Universidade de Évora - Escola de Ciências e Tecnologia

Mestrado em Biologia da Conservação

Dissertação

Sex-based breeding behaviour and space use in the Eurasian Stone-curlew (Burhinus oedicnemus) in Southwest Iberia

Inês da Costa Medeiros

Orientador(es)	João Miguel Camacho Gameiro da Silva Rui Lourenço Ana Teresa Dias dos Santos Marques

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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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Évora 2025

UNIVERSIDADE DE ÉVORA
ESCOLA DE CIÊNCIAS E TECNOLOGIA

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Resumo

Comportamento reprodutor e uso do espaço com base no sexo do alcaravão (*Burhinus oedicnemus)* no Sudoeste da Península Ibérica

O alcaravão *Burhinus oedicnemus* é uma ave estepária sem dimorfismo sexual. Esta dissertação pretende avaliar se fêmeas e machos exibem diferenças nos papéis reprodutores e parentais. Foram utilizados dados de movimento de toda a época reprodutora de 15 fêmeas e 13 machos na Península Ibérica entre 2021 e 2024, para comparar o comportamento espacial e temporal. Foram calculados modelos de movimento *Brownian Bridge* (BBMMs) para calcular áreas núcleo e áreas vitais, bem como a centralidade em relação ao ninho. Para a escala temporal, foram aplicados Modelos Aditivos Generalizados Mistos (GAMMs) para compreender a fenologia diária de visita por cada sexo. Não foram encontradas diferenças significativas em nenhum dos parâmetros estudados, embora os machos pareçam afastarem-se mais dos ninhos durante os cuidados parentais. O comportamento espacial e temporal semelhante entre sexos poderá estar relacionado com a ausência de dimorfismo sexual, resultando na igual partilha de responsabilidades durante a reprodução.

Palavras-chave: Charadriiformes; Pseudo-estepes; Uso do espaço; Cronobiologia; Conservação.

Abstract

Sex-based breeding behaviour and space use in the Eurasian Stone-curlew (*Burhinus oedicnemus*) in Southwest Iberia

The Eurasian Stone-curlew *Burhinus oedicnemus* is a steppe species with no sexual dimorphism. This study aimed to assess whether females and males exhibit differences in breeding and parental roles. Movement data from the entire breeding season of 15 females and 13 males were collected in the Iberian Peninsula between 2021 and 2024 to compare the spatial and temporal behaviour. Brownian Bridge Movement Models (BBMMs) were calculated to determine core areas and home-range areas, as well as centrality to the nest. For the temporal scale, Generalized Additive Mixed Models (GAMMs) were performed to investigate daily patterns on nest visit by each sex. No significant differences were detected, although males tended to step further away from the nests during parental care. The overall similarity in spatial and temporal behaviour between sexes may be related to the lack of sexual dimorphism, suggesting an equal division of responsibilities throughout reproduction.

Keywords: Charadriiformes; Pseudosteppes; Space use; Chronobiology; Conservation.

Introduction

One of the most important direct drivers of biodiversity loss and ecosystem service change worldwide is habitat change and degradation. Cultivated systems, such as croplands, have been among the main causes of ecosystem transformation, now representing 24% of Earth's terrestrial surface (Duraiappah et al., 2005). In Europe, croplands expanded rapidly after 1700, and by 1950 around 70% of the original temperate and Mediterranean forests and grasslands had been lost. In response to such large-scale habitat loss, the European Union created the Natura 2000 network of protected areas, aimed at safeguarding many threatened species and habitats, including those occurring in farmland environments (Dudley, 2008; Blicharska et al., 2016).

Within Europe, the pseudosteppes of the Iberian Peninsula stand out as supporting one of the highest numbers of bird species with unfavourable conservation status (Suárez et al., 1997). However, in recent decades, the pseudosteppes have been abandoned or converted to intensive agriculture (Brotons et al., 2004; Moreira et al., 2007). Changes in agricultural management practices, often driven by policy shifts such as those associated with the European Union's Common Agricultural Policy (CAP), have further contributed to habitat degradation (Suárez et al., 1997; Duarte et al., 2006). The reforms to the CAP in the 1990s, particularly the 2003 revision, brought major modifications to agricultural incentives and land-use patterns (Brady et al., 2009; Gameiro et al., 2024), with significant ecological consequences.

