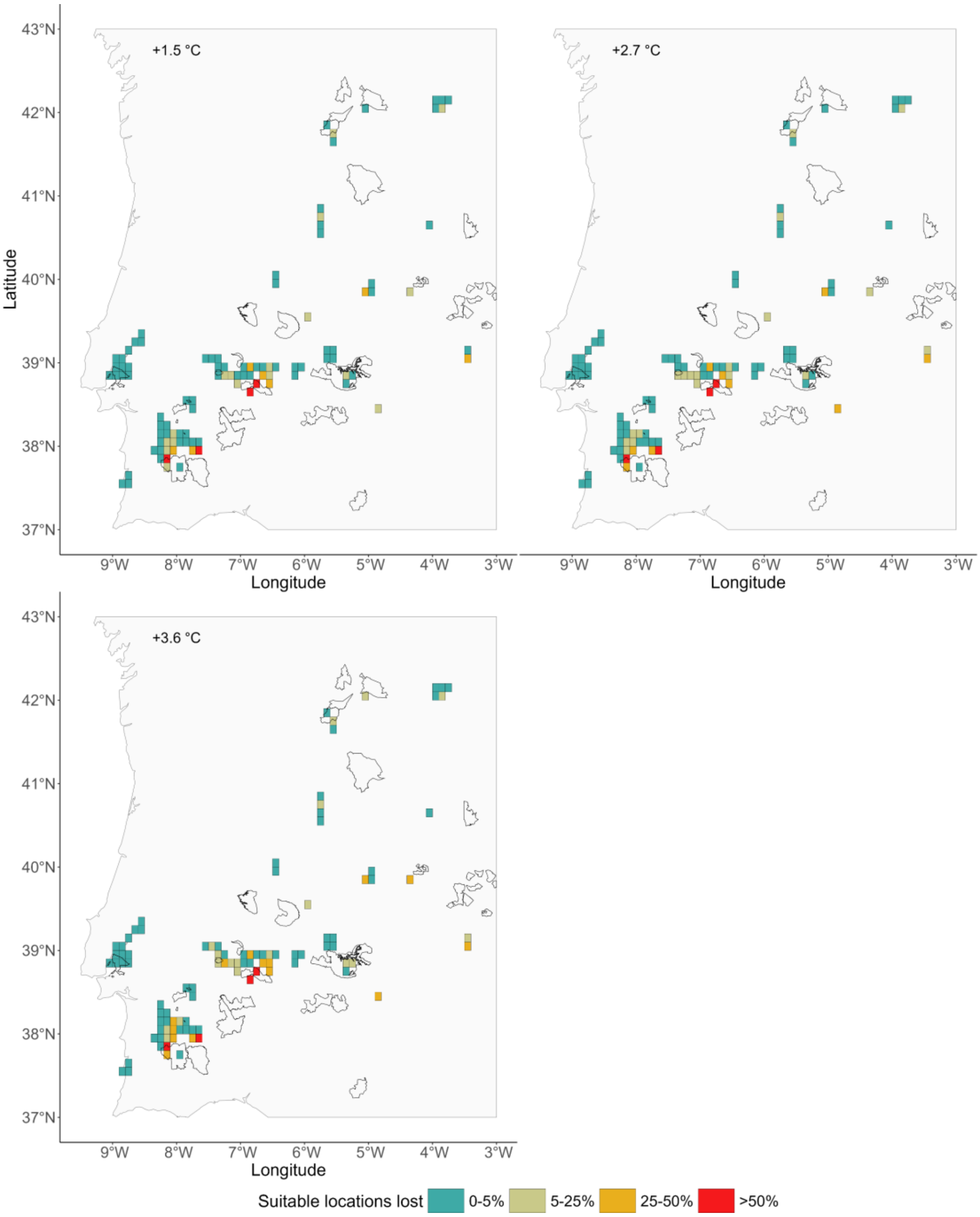

Figure S3.10. The proportion of locations that become unsuitable for little bustards with a 1.5°C, 2.7°C, or 3.6°C temperature increase within each grid cell (resolution = 0.1°), predicted from the generalized linear model. Predicted site usage determined using a probability cut-off of 0.6.

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The effects of extreme temperatures on use of micro-refugia and behaviour of a European raptor

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AUTHOR CONTRIBUTIONS

K.Z.: conceptualization, data acquisition, methodology, data curation, formal analysis, visualization, writing – original draft, review and editing; I.C.: data acquisition, methodology, supervision, writing – review and editing; J.B.: data provision, writing – review and editing; D.R.M.: data provision, writing – review and editing; A.M.A.F.: conceptualization, funding acquisition, data acquisition, methodology, supervision, writing – review and editing;

ABSTRACT

Extreme weather events such as heatwaves can have a range of negative effects on individuals, including mortality through thermal stress, or indirectly affecting survival and fitness through changes in activity and behaviour patterns. While the understanding of these mechanisms is crucial for predicting the effects of global warming on species and populations, these fine-scale individual behavioural responses are largely unknown. Here, we use fine spatial and temporal scale GPS tracking data of 48 Eurasian kestrels (*Falco tinnunculus*) in southwest Europe to investigate activity levels and use of micro-refugia with increasing temperature. We estimate the probability of being active and calculate total distances moved across the day to investigate changes in activity levels. Moreover, we identify fixes falling on nest sites or locations with trees to examine frequency of use of trees and nest sites as potential refugia. We find that level of activity and distances travelled change with increasing temperature, but these patterns differ across the day. We determine that the temperature range between 15.54 and 30.87°C is optimal for kestrel activity. We show that kestrels use trees but not nests as refugia, particularly during the middle of the day, when the rate of tree use almost triples between 14 and 46°C. Our findings highlight the potential intricate behavioural thermoregulation patterns of individuals in the warmest parts of Europe. With global warming, the time per day that is suitable for activity is decreasing. This in turn may have direct and indirect consequences for individuals, as fewer opportunities for foraging will likely induce fitness losses and lower breeding success. Access to refugia, such as trees, which are limited in open arable landscapes, can help minimise exposure to potentially dangerously high temperatures.

Keywords: Micro-refugia use, Eurasian kestrel, behavioural responses, extreme temperatures

4.1. Introduction

High ambient temperatures may have negative effects on populations through individual survival and fitness. High temperature exposure may directly cause adult and juvenile mortality through thermal stress or dehydration (Catry et al. 2015, Albright et al. 2017, Corregidor-Castro et al. 2023). Moreover, remaining active during such periods will likely cause physiological strain that may be associated with reduced movement and cognitive efficiency (Danner et al. 2021), and therefore, individuals may be less successful at obtaining food for themselves or provisioning their young (du Plessis et al.

2012). These negative effects on population demography may result in local extinctions and distributional shifts where conditions become uninhabitable (Parmesan and Yohe 2003, Chen et al. 2011, Gillings et al. 2015). Furthermore, the occurrence of extreme weather events, which are expected to become increasingly frequent as a result of climate change, may have a more severe impact on individuals and populations than overall temperature increases (Marcelino et al. 2020).

Susceptibility to extreme events such as heatwaves has been shown to differ among species groups, for example in relation to their traits, such as diet body mass, or movement strategies (Ding et al. 2024). Individuals are likely affected by a combination of different environmental factors, hence the extent to which populations are affected may also depend on the type of habitat they inhabit, its structure (Sumasgutner et al. 2023) and availability of microclimate (Kim et al. 2022). These interconnected effects can challenge our ability to identify the main threats to populations, which is crucial to identify management measures for biodiversity conservation that account for detrimental impacts of global warming (Rubenstein et al. 2023, Howard et al. 2023).

Individuals may adopt a variety of behavioural strategies to avoid or mitigate the negative effects of exposure to extended periods of extreme temperatures (e.g. Smit et al. 2016; Ben Mocha et al. 2025). This includes reducing or stopping activity when temperatures increase leading to a decrease in the time available for foraging, which has also been shown to impact other behaviours such as lekking (Gudka et al. 2019), or the levels of vigilance and alarm to potential threats (Gutiérrez et al. 2023, Cordonnier et al. 2023). Inactivity, may also result in fewer opportunities to successfully obtain food or attract a mate, thus introducing a trade-off between avoiding strain or potential mortality from extreme heat exposure, and reductions in foraging time and fitness from lack of resources (Cunningham et al. 2021).

To protect themselves from the heat, individuals may also select habitats with features that provide shelter from high temperatures, known as micro-refugia (Ramos et al. 2023a). These patches may be critical for survival during heatwaves (Finocchiaro et al. 2024), but also have been shown to be important for shielding from cold (Pérez-Ordoñez et al. 2022). Landscapes with diverse characteristics that provide micro-refugia may enable biodiversity persistence in areas that would have otherwise become uninhabitable due to climate change (Kim et al. 2022). As global temperatures continue to increase and extreme weather events become more frequent, it is urgent to understand how species, populations and individuals may respond to these challenging and rapidly changing conditions. Climate refugia have been assessed at broad spatial scales to identify areas where species may persist with climate change (Warren et al. 2018, Brambilla et al. 2022) but the finer scale understanding of micro-scale refugia use, at the scale used by individuals, remains limited. The increasing availability of GPS tracking data provides a unique opportunity to observe individual behaviour and identify which features may be used as micro-refugia (López-López 2016).

Here, we use GPS tracking data of 48 Eurasian kestrels to investigate activity and habitat use across a temperature gradient. These individuals were tracked in southern Portugal and Spain, an area that has already been exposed to warming in recent decades. The kestrel is widespread across Europe, however, populations within the Iberian Peninsula are likely to be exposed to the highest temperatures within the species' range, making them an ideal case study for investigating behavioural responses to extreme temperatures. Hence, we characterise the species' climatic niche across the European range as well as for the Iberian Peninsula. We identify when individuals are active and inactive and determine their activity levels. For each location we determine if there is potential use of micro-refugia, i.e. trees or nest structures, to determine if the use of these features changes with temperature. We predict that at higher temperatures, kestrels will be less active and will use micro-refugia sites more frequently.

4.2. Methods

Study area and study system

Eurasian kestrels were tracked within monitored breeding populations in Castro Verde (Portugal), as well as in Doñana National Park and around Seville (Spain). These study areas in the Iberian Peninsula (Southwest Europe; Portugal and Spain) are characterised by extensive arable agriculture with sparse patches of shrub and trees and abandoned rural buildings. Between 2020 – 2024, the average maximum monthly temperature varied across the study area between 15 and 35 °C in May and June (breeding season), and 20 to 40 °C between July and September (non-breeding season), with an average temperature anomaly in relation to 1970-2000 of 1.31-2.56 °C in May-June and 0.85-1.97 °C in July-September (WorldClim, Fick & Hijmans 2017; Supporting Information). Extreme temperatures (those above the 95th percentile of temperatures observed within our dataset; 39.03 °C) occur frequently within the area, with on average 1.64% of days within the breeding season and 20.87% days in the non-breeding season in 2020 – 2024 across the Iberian Peninsula having a maximum temperature exceeding 39 °C.

A total of 69 Eurasian kestrels (*Falco tinnunculus*) were tracked in Portugal and Spain (15 and 58 individuals respectively), between the years 2020 and 2024. The tracking devices and frequency of GPS locations obtained varied between studies (Supporting information). The devices weight did not exceed 4% of the individual's body mass ($\bar{x}$ = 3.13%). Permissions to trap and deploy devices on Eurasian kestrels were obtained from ICNF (PT; permits 84/2021, 92/2023, 104/2024), Consejería de Sostenibilidad y Medio Ambiente, and Consejería de Agricultura Pesca y Desarrollo Rural, Junta de Andalucía (ES; Dirección General de Gestión del Medio Natural, DGMN 02/02/2018, DGMN 10/08/2018, DGMN 11/120/2021 and DGMN 28/07/2023 and Dirección General de la Producción Agrícola y Ganadera DGPAG 14/05/2018/086 and DGPAG 29/01/2024/015).

Data within the first 24 hours of deployment was removed to avoid the influence of any possible unusual behaviour as a result of capture and handling of the individual. Only day-time fixes and data collected between May and September were used, capturing the warmest period of the year when the birds are more likely to be exposed to temperature extremes. To obtain independent observations and reduce sample size discrepancy between individuals, data were temporally thinned to a minimum between-fix time interval of 30 minutes. Finally, data for any individual with fewer than 20 days of data was removed. The final sample consisted of 48 individuals, including 24 females and 24 males (Supporting Information).

To account for behavioural differences within the annual cycle, we classify observations as in the breeding or non-breeding period. Where known and possible, nests were monitored directly or using camera traps. To standardise the data used in the analysis, the breeding season data collection started on the 1st of May for all individuals. Field surveys or camera traps were used to determine the end of the breeding season for each tracked individual. The breeding end date was defined for individuals whose nests were monitored as either the date when the chicks fledged (assessed using camera trap images) or when they reached the age of 30 days (assessed through field surveys). For individuals whose nests were unknown or inaccessible and not monitored, the end of breeding date was assigned as the average date across all years (due to low per-year sample size), which was the 25th of June in Portugal, and the 1st of July in Spain (Supporting information).

Environmental data and refugia use

We characterised the Eurasian kestrel climatic niche within the European range (longitude range -24.3° to 59.0°, latitude range 34.9° to 75.0°) using the 19 bioclimatic variables averaged over 1970-2000 at 5-arcminute resolution obtained from WorldClim (Fick and Hijmans 2017) following the PCA-env approach outlined by (Broennimann et al. 2012). The bioclimatic variables were transformed into two axes (principal components (PC), cumulatively explaining 73.47% of the variation of the raw variables) using a principal component analysis (PCA), representing the climatic niche. The niche shape was produced from the minimum convex polygon (MCP) of the PC scores using the package *adehabitatHR* (Calenge & Fortmann-Roe 2023). We identify the position of the climatic niche of the Iberian Peninsula within the European niche, to explore whether our study area falls on the warm edge of the climatic niche of the kestrel European population. Full details and outputs of the PCA-env are available in the Supporting Information.

Climate variables at a resolution of 2.5x2.5° were obtained from the NCEP/DOE Reanalysis 2 dataset (Kanamitsu et al. 2002) and interpolated to obtain hourly maximum temperature for each GPS location using the *microclima* package (Maclean et al. 2019). The habitat across the study area is highly homogenous, with almost 92% of all locations obtained in areas with over 90% of herbaceous habitat (Supporting information). Hence, habitat was not included in further analyses.

The main landscape features that common kestrels may use in the study areas as micro-refugia from extreme temperatures are trees or nest cavities. To determine tree coverage and if a location falls on a tree, we combined two datasets: tree density data at 10m resolution from Copernicus Land Monitoring (CLMS), and the Global Canopy Height Maps at 1m resolution (Tolan et al. 2024) which was extracted using Earth Engine (Gorelick et al. 2017). Any GPS location overlapping with a maximum tree density > 0% or canopy height > 3 m was defined as use of tree. Alternatively, during the breeding season, kestrels may use nest structures to seek shade and shelter from high temperatures. Nest locations for each individual were either known or estimated from GPS locations (for inaccessible nests; Supporting Information). To account for GPS error, a 10m buffer around each GPS location was overlapped with tree density and nest sites.

