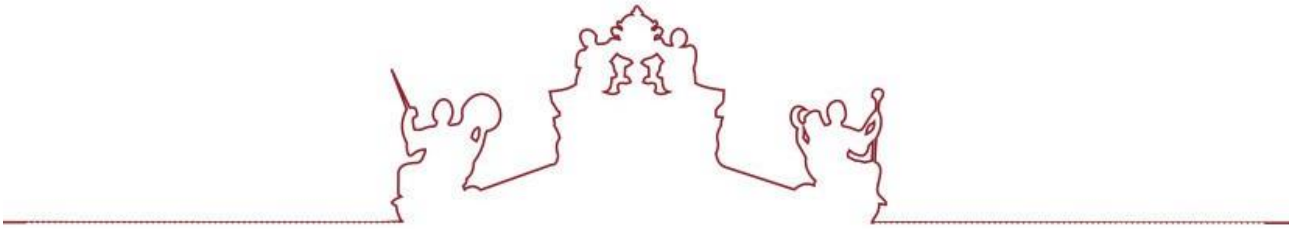

Universidade de Évora - Escola de Ciências e Tecnologia
Universidade de Lisboa - Instituto Superior de Agronomia

Mestrado em Gestão e Conservação de Recursos Naturais

Dissertação

Environmental and climatic factors triggering little bustard *Tetrax tetrax* migration

Diana Maria Roussado Batalha

Orientador(es) | João Paulo Campbell Alves da Silva
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A dissertação foi objeto de apreciação e discussão pública pelo seguinte júri nomeado pelo Diretor da Escola de Ciências e Tecnologia:

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Vogais | João Gameiro (Instituto Superior de Agronomia - Jardim Botânico da Ajuda) (Arguente)
João Paulo Campbell Alves da Silva (Universidade do Porto) (Orientador)

Évora 2024

Acknowledgements

O caminho até à entrega deste trabalho foi desafiante em vários aspetos. Felizmente, tive ao meu redor pessoas que me apoiaram e sem as quais não teria tido o mesmo desfecho.

Começo por agradecer ao João Paulo Silva, meu orientador, por me ter dado a conhecer o sisão, pela oportunidade de o acompanhar em trabalho de campo e por todo o apoio e conhecimento transmitido durante este trabalho. Obrigada também por, mesmo depois da minha ausência, me ter recebido de braços abertos para terminar esta etapa.

Obrigada ao meu orientador, professor João Rabaça, por me ter aceitado como sua orientanda antes mesmo de nos conhecermos, pela partilha de conhecimentos e por se mostrar disponível para rever o trabalho num tão curto espaço de tempo.

Agradeço à Teresa Marques, pelo seu enorme contributo na análise de dados, discussão e revisão do trabalho.

Agradeço ao Álvaro Silva, por recomendar onde tirar dados relativos à temperatura e nebulosidade e pela disponibilidade em ajudar.

À Christina Juhlin, agradeço a partilha das imagens, do script e de toda a informação necessária para calcular o NDVI.

À Alice Cutroneo, agradeço a partilha dos scripts para o cálculo das variáveis do vento que foram também muito úteis na extração de outras variáveis.

À minha querida amiga Catarina Jorge, agradeço pelo seu contributo no tratamento de dados, pelas aulas de R, pelo incentivo, paciência e amizade durante todo este caminho.

Aos meus pais, por terem o papel de dar na cabeça mas também serem porto de abrigo, o meu muito obrigada!

Agradeço também à minha irmã, por todo o apoio e incentivo e por ser um exemplo para mim de empenho e dedicação.

Às minhas grandes amigas Bárbara, Inês, Joana, Mariachi e Sara, que foram e continuam a ser também porto de abrigo, muito obrigada! São elas também fonte de inspiração pela sua garra e empenho.

Agradeço aos elementos da minha querida Tunassa, por preencherem o meu percurso académico de amizades, ensinamentos e valores que levo para a vida; por tantos bons momentos, mas também pelo apoio nos menos bons. Muito obrigada, meninas!

A estas pessoas, aos meus colegas e professores, e a tantas outras que me faltaram referir, o meu muito obrigada!

Resumo

Fatores ambientais e climáticos que desencadeiam a migração do sisão *Tetrax tetrax*

O sisão (*Tetrax tetrax*) é uma ave prioritária em termos de conservação que se reproduz em áreas dominadas por pastagens extensivas e agricultura tradicional. Quando a época de reprodução termina, a maioria das aves realiza movimentos em direção a áreas com maior disponibilidade de alimento, no entanto, o que desencadeia a decisão migratória é desconhecido. Este estudo visa identificar fatores ambientais e climáticos que desencadeiam as decisões migratórias do sisão. Foram utilizados dados de 10 anos de seguimento por GPS, envolvendo mais de 80 sisões. As variáveis ambientais e climáticas foram obtidas a partir de dados de deteção remota e de medições de estações meteorológicas locais. Foram efetuadas análises univariadas através de regressões lineares e uma abordagem multivariada usando um GLMM. Este estudo mostra que os sisões, quando expostos a um maior número de dias com temperaturas superiores a 25ºC, abandonam os locais de reprodução mais tarde; de igual modo, quando expostos a menor disponibilidade de alimento e quando há vento favorável (*tailwind*); as aves que percorrem menores distâncias partem também mais tarde. Com as alterações climáticas a fazerem prever um maior número de dias de temperatura elevada no final da primavera e do verão e, com as práticas agrícolas atuais a reduzirem a biomassa vegetal, os resultados deste estudo sugerem que existe um risco de redução da duração da época de reprodução.