As these landscapes continue to undergo rapid change, it becomes essential to examine how birds respond at the behavioural level. In particular, understanding breeding behaviour is essential for clarifying how birds adapt to these anthropogenic dynamic landscapes, allocate resources, and respond to ecological pressures. Such studies provide insights into the mating systems, parental care, and reproductive success, all of which directly influence population viability and evolutionary fitness. They also help predict population responses to environmental change, as behavioural flexibility underpins resilience to climate shifts and habitat loss (Székely et al., 2023). Importantly, incorporating behavioural perspectives into conservation planning is critical, since neglecting sex-specific strategies may lead to ineffective management and misinterpretation of demographic trends (Militão et al., 2023; Wu et al., 2025). Sex-specific roles in reproduction, including differences in courtship, mate competition, parental care, and foraging, are central to avian breeding systems. These roles are shaped by both ecological drivers, such as food availability and predation risk, and by social context, including adult sex ratios and mating opportunities (Kappeler et al., 2022). Such behavioural divergence often results in resource partitioning, differential exposure to threats, and distinct reproductive investments, with clear implications for survival and reproductive output (Militão et al., 2023). Ignoring these differences risks obscuring key ecological processes, as males and females may exploit habitats differently, experience unequal mortality, and respond divergently to environmental pressures (Militão et al., 2023; Wu et al., 2025). Several adaptive strategies illustrate the importance of sex-specific behaviours. In ground-nesting birds, changes in preen oil composition support the olfactory crypsis hypothesis, whereby incubating individuals, often females, reduce their scent to minimise predation risk, an adaptation particularly relevant in species exposed to olfactory predators (Grieves et al., 2022). Nest attendance routines also reveal functional specialization. In some species, one sex incubates predominantly during the night, while the other takes over by day, ensuring continuous coverage while balancing foraging opportunities (Ferraz et al., 2024). For example, in Eurasian spoonbills *Platalea leucorodia leucorodia*, males and females alternate nest attendance and foraging, likely reflecting adaptations to maximise incubation efficiency and energy allocation (Lok et al., 2024). Furthermore, differences in foraging habitats and nest attendance patterns may balance parental investment, reduce intra-pair competition, and account for sex-specific nutritional needs or risk tolerance (Baert et al., 2018; Lok et al., 2024). These adaptations are especially important in ground-nesting birds, which experience high levels of predation and disturbance. Coordinated strategies, such as olfactory camouflage and division of parental duties, are critical for ensuring reproductive success and chick survival under such selective pressures (Grieves et al., 2022; Lok et al., 2024). Empirical evidence demonstrates that seasonal and sex-based differences in anti-predator strategies, including preen oil modifications, are more prevalent in ground-nesting species, underlining their ecological importance in high-risk environments (Grieves et al., 2022). These sex-specific behaviours are particularly evident in sexually dimorphic species, where pronounced morphological differences often coincide with clearly defined reproductive roles. In such systems, males may be primarily associated with display territories and courtship activities, participating mainly in mating, while females assume responsibility for incubation and chick care (Alonso et al., 2000; Morales et al., 2000; Morales et al., 2008; Silva et al., 2017). In other cases, sex-specific division of labour is expressed temporally, with males predominantly incubating during the night and females during the day (del Hoyo et al., 1997; De Juana, 1997). Conversely, the absence of sexual dimorphism is often associated with reduced sexual selection pressures and is frequently correlated with more balanced parental responsibilities between sexes (Wang et al., 2023).

In recent years, animal tracking technologies, such as GPS, have allowed researchers to collect detailed and continuous data on animal movements and behaviours in natural settings. This overcomes the limitations of direct observation and manual tracking, reducing observer bias, and enables quantification of individual and group behaviours, activity patterns and habitat use with high spatiotemporal resolution (Weissbrod et al., 2013; Kays et al., 2015; Nathan et al., 2022; Koger et al., 2023). These tracking systems are even more valuable for elusive species or species that show predominant nocturnal activity, where direct observation is challenging (Kays et al., 2015; Hertel et al., 2019). Tracking data can be used to identify and quantify sex-specific patterns in space use, movement and behaviour. For example, Ferraz et al. (2024) determined sex-specific time windows to identify incubation behaviours to correctly identify nests using high resolution GPS devices in two steppe bird species. These analyses are critical to understanding ecological roles, reproductive strategies and informing conservation management (Stehfest et al., 2015; Hertel et al., 2020; Nathan et al., 2022), as this reduces nest visits and disturbance (Ferraz et al., 2024).