Statistical analyses

Each GPS location obtained was classed as active or inactive. Individuals were considered active if the distance between consecutive fixes was greater than 25 m (Supporting Information). Only fixes collected at intervals between 30 (i.e. the minimum data frequency) and 70 minutes were retained, as assessing activity based on between-fix distance is less likely to produce a realistic representation of individual activity the longer the time intervals between consecutive observations. To assess how kestrel activity may change across the day, we fit a Generalized Additive Model (GAM) with a binomial error distribution with individual activity (0/1) as the response variable, a thin plate spline of hour of GPS locations in each season (breeding and non-breeding) as the explanatory variable, and an individual random effect (Supporting Information). From visually inspecting model predictions, we identify three distinct time-of-day periods that capture the kestrel activity patterns: morning from sunrise until 11am, midday from 11am until 4pm, and afternoon from 4pm until sunset (Fig.4.3).

To investigate changes in activity across the temperature gradient, we first fit a Generalized Additive Mixed Model (GAMM) with a binomial error distribution (active/inactive) and logit-link. The model included a thin plate spline for temperature, a linear effect of time of day, and an interaction between sex and season to explain the probability of activity (GAMM1). The number of basis used for the splines was restricted to avoid overfitting. To account for residual autocorrelation as a result of observations being collected consecutively within relatively short time intervals, a first-order autoregressive (AR1) correlation structure was estimated using the dates of GPS locations (Zuur et al. 2009). Moreover, we fit a second GAMM as above but with a two-dimensional thin plate spline of temperature across the three times of day (morning, midday, afternoon; GAMM2).

Extreme temperatures may limit the time available for individuals to be active. To obtain the temperature thresholds outside of which activity is affected, we used the activity GAMM with a temperature only smooth term (GAMM1) and calculated the probability threshold using the “closest-to-(0,1)” criterion (i.e. closest to perfect sensitivity and specificity) using the *pROC* package (Perkins & Schisterman 2006, Robin et al. 2011). This threshold marks the cut-off probability where predicted probabilities below that threshold indicate inactivity. We then extracted the temperature values corresponding to conditional predicted probabilities equal to the calculated threshold, producing a range of temperatures considered optimal for kestrel activity. The change in the frequency of occurrence of optimal temperatures for activity between 1979 – 2024 was determined for both the breeding and the non-breeding season using the NCEP Reanalysis 2 mean air temperature at 2 m (Tk; Kanamitsu et al. 2002) in 6-hour intervals at a 2.5x2.5° resolution. The number of 6-hour intervals within the optimal temperature range was counted separately for the breeding and non-breeding seasons across the whole study area. We only included temperature data from the areas used by the tracked individuals in each season (Supporting Information).

The between-fix distance moved per individual was divided by the corresponding between-fix time interval and summed within each day and each time-of-day period. Individual days with fewer than five observations and individual time-of-day periods with fewer than two observations were removed from the analysis. To test how temperature affected the distance moved we fit two linear mixed effects models (LMM): one with total daily distance (LMM1) and distance travelled per time of the day (LMM2; morning, midday and afternoon) as a response variable (both natural logarithm-transformed). Temperature and an interaction between sex and season were included as explanatory variables. In the daily distance model (LMM1) time of day was also included as an explanatory variable, while the distance per time-of-day model (LMM2) included an interaction between temperature and time of day.

To investigate the use of trees as possible micro-refugia sites we removed from the analysis locations obtained at the nests during the breeding season which were considered separately to determine if the nests are used as a micro-refugia. Furthermore, kestrel habitat use may be constrained by proximity to the nest during the breeding season, and therefore, some individuals may not have access to trees during that time. Four individuals did not have access to trees within their breeding utilization distribution, and therefore, all breeding season data for these individuals was removed from this analysis (Supporting Information). To prevent residual autocorrelation within the model, for each individual, on each day and in each time-of-day period, we counted the total number of GPS locations collected and the total number of locations falling on a tree. All individual/time-of-day periods with fewer than two GPS locations were removed. We then fitted a Zero-inflated Generalized Linear Mixed Model (ZI GLMM) with a Poisson conditional distribution and a logistic zero-inflation component, using the *glmmTMB* package (Brooks et al. 2017). The conditional model included the following explanatory variables: season (breeding, non-breeding), sex (male, female), an interaction between temperature (maximum temperature of the time of day) and the time of day (morning, midday, afternoon), and offset by the total number of GPS locations obtained for that individual in that time-of-day period. The zero-inflation component was modelled using an intercept only model with a random effect of individual. We followed the same process and fitted a GLMM with zero-inflated negative binomial distribution to investigate the relative frequency of nest use during the breeding season only (Supporting Information).

All models included a random effect of individual. Data handling and analyses were carried out in R v.4.4.1 (R Core Team 2024), with the spatial data handling carried out using the *terra* package (Hijmans et al. 2024). In all aggregated datasets (indv/day and indv/time-of-day) we selected the maximum temperature recorded by any individual on that day and time within the same grid (2.5x2.5° resolution), thus obtaining the maximum temperature that the individual could have been exposed to. In models explaining the relative frequency of tree or nest use, we tested for the interactions between temperature and time of day, and/or season and sex. Non-significant interaction terms were removed from models.

4.3 Results

The kestrel climatic niche within the Iberian Peninsula when compared to the total kestrel climatic niche in Europe, is characterised by low PC2 and intermediate PC1 values, corresponding to high mean and maximum temperatures and diurnal temperature range (PC2), low annual temperature variation (PC1), high precipitation during the coldest and wettest months (PC1), but low precipitation during the warmest parts of the year (PC2; Fig.4.1; Supporting Information).

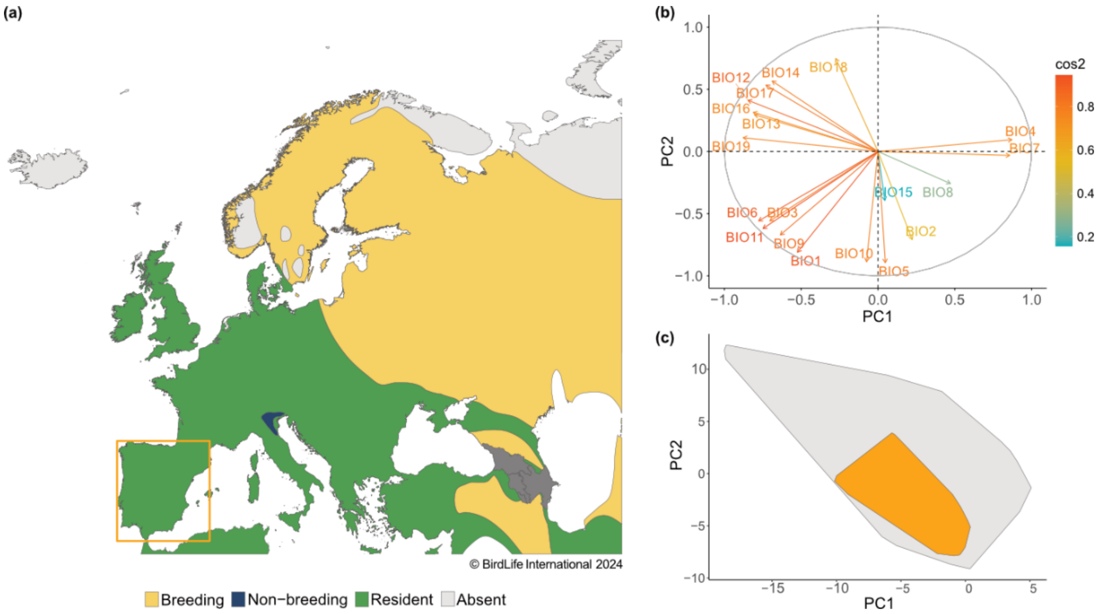

Figure 4.1. Eurasian kestrel breeding (yellow), non-breeding (blue), and resident (green) distribution within Europe (a), variable contributions (quality of representation (cos2)) to principal component one (PC1) and two (PC2) representing the two dimensions of the kestrel realised climatic niche within Europe (b), and the overlap of the minimum convex polygon (MCP) representing the Eurasian kestrel realised climatic niche in Europe (grey) and within the Iberian Peninsula (orange; c). Orange square on the distribution map represents the area for which the kestrel climatic niche for the Iberian Peninsula was obtained. Bioclimatic variables BIO1-12 are related to temperature, and BIO13-19 to precipitation.

A total of 117,914 GPS locations across 6,316 individual/days were included in the final dataset (Fig.4.2). The minimum number of days any individual was tracked for was 27 while the maximum was 448 days across 3 years (Supporting Information). Out of the 48 individuals included in the analyses, 14 were tracked for more than 1 year. 7.45% of all GPS location collected fall on trees (Fig.4.2).

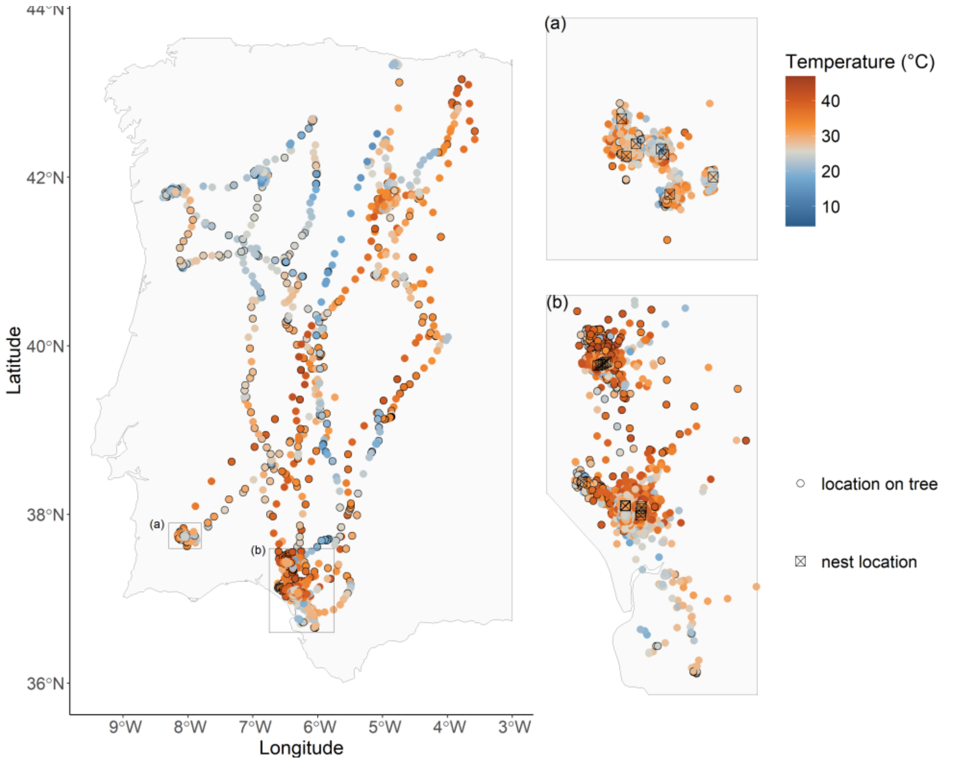

Figure 4.2. Eurasian kestrel GPS breeding and nonbreeding locations collected from 48 individuals between 2020 – 2024 across both breeding (May-June) and non-breeding (July-September) seasons, with a zoomed-in view of the monitored breeding areas where kestrels were captured in Portugal (a) and Spain (b). The colour gradient shows the hourly temperature for each observation, while locations in trees are marked with a black outline, and nest locations are marked with squares.

Activity

The median temperature experienced by individuals based on their GPS locations was 28.18 °C while the lowest and highest were 4.34 and 46.79 °C, respectively (Fig.4.3a). On average, the highest diurnal temperatures occurred at approximately 1-2 PM (Fig.4.3b), which also corresponded with a reduction in kestrel activity (Fig.4.3c-d).

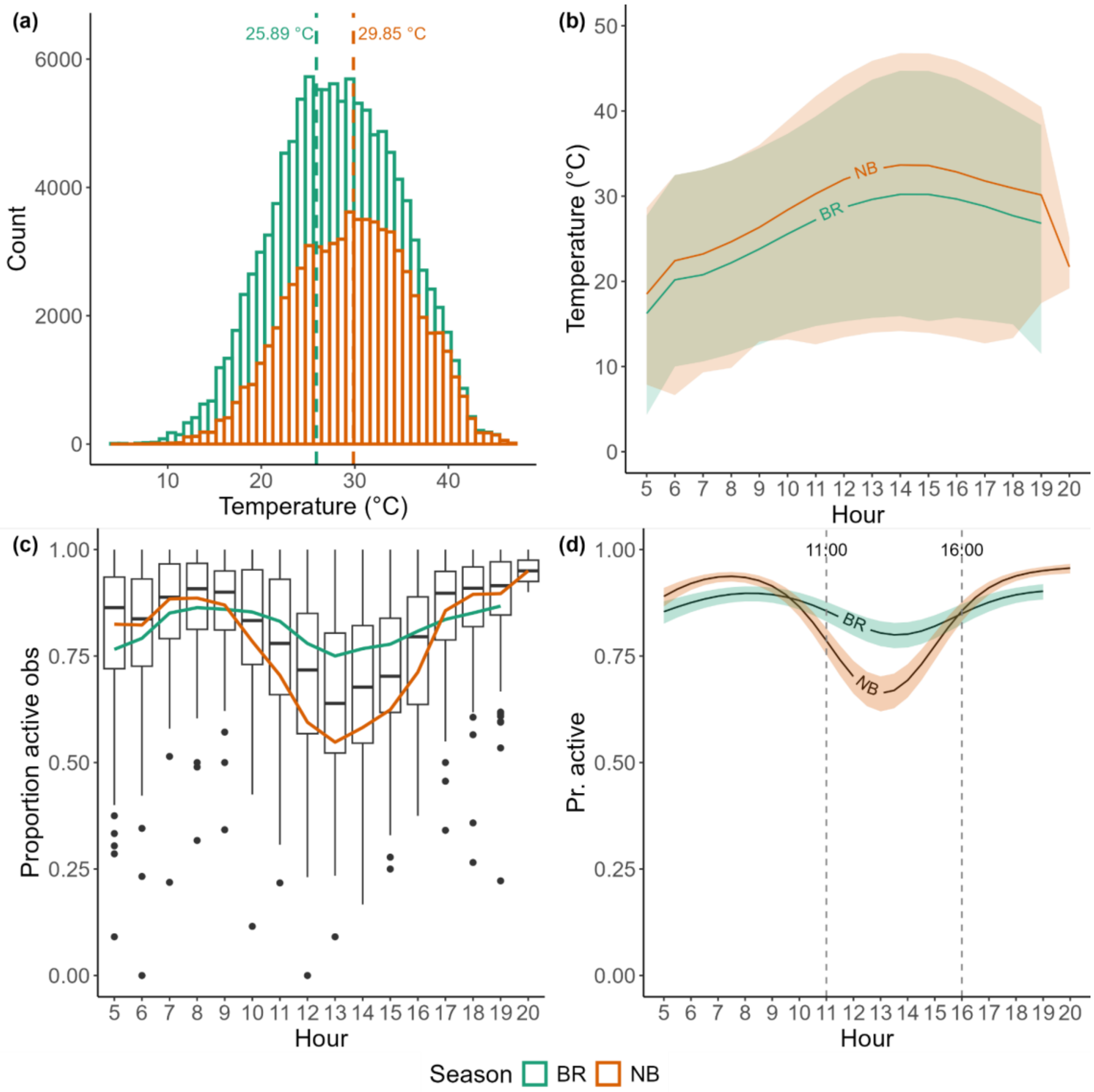

Figure 4.3. Frequency distribution of temperatures at each GPS location with median temperature for the breeding (25.89 °C) and non-breeding season (29.85 °C; a), average temperature at each hour of the day in the breeding and non-breeding seasons included in the dataset with the shaded area indicating the temperature range of each hour (b), the distribution of the proportion of active observations at each hour with the lines showing the mean proportion in the breeding (green) and non-breeding (orange) seasons (c), and activity probability (shaded area shows CI95%) across hour for breeding and non-breeding season predicted from GAM (d). Dashed lines in (d) show the hours 11:00 and 16:00 which were used as a cut-off between morning and midday, and midday and afternoon.