Palavras-chave: Sisão; ecologia do movimento; análise multivariada; *triggering factos*

Abstract

Environmental and climatic factors triggering little bustard *Tetrax tetrax* migration

The little bustard (*Tetrax tetrax*) is a threatened grassland bird that breeds in areas dominated by extensive pasture lands and traditional agriculture. When the breeding season ends, most birds perform movements towards areas with greater food availability, however what triggers the migratory decision is unknown. This study aims to understand the environmental and climatic factors that trigger the migratory decisions of little bustards. An existing dataset of 10 years of tracking GPS data, with over 80 tagged bustards was used. Environmental and climatic variables were derived from a combination of remote-sensed satellite data and local weather station measurements. Detailed univariate analysis was carried out into linear regressions, and a multivariate approach into a GLMM. This study shows that when exposed to a greater number of days with temperatures above 25ºC, little bustards leave breeding grounds later; the same happens when birds are exposed to lower food availability and when tailwinds are available; still, little bustards that travel shorter distances also depart later. With climate change predicting a greater number of days of elevated temperature at the end of spring and summer and current agricultural practices reducing vegetation biomass, this study's findings suggest there is a risk of the breeding season’s length being reduced.

Keywords: Little bustard; movement ecology; multivariate analysis; triggering factors

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List of Abbreviations, Acronyms and Symbols

AIC - Akaike Information Criterion

GLMM – Generalized Linear Mixed Model

NDVI - Normalized Difference Vegetation Index

1. Introduction

Migration is a survival strategy principally related to seasonal shifts in food availability (Rockewll *et al.*, 2017). Migratory behaviour can be culturally transmitted or, more commonly, genetically determined (Burnside *et al.*, 2021). The migration behaviour is internally regulated, such as by the photoperiod, but external environmental and climatic factors (e.g. food availability and temperature) can fine-tune the timing of migration (Burnside *et al.*, 2021). Understanding what triggers migration is crucial for analysing how species respond to changing environmental and climatic factors and assess their ecological effects (Northrup *et al.*, 2019).

The little bustard [*Tetrax tetrax* (Linnaeus, 1758)] is a grassland bird from the Otididae family with a Palearctic distribution, ranging from Mongolia, China and Russia - to the east - to the Iberian Peninsula and Morocco - to the west. These birds live in open habitats with low vegetation (lower than 30-40 cm) showing preference towards hilltops, providing cover and at the same time the possibility of surveillance (Silva *et al.*, 2004a). Areas with small fields with high levels of diversity are also important for food resources (Morales *et al.*, 2008). Adult little bustards feed mainly on green plants showing a preference towards legume crops such as lucerne, chickpeas, peas and vetches crops, but in the first two to three weeks of life, the chicks feed exclusively on arthropods (Jiguet, 2002).

This is one of the most endangered species in Europe (BirdLife International, 2021) classified globally as Near Threatened (IUCN, 2021) and Vulnerable in Europe (BirdLife International, 2021). Since the end of the XIX century, European populations have been declining sharply and are now extinct in several countries of Central and Southern Europe and North Africa (IUCN, 2021). Presently the species' distribution is highly fragmented (Moreira *et al.*, 2012). The Iberian Peninsula is the stronghold of the western Europe population (Iñigo & Borov, 2010), depending greatly on the vast extents of grasslands and cereal fields which offer suitable conditions for the species, throughout the yearly cycle (Silva *et al.*, 2004b; Moreira *et al.*, 2012). However, the population in Iberia has been in sharp decline (De la Morena, 2018; Silva *et al.*, 2023), threatened principally by agricultural conversion towards more intensified agricultural systems and expansion of anthropogenic linear infrastructures (Marques *et al.*, 2020; Santos *et al.*, 2016; Traba *et al.*, 2008). Dryland cereal farmland has given way to intensive permanent pastures, industrial olive groves, vineyards and other permanent crops (Alonso *et al.*, 2019; Silva *et al.*, 2023). This intensification can lead to a decrease in the abundance of insects, which is a key source of protein for chicks during the first two weeks of live (Jiguet, 2000) but also to the destruction of nests and killings of females and juveniles by agricultural machinery during harvests (Inchausti & Bretagnolle, 2005; Iñigo & Barov, 2010). On the other hand, overhead powerlines pose a risk to the species, as little bustards are particularly susceptible to colliding with these utility infrastructures (Marques *et al.*, 2021; Silva *et al.*, 2022). The species is classified as Endangered, in Spain (BOE, 2023) and Vulnerable, in Portugal (Cabral *et al.*, 2005) but is likely to be considered Endangered in the next review due to its ongoing and severe decline.

For these reasons, it is listed as the SPEC 1 (Species of European Conservation Concern; most concerning conservation status) (Birdlife, 2004) and is a priority species under the European Birds Directive (2009/147/EC).

The little bustards breed in a lek mating system, where males defend their territory in more or less dispersed areas (arenas) that are then visited by females to mate (Ponjoan *et al.*, 2012; Iñigo & Barov, 2010). The social organization of the males in lek is hierarchical and only a few males contribute to the next generation. According to Ponjoan *et al.* (2012), most males have more than one arena. Older adults defend smaller territories while younger adults show a higher probability of being floaters, parasitizing the attractiveness of territorial males (Silva *et al.*, 2017). In Portugal, the breeding season starts in late March or beginning of April; males leave displaying grounds in the second half of May - but females deal with the chick rearing, usually until mid-July (Silva *et al.*, 2004a).

When it comes to migration, populations of northern and eastern Europe are totally migratory, while the Iberian populations were described as sedentary (Cramp & Simmons, 1980). However, a study by de La Morena *et al.* (2015) reported that most individuals performed seasonal movements and only a few were truly sedentary individuals. There is thus evidence for a partially migratory population, showing a wide variety of migration patterns. The wide range of environmental conditions (orographic, climatic and land use conditions) covered by the Iberian Peninsula's area of distribution can help understand the reasons for the variability in its migratory behaviour.