The Eurasian Stone-Curlew *Burhinus oedicnemus* (hereafter designated as Stone-curlew only), a member of the family Burhinidae within the order Charadriiformes, is a terrestrial wader without sexual dimorphism, characteristic of open habitats with sparse low vegetation and gentle slopes, including agricultural and steppe areas (Figure 1). The absence of sexual dimorphism may grant certain advantages, such as reduced levels of sexual selection and intersexual conflict when compared to other sexual dimorphic species. This can contribute to more stable social structures and lower antagonism between sexes, reducing evolutionary pressures for traits that benefit one sex over the other (Xu et al., 2024). Reduced dimorphism may also facilitate a more equal sharing of parental duties, with both parents contributing to incubation and chick rearing (Blondel et al., 2002). This trait is not unique to the Stone-curlew but is also observed in other members of the Burhinidae family, such as the Bush Stone-curlew *Burhinus grallarius* (Andrews, 2000). The Stone-curlew has a distribution range that extends across most of Europe, Central Asia, the Middle East and North Africa (BirdLife International, 2021), but it is restricted to small, fragmented patches of suitable habitat (Snow & Perrins, 1998). The Iberian Peninsula holds the largest and most important breeding population in Europe (Bas & Guitián, 1983; Barros, 1994). However, declines documented in North-Western and Central Europe due to nesting habitat loss are believed to be mirrored in the Iberian Peninsula (SEO/BirdLife, 2021; Almeida et al., 2022; Rocha, 2022; De Juana, 2022). Although globally classified as Least Concern (LC), the species is of European conservation concern (Snow & Perrins, 1998; BirdLife International, 2018; BirdLife International, 2021), as it is classified as Vulnerable (VU) in Portugal (Almeida et al., 2022) and Near Threatened (NT) in Spain (SEO/BirdLife, 2021). This highlights the urgent need for a better understanding of how steppe birds, such as the Stone-curlew, use their environment throughout the year, particularly during breeding (Suárez, 1988; De Juana, 1989). Due to its nocturnal and elusive habits, several aspects of the Stone-curlew ecology remain unstudied (Fuentes, 1994; Green et al., 2000; Geen et al., 2019). The species is known to be monogamous and solitary (Fuentes, 1994; Snow & Perrins, 1998), often breeding in spring with a two-egg single brood, although more nesting attempts can occur (Snow & Perrins, 1998; Harrison & Castell, 2002; Al-safadi, 2006). Nests are placed in shallow depressions on stony, bare ground, often in areas with low or no vegetation (Cramp & Simmons, 1983; Fuentes, 1994; European Environment Agency, 2012). Previous studies using direct observation have shown that incubation is shared by both sexes, with changeovers occurring at similar frequencies during day and night (Green et al., 2000; Harrison & Castell, 2002). This pattern happens with other members of the Burhinidae family, including the Indian Stone-curlew *Burhinus indicus* (Sharma & Sharma, 2015), Spotted Thick-knee *Burhinus capensis* (Josiah & Downs, 2023) and Bush Stone-curlew (Andrews, 2000). However, despite these examples, studies on breeding behaviour within this family remain limited, and detailed comparative information is still scarce. According to Cramp & Simons (1983), the Stone-curlew chicks are precocial, leaving the nest soon after hatching, although Green et al., (2000) reported that chicks rarely moved away from the nest more than a few hundred meters. Nevertheless, studies using GPS-tagged individuals are still lacking, and detailed information on sex-based breeding behaviour remains scarce.

Figure 1. Eurasian Stone-Curlew, *Burhinus oedicnemus*. Photo taken by Gonçalo Ferraz.

The aim of this study is to advance our understanding of the breeding behaviour of Stone-curlews by investigating potential sex-based differences during the breeding period, using high-resolution movement data from GPS/GSM tagged individuals. Specifically, the study addresses two complementary dimensions: spatial and temporal. In the spatial dimension, it was tested whether females and males differ in their space use by comparing core area, home-range size, and nest centrality at three data subsets: the entire breeding season, individual nests, and breeding phases (incubation and parental care). In the temporal dimension, it was examined whether females and males differ in their daily nest attendance patterns, focusing on the incubation phase. It was expected that females and males of Stone-curlews would not show breeding behavioural differences in both dimensions. This hypothesis was established according to the Green et al., (2000) study based on direct observation that affirmed the Stone-curlews shared incubation duties by both sexes. Also, as this species has no sexual dimorphism, it was expected no differences in the breeding behaviour (Cramp & Simmons 1980; del Hoyo et al., 1997; De Juana, 1997; Alonso et al., 2000; Morales et al., 2000; Martín, 2001; Morales et al., 2008; Silva et al., 2017).