Out of a total sample of 110,667 GPS locations collected, 83,098 instances were marked as active, and 27,569 as inactive. Activity probability increased from 0.580 at 4.34 °C until a peak probability of 0.814 at 24.04 °C, followed by a decrease until a temperature of approximately 38.00 °C, after which activity probability remained stable (Table 1; Fig.4.4a). Individuals were predicted to have overall lowest activity levels during the midday period (0.666), with their activity being similar but slightly higher in the afternoon than during the morning: 0.826 and 0.783, respectively.

Table 4.1. Parameter estimates from the generalized additive mixed model (GAMM) explaining the activity probability as a function of either a smooth term of temperature (GAMM1) or of temperature across each of the three time-of-day periods (morning, midday, afternoon; GAMM2), as well as an interaction between season and sex. Abbreviations: TOD = time of day; BR = breeding season; NB = non-breeding season; F = female, M = male; edf = effective degrees of freedom. N = 110,667 across 48 individuals.

GAMM1; AUC = 0.724				
Parametric coefficients:				
Parameter	Estimate	Std. Error	t-value	p-value
Intercept	1.178	0.105	11.270	<0.001
TOD morning:midday	-0.593	0.025	-23.739	<0.001
TOD morning:afternoon	0.272	0.026	10.546	<0.001
Season BR:NB	0.356	0.035	10.182	<0.001
Sex F:M	1.067	0.145	7.337	<0.001
Season BR:NB : Sex F:M	-1.304	0.043	-30.060	<0.001
Approximate significance of smooth terms:				
Parameter	edf	Ref.df	F	p-value
Temperature	3.944	3.944	214.13	<0.001
Individual (RE)	44.242	46.000	48.27	<0.001
GAMM2; AUC = 0.716				
Parametric coefficients:				
Parameter	Estimate	Std. Error	t-value	p-value
Intercept	1.040	0.101	10.286	<0.001
Season BR:NB	0.355	0.035	10.128	<0.001
Sex F:M	1.059	0.142	7.435	<0.001
Season BR:NB : Sex F:M	-1.287	0.044	-29.570	<0.001
Approximate significance of smooth terms:				
Parameter	edf	Ref.df	F	p-value
Temperature : TOD morning	2.941	2.941	122.98	<0.001
Temperature : TOD midday	2.927	2.927	589.88	<0.001
Temperature: TOD afternoon	2.944	2.944	91.14	<0.001
Individual (RE)	44.159	46.000	46.15	<0.001

Activity was correlated with temperature following a similar non-linear pattern during the morning and afternoon (Fig.4.4b). During those times of day, activity probability increased to a peak of 0.811 at 24.34 °C in the morning, and 0.786 at 28.50 °C in the afternoon, followed by a decline to 0.488 at a maximum temperature of 38.34 °C in the morning, and 0.447 at 45.50 °C in the afternoon (Fig.4.4b). At midday, activity probability rapidly decreased then reached a plateau, with a minimum predicted activity probability of 0.526 at 46.6 °C (Fig.4.4b).

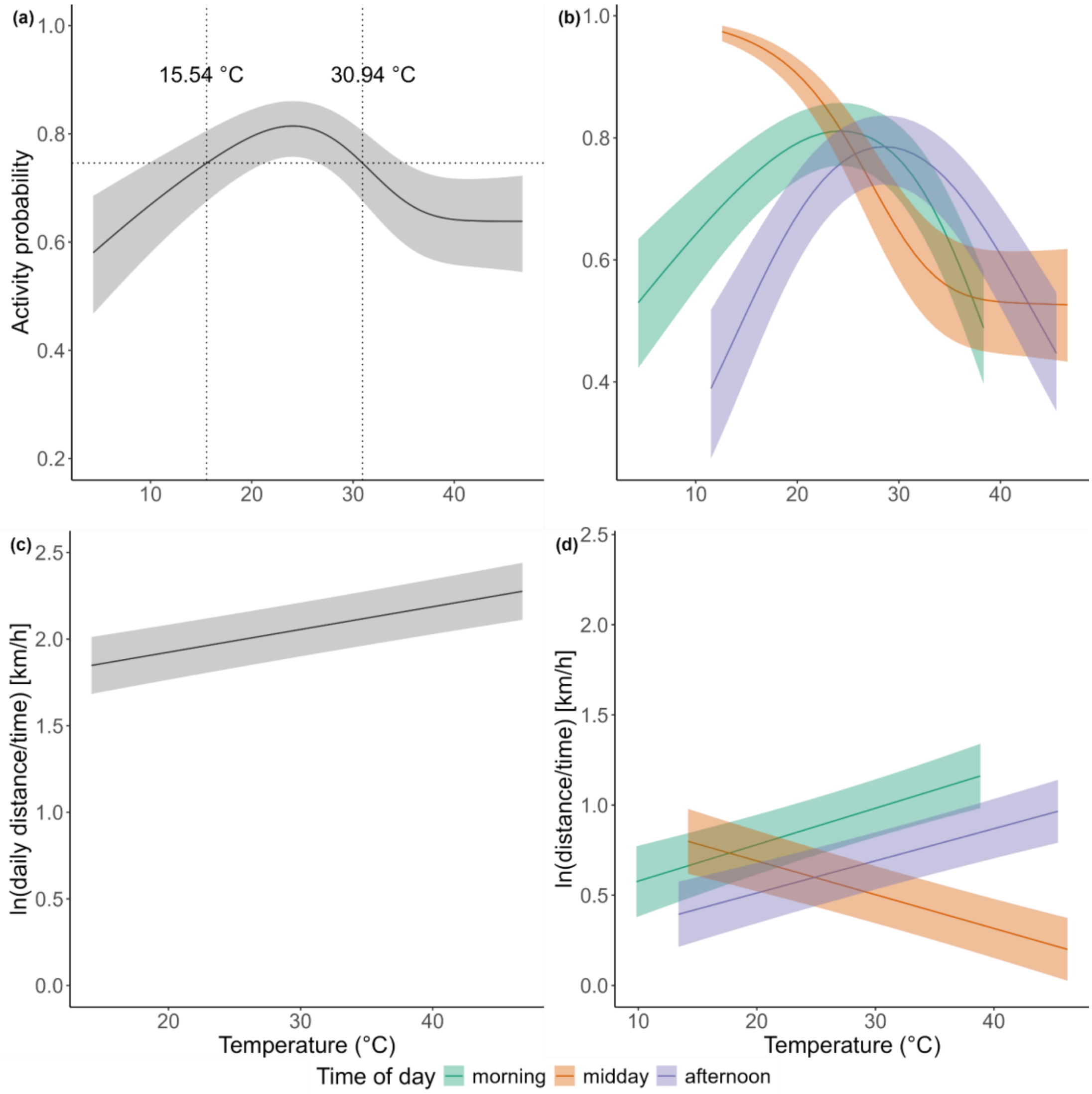

Figure 4.4. Conditional predictions from GAMM explaining activity probability across temperature gradient (GAMM1; a) and across the temperature gradient in the morning (green), midday (orange), and afternoon (purple; GAMM2; b), and conditional prediction from the LMM of daily distance (LMM1; c) and distance per time of day (LMM2; d) across the temperature gradient. The dotted lines in (a) show the temperature and probability threshold. Shaded areas indicate the 95% confidence intervals.

Daily distance moved by tracked individuals increased with increasing temperature (Table 4.2; Fig.4.4c), however, this pattern differed across times of day (Fig.4.4d). In both mornings and afternoons, the distance moved increased with temperature, but the opposite trend was observed in the midday, with tracked individual moving overall shorter distances as temperature increased (Fig.4.4d).

In the non-breeding season, males and females had similar activity levels and moved similar distances daily and across the three time-of-day periods (Tables 4.1-4.2), while in the breeding season, males had considerably higher activity probabilities and moved over twice as much as the females. Female activity and distance moved were similar between seasons, with a small increase in both metrics, particularly in distance moved, in the non-breeding season. The activity and distance moved by males decreased considerably in the non-breeding season (Fig.4.5).

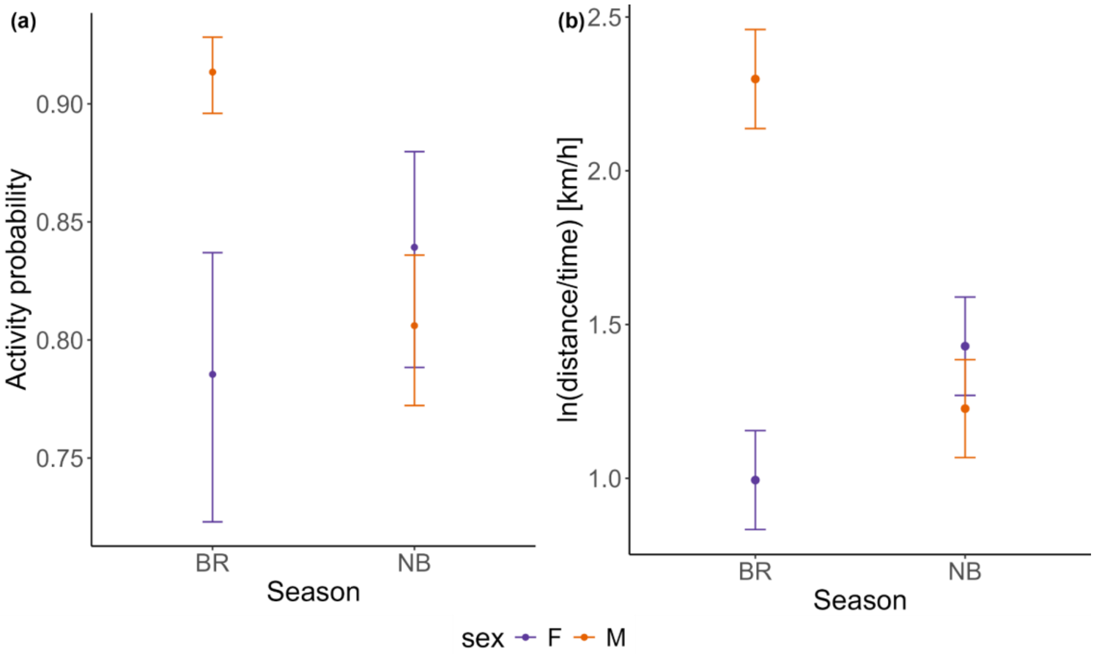

Figure 4.5. Conditional predictions from the GAMM explaining activity probability (a) and conditional predictions from LMM explaining distance moved per time-of-day period (b) in the breeding (BR) and non-breeding (NB) season for females (purple) and males (orange). Error bars show the 95% confidence intervals.

Table 4.2. Parameter estimates from the linear mixed model (LMM) explaining the daily distance moved and the distance moved within three time-of-day periods (morning, midday, afternoon), as a function of temperature (daily distance model) or of temperature across each of the three time-of-day periods (distance per time of day model), as well as an interaction between season and sex. Abbreviations: TOD = time of day; BR = breeding season; NB = non-breeding season; F = female, M = male. N = 110,667 across 48 individuals

Parameter	Estimate	Std. Error	df	t-value	p-value
Daily distance (LMM1); N = 5937 (indv/days) across 48 individuals					
Intercept	1.662	0.094	94.262	17.592	<0.001
Temperature	0.013	0.002	5924.539	7.667	<0.001
Season BR: NB	0.328	0.032	5913.345	10.195	<0.001
Sex F:M	1.149	0.112	45.997	10.287	<0.001
Season BR:NB : Sex F:M	-1.361	0.041	5931.022	-33.068	<0.001
Distance per time of day (LMM2); N = 16,160 (indv/TODs) across 48 individuals					
Intercept	0.376	0.124	277.918	3.038	0.003
Temperature	0.020	0.003	16134.162	5.794	<0.001
TOD morning:midday	0.688	0.123	16112.151	5.607	<0.001
TOD morning:afternoon	-0.221	0.123	16109.526	-1.801	0.072
Season BR:NB	0.435	0.030	15841.261	14.555	<0.001
Sex F:M	1.304	0.113	48.177	11.548	<0.001
Temperature : TOD morning:midday	-0.039	0.004	16109.996	-9.348	<0.001
Temperature : TOD morning:afternoon	-0.002	0.004	16108.727	-0.564	0.573
Season BR:NB : Sex F:M	-1.507	0.038	16041.794	-39.526	<0.001

The probability threshold maximising the sensitivity and specificity of the activity probability model was 0.7460 and temperature range corresponding to predicted probabilities equal or higher than this threshold was 15.54 – 30.94 °C (Supporting Information). The proportion of temperatures within this threshold was overall lower in the non-breeding than in the breeding season in most years (Fig.4.6). The highest proportion of periods with the optimal temperature range was 0.940 in 1990 in breeding and 0.736 in 1996 in non-breeding, while the lowest 0.645 in 2004 in breeding and 0.467 in 2016 in non-breeding (Fig.4.6). On average, the proportion of time within the optimal temperature threshold decreased by 0.00078 (SE = 0.00075, t = -1.033, p = 0.307) per year in the breeding season and 0.00122 (SE = 0.00063, t = -1.941, p = 0.0587) per year in the non-breeding season.