Outbound migration movements occur at the end of spring, marking the conclusion of the breeding season. During this time, birds move towards post-breeding areas, typically choosing sites with higher food availability (Silva *et al.*, 2007). Nevertheless, the precise triggers behind the decision to migrate remain unknown.

There is evidence that the large majority of the migration movements by the little bustard occur at night. In a study by Alonso *et al.* (2020), the large majority of the post-reproduction movements of males were nocturnal or partially nocturnal and the birds avoided flying during most of the daytime period. Night migration strategy may aid in preventing predation (Alerstam, 2009), taking advantage of daylight hours for feeding, leading to a minimization of loading costs (Delingat *et al.*, 2006), as well as minimizing metabolic effort by avoiding the high temperatures recorded during day time, thus minimizing water loss (Klaassen, 1996). However, this behaviour may pose an increased collision risk with power lines, since they will have reduced visibility during migratory movements (Alonso *et al.*, 2020). Therefore, moonlight may be an important source of light for nocturnal activities. From corals to amphibians, birds and mammals, many species regulate their activities and life cycle according to the moon cycle (Kronfeld-Schor *et al.*, 2013; Penteriani *et al.*, 2014). On the other hand, cloud cover may reduce the available night glow which could cause disorientation, precluding migrants from detecting the post-breeding areas with suitable habitat (Pyle *et al.*, 1993).

Throughout the breeding season, decreasing food resources and rising temperatures in late spring/early summer may reduce habitat suitability and increase metabolic rates. Thus, these factors may play an important role in triggering migratory events (Alonso *et al.* 2020).

Precipitation also plays a significant role in bird migration, both directly by influencing thermoregulation, visibility, and flight orientation (Erni *et al.*, 2002), and indirectly by affecting the primary productivity of vegetation, which is used as a food source for the birds (Bunting, 2002).

Wind speed and direction are known to have a significant effect on birds' flight (Weber & Hedenström, 2000). In a study with four species of nocturnal passerine migrants, Åkesson & Hedenström (2000) show that passerines took the wind intensity and direction into account when departing on migratory flights. Migratory flights coincident with wind direction (tailwinds) are advantageous to perform movements with low energetic expenditure, as this extends the flight range (Åkesson & Hedenström, 2000; Weber & Hedenström, 2000).

The fact that individuals do not all migrate at the same time, in addition to the existence of distinct migrations strategies (de La Morena *et al.*, 2015), may be an indicator that more than one factor triggers the decision to migrate. Understanding the factors that trigger migration is key to predict future migratory responses to changes such as climate change and land use (Burnside *et al.*, 2020) and to be able to make decisions to protect this species.

The present work aims to understand the environmental and climatic factors that trigger migratory decisions of little bustards. For this purpose, I used an existing dataset from 80 little bustards tagged with GPS devices collected over a 10-year period and tested the following hypothesis related to migratory decision from breeding areas:

i. Do wind speed and direction influences departure time?

ii. Can reduced food availability of breeding areas (using NDVI as a proxy) prompt migration and drive the outbound movements?

iii. Do migratory movements occur on nights with greater lights levels?

iv. Will temperature affect the migration decision?

v. Does the distance travelled influence the moment of their departure?

vi. Does precipitation affect the migration decision?

2. Materials and Methods

2.1. Study Area

The study took place in Southwestern Europe, within the regions of Alentejo, Portugal and Extremadura, Spain (Fig.1).

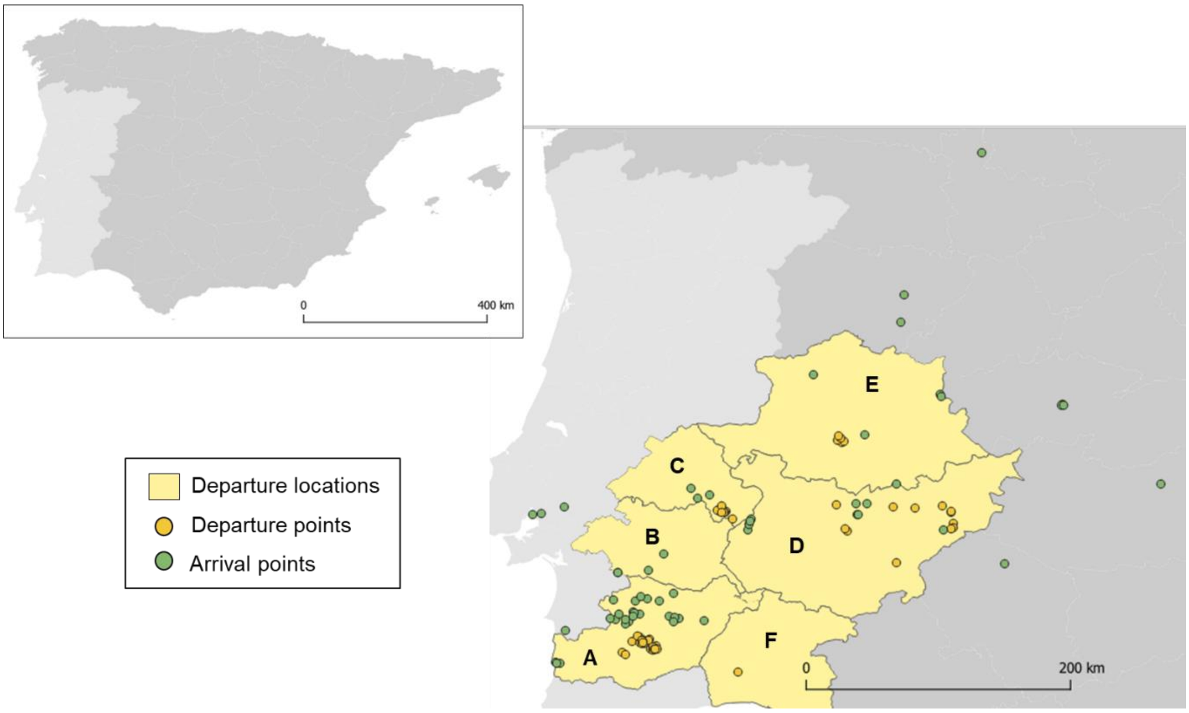

Figure 1. Map of the study area in the Iberian Peninsula (Portugal and Spain) featuring departure locations of little bustard in Alentejo (A: Beja, B: Évora, and C: Portalegre) and in Extremadura (D: Badajoz, E: Cáceres, and F: Huelva). The departure and arrival points of the migration journey are presented.