Methods

Study area and system

This study was conducted in Southwest Iberia (Portugal and Spain, Western Europe). The Peninsula has some special attributes given by the diverse geological, physiographic, climatic and ecological characteristics along with its strategic location that gave its role of a glacial refuge in the Pleistocene and historical human activities. All this contributed to high biodiversity levels, including endemisms (Gibert et al., 2003; Gómez & Lunt, 2007; García-Vázquez et al., 2019). It has also an important role in the migratory routes of avifauna (Finlayson, 1992). Almost all the Iberian Peninsula is within the Mediterranean ecoregion and is subdivided into seven major ecological units (Goicolea & Mateo-Sánchez, 2022). Because of this high environmental heterogeneity, this region has diverse habitats of interest, being one of them steppes, including natural or agricultural pseudosteppes (European Environment Agency, 2018). Therefore, the Iberian Peninsula has the highest contribution to the European Natura 2000 network having an area of 222 000 km^2 and 2 130 protected spaces (Alcaraz et al., 2006). According to Instituto Nacional de Estatística (2023), Spain had 28% of its territory protected for biodiversity and Portugal had only 22% of its territory protected in 2021.

For Portugal, it was only monitored nests in the South of Portugal in the district of Beja and only three of them were included in the subsequent analysis. For Spain, nests were monitored in the autonomous communities of Extremadura, Castilla-La Mancha and Castilla y Léon. However, only nests of Extremadura and Castilla y Léon were used for the analysis of successful nests. Extremadura had eight nests and Castilla y Léon had only one nest (Figure 2).