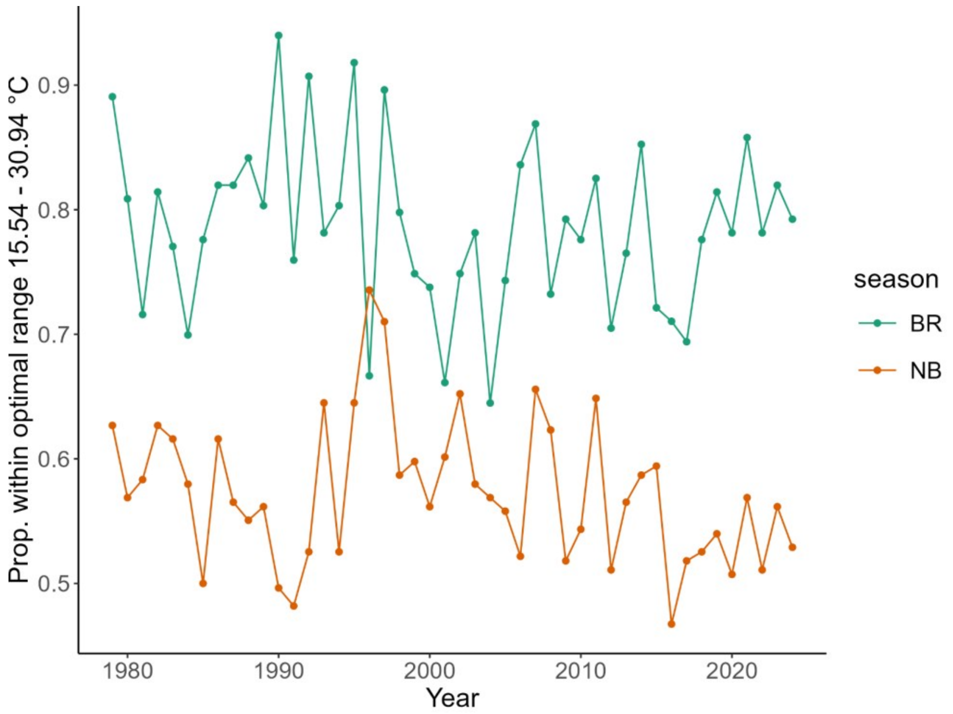

Figure 4.6. The proportion per year with temperatures within the optimal range for activity corresponding to the probability cut-off maximising model sensitivity and specificity of the GAMM1 in the breeding (green) and non-breeding (orange) seasons.

Micro-refugia use

During the breeding season nest structures were more frequently used during midday and in the afternoon, but the relative rate of nest structure use decreased with increasing temperature (Supporting Information).

Females and males used sites with trees with the same frequency and tree use was more frequent in the non-breeding than in the breeding season (Table 4.3). The relative rate of use of sites with trees increased with increasing temperatures, however, the slope of this increase differed depending on the time of day (Fig.4.7). In both the morning and afternoon sites with trees were used at a similar, relatively low frequency, while during midday the rate of tree use by the tracked individuals almost triples between 14.2 and 46.2°C (Fig.4.7).

Table 4.3. Parameter estimates from zero-inflated GLMM explaining the relative rate of tree use (conditional model) and the probability of a location with trees not being used (probability of the rate of tree use being 0; zero-inflation component). Abbreviations: TOD = time of day; BR = breeding season; NB = non-breeding season; F = female, M = male. N = 15958 (indv/tods) across 48 individuals

Parameter	Estimate	Std. Error	z-value	p-value
Zero-inflation model (probability of rate = 0):				
Intercept	1.399	0.293	4.780	<0.001
Conditional model (relative rate of tree use):				
Intercept	-2.459	0.188	-13.102	<0.001
Temperature	0.017	0.005	3.391	<0.001
TOD morning:midday	-0.132	0.169	-0.783	0.433
TOD morning:afternoon	-0.094	0.214	-0.440	0.660
Sex F:M	0.068	0.168	0.406	0.684
Season BR:NB	0.210	0.032	6.597	<0.001
Temperature : TOD morning:midday	0.016	0.006	2.897	0.004
Temperature : TOD morning:afternoon	-0.006	0.007	-0.810	0.418

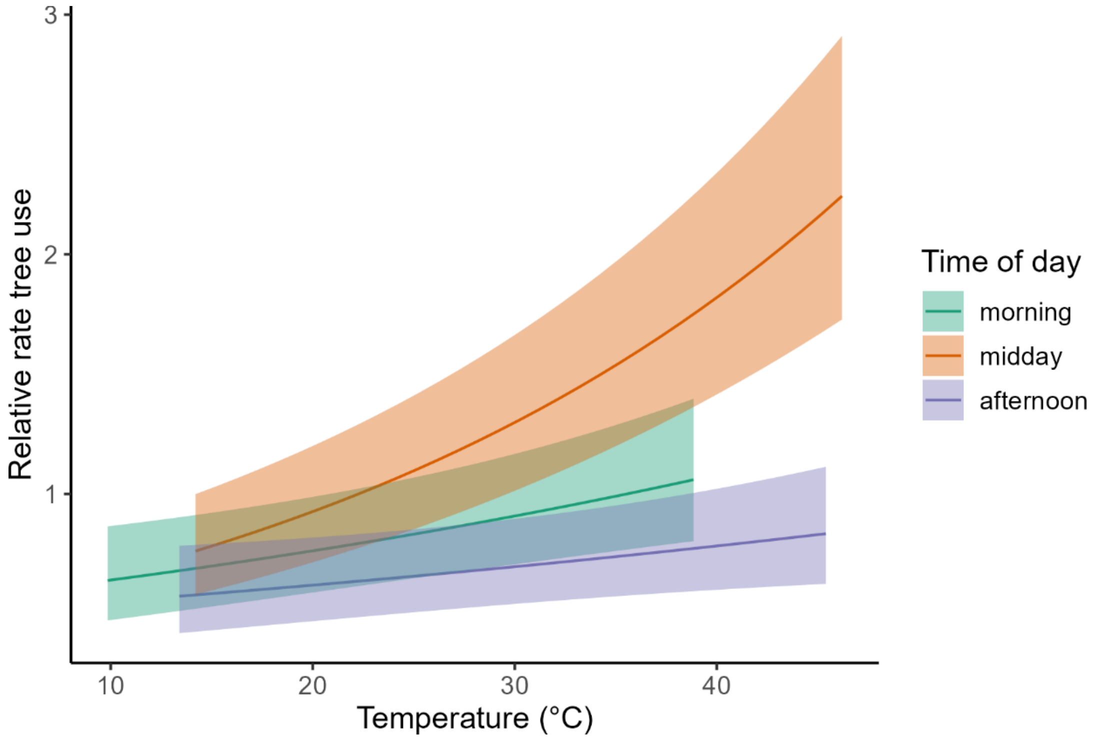

Figure 4.7. Conditional predictions from the GLMM explaining the relative rate of tree use in the morning (green), midday (orange), and afternoon (purple) across the temperature gradient. Shaded areas show the 95% confidence intervals.

4.4 Discussion

With increasing global temperatures, understanding individual responses to extreme temperatures is becoming crucial for providing conservation strategies that may help mitigate the negative effects of potential thermal strain and protect populations. We use fine-scale GPS tracking data of Eurasian kestrels at the warm and dry edge of their European distribution, coinciding with the edge of the species' environmental space, to investigate behavioural strategies across temperature gradients in the breeding and non-breeding season. We show that kestrel activity declines with increasing temperatures and individuals use trees but not nests as micro-refugia at higher temperatures. However, the patterns observed in this study differed across the day, with the midday period, a time when individuals are likely exposed to the highest temperatures, being characterised by different behavioural patterns compared to the morning or afternoon periods. We identify an optimal temperature range for activity and show that over the last five decades the proportion of the day with temperatures within that range has been declining particularly in the non-breeding season, suggesting that the proportion of time available per day for individuals to forage is being reduced with global warming.

Our findings are in agreement with previous evidence showing that bird species may use resting or heat dissipation techniques such as panting, to cope with exposure to high temperatures (Smit et al. 2016, Schoenjahn et al. 2022). A study of Southern Pied Babblers (*Turdoides bicolor*) found that although activity levels did not change, individual foraging efficiency decreased with increasing temperature (du Plessis et al. 2012). Increasing thermal strain may be hindering the activity of not only the kestrels but also their prey. This may be due to concurrent reduction in the activity levels of their prey, however, for this part of Europe the prey activity patterns are still unknown. If food is abundantly available, foraging effort may be lower, therefore, buffering against the negative effects of heat exposure on food acquisition (Stofberg et al. 2022). Furthermore, individuals may switch to foraging on prey types that are less affected by high temperatures (Cuff et al. 2023). For example, kestrels may feed more on insects rather than rodents. Nevertheless, while these prey items may remain readily available, they may be relatively smaller, and therefore, the energetic benefit per prey item will also be lower. This in turn may mean that to obtain sufficient food quantities, foraging effort would need to increase. As ambient temperatures rise, the thermal strain may limit individual ability to forage continuously, even when prey items are abundant. This introduces a trade-off between food quantity and quality, where individuals may prioritise foraging on less abundant but more energetically beneficial prey (high cost and high reward) or more abundant but smaller prey (low cost, low reward) to meet food intake demands. Finally, prey availability may vary spatially where prey are more abundant or more active in cooler, shaded areas when ambient temperatures are high, and the predator may also switch to foraging in such areas (Wiebe and Gow, 2015), or the prey may become inaccessible. Hence, periods of extremely high temperatures or heatwaves may have a negative effect on foraging opportunities, as individuals may need to balance risk of thermal stress and the need for obtaining sustenance (Cunningham et al. 2021), while their prey may also be less active, as well as on foraging success due to reduction in motor and cognitive performance (Danner et al. 2021).

Furthermore, with global warming, high temperatures will become more frequent and more extreme (Meehl and Tebaldi 2004). We find that the optimal temperature range for kestrel activity is approximately 15.54 – 30.94°C. Since 1979, periods with temperatures within the optimal range of activity have declined particularly for the non-breeding season, however, this decline was not significant. Nevertheless, this may mean that the proportion of the day that is available for individuals to be active has been decreasing and will likely continue to do so with future warming. Thus, individuals will be faced with these trade-offs between resting and missing opportunities to forage, and exposing themselves to potentially lethal temperatures, more frequently (Cunningham et al. 2021). Nestlings of a similar species, the lesser kestrels (*Falco naumanni*), was shown to experience increased mortality when exposed to within-nest temperatures of 44°C (Catry et al. 2015). Our results contribute to these findings, highlighting that negative effects of heat exposure, in the form of reduced activity, may occur at temperatures considerably lower than the thermal limit. We observed no change in the proportion of temperatures within the optimal range during the breeding season. This season is characterised by relatively more frequent lower temperatures compared to the non-breeding season, and therefore, the reduced frequency of temperatures falling below the lower limit may balance the increased frequency of temperatures above the upper limit of the optimal temperature range.

Daily distances moved increased with temperature, but when the distance per each time-of-day period was considered, distances moved in the morning and afternoon increased, while during the midday, kestrels on average moved less. These opposing patterns, particularly between the midday and afternoon, may be a result of compensatory activity. The midday coincides with the warmest part of the day. On warm days, temperatures during that period may be too high for individuals to continue being active. The afternoon on such days is also likely to be characterised by relatively high temperatures, however, as individuals may have been unable to forage earlier in the day, they may now be forced to increase activity or risk not being able to obtain food for themselves or their young. Furthermore, prey may be less active at higher temperatures, resulting in individuals needing to forage longer and across larger areas to forage successfully.

We observed differences in activity levels and distances moved between sexes and seasons. Individuals were overall less active in the non-breeding than the breeding season. This increased activity may be related to the need for provisioning young, and has been observed in Eurasian kestrels in Italy, where the tracked individuals' home ranges were broader during the chick-rearing period (Damiani et al. 2022). However, when considered separately, female activity and movement distances were relatively similar between the seasons, and during breeding females were considerably less active and travelled much shorter distances compared to males. This is in agreement with previous studies of Eurasian kestrels (García-Silveira 2024), as well as studies of lesser kestrel movement behaviour during breeding and chick-rearing, where males were found to be more active than females, undertaking frequent short-distance provisioning trips (Hernández-Pliego et al. 2017). A reason for these differences may be that in the period shortly after chicks hatching, the females may stay in the nest for extended periods incubating or defending the nests, while foraging is mainly done by males (García-Silveira 2024).

Tracked kestrels used nest sites less frequently at higher temperatures. The range of temperatures within nests are likely to differ depending on the location and type of nest (Catry et al. 2015). Furthermore, during the breeding season, the additional presence of an adult individual within the nest may negatively impact the chicks, which are already likely under considerable thermal strain. Hence, avoiding the nest during peak heat-exposure periods may minimise additional stress to juveniles. On the other hand, the reduced visitation means reduced provisioning, which may result in decreased juvenile growth rates and contribute to increased offspring mortality (Oswald et al. 2021, Bourne et al. 2021).

The relative rate of usage of sites with trees increased at higher temperatures, suggesting that adult kestrels may be utilizing trees as micro-refugia. To our knowledge, this is the first study demonstrating micro-refugia usage in the Eurasian kestrel. The use of microclimate refugia has been shown in other bird species (Ramos et al. 2023a), and the importance of their availability within the landscape for persistence and reduction of local extinctions has been shown in other taxa (Suggitt et al. 2015, 2018, Williamson et al. 2021). Refugia availability is likely to be a key management action for maintaining climatic suitability within protected areas (Brambilla et al. 2022). Nevertheless, at certain levels of thermal exposure refugia may not be enough for individuals to maintain use of some sites. Little bustards (*Tetrax tetrax*) left their breeding areas earlier in the season when microclimate refugia availability was limited, but this effect was dampened as temperature increased (Ramos et al. 2023b), suggesting microclimate availability may not be sufficient to allow individuals to persist in heat-extreme areas if global temperatures continue to rise.

This study draws inference on individual behaviour based on their GPS location, and therefore, does not identify or distinguish between activity types. This may mean that while individual is in the proximity of a tree or the nest, it may not actually be using it, but instead may simply be flying next to it. Due to the relatively long minimum time intervals between consecutive observations, we may also be misidentifying observations as inactive, as an individuals may have briefly moved and returned to the same location within the 30-minute interval. Nevertheless, the frequency of inactive observations within our data is relatively low (25%) suggesting we successfully captured kestrel activity. Finally, the rate of misidentifying the habitat use in relation to activity, as well as the active/inactive status of the individuals, will likely be the same regardless of temperature. Thus, while the frequency values of the behaviours may be inaccurate, the behavioural differences observed here are likely true.

In conclusion, kestrels were exposed to a median temperature of 29 °C but the optimal temperature for foraging recorded for the tagged birds was between 15.54 and 30.94°C. As temperatures increased, kestrels were less active and used trees as refugia. We observe evidence of potential compensatory behaviour, where on particularly warm days, kestrels may increase their activity later in the day to make up for previous reduced activity and lost foraging opportunities as a result of heat exposure avoidance. With global warming, more hours per day may be characterised by temperatures exceeding a threshold suitable for foraging activity, resulting in fewer opportunities to successfully obtain food for themselves or their young. Having access to refugia such as trees, might become essential to minimise exposure to potentially dangerously high temperatures, which may otherwise cause considerable strain or even be the cause of mortality.