According to the Köppen-Geiger classification, this region of the Iberian Peninsula is mostly characterised by a temperate climate with hot, dry summers (the average temperature of the hottest month is over 22 °C). A small part of the Beja region and Extremadura are characterised by a dry climate (Cunha *et al.* 2011).

2.2. Capture and data collection

I used a dataset of movements of males' little bustards that were tagged with GPS tracking devices between the years 2009 and 2019. Different tracking technologies were used: between 2009 and 2012 birds were tagged with Microwave Telemetry solar GPS

PTT (Platform Transmitter Terminal) devices that transmitted the data to the ARGOS satellite constellation. After 2012 it was used GPS GSM that transmitted data via cell phone network. In all cases the tags weight less than 5% of the bird's body mass.

To better understand the factors that influence little bustard migration, I extracted the data and GPS locations of (1) the departure point, which was considered the last GPS position within the breeding grounds before it began moving towards the post-reproductive area, and (2) the arrival point, which was considered the first GPS location at the post-breeding area, where they stayed for more than 7 days. The explanatory variables were extracted for the start and end points of the movement. I considered post-breeding migration movements distances greater than 15 km between May and August (Alonso *et al.*, 2019).

2.3. Climatic and environmental variables

2.3.1. Brightness variables

The variables regarding brightness are shown in the Table 1.

The data related to the moon was obtained from the platform timeanddate.com.

Cloud cover was annotated using the Env-DATA System (Environmental Data Automated Track Annotation System) on Movebank (movebank.org; Dodge *et al.,* (2013)). I considered "cloud cover" the proportion of the model grid cell covered by cloud, calculated for the total atmospheric column from cloud occurring at all model levels, interpolation: bilinear; spatial granularity: 0.75 degrees; temporal granularity: 3 hourly.

Table 1. Brightness Variables

Variable	Description	Range
MoonLight	Percentage of illumination from the moon on the day of departure	0.024 - 0.999
MoonPosition	*Visible* if at the departure time the moon was above the horizon line; *not visible* if at the departure time the moon was under the horizon line	0 or 1
Moon	"MoonLight" x "MoonPosition"	0 – 0.999
CloudCover	Total cloud cover percentage	0 – 1

2.3.2. Temperature variables

Variables regarding temperature are shown in the Table 2. The variables were based on minimum and maximum temperatures from 2009 to 2019 for the Iberian Peninsula from the Copernicus Climate Change Service website (https://cds.climate.copernicus.eu/; Cornes *et al.*, 2018).

Table 2. Temperature Variables

Variable	Description	Range
TMaxday	Maximum temperature on departure day	22.77 - 42.39 °C
MeanMax3	Mean of maximum temperatures in the three days before departure	21.28 - 42.79 °C
MeanMax8	Mean of maximum temperatures in the eight days before departure	22.64 - 37.92 °C
SubMax3	“Tmaxday” – “MeanMax3”	-9.12 - 7.17 °C
SubMax8	“Tmaxday” – “MeanMax8”	-10.53 - 8.41 °C
TMinday	Minimum temperature on departure day	8.52 – 24.94 °C
MeanMin3	Mean of minimum temperatures in the three days before departure	9.51 - 23.56 ° C
MeanMin8	Mean of minimum temperatures in the eight days before departure	10.83 - 19.45 ° C
SubMin3	“TMinday” – “MeanMin3”	-4.66 - 3.21 ° C
SubMin8	“TMinday” – “MeanMin8”	-4.76 - 6.53 ° C
Meanday	Mean temperature on departure day	16.08 - 33.66 ° C
Mean3	Average of the mean temperatures over the three days prior to departure	15.49 - 33.10 ° C
Mean8	Average of the mean temperatures over the eight days prior to departure	16.75 - 28.53 ° C
SubMean3	“Menday” – “Mean3”	-6.81 - 5.19 ° C
SubMean8	“Meanday” – “Mean8”	-7.31 - 6.43 ° C
NdT35.3d	Number of days with maximum temperature above 35 ºC in the three days prior to departure	0 – 3
NdT35.8d	Number of days with maximum temperature above 35 ºC in the eight days prior to departure	0 – 6
NdT25.3d	Number of days with maximum temperature above 25 ºC in the three days prior to departure	0 – 3
NdT25.8d	Number of days with maximum temperature above 25 ºC in the eight days prior to departure	1 - 8

2.3.3. Precipitation variables

The variables regarding precipitation are shown in the Table 3.

The variables were based on daily values from 2009 to 2019 for the Iberian Peninsula from the Copernicus Climate Change Service website (https://cds.climate.copernicus.eu/; Cornes *et al.*, 2018).

Table 3. Precipitation Variables

Variable	Description	Range
Precip3dias	Accumulated precipitation in the three days prior to departure	0 – 16.01 mm
Precip3diasbi	Occurrence/absence of precipitation in the three days prior to departure	0 or 1
Precip8dias	Accumulated precipitation in the eight days prior to departure	0 – 19.50 mm
Precip8diasbi	Occurrence/absence of precipitation in the eight days prior to departure	0 or 1

2.3.4. Distance variable

The variable *Distance* is the distance (km) between the departure and arriving point (Table 4). It was calculated with the standard distance matrix (NxT) from QGIS (3.16.6) tool.