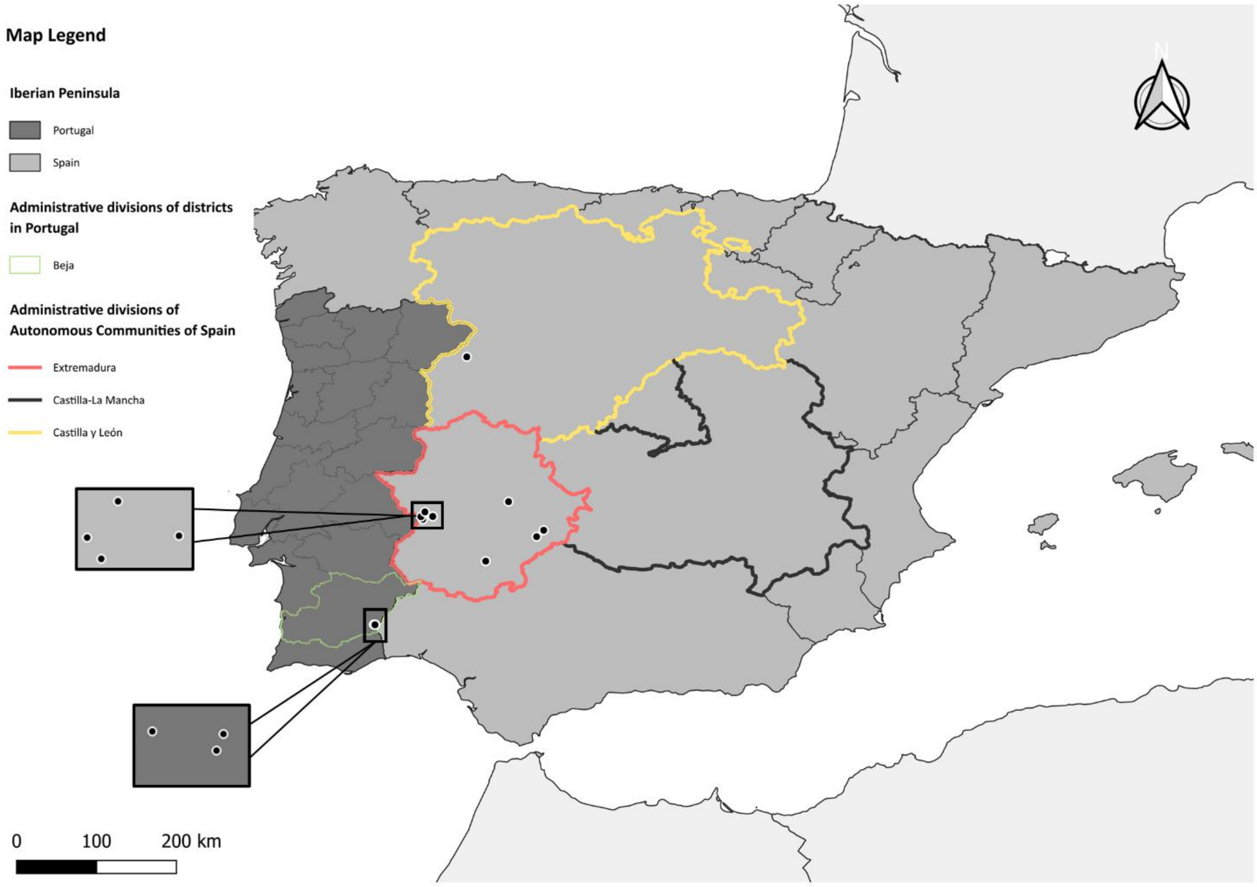

Figure 2. Map of the Iberian Peninsula with the locations of the successful nests (black dots). The administrative divisions that included the nests are in bold and administrative divisions that included successful nests are colored (Portugal: Beja (green); Spain: Extremadura (red) and Castilla y Léon (yellow)) (Nature Earth (https://www.naturalearthdata.com/downloads/10m-cultural-vectors/), Organismo Autónomo Centro Nacional de Información Geográfica (https://centrodedescargas.cnig.es/CentroDescargas/limites-municipales-provinciales-autonomicos), Direção Geral do Território (https://www.dgterritorio.gov.pt/cartografia/cartografia-tematica/caop) and data from Steppe Birds Move (2021 – 2024)).

Data collection and sexing

Stone-curlews were captured during the breeding season using clap nets near nesting sites and on wintering roosting areas using mist nets. These birds were marked with *Ornitela* GPS/GSM loggers, programmed to provide GPS data and tri-axial accelerometer data at 30-minute intervals. Tagged birds were monitored remotely through their movements. Potential nests were inferred from a "star-shaped" movement pattern and were then confirmed *in situ*. Incubation starting date was estimated either via an egg density test to record the buoyancy level in a jug of water to assess the embryonic development stage (Brito, 1996), or by subtracting 28 days to the date the tagged bird leaves the nest (following the incubation duration mentioned in Harrison, 1982). Incubation periods of less than 28 days were classified as incomplete or unsuccessful. Parental care would last ca. 35 days until chicks are considered fully fledged. Similarly, parental care with a duration of less than 35 days was classified as unsuccessful (e.g. chicks died). All these stages (failed or successful incubation or parental care periods) were confirmed *in situ* through direct observation of nests and/or tagged birds with their chicks. Biometric readings and feathers were collected during bird tagging to aid in sex identification through DNA analysis (Silva et al., 2022).

Data filtering

All data filtering, calculations, and analyses were conducted using R software (R Core Team, 2024; version 4.4.2). Movement data of Stone-curlew was downloaded from the online platform *Movebank*. This platform was designed for managing, sharing, and archiving animal tracking and behaviour data (https://www.movebank.org/cms/movebank-main). This data had previously been collected as part of five ongoing projects. After downloading the data, it was filtered to match the objectives of the study. Initially, the five datasets were standardized using R to enable their subsequent merging. Specifically, the following variables were retained: bird identification code, geographical coordinates, timestamp and ground speed. The 'dplyr' package (Wickham et al., 2023; version 1.1.4) was used to remove unnecessary columns.

For this study, data was filtered to retain only one random location per hour for the breeding season (February to September), and only locations with ground speed below 3 m/s (to exclude locations during flights). Additionally, individuals located outside the Iberian Peninsula were excluded. Once this initial filtering was complete, the start and end dates of the breeding attempt were added for each individual. Only individuals tracked between 2021 and 2024 were included. In total, 28 stone-curlews were monitored in this study. The breeding phase dates were obtained from an existing dataset developed for a previous study (García-Baltasar, in prep.). Each reproductive phase includes a start and end date for incubation, as well as a start and end date for the parental care phase. Not all birds had both phases. In those cases, only the phase for which data was available was retained. The start of parental care was defined as the first day following the end of incubation. If the start and end dates of a breeding phase were present, but the movement data did not cover the full phase, that record was excluded from the dataset. The sex of each bird was also added and birds with unknown sex were excluded from comparisons. This final dataset was used for subsequent calculations. It includes each bird's identifier, geographic coordinates (longitude and latitude) and timestamps (date and time of each location). In all plots comparing area and distance metrics between males and females, the colour scheme of pink for females and blue for males was used.

To conduct this study, three data subsets were considered. For reference, a nest was considered successful in the incubation phase if eggs had hatched and successful in the parental care phase if chicks fledged. The three data subsets were defined as follows: (1) Breeding season, coinciding with locations from the full breeding season, including all the nests in the database without accounting if the nest failed or had success during incubation or parental care phases, including multiple nesting attempts per year; (2) Nest, coinciding with locations only from nests that succeeded in both incubation and parental care phases; and (3) Phase, it was subdivided into (3.1) Incubation, coinciding with locations only during successful incubation phase, and (3.2) Parental care, coinciding with locations only during successful parental care phase.