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NOAA PSL, Boulder, Colorado, USA, and are available from their website at https://psl.noaa.gov. This work uses species distribution data provided by BirdLife International (BirdLife International and Handbook of the Birds of the World (2024) Bird species distribution maps of the world. Available at https://datazone.birdlife.org/contact-us/request-our-data). The research presented in this paper was carried out on the High-Performance Computing Cluster supported by the Research and Specialist Computing Support service at the University of East Anglia.

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Chapter 4 Supporting information

Tracking data

In Portugal LoRa GPS tracking devices were used (≤6.5g; Movetech Telemetry) and in Spain Axy-Trek (4g; TechnoSmart, Italy), UVA-BITS (7g; University of Amsterdam, The Netherlands), Pathtrack nanofix GEO+RF (4.7g) and MINI loggers (5g; INTERREX Poland). The data were checked for any unusual fixes and cleaned using the *CoordinateCleaner* package (Zizka et al., 2019). Locations during the day were selected by obtaining the sunrise and sunset times for each location and date, using the package *suncalc* (Thieurmel & Elmarhraoui, 2017).

Table S4.1. Number of individuals tracked in each year, the total number of days per year period on which at least one observation was collected, and the total number of observations per year period. Each year is defined as the period from the 1st of May to the 30th of September (153 days). The same individual can be tracked over multiple years, the total number of individuals in the study was 48 and the total number of observations N = 117,914.

Year	N individuals	N days	Total N
2020	5	147	11,623
2021	18	153	40,647
2022	19	153	31,685
2023	18	153	30,348
2024	4	145	3,611

Table S4.2. Number of days tracked and GPS locations collected per individual per year.

Year	Individual ID	Study ID	N days tracked	Total N
2020	M15219	ES	116	2641
	MX5061	ES	122	2458
	MX5088	ES	143	3067
	MX5837	ES	47	1003
	MX5900	ES	120	2454
2021	M15219	ES	141	3090
	MX4417	ES	79	1898
	MX4423	ES	66	1441
	MX4424	ES	71	1524
	MX4435	ES	36	857
	MX4491	ES	40	963
	MX4659	ES	145	3127
	MX5057	ES	133	2997
	MX5061	ES	153	3162
	MX5088	ES	113	2319
	MX5893	ES	125	2703
	MX5900	ES	149	3212
	MX6131	ES	50	1187
	MX8133	ES	123	2138
	MX8136	ES	105	1779

	MX8158	ES	150	3309
	MX8159	ES	106	2530
	MX9168	ES	122	2411
2022	M9206	ES	31	742
	MX4473	ES	61	1454
	MX4474	ES	119	2572
	MX4475	ES	49	1151
	MX4476	ES	104	2061
	MX4477	ES	114	2537
	MX4659	ES	153	3266
	MX5061	ES	153	2982
	MX5874	ES	112	2387
	MX5875	ES	50	1183
	MX5893	ES	133	2792
	MX6199	ES	97	2160
	MX8153	ES	101	2291
	MX8158	ES	89	1892
	dev3C64_Desgastes	PT	61	731
	dev7482_Belver	PT	28	171
	dev8248_Vale_Goncalinho	PT	27	347
	devA25C_Vale_Mertola	PT	65	818
	devAD54_Cegonhas_M	PT	39	148
2023	MX4467	ES	135	2103
	MX4471	ES	134	1526
	MX4474	ES	83	1568
	MX4476	ES	129	2192
	MX4477	ES	150	2758
	MX4659	ES	150	2857
	MX5892	ES	150	2909
	MX8137	ES	120	1054
	MX8153	ES	150	2681
	MX9206	ES	145	1508
	MX9209	ES	36	446
	MX9210	ES	131	1663
	MX9216	ES	122	1993
	MX9220	ES	88	1482
	dev3C64_Desgastes	PT	27	281
	dev7803_Cegonhas_M23	PT	68	1110
	dev8BD8_Vale_Goncalinho_F23	PT	28	417
	devEB60_Desgastes_F	PT	119	1800
2024	MX9216	ES	43	350
	dev7802_VG_tower24	PT	126	1811
	dev95EC_Reguengo_F24	PT	86	901
	devEB60_Desgastes_F	PT	55	549

Nest location was either known (N = 45) or determined from GPS locations (N = 3). The start of the breeding season was defined as the 1st of May for all individuals (i.e. the start of the data collection period included in this study), because while some individuals may start incubating in late April, temperature extremes are more likely to occur later in the spring and summer. Nests were monitored directly (N = 6) or using camera traps (N = 35). The end of breeding was defined as the date when the chicks fledged and were no longer in the nest. For nests where chicks were monitored but not seen fledged, the end of breeding was taken as the date on which the chicks would reach the age of 30 days, and when no such data was available (due to nests being inaccessible), the average end-of-breeding date, calculated for the monitored nests each year and separately for Portugal and Spain, was used (Table S4.3). Due to the relatively low sample size of individuals with known end-of-breeding dates in Portugal, the average end-of-breeding date assigned to individuals with no breeding data available was calculated over all years and across all individuals tracked in Portugal. Similarly, only one individual with no breeding data available was tracked in Spain in 2024, and was therefore, assigned the average end-of-breeding date across all individuals tracked in Spain in this study.

Table S4.3. The average date across all years and individuals with available end-of-breeding dates (25-06). Spain 2024 only one individual with unknown status so average across all individuals in Spain in all years (01-07)

year	Country (study ID)	N individuals	Mean end of breeding
2020	ES	3	2020-06-25
2021		15	2021-07-04
2022		13	2022-07-05
2023		13	2023-06-24
2024		1	NA
2022	PT	4	2022-06-21
2023		1	2023-07-02
2024		1	2024-07-04

Environmental data

To characterise the foraging habitat, we used the CLMS CORINE Land Cover 2018 data at a 100m resolution. The 44 habitat classes were grouped into one of the following categories: arboreous, shrubby, herbaceous, or other. This classification was based on previous work done for the same region (Ramos et al., 2023; Table S4.4). The proportion of each habitat category within a 500m buffer around the GPS location was then extracted. However, herbaceous vegetation largely dominates the study area, with almost 92% of all GPS locations collected failing in areas consisting of over 90% herbaceous land cover (Fig.S4.1). Hence, this variable was not used in further analyses.

Table S4.4. Habitat category conversion between CLMS Corine, MODIS, and vegetation type based on (Ramos et al., 2023).

CORINE	MODIS	Vegetation type
Fruit trees and berry plantations	Evergreen Broadleaf forest	Arboreous
Olive groves	Evergreen Broadleaf forest	
Annual crops associated with permanent crops	short grasslands	
Agro-forestry areas	savannas	
Broad-leaved forest	Evergreen Broadleaf forest	
Coniferous forest	Evergreen needleleaf forest	
Mixed forest	Mixed Forests	
Non-irrigated arable land	short grasslands	Herbaceous
Permanently irrigated land	cropland	
Rice fields	cropland	
Pastures	short grasslands	
Complex cultivation patterns	savannas	
Land principally occupied by agriculture, with significant areas of natural vegetation	short grasslands	
Natural grasslands	short grasslands	
Beaches, dunes, sands	Barren	
Sparsely vegetated areas	Barren	
Inland marshes	Permanent Wetlands	
Salt marshes	Permanent Wetlands	
Salines	Permanent Wetlands	
Water courses	Water Bodies	
Water bodies	Water Bodies	
Continuous urban fabric	Urban and Built-up Lands	Other type of habitat
Discontinuous urban fabric	Urban and Built-up Lands	
Industrial or commercial units	Urban and Built-up Lands	
Road and rail networks and associated land	Urban and Built-up Lands	
Port areas	Urban and Built-up Lands	
Airports	Urban and Built-up Lands	
Mineral extraction sites	Barren	
Dump sites	Urban and Built-up Lands	

Construction sites	Urban and Built-up Lands	
Green urban areas	Urban and Built-up Lands	
Sport and leisure facilities	Urban and Built-up Lands	
Bare rocks	Barren	
Burnt areas	Barren	
Glaciers and perpetual snow	Permanent Snow and Ice	
Peat bogs	Permanent Wetlands	
Intertidal flats	Permanent Wetlands	
Coastal lagoons	Water Bodies	
Estuaries	Water Bodies	
Sea and ocean	Water Bodies	
NODATA	Unclassified	
Vineyards	Open shrubland	Shrubby
Moors and heathland	Closed Shrublands	
Sclerophyllous vegetation	Open shrubland	
Transitional woodland-shrub	savannas	

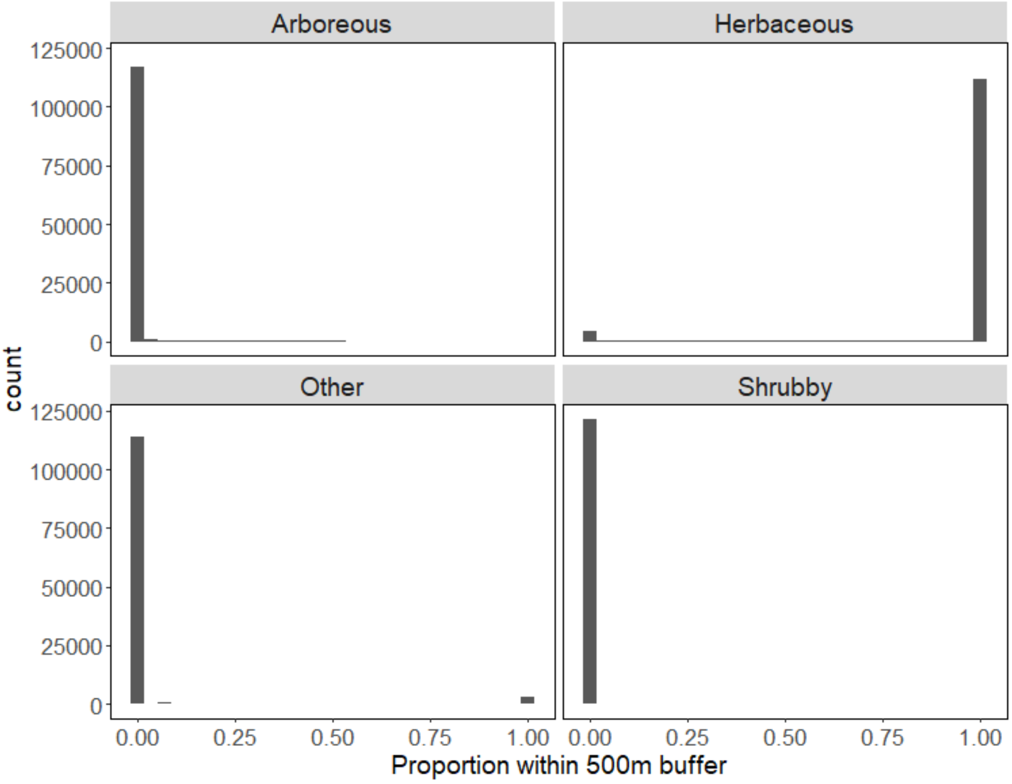

Figure S4.1. Frequency distribution of land cover types within a 500 m buffer around all GPS locations.

The Eurasian kestrel climatic niche was characterised by the first two principal components, which collectively explained 73.47% of the variation within the data. The first component was characterised by annual temperature variation (BIO4, BIO7) and precipitation of coldest and wettest parts of the year (BIO19,16, 13), while the second principal component was associated with diurnal temperature range (BIO 2) as well as the temperature and precipitation of the warmest parts of the year (BIO 10, 5, 18, 1; Table S4.5).

Table S4.5. Contributions of the 19 bioclimatic variables to the first and second principal components describing the Eurasian kestrel climatic niche within Europe, including breeding, resident, and non-breeding ranges.

Code	Variable name	PC1	PC2
BIO19	Precipitation of Coldest Quarter	-0.310	0.045
BIO4	Temperature Seasonality	0.309	0.039
BIO7	Temperature Annual Range	0.303	-0.013
BIO12	Annual Precipitation	-0.299	0.169
BIO16	Precipitation of Wettest Quarter	-0.287	0.129
BIO13	Precipitation of Wettest Month	-0.284	0.121
BIO6	Minimum Temperature of Coldest Month	-0.275	-0.228
BIO11	Mean Temperature of Coldest Quarter	-0.265	-0.254
BIO17	Precipitation of Driest Quarter	-0.258	0.219
BIO3	Isothermality	-0.249	-0.229
BIO14	Precipitation of Driest Month	-0.244	0.232
BIO9	Mean Temperature of Driest Quarter	-0.225	-0.275
BIO1	Annual Mean Temperature	-0.186	-0.332
BIO8	Mean Temperature of Wettest Quarter	0.167	-0.105
BIO18	Precipitation of Warmest Quarter	-0.097	0.306
BIO2	Mean Diurnal Range	0.079	-0.290
BIO10	Mean Temperature of Warmest Quarter	-0.026	-0.363
BIO5	Max Temperature of Warmest Month	0.017	-0.366
BIO15	Precipitation Seasonality	0.016	-0.161