Table 4. Distance Variable

Variable	Description	Range
Distance	Distance between the departure and arriving point.	15.26 - 346.58 km

2.3.5. Wind variables

The variables regarding wind are shown in the Table 5.

Wind speed (m/s) and direction (degrees) were obtained from u and v components 10 m above the surface of the Earth. U component is the velocity of the east-west (zonal) component of wind (positive values indicate west to east flow). V component is the velocity of the north-south (meridional) component of wind (positive values indicate south to north flow). These components were annotated using the Env-DATA System on

Movebank (movebank.org; Dodge *et al.,* (2013)). The interpolation was bilinear; spatial granularity: 0.75 degrees; temporal granularity: 3 hourly.

Table 5. Wind Variables

Variable	Description	Range
WindSpeed	Wind speed at the time of departure	0.79 - 5.69 m/s
WindSpeed7mean	Mean of wind speed at the departure location in the seven days prior	1.79 - 4.78 m/s
WindVariation	“WindSpeed” – “WindSpeed7mean”	-1.72 - 2.64 m/s
DiferDirec4	Difference in directions of movement and wind in 4 parts (see Fig. 2)	0 - 2
DiferDirec8	Difference in directions of movement and wind in 8 parts (see Fig. 2)	0 - 4

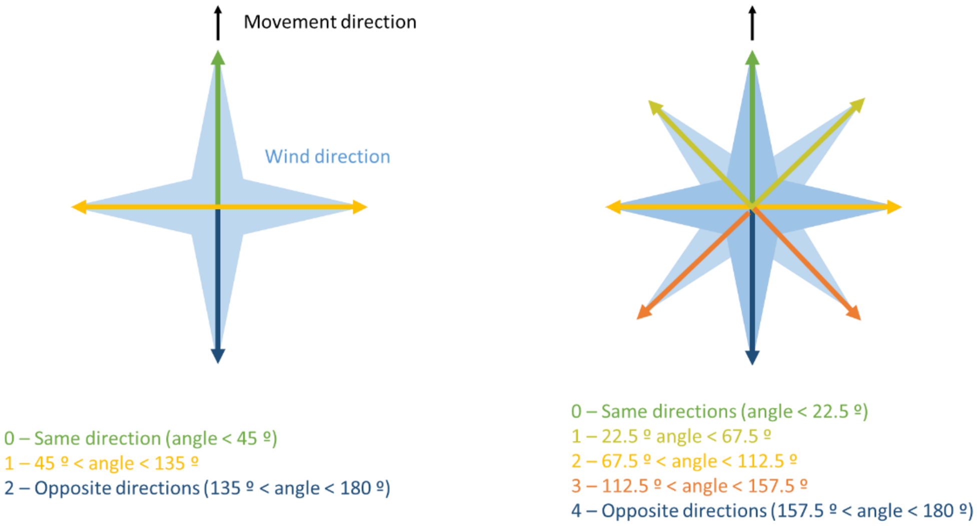

Figure 2. Description of the difference between movement and wind directions classification in four (left) and eight (right) parts.

2.3.6. Food availability variables

The variables regarding food availability are shown in the Table 6.

The variables were based on the Normalized Difference Vegetation Index (NDVI), an indicator of vegetation greenness. Because adult little bustards feed almost exclusively on green plants, NDVI is thought to be a good proxy of food availability (Shariatinajafabadi *et al.*, 2014). NDVI was calculated from MODIS Land Surface Reflectance from the NASA LPDAAC collections (https://search.earthdata.nasa.gov/). The data was converted into images using R software. Taking into account the average breeding home range of 131 ha for breeding males (Silva *et al.*, 2017), I determined the average NDVI value cantered at the departed point and date considering a radius of 650 m using the QGIS. As the little bustard lives in open habitats of herbaceous vegetation, I identified the areas that corresponded simultaneously the home range area and open areas. Open areas were identified using Corine Land Cover (2018, v.20) and considering the following land uses: 211 - Non-irrigated arable land, 212 - Permanently irrigated land, 231 – Pastures, 321 - Natural grassland. Therefore, within 650 m radius area I overlayed the MODIS 250 m grid, only selecting the cells that were at least 95% covered by open area land uses. As each territory had more than one square, the NDVI value of each home range was the average of the NDVI values of the squares that made it up.

Table 6. Food Availability Variables

Variable	Description	Range
NDVI650	Average NDVI values within a 650m radius of the departing point	0.184 - 0.533
NDVI650c	Average NDVI values within a 650m radius of the arrival point	0.174 – 0.748
NDVI650variation	NDVI650c/NDVI650	0.884 – 3.502
NDVI650Difer	NDVI650c-NDVI650	-0.026 – 0.484

2.4. Data analysis

I started to do univariate analysis (linear regression) with the predictive variables, using departure date (Julian day, 1 = 1st of January) as dependent variable to search for significance. I considered a variable is significant if the p-value <0.05. The values of the distance variable have a very large range. In an attempt to reduce skewness, logarithmic transformation was made.

A Spearman correlation matrix was made to ensure that no correlated variables were included. When two variables were strongly correlated ($r < -0.7$ or $r > 0.7$), I chose the one that has had a smaller p-value at the linear regression.

For the multivariate models, Generalized Linear Mixed Models (GLMM) were performed as the response variable (Julian day) has a Poisson distribution. These models offer a more adaptable method for analysing non-normal data in the presence of random effects (Bolker *et al.*, 2009). The predictive variables used in the models were only the ones that were significant in the univariate analysis and were not correlated with each other. Heterogeneity of the variables is expected between locations as well as between the years. I considered all combinations of the four predictors while keeping Year and Local of Departure as random variables.