Statistical analysis

Sex-based differences in core and home-range area size

To compare the space use between female and male Stone-curlews during breeding, we calculated core areas and home-ranges using 50% and 95% kernels, respectively, with Brownian Bridge Movement Models (BBMM). The BBMM takes into consideration the spatial and temporal relationship of bird locations, explicitly modelling the movement path (Horne et al., 2007). This model has been increasingly used because it provides straightforward results (Lonergan et al., 2009; Ovaskainen & Crone, 2009; Willems & Hill, 2009) and has been recognized for its broad potential in ecological studies (Farmer et al., 2010; Takekawa et al., 2010).

The BBMMs were calculated to estimate bird home-ranges for three different data subsets, breeding season, nests, incubation and parental care phase. Before generating the BBMMs, a raster representing the study area, the Iberian Peninsula, was created with a spatial resolution of 100 meters. The raster and bird GPS locations were projected into UTM (Universal Transverse Mercator Zone 30N, WGS84) to construct the BBMMs. Duplicate timestamps were removed, and missing data points were interpolated to ensure regular trajectories with fixed one-hour intervals. Each bird's trajectory was processed using the 'adehabitatHS' package (Calenge, 2024a; Version 0.3.18) and movement trajectories were created using the 'as.ltraj' function (Calenge, 2024b; version 0.3.28) to ensure data were discretized into one-hour intervals, standardizing the time between locations. The diffusion parameter (D), representing spatial variance in movement, was calculated using the 'BRB.D()' function (Calenge, 2024c; version 0.4.22). Finally, space use was estimated with the 'BRB' function (Calenge, 2024c; version 0.4.22), applying the following parameters recommended for smoothing: maximum interval between locations (Tmax) of 24 hours, tau = 300, and Lmin = 20. These parameters were chosen because tau and Lmin help tune how the kernel balances directed interpolation versus localized use of space: tau controls the randomness of movement, while Lmin determines how uncertain nearly identical locations are considered as movement. For hourly locations and a GPS accuracy of approximately 10 m, a tau of 300 and an Lmin of 20 is considered standard.

Probability contours were extracted at two kernel levels (50% and 95%) using the 'contourLines' function, and polygons were generated using 'st_polygonize' from the 'sf' package (Pebesma & Bivand, 2023; version 1.0.19). These polygons were saved as shapefiles for further visualization in Geographic Information Systems (GIS); in this study, QGIS was used (QGIS Development Team, 2024; version 3.36.1. Even with adjusted parametrization, BRB function can still create some "artifacts", e.g. polygons without actual locations. Each polygon was inspected to ensure correct geometry (Figure 3). For the breeding season, successful nests, and incubation phase components, only 50% kernels containing the nest location were maintained. For the parental care phase, core areas were kept if location data existed within the polygon. For 95% probability contours, polygons were retained if a location was present. However, overall, it was only eliminated small polygons which could clearly indicate that it was an artefact. Next, polygon areas were calculated in square meters using ‘st_area’ from the ‘sf’ package (Pebesma & Bivand, 2023; version 1.0.19) and then converted to hectares to facilitate interpretation across the three data subsets. A unique identifier was created for each polygon, combining the bird ID, BBMM probability level and bird sex.

To compare BBMM areas between females and males for each of the three data subsets, normality of the data was assessed separately for females and males using the ‘shapiro.test’ function (R Core Team, 2024; version 4.4.2). Additionally, variance homogeneity was also tested using Levene’s test from the ‘car’ package (Fox & Weisberg, 2019; version 3.1.3). Based on these tests results, non-parametric Mann-Whitney U test was applied. Boxplots were created to visualize results using ‘ggplot’ from the ‘ggplot2’ package (Wickham, 2016; version 3.5.1).