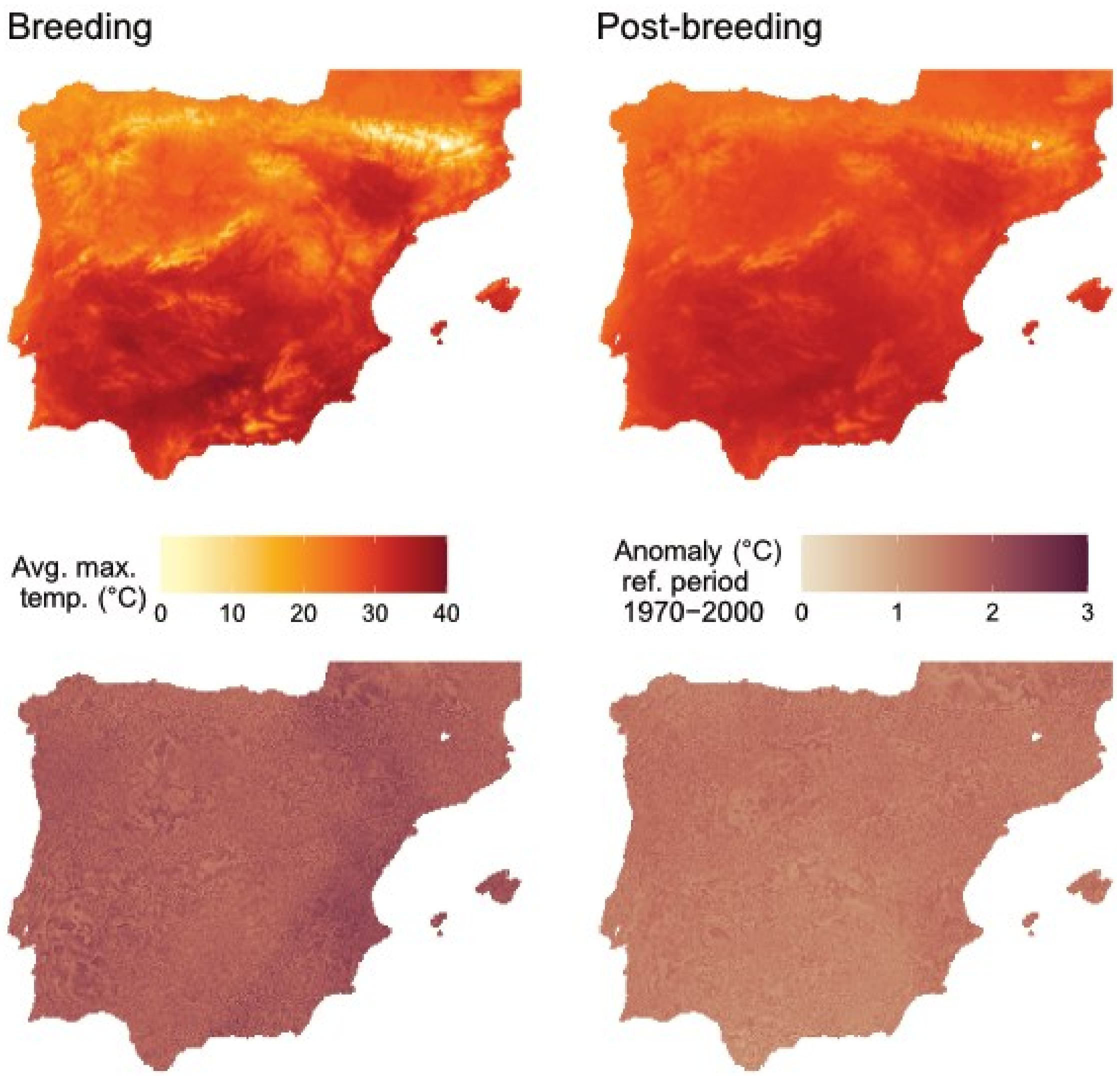

Figure S4.2. The average maximum temperature for May-June (breeding) and July-September (non-breeding) for years 2020-2021, and the average anomaly in relation to the period 1970-2000, obtained from WorldClim2 (Fick & Hijmans, 2017).

Defining kestrel activity

To investigate how activity levels change with increasing temperature we first calculated the time interval and distance between consecutive fixes. The distance between locations was calculated with the haversine method using the *geosphere* package (Hijmans et al., 2024). This calculation was re-started on each day an individual was tracked and any fixes with a time interval >70 minutes were removed as those are unlikely to be a realistic representation of individual activity. For each location, we determined whether an individual was active based on the between-location distance: if this distance was greater than 25m, we assumed the individual was active, otherwise, if the distance was less than 25m, that the individual was inactive. To ensure that the distance threshold was not biasing activity levels, we repeated the process of determining whether an individual was active or inactive using a further three distance thresholds: 50, 75, and 100 m. We find agreement across all distance thresholds in the assigned activity status for 88.2% of observations (N = 97,629 out of N = 110,667), and 5.2% of observations (N = 5,757) are only assigned as 'active' when using the 25 m threshold ('inactive' at 50-100 m thresholds). This suggests that the selection of the distance threshold is unlikely to bias our results.

From sunrise, kestrel activity remained relatively constant from sunrise until 8:00 (0.897, CI95% 0.878 – 0.914) in breeding and 7:30 (0.937, CI95% 0.925 – 0.947) in the non-breeding season, when it began to decline, reaching a minimum probability of 0.800 (CI95% 0.768 – 0.828) at around 13:30 during the breeding and 0.662 (CI95% 0.620 – 0.702) at 13:00 during the non-breeding season (Table S4.6; Fig.S4.3). This was followed by an increase in activity probability until a second peak of 0.902 (CI95% 0.883 – 0.919) at 19:00 during breeding, and 0.956 (CI9% 0.944 – 0.966) at 20:00 in the non-breeding season (Table S4.6; Fig.S4.3).

Table S4.6. Parameter estimates from the Generalized Additive Model (GAM) explaining activity status (active/inactive) using a smooth of hour during which observation was recorded by season (BR = breeding; NB = non-breeding), and including an individual random effect (RE). N = 110,667 across 48 individuals. edf = effective degrees of freedom.

Parametric coefficients:				
Parameter	Estimate	Std. Error	t-value	p-value
Intercept	1.422	0.100	14.21	<0.001
Approximate significance of smooth terms:				
Parameter	edf	Ref. df	F	p-value
Hour : season BR	4.883	4.993	599.10	<0.001
Hour : season NB	4.947	4.998	5896.00	<0.001
Individual (RE)	46.179	47.000	4563.20	<0.001

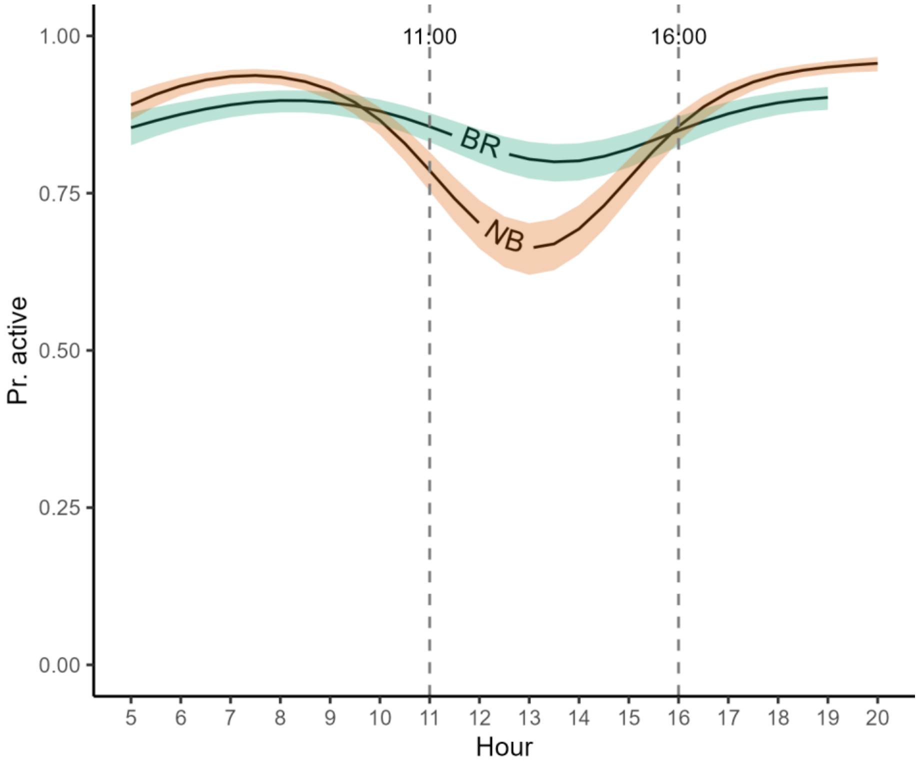

Figure S4.3. Conditional predictions from GAM explaining activity probability for all hours of the day in the breeding (B; green) and non-breeding (NB; orange) seasons. Shaded areas show the 95% confidence intervals and dashed lines indicate the selected cut-off times for the three time-of-day periods (morning, midday, afternoon).

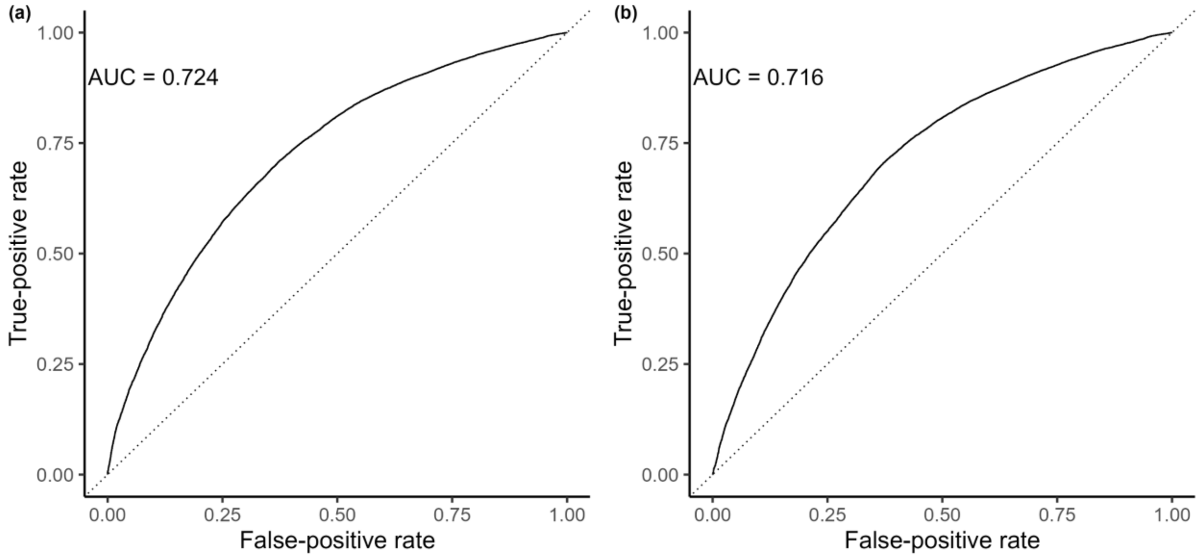

Figure S4.4. The receiver operating characteristic (ROC) curve for GAMM with a spline of temperature (GAMM1; a) and spline of temperature by time of day (GAMM2; b). The area under the curve (AUC) is show on the corresponding figure and the dotted line shows the line of equal true-positive and false-positive rate.

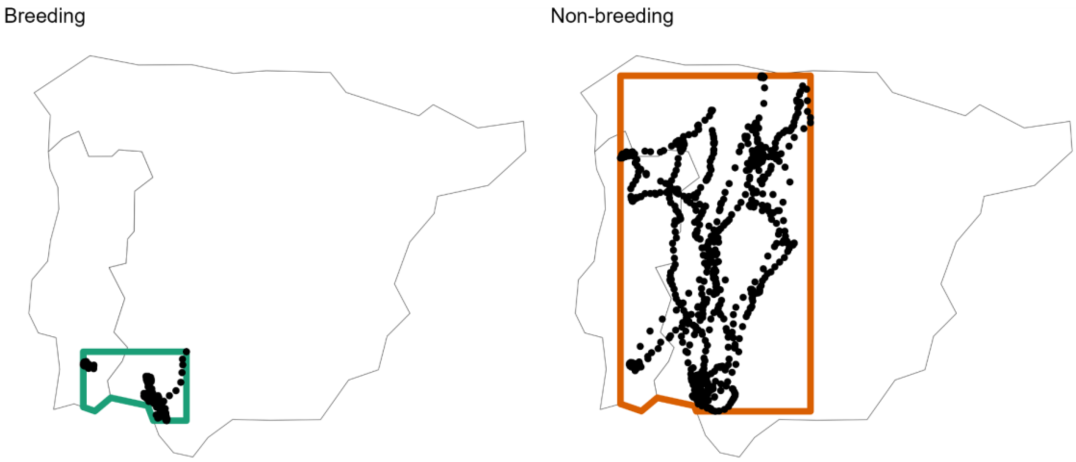

Figure S4.5 The spatial extent for calculating the proportion of time (6-hourly observations) with temperatures within the optimal temperature range for kestrel activity for the breeding (green area) and non-breeding (orange area) seasons. The dots show the GPS tracking data recorded during each season.

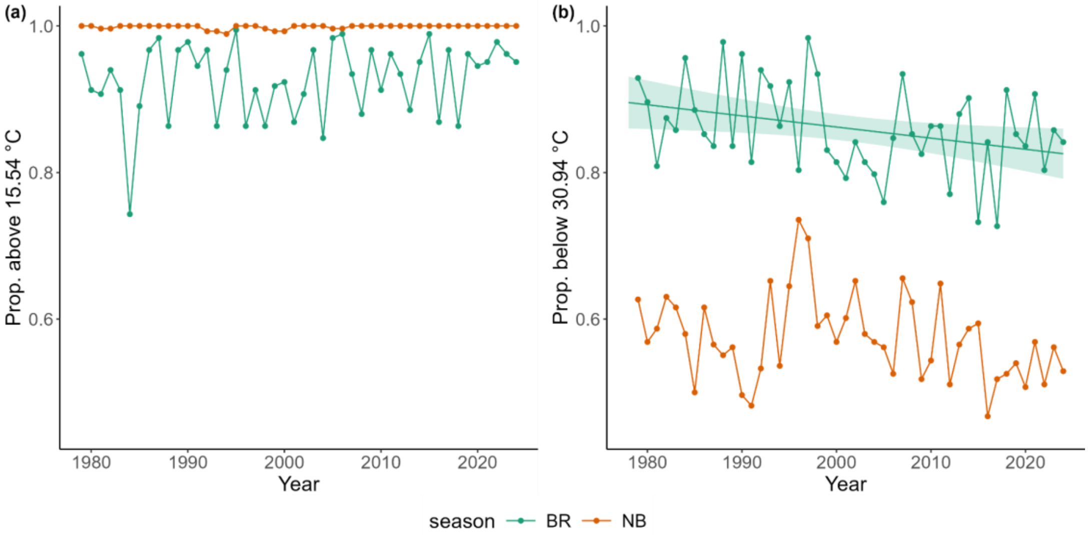

Figure S4.6. Proportion of time per year above the lower threshold (a) and proportion below the upper threshold (b) of the predicted optimal temperature range for kestrel activity in breeding (green) and non-breeding (orange) for years 1979 – 2024. The trendline is given only for the significant relationships and shows the predicted relationship from the linear model and the shaded areas show the 95% confidence intervals.

Table S4.7. Parameter estimates from the linear model (LM) explaining the proportion of time with temperatures above the minimum threshold and below the maximum threshold of the optimal temperature range as a function of year, separately for the breeding and non-breeding seasons.

Parameter	Estimate	Std. Error	t-value	p-value
		Prop. above 15.54°C		
		Breeding		
Intercept	-0.553	1.117	-0.495	0.623
year	0.001	0.001	1.325	0.192
		Prop. below 30.94°C		
		Breeding		
Intercept	3.898	1.299	3.001	0.004
year	-0.002	0.001	-2.339	0.024
		Non-breeding		
Intercept	3.009	1.254	2.399	0.021
year	-0.001	0.001	-1.941	0.059

Home ranges and availability of trees

We estimated individual utilization distribution (UD) during the breeding season as the 100% minimum convex polygon (MCP) of all GPS locations collected during the individual's breeding season using the *adehabitatHR* package (Calenge & Fortmann-Roe, Scott, 2023). We then extracted the maximum tree cover density and canopy height within each individual UD to determine tree availability as above. If no trees were available within an individual's UD, all data for that individual during the breeding season was removed from the tree refugia analysis, as the aim of this study was to investigate whether individual use of trees become more frequent with increasing temperature, rather than whether individuals use trees at all.