To test which model fitted better, Akaike Information Criterion (AIC) was used.

All statistical analyses were performed with R (version 1.4.1106). All geographical analyses and plots were carried out using QGIS 3.16.6.

3. Results

A total of 36 birds was used for this study. 64% of the individuals were tracked for only one year (n=23), 14% for two years (n=5), 19% for three years (n=7) and 3% for four years (n=1)). The total number of post-breeding movements was 58.

Recorded migratory movements occurred in Portugal (Alentejo, n = 40) and Spain (Extremadura, n = 18) (Table 7). The summary statistics of the response variable (Julian Day) are presented in Table 8.

Table 7. Number of movements per departure location and year. On the left: Number of movements per departure location; on the right: Number of departures per year.

Portugal	Beja	31
	Évora	1
	Portalegre	8
Spain	Badajoz	12
	Cáceres	5
	Huelva	1
	Total	58

Year	n
2009	12
2010	9
2011	10
2012	1
2014	2
2015	5
2016	1
2017	3
2018	4
2019	11
Total	58

Table 8. Statistical Summary of the Response Variable, Julian Day

Julian day	
Min	131
Median	182
Mean	176
Max	217
Variance	497.23
Standard Deviation	22.30

Table 9 shows the results of the univariate analysis with significant predictive variables (p-value <0.05). The variables highlighted in green are the ones that were used in the model.

None of the variables related to brightness were significant. The cloud cover of the departure times was mostly below 0.2 (71%, n=58).

Regarding temperature variables, the majority was significant with the exception of the variables that were the result of the subtraction of the values three and eight days before departure with the departure day value (SubMax3, SubMax8, SubMin3, SubMin8, SubMean3 and SubMean8 were not significant) and the variable NdT35.3d (Number of days with maximum temperature above 35 ºC in the three days prior to departure). The estimates of all temperature variables had a positive relation with the departure date (Table 9). Taking into account that temperature variables were strongly correlated with each other (Appendix A), I choose the variable NdT25.8d as it had the lowest p-value and the highest adjusted R-squared in the linear regression.

Table 9. Results of the univariate analysis. In this table, only the significant predictive variables (p-value < 0.05) are included. The variables highlighted in green cells are the ones that were used in the GLMM.

Variable	p-value	Adjusted R-squared	Estimate Signal
LogDistance	*	0.09126	-
NDVI650	***	0.2309	-
DiferDirec8	*	0.06647	-
MeanMax3	**	0.1577	+
MeanMax8	***	0.3991	+
TMaxday	**	0.1567	+
MeanMin3	***	0.2012	+
MeanMin8	***	0.2978	+
TMinday	**	0.1384	+
Meanday	***	0.1713	+
Mean3	***	0.1852	+
Mean8	***	0.3752	+
NdT35.8d	*	0.07825	+
NdT25.3d	***	0.2003	+
NdT25.8d	***	0.533	+

None of the variables related to precipitation was significant. The accumulated precipitation was under 1 mm in 91% and 69 % (n = 58) of the cases three and eight days prior to departure, respectively.

Although the variable related to distance had a p-value of 0.081, with the log transformation (logDistance) it turned out significant. The estimate signal was negative.

Concerning wind variables, only the Difference in directions of movement and wind in 8 parts (DiferDirec8) showed significance. The estimate signal was negative.

Regarding food availability variables, only the variable NDVI650 (Average NDVI values within a 650m radius of the departing point) showed significance. The estimate signal was negative.

The combination of the four explanatory variables selected (NDVI650, DiferDirec8, NdT25.8d and logDistance) resulted in 15 GLMM (Table 10). Due to convergence problems with the established models, the variables were scaled. The model with all four explanatory variables (Mo1) was the one with the lowest AIC (470.3962). The difference between this model AIC and the other models was greater than two in all cases, so Mo1 was selected as better model.

Table 10. GLMMs ordered from lowest to highest AIC

Name	Model	AIC	Δ AIC
Mo1	NDVI650 + DiferDirec8 + NdT25.8d + logDistance	470.40	-
Mo2	NDVI650 + DiferDirec8 + NdT25.8d	472.52	2.13
Mo5	DiferDirec8 + NdT25.8d + logDistance	473.88	3.48
Mo4	NDVI650 + NdT25.8d + logDistance	474.60	4.20
Mo9	DiferDirec8 + NdT25.8d	475.84	5.45
Mo7	NDVI650 + NdT25.8d	476.26	5.86
Mo11	NdT25.8d + logDistance	479.85	9.45
Mo14	NdT25.8d	481.31	10.91
Mo3	NDVI650 + DiferDirec8 + logDistance	494.78	24.38
Mo6	NDVI650 + DiferDirec8	495.09	24.69
Mo8	NDVI650 + logDistance	497.38	26.98
Mo12	NDVI650	497.40	27.01
Mo10	DiferDirec8 + logDistance	531.58	61.18
Mo13	DiferDirec8	532.37	61.97
Mo15	logDistance	540.22	69.82

The best model showed that little bustards depart latter when the NDVI values are lower, there are smaller differences between the directions of movement and wind (favourable tailwind), in the 8 days before departure, the maximum temperature is always above 25°C and the distances travelled to the post-breeding areas are shorter. Table 11 displays the estimators and summary statistics of the best model. The percentage of explained deviance (14.6 %), as well as the marginal (R^2m) and conditional (R^2c) coefficients of determination of Mo1, were calculated as measures of goodness-of-fit

Over dispersion was checked by means of the package ‘DHARMa’ 0.4.6. (Harting, 2022). There was no overall deviations from the expected distribution of residuals (Appendix B).