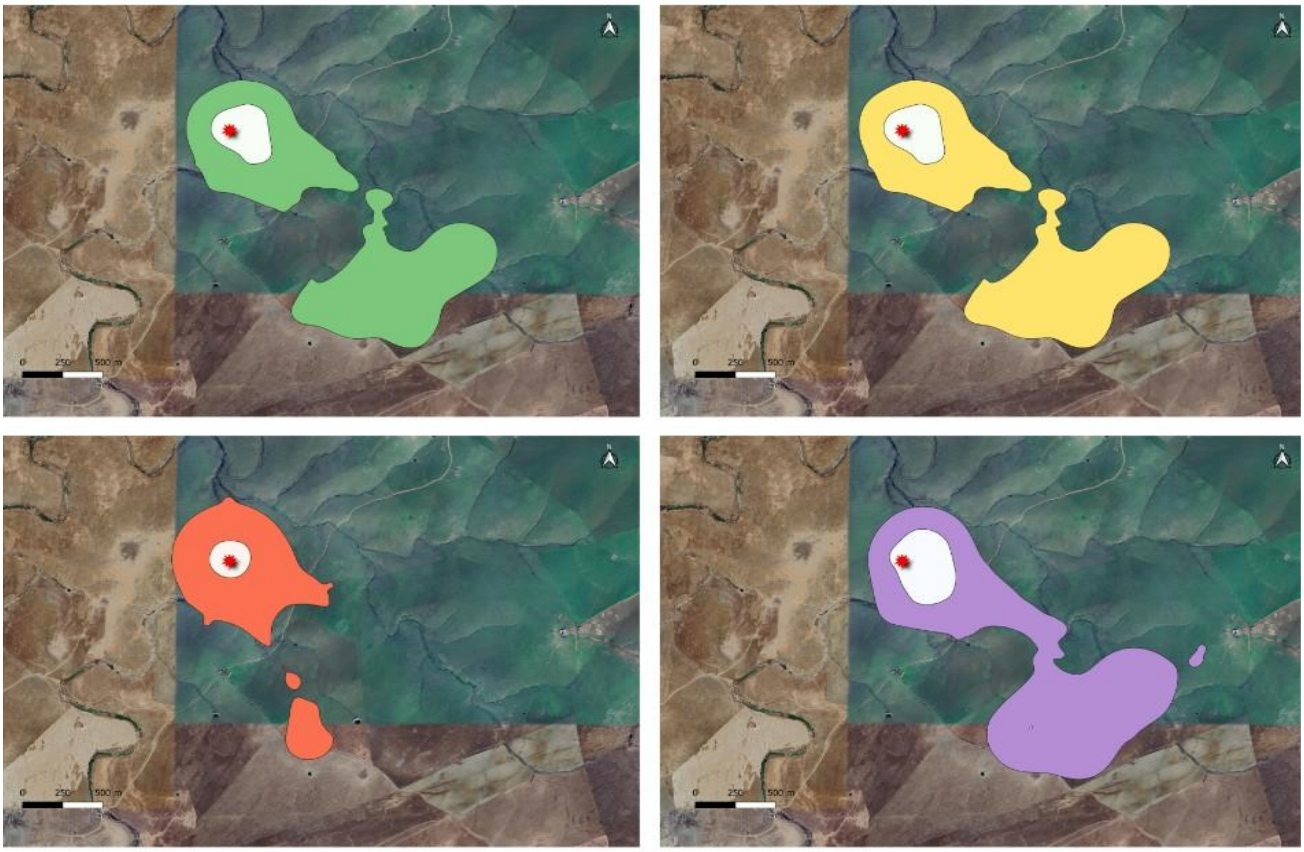

Figure 3. Brownian Bridge Movement Models (BBMM) visualization on Geographic Information Systems (GIS; QGIS). All data subsets are represented above in the four pictures. The core area (50% kernel) is represented by the white core, and the home-range area (95% kernel) is the area around the white core. Additionally, the nest location is represented by the red star in the middle of the core area. The five pictures are as follows: A) BBMM of the breeding season data subset; B) BBMM of the nest data subset; C) BBMM of the incubation phase data subset; and D) BBMM of the parental care phase data subset.

Sex-based differences in movement centrality based on distance to the nest

Centrality was calculated as the mean distance (MD) of all GPS locations to the exact location of the nest to understand sex-based differences between females and males of tracked Stone-curlews at three different data subsets already mentioned. This metric serves as a proxy for space centrality. Lower values indicate more restricted and centrally focused movements around the nest.

The geodesic distance (in meters) between each GPS point and its respective nests was calculated using the Haversine formula using the function 'disHaversine' from the package 'geosphere' (Hijmans, 2024; version 1.5.20; Figure 4). Subsequent analyses tested whether females and males had different spatial centrality in their movements around the nest location. Prior to statistical testing, normality was assessed for each sex using the Shapiro-Wilk tests using the function 'shapiro.test' (R Core Team, 2024; version 4.4.2) and tested variance homogeneity with Levene's test using the function 'leveneTest' from the 'car' package (Fox & Weisberg, 2019; version 3.1.3). When the assumption of normality was denied for at least one group, a non-parametric test was justified, being used the Mann-Whitney U test. When the assumption of normality was proven, a T-Test was applied. The respective results were visualized in boxplots that were generated using the package 'ggplot2' (Wickham, 2016; version 3.5.1). Outliers were maintained, unless there were extreme values that skewed interpretation (> 2000m). In those cases, the data was filtered accordingly (it was removed four outliers for the breeding season; see Annex 1).