Table S4.8. Individual utilization distribution (UD) area, the sample size (N) and number of days (days) over which the data used to calculate the UD was collected, and whether trees were available within the UD (trees).

Individual ID	Study ID	Area (km^2)	trees	N	days
dev3C64_Desgastes	PT	10.840	1	646	48
dev7482_Belver	PT	17.576	1	133	14
dev7802_VG_tower24	PT	10.643	1	689	37
dev7803_Cegonhas_M23	PT	37.300	1	474	25
dev8248_Vale_Goncalinho	PT	1.796	1	245	20
dev8BD8_Vale_Goncalinho_F23	PT	3.407	1	328	23
dev95EC_Reguengo_F24	PT	7.020	1	476	35
devA25C_Vale_Mertola	PT	10.000	1	66	4
devAD54_Cegonhas_M	PT	2.453	0	31	7
devEB60_Desgastes_F	PT	4.089	1	817	65
M15219	ES	23.016	1	1145	53
M9206	ES	6.005	1	742	31
MX4417	ES	5.946	1	1528	63
MX4423	ES	1.980	0	564	29
MX4424	ES	9.876	1	989	49
MX4435	ES	8.316	1	857	36
MX4467	ES	41.819	1	546	29
MX4471	ES	5.649	1	392	26
MX4473	ES	57.221	1	767	32
MX4474	ES	13.342	1	1848	89
MX4475	ES	17.642	1	937	40
MX4476	ES	5.399	1	1406	65
MX4477	ES	12.783	1	1374	58
MX4491	ES	33.744	1	356	15
MX4659	ES	36.109	1	4851	214
MX5057	ES	6.483	1	418	18
MX5061	ES	255.105	1	4086	172
MX5088	ES	5.855	1	619	31
MX5837	ES	618.484	1	677	31
MX5874	ES	2413.611	1	733	34
MX5875	ES	166.292	1	1179	49
MX5892	ES	18.984	1	1405	61
MX5893	ES	3.208	1	1248	59

MX5900	ES	62.140	1	3032	125
MX6131	ES	2.726	0	586	25
MX6199	ES	84.167	1	758	32
MX8133	ES	11.044	1	1378	73
MX8136	ES	28.771	1	750	37
MX8137	ES	0.183	1	47	13
MX8153	ES	178.743	1	1536	71
MX8158	ES	20.309	1	2338	104
MX8159	ES	13.714	1	1375	57
MX9168	ES	4.914	1	549	24
MX9206	ES	1451.930	1	532	52
MX9209	ES	2.814	0	352	23
MX9210	ES	16.381	1	670	48
MX9216	ES	5.229	1	812	70
MX9220	ES	39.191	1	728	33

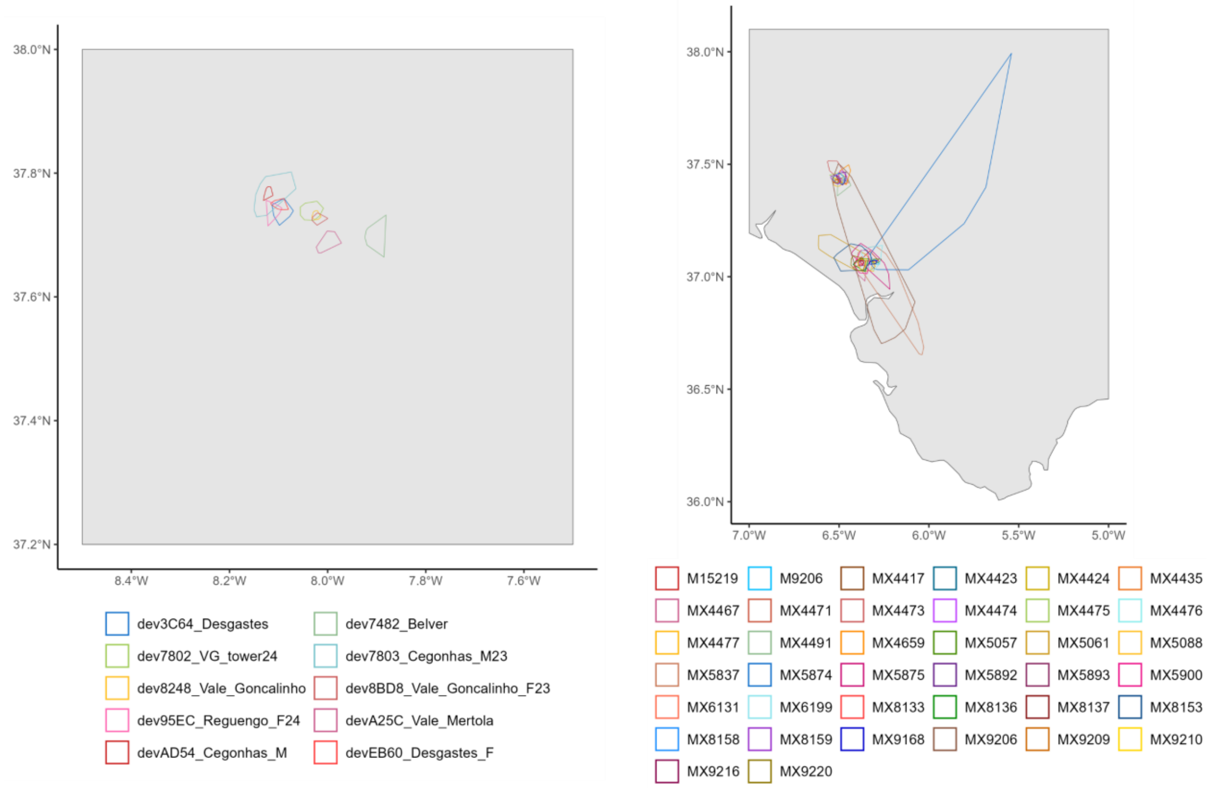

Figure S4.7. Individual breeding utilization distributions in Portugal (left) and Spain (right).

Use of nest structures

To determine nest usage for each location collected, we create a 25m buffer around the point locations of all nests. We extract information both on whether the individual is using their nest or any other known nesting location. To investigate the relative frequency of nest use, we first extracted data from the breeding season only, then all locations were summed per individual and time-of-day period, and the number of on-nest locations was counted. Any individual with fewer than 10 locations collected during that season and individual/time-of-day periods with fewer than two GPS locations were removed from the dataset. We then fit a Generalized Linear Mixed Model (GLMM) with a zero-inflated negative binomial distribution from the *glmmTMB* package (Brooks et al., 2017) explaining the number of on-nest locations offset by the total number of locations per individual/time-of-day period with temperature (maximum temperature of the time of day), time of day (morning, midday, afternoon), and individual sex as explanatory variables.

Table S4.9. Parameter estimates from zero-inflated negative binomial GLMM explaining the relative rate of nest use. Abbreviations: TOD = time of day; BR = breeding season; NB = non-breeding season; F = female, M = male. N = 6425 (indv/tods) across 46 individuals (BR only data; two individuals removed because their N < 10 in BR)

Parameter	Estimate	Std. Error	z-value	p-value
Intercept	-1.242	0.267	-4.650	<0.001
Temperature	-0.035	0.003	-11.843	<0.001
TOD morning : midday	0.347	0.036	9.670	<0.001
TOD morning : afternoon	0.112	0.039	2.898	0.004
Sex F : M	-0.538	0.363	-1.484	0.138

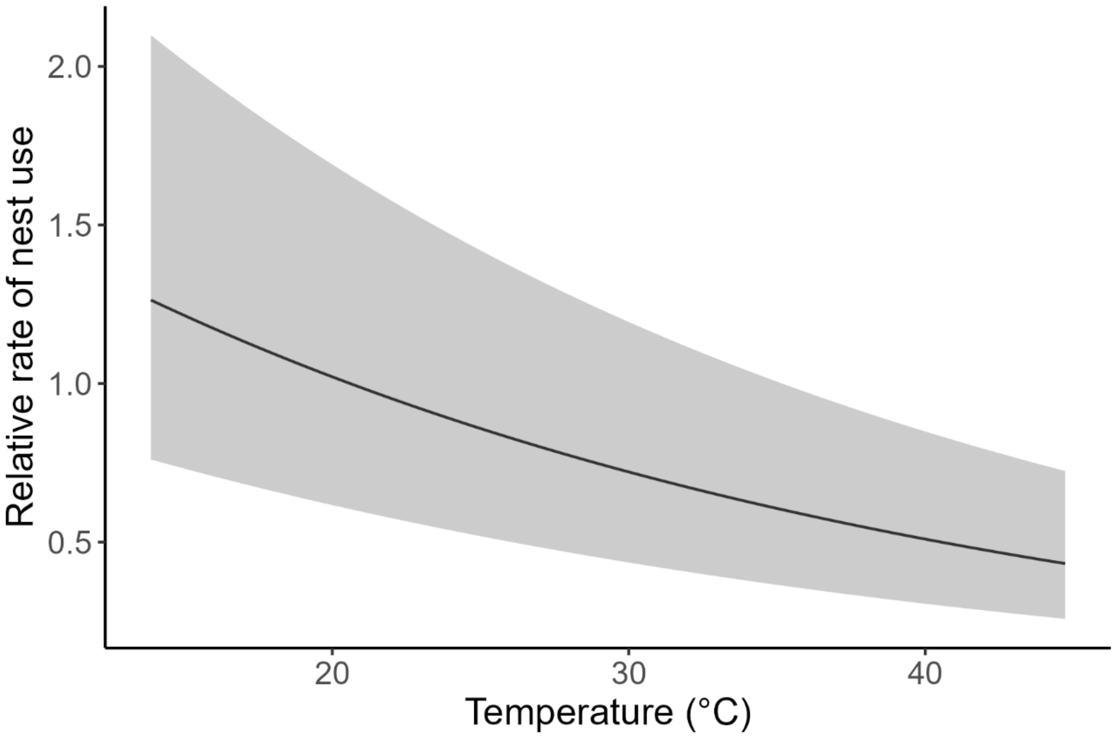

Figure S4.8. Conditional predictions from the GLMM explaining the relative rate of nest use across the temperature gradient. Shaded areas show the 95% confidence intervals

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Chapter 5: General conclusions

5.1 Summary of findings

Environmental change and anthropogenic activity are major threats to global biodiversity, and therefore, identifying characteristics that may make species most vulnerable as well as understanding how populations or individuals may respond is crucial for planning effective conservation action. We produced an index of climatic niche breadth to range area of multiple bird species breeding in Europe, and link this to the species' trends over the last 40 years. We show that, for two species with a similar range area, those able to tolerate a broader range of climatic conditions (i.e. those with broader climatic niches) were less likely to be declining (Chapter 2). This suggests that species which are generalists in terms of the climatic conditions where their populations persist, may be more resilient to environmental change compared to climate specialist or species exposed to a limited range of climatic conditions. We examine the relationship between the climatic niche breadth and range area, and while those variables are correlated, we observe considerable variation in niche breadth, particularly among species with relatively small range areas. The findings of Chapter 2 highlight the importance of considering the species' climatic niches when trying to understand population responses to environmental change and show that our index of climatic niche breadth to range area developed in this chapter could be a useful tool in vulnerability assessments.

Responses to environmental change are likely to vary across different taxonomic groups. In Chapter 2, we assessed the relationship between the long-term population trends of 159 European bird species and a number of their traits. In agreement with previous studies (Douglas et al. 2023, Rigal et al. 2023), we find that farmland-associated species are more likely to be declining than species primarily associated with any other habitat type. Furthermore, we found that species that have a higher tolerance to human-modified environments (i.e. are known to use more types of human-modified habitats) were less likely to be declining. Finally, migratory status (resident, full- and partial-migrant) did not affect the slope of the population trend. This is in contrast to previous studies which have shown that long-distance migrants may be particularly at risk and have already declined (Howard et al. 2020, Lees et al. 2022, Vickery et al. 2023), and could be a result of the relatively simple classification of the three broad migratory status categories used in this study.

Anthropogenic activity has significantly transformed large parts of the planet, causing areas to become uninhabitable, and forcing many species to be restricted to protected areas or face extinction (Santiago-Ramos & Feria-Toribio 2021, Brennan et al. 2022, Semenchuk et al. 2022). Protected areas are an important tool for conservation in the face of the threats posed by environmental change. However, as these areas are static, any change in conditions, either seasonal or permanent, may render them unsuitable. Understanding the conditions that make sites suitable, especially in periods when individuals are exposed to particularly harsh conditions, is therefore, key to managing protected areas to best shelter individuals. In Chapter 3, we use GPS tracking data of male little bustards (*Tetrax tetrax*), a species that has faced significant declines in recent years (Silva et al. 2023) and compare the postbreeding microclimate and habitat conditions at sites used exclusively during breeding to those used during the warm postbreeding season. We find that site usage was associated with lower temperatures and higher microclimate refugia availability, but low shrubby cover. While shrubs may be a source of microclimate refugia for the little bustards, dense shrub is avoided in favour of more open patches. Site usage probability also increased with NDVI, which we included in our analysis as a proxy for food availability. Food availability is an important factor in site selection and may be linked to the negative relationship between site usage and shrub cover, as shrubby patches occur in rocky outcrops where food availability is likely to be lower. During the postbreeding season, little bustards scarcely use sites within protected areas, showing this species is not well protected across its annual cycle, and in particular in the period of the year when individuals are exposed to extremely high temperatures. These findings highlight the urgent need for protected areas to be expanded to cover sites which are suitable for use by little bustards during the postbreeding season and provide microclimate refugia that may allow individuals to persist in those areas even under extreme thermal conditions.

Furthermore, we predict site usage probability change under three warming scenarios: 1.5, 2.7, and 3.6 °C temperature increase (Chapter 3). While overall suitability losses are low, we find that areas which have already been particularly affected by climate change, will continue to face considerable declines in suitability. Under global warming, the availability of habitat patches with diverse microclimate characteristics may become crucial for the persistence of the little bustard within the Iberian Peninsula.

Individuals may adjust their spatiotemporal activity in response to high temperatures. This may occur through reduction of activity at peak temperatures or selecting patches with features that may offer shelter from extreme heat. In Chapter 4, we explore how temperature affects activity levels and the frequency of tree use for the Eurasian kestrel during the breeding and non-breeding seasons. We find that kestrels increase the use of trees but not nests at high temperatures, suggesting trees are providing important micro-refugia for this species. Furthermore, we show that temperature affects both activity levels and the distances moved by individuals, although the observed patterns differ across the day. During the middle of the day, when temperatures are highest, kestrels moved less and increased their use of trees as temperatures increased. During morning and afternoon, the distance moved by individuals increased with increasing temperature. In the morning, kestrels are less exposed to extreme temperatures and increase their activity as temperatures increase. In the afternoon, this relationship may suggest that there could be some compensatory activity, where individuals may be forced to become active at unfavourable temperatures if they were unable to be active in earlier periods due to extremely high temperatures.