Table 11. Estimates and summary statistics of the final model.

Variable	**Estimate**	**SE**	**z-value**	**p-value**
(Intercept)	5.29331	0.060	89.548	< 2e-16 ***
NdT25.8d	0.07789	0.015	5.154	2.54e-07 ***
DiferDirec8	-0.02715	0.012	-2.304	0.021 *
NDVI650	-0.03149	0.014	-2.248	0.025 *
LogDistance	-0.03186	0.015	-2.093	0.036 *

AIC	**Deviance**	**Explained Deviance**	**R2m**	**R2rc**
470.40	456.40	14.6 %	0.647	0.689

4. Discussion

The little bustard is a partially migratory species in the Iberian Peninsula (De La Morena *et al.*, 2015), with some individuals being more prone to migrate than others. As mentioned in section 1. Introduction, most birds perform seasonal movements towards areas with greater food availability (Alonso *et al.*, 2019) and understanding the environmental and climatic cues that trigger migration is crucial to better understand how migration patterns may shift with changing environment and climate. In this study I tried to identify for the first time the drivers that influence the timing of little bustards' migration departure. In fact, I show that when exposed to a greater number of days with temperatures above 25ºC little bustards leave breeding grounds later; the same happens when birds are exposed to lower food availability and when tailwinds are available; still, birds little bustards that travel shorter distances also depart later.

Birds departed when a higher frequency of days with daily temperatures over 25 ºC was recorded in the previous week. Although this is an expected result as the number of hotter days increases at the end of the breeding season, maximum temperatures tend to become stable from June to August (Iberian Climate Atlas, 2011) which is the bulk of this study period and when the large majority of migratory events took place. Even though birds have a thermoregulatory behaviour to adapt to higher temperatures (McCafferty *et al.*, 2017) reducing activity during the day, this may not be enough when having to deal with very high temperatures that persist for several days. The thermal stress associated with exposure to intense heat, such as heatwaves, can lead to heat stress and ultimately to mortality due to overheating (Stillman, 2019). Temperature has already been shown to be a relevant variable for the migration of various species (e.g. Burnside, 2021). A previous work carried out by Silva *et al.* (2015) found that birds start inhibiting activity with elevated temperatures starting at 25 ºC, which can compromise foraging activity since little bustards are not nocturnal and do not compensate being active during night-time at cooler hours. This could help explain the pattern found, as having a reduced time window to forage may trigger migratory decisions.

Wind direction is a known variable influencing migration timing (e.g. Pyle *et al.*, 1993, Ramos *et al.*, 2019). The wind model of optimal migration theory predicts that there is a period of days in which birds will wait for the best wind conditions (tailwind) before leaving (Åkesson & Hedenström, 2000). If these conditions have not arisen by the end of that period, birds will depart regardless of the wind. In this study, wind speed was low in the majority of cases, with only a few values considered moderate. Even so, the presence of tailwind was a significant variable explaining the day of departure. Earlier departures are associated with greater differences in direction, while later departures have smaller differences (i.e. with tailwind), suggesting that tailwind is available towards later in study period. At a time that food availability is scarce and energy expenditure is higher, tailwinds may be crucial in lowering the energy expenditure of migratory movements, especially for a flapping bird like the little bustard (Åkesson & Hedenström, 2000).

Food supply is an important component for the success of migration (Åkesson & Hedenström, 2007). The use of NDVI as an indicator of food availability has been used in other studies (e.g. Shariatinajafabadi *et al.*, 2014) and is well adjusted to the little bustard since adults birds feed mainly on green plants (Jiguet, 2002). My results show that little bustards leave their breeding grounds when exposed to lower food availability. Most likely, birds leave when they perceive that food is becoming scarce (Silva *et al.*, 2007) and not when food availability is depleted since it is necessary for them to leave when they still can accumulate enough energy for the journey. This result may be rather related to the impact that time of the year has on the variable since, as the days pass, vegetation gradually dries up.

Earlier departures are associated with longer distances travelled to post-breeding sites. Alonso *et al.* (2019) have demonstrated that little bustards show a high fidelity to post-breeding areas. Considering that my work is based on movements recorded singly in adult little bustards, birds have experienced previous post-migratory journeys. The knowledge gained from past years' experiences could be valuable for their migration. It is therefore expected that little bustards that travel longer distances, by migrating sooner are benefiting from greater food availability and fresher temperatures with lower metabolic effort.

Visual cues can play a vital role for animals navigating in the darkness of night (Penteriani *et al.*, 2014). A study by Norevik *et al.* (2019) with nightjars, argues that migration will begin after days of greater brightness as this allows the animals to feed for longer during the night and accumulate more reserves for the journey. The final model did not find brightness a relevant variable explaining the timing of migration of little bustards. An alternative explanation could be the use of other clues such as stars (Pyle *et al.*, 1993). For this case, a clear sky like those seen in the results would be a good condition eventually supporting this possibility.

None of the variables relating to precipitation were significant. In most cases, the precipitation was either negligible or extremely low. This result was expected as it coincides with the summer period characteristic of the Mediterranean climate (Cunha *et al.*, 2011).

According to the explained deviance, the final model can account for 15% of the variation in the observed data. There are numerous variables influencing the timing for migration that were not included in this study, so it was expected that the model would explain just a limited portion of the variability in the data. Variables such as genetic predisposition, photoperiod, atmospheric pressure, and intra- and interspecific competition were not taken into account. Comparing the values of marginal (R2m) and conditional (R2c) coefficients of determination of the final model (Table 11), we observe that random effects play a significant role in explaining the model. The variance explained by the random effects (R2m) accounts for 65% of the model, whereas the variance explained by the entire model, including both fixed and random effects, has a value of 69%. Therefore, breeding area and year prove to be crucial in explaining the observed patterns.

Climate change and modifications in agricultural practices induced by Common Agricultural Policies of European Union may potentially affect the timing of migration of little bustards. Because the Iberian Peninsula is a hotspot for climate change, being particularly vulnerable to heat waves (Bento *et al.*, 2021), it is plausible that bustards may depart from their breeding grounds earlier with a higher frequency of elevated temperatures in late spring / beginning of summer. According to the results, a higher frequency of elevated temperatures influences the departure date for migration. On the other hand the conversion of extensive cereal farming towards pasture land has greatly degraded breeding habitat, reducing significantly vegetation biomass (Silva *et al.*, 2023), which could possibly lead bustards to leave towards their post-breeding areas earlier.

5. Conclusion

This dissertation had the overall objective of understanding the environmental and climatic factors that trigger little bustard migratory decisions. To my knowledge, this is the first work identifying drivers that influence the timing of migration departure for the species.

The final model obtained supports the hypotheses that indeed tailwind, food availability, temperature, and distance travelled influence the migration decision of the species under study. The little bustard departs latter when the days leading up to the departure have maximum temperatures above 25°C; the direction of the wind is favourable to the movement (tailwind); there is low food availability and the distances travelled to the post-breeding areas are shorter.

Precipitation and brightness were not found to have an impact on little bustard migration.

While the findings of this study provide valuable insights into what environmental and climatic factors trigger little bustard migratory decisions, it is important to acknowledge the limitations of this research. The sample size was one of the limitations of the study. Having a larger sample would have allowed for a more complex model, with more explanatory variables.

For future studies, it would be interesting to include the tracking of females, as their departure timings are already different due to chick rearing obligations. It would also be interesting to test whether 'Breeding Strategy Type' would influence the timing of migration, as territorial birds tend be older, and therefore more experienced adults (Silva *et al.*, 2017). While older adults defend smaller territories, younger adults show a higher probability of being floaters, exploiting the attractiveness of territorial males.

With climate and environmental change affecting the frequency of days with high temperatures and vegetation biomass, the findings in this study shed light on the risks in reducing the length breeding season.

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7. Appendix

Appendix A: Correlation Matrix. Correlations greater than 0.7 highlighted in yellow.

	Distancia	NDVI650	DiferDirec8	MeanMax3	MeanMax8	TMaxday	MeanMin3	MeanMin8	TMinday	Meanday	Mean3	Mean8	NdT35.8d	NdT25.3d	NdT25.8d
Distancia	1	-0.12012	0.09321124	-0.0016918	-0.1308253	-0.19585	-0.0576148	-0.141407	-0.11022	-0.19278	0.0117	-0.151	0.077874	-0.07208	-0.19719
NDVI650	-0.12012	1	-0.0472975	-0.3481805	-0.4624873	-0.31108	-0.4687625	-0.4704851	-0.31496	-0.33034	-0.389	-0.471	-0.35509	-0.17538	-0.43034
DiferDirec8	0.093211	-0.0473	1	-0.0178623	0.02578718	-0.218	0.0667951	0.0418885	-0.0556	-0.1663	0.0547	0.0282	0.116155	-0.10172	-0.10004
MeanMax3	-0.00169	-0.34818	-0.0178623	1	0.76221969	0.614937	0.8537636	0.6034329	0.82251	0.755391	0.9733	0.7205	0.672349	0.593397	0.455029
MeanMax8	-0.13083	-0.46249	0.02578718	0.76221969	1	0.484881	0.8575779	0.9083946	0.678	0.594697	0.8165	0.9829	0.818813	0.534304	0.74886
TMaxday	-0.19585	-0.31108	-0.2179961	0.6149374	0.48488111	1	0.5153957	0.3662063	0.73238	0.954597	0.5641	0.4499	0.265805	0.404617	0.45344
MeanMin3	-0.05761	-0.46876	0.0667951	0.85376357	0.8575779	0.515396	1	0.8436741	0.77483	0.648405	0.9347	0.8735	0.718375	0.593448	0.626354
MeanMin8	-0.14141	-0.47049	0.04188845	0.6034329	0.9083946	0.366206	0.8436741	1	0.54326	0.451044	0.7099	0.9614	0.715513	0.554121	0.730752
TMinday	-0.11022	-0.31496	-0.0555997	0.82251069	0.67799686	0.732382	0.7748316	0.5432649	1	0.880033	0.8066	0.6304	0.564423	0.540208	0.560647
Meanday	-0.19278	-0.33034	-0.1662959	0.75539082	0.59469685	0.954597	0.6484051	0.4510443	0.88003	1	0.7052	0.5495	0.39686	0.47557	0.527424
Mean3	0.01172	-0.38915	0.05471915	0.9732997	0.81648159	0.564121	0.9347258	0.7099265	0.80658	0.705189	1	0.7968	0.721969	0.597812	0.508725
Mean8	-0.15131	-0.47098	0.02817722	0.72050817	0.98289704	0.449875	0.873512	0.9613645	0.63038	0.549479	0.7968	1	0.799344	0.541235	0.741617
NdT35.8d	0.077874	-0.35509	0.11615454	0.67234912	0.81881294	0.265805	0.7183749	0.7155129	0.56442	0.39686	0.722	0.7993	1	0.297833	0.392457
NdT25.3d	-0.07208	-0.17538	-0.1017209	0.59339715	0.53430387	0.404617	0.5934485	0.5541214	0.54021	0.47557	0.5978	0.5412	0.297833	1	0.611369
NdT25.8d	-0.19719	-0.43034	-0.1000431	0.45502925	0.74885996	0.45344	0.6263535	0.7307519	0.56065	0.527424	0.5087	0.7416	0.392457	0.611369	1

Appendix B: DHARMA Results