We obtain the range of temperatures optimal for foraging for Eurasian kestrels and use this to calculate the proportion of periods between 1979 – 2024 that have been characterised by temperatures within this range in the breeding and non-breeding periods within the study extent. We observe an overall decrease in the proportion of periods within the optimal temperature range, particularly in the non-breeding season. In the future, temperatures are likely to continue increasing, and therefore, this decrease in time available for individuals to forage is also likely to continue. This may have important implications for individual survival and productivity, as fewer foraging opportunities likely reduce foraging success, with consequences for food provisioning and productivity. Hence, availability of micro-refugia, such as trees, will likely be key to allowing populations to persist in the face of warming temperatures and increasingly frequent heatwaves. The consequences of exposure to heatwaves and micro-refugia availability for survival and productivity should be further studied to better understand individual responses to extreme weather events.

In conclusion, this work emphasizes the importance of understanding individual responses to climate extremes, and in particular, to high temperatures. We show that birds select habitats that offer microclimate refugia and respond to high ambient temperature by reducing their activity and utilising potential micro-refugia sites. These responses likely allow individuals to persist when exposed to extreme weather, and their identification may be key to effective conservation under climate change. The findings of this thesis also contribute to evidence of a more nuanced relationship between climatic niches and range areas and the need for incorporating metrics of the climatic niche into vulnerability assessments (e.g. IUCN Red List; Foden et al. 2019, IUCN 2025).

5.2 Broader context and implications

Climatic niches

My work contributed to a better understanding of the importance of climatic niche breadths and species vulnerability to environmental change. While range area may help predict species responses to environmental change (Schwartz et al. 2006, Staude et al. 2020), a large range is not necessarily synonymous with a tolerance to a wider range of climatic conditions. This more nuanced relationship between niche breadth and range area has been previously demonstrated (Dallas & Kramer 2022), however, it has not yet been explicitly incorporated into a niche breadth metric, and vulnerability assessments often consider range area and niche breadth as separate metrics. Furthermore, the link between climatic niches and population trends has also been show in past studies, however, these often considered the thermal aspect of the climatic niche only (Jiguet et al. 2007; 2010; Tayleur et al. 2016; but see: Stephens et al. 2016; Gregory et al. 2023). Our results (Chapter 2) highlight the complex relationship between niche breadth and range size, and provide a tool for incorporating the range of climatic conditions experienced while accounting for the area considered. We quantify the niche in two dimensions, but the methodology used (hypervolume) enables the use of an unrestricted number of dimensions to define the climatic niche. Finally, our approach allows for a relative comparison of the relationship between niche breadth and range area across species.

Implications for the management of protected areas

The landscape outside of protected areas has been undergoing rapid changes, particularly in terms of farmland and agricultural habitats (Busana et al. 2025). While protected areas may buffer against these changes (Gameiro et al. 2020), the higher rate of land use change outside protected areas may cause them to become isolated patches surrounded by unsuitable areas (Seiferling et al. 2012). As a result of this limited connectivity many species are becoming more restricted to protected areas (Brennan et al. 2022). Moreover, while protected areas may buffer some of the threats of global environmental change, the conditions within them may still decline with climate change for some species (Araújo et al. 2011). This reduction in climatic suitability within protected areas may drive distributional shifts and increase usage of non-protected sites (Garden et al. 2015, Cimatti et al. 2025). To combat these challenges, we need to understand what characteristics make sites suitable and use this information to design targeted protected areas (Wauchope et al. 2022). The results of this thesis emphasize the need for improving the resilience of existing protected areas to environmental change, as well as the expansion of protected areas to sites with features that offer key characteristics, such as microclimate refugia, that allow individuals to persist in these sites under environmental change.

Impact of extremes and adaptation

Extreme weather events have been shown to have a more pronounced negative effect on populations than overall, gradual changes in climatic conditions (Marcelino et al. 2020, Maresh Nelson et al. 2024). The frequency of these extreme events is predicted to increase (IPCC 2023), intensifying the threat to global biodiversity. However, the understanding of species vulnerability to those changes and the extent to which different groups will be affected is still lacking (van den Bosch et al. 2025). Changes in the frequency and intensity of extreme events are likely to vary spatially as well as depend on the type of event (Tan et al. 2018). In agreement with recent studies (van den Bosch et al. 2025), the results of this thesis emphasise that to predict the impacts of global environmental change, metrics of the range of climatic conditions that species or populations can tolerate need to be incorporated into vulnerability assessments (Chapter 2).

Furthermore, to effectively protect vulnerable species groups, we first need to understand what behavioural mechanisms are employed to respond to and persist under extreme weather events. The results of this thesis show that at higher temperatures, individuals may change their behaviour through reducing activity and altering patterns of spatial utilisation of the landscape (Chapters 3-4). Mechanisms that species may use to cope with unfavourable ambient conditions have received considerable attention in literature, particularly regarding the ability of desert species to tolerate exposure to extreme temperatures (e.g. Smit et al. 2016; Ma et al. 2023). For example, Arabian babblers (*Argya squamiceps*) have been shown to adjust their diel activity in response to temperature, by being active early in the morning and remaining active in the evenings, therefore, avoiding periods when ambient temperatures are highest (Ben Mocha et al. 2025). Similarly, the Grey Falcon (*Falco hypoleucos*) was found to be overall less active compared to a related species inhabiting both arid and temperate habitats (Schoenjahn et al. 2022). Finally, species occupying areas characterised by higher temperatures may have evolved to be able to persist in extreme thermal conditions through having an overall higher maximum body temperature (Freeman et al. 2022).

Within the same geographical area, behavioural mechanisms may vary across taxa, including due to morphological, physiological, or life history traits, and therefore, effective conservation strategies require species-specific response and adaptation mechanisms (Pattinson and Smit 2017; Cohen et al. 2020). Different behavioural strategies may be utilized depending on the species' body size. For example, heat dissipation behaviours such as panting were shown to be more important for relatively smaller bird species (Smit et al. 2016). Furthermore, the temperature thresholds at which these mechanisms may be employed have also been shown to differ with body mass, as larger species reduced activity and increased their use of shaded patches of habitat at relatively lower temperatures (Smit et al. 2016). Individuals may also be locally adapted to the ambient conditions within their ecosystem, and therefore, responses to extreme temperatures may vary across populations as well as location within the species distribution (Melero et al. 2025). This ability to adapt to local conditions may also suggest that populations previously exposed to change in climatic conditions are less susceptible to further changes in the future (Bailey et al. 2022).

Use and importance of micro-refugia

The importance of considering microclimate and the availability of micro-refugia for shielding biodiversity against climate change has been increasingly frequently studied in recent years (e.g. Nadeau et al. 2022; Thorne et al. 2023; Kemppinen et al. 2024), with many studies focusing on plants as model systems (e.g. Finocchiaro et al. 2022; Pastore et al. 2022; Malanson et al. 2024). In contrast, evidence linking individual habitat use and features within the habitat that may be used as micro-refugia by animals is still relatively limited (e.g. Massimino et al. 2020; Ramos et al. 2023). My thesis contributes to this literature, showing that at higher ambient temperatures, kestrels used trees more frequently, while little bustards were more likely to use sites that were cooler and had greater microclimate refugia availability during the warmest part of the year (postbreeding season; Chapters 3-4). These results highlight that providing features that could shelter individuals from extreme weather may be a key strategy for habitat conservation under climate change.

Moreover, the distribution of micro-refugia may affect and limit the distributions of the species utilising them, particularly as climatic suitability outside of the refugia declines (Massimino et al. 2020). Micro-refugia availability was also found to be one of the main drivers of American pika (*Ochotona princeps*) site usage, having a stronger effect than food availability (Hall et al. 2016). Hence, protecting habitat patches which may provide micro-refugia or the creation of such features within protected areas is of key importance for the facilitation of species conservation under global warming (Shimokawabe et al. 2015; Massimino et al. 2020). Artificial structures may also be an important source of refugia from unfavourable ambient conditions. For example, man-made fabric canopies, deployed in desert habitats in North America were shown to be used as micro-refugia by multiple species (Ghazian et al. 2026).

As the magnitude and direction of climate change effects is likely to differ between species, the requirement for micro-refugia as well as the type of feature that may serve as a refugium may not be universal (Hylander et al. 2015). The effectiveness of micro-refugia in buffering against ongoing climate change may be dependent on the patch characteristics, as well as its surroundings, with the potential for creating patches that may facilitate not just population persistence but also distributional shifts to areas with suitable climates (Hannah et al. 2014). Thus, both the availability and quality of micro-refugia need to be considered when assessing the potential of a patch to provide a buffer against declining climatic suitability (Hall et al. 2016; Zhou et al. 2025).

Use of micro-scale environmental information

While predictions of the effects of climate change are frequently investigated across broad spatial scales (Warren et al. 2018), previous studies have shown the importance of considering the microclimatic variation within the landscape (Suggitt et al. 2011), as this may provide a more realistic representation of the conditions actually experienced by individuals. Models based on macroclimate information can overestimate species responses to climate change (Maclean & Early 2023) because these data fail to capture micro-scale availability of suitable refugia which may allow species persistence in areas where macro-scale climate is expected to become unsuitable (Stark & Fridley 2022). For example, the predicted population distribution changes of two passerine species showed opposite trends when modelled using macro- and micro-climate (Jähnig et al. 2020). Omitting microclimatic heterogeneity when forecasting climatic suitability can therefore miss areas that may offer crucial refugia which should be prioritised for conservation (Nadeau et al. 2022).

While fine-scale information may be crucial for capturing responses to environmental change, utilising microclimate data may not always be necessary (Kemppinen et al. 2024). In this thesis, I took two approaches to micro-scale information: Chapter 3 uses micro-scale (30 m) temperature data generated from a microclimate model to define microclimate refugia availability, while Chapter 4 uses macro-scale temperature (~250 km) and micro-scale habitat (1-10 m) information for investigating potential micro-refugia use across the temperature gradient. This suitability of macro- vs micro-climate methods is context dependent. By defining microclimate refugia based on the difference between the median and minimum temperatures within a patch, we allow for a variety of source of refugia. These could be habitat-related features, including taller vegetation such as shrubs or trees, as well as terrain characteristics, for example, shaded slopes. Such features are likely to be utilised by a species such as the little bustard, which may spend its time on the ground. On the other hand, a kestrel is unlikely to use most of these features, and therefore, using a definition of microclimate refugia based on differences in micro-scale temperature, rather than specific features that may provide refugia, would not have been informative in this context. This highlights that while microclimate information may provide greater insight into fine-scale patterns across the landscape, these approaches should not be used as a “one-size-fits-all” default methodology for understanding individual responses to global environmental change without a consideration for the behavioural ecology of the species.

5.3 Future directions

Consequences of exposure to climate change

Changing climatic conditions may drive shifts in species distributions, and as a result the observed realised climatic niche of the species may also change (Chevalier et al. 2024). This poses a challenge to using metrics of climatic niche breadth in vulnerability assessments as the full range of climatic conditions that a species may persist in, i.e. the fundamental niche, may likely be underestimated. To better understand these processes, a more dynamic view of the climatic niche is needed, through the combination of evidence of distributional shifts and assessment of climatic niche shifts.

The velocity of climate change is spatially heterogenous, and therefore, the extent of its impact will vary across habitats and species' ranges (Loarie et al. 2009, Cimatti et al. 2025). Hence, the extent to which populations may be affected will also likely vary depending on their geographic location. This link between the range of climatic conditions that can be tolerated and the rate or level of exposure to climate change is largely missing. The findings of Chapter 2 suggest that species with a broader climatic niche may be more resilient to environmental change, as they were relatively less likely to be declining than species with a similar range size but a narrower climatic niche. To further test this, the velocity of climate change across the species or population range could considered in addition to climatic niche breadth when investigating population trends. This would allow for assessment of the impact of exposure to climate change on population trends as well as to explore whether climatic niche breadth may be a good predictor of the impact of climate change on populations.

Assessment of case-dependent vulnerability and identification of refugia needs

Understanding how individuals use their habitat is crucial for producing targeted management of protected areas for species of conservation concern (Wauchope et al. 2022). However, the vulnerability to environmental change differs among species, populations, or even individuals (Maresh Nelson et al. 2024). Hence, conservation action cannot be reliant on global or distribution-wide vulnerability assessments. Fine scale GPS tracking data provides a unique opportunity to obtain detailed observations of individual behaviour which is necessary for the monitoring of the impact of changes and threats they may be exposed to (Costa-Pereira et al. 2022, Ellis-Soto et al. 2025). Depending on species ecology different features may be used as micro-refugia. We show that kestrels use sites with trees more frequently at higher temperatures, suggesting trees may be serving as micro-refugia (Chapter 4). On the other hand, we find no effect of proportion of tree cover on site usage probability by little bustards (Chapter 3). The refugia availability that is needed to effectively shelter from global warming is also likely to be species dependent. The presence of micro-refugia within a patch may allow individuals to persist under unsuitable climatic conditions. However, simply increasing the availability of micro-refugia may not be as beneficial, as shown by the negative relationship between little bustard site usage probability and proportion of shrubby cover (Chapter 3). Shrubs have been shown to provide microclimate refugia (Ramos et al. 2023). Although a patch with dense shrubby cover will have abundant microclimate refugia, it is unlikely to be suitable for a species that favours open landscapes, such as the little bustard. These nuanced relationships highlight the need for in-depth investigation of individual requirements under climate change. Exploring these patterns may allow for maximising refugia availability and producing buffers against unfavourable environmental conditions in areas that are particularly affected.

Demographic consequences and micro-refugia availability

Microclimate refugia provide shelter from extreme weather events such as heatwaves (Williamson et al. 2021, Finocchiaro et al. 2024) and may allow for individual persistence in the face of global warming (Stark & Fridley 2022). The availability of microclimate refugia may be particularly important for preventing retraction at the warm margins of the species range, where individuals are already being exposed to extremely high temperatures. While the availability of buffers against extreme weather may have a range of direct and indirect positive effects on individuals, the relationship between micro-refugia availability and population demographic parameters has not been sufficiently considered. Linking micro-refugia availability within an individual's home range to their survival or reproductive success would help to further disentangle the mechanisms of microclimate buffering against global warming.

Consequences for individual movement strategies

Chapter 3 explores the postbreeding conditions at sites used and non-used during that time, and therefore, providing insights into why individuals may move away from some areas after breeding. In particular, individuals may be moving from sites because of exposure to higher temperatures and fewer microclimate refugia available, as well as lower food availability. This coincides with movement to sites outside of protected areas, which poses a challenge to the conservation of the species, as individuals may be exposed to a higher intensity of anthropogenic threats outside of protected areas (Pérez-Granados et al. 2025). Understanding how climate change may be driving individual-level selection of a particular movement strategy may, therefore, aid in not only improving our knowledge of individual responses to environmental change, but also in identifying areas that need to be protected.

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