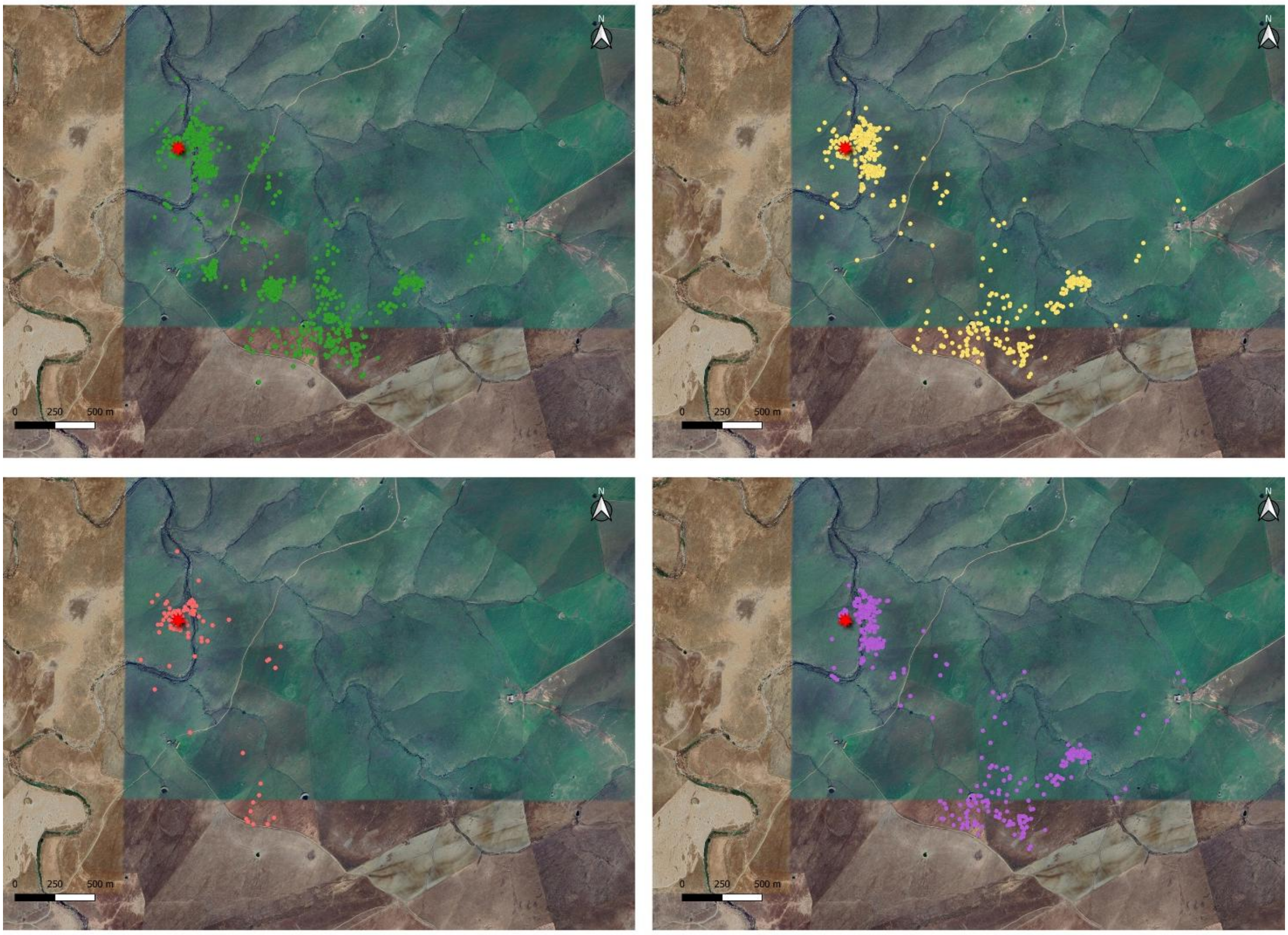

Figure 4. Mean distance (MD) represented by the visualization of each GPS point and the nest location (red star) on Geographic Information Systems (GIS), in this case QGIS. The four pictures are as follows: A) MD of the breeding season data subset; B) MD of the nest data subset; C) MD of the incubation phase data subset; and D) MD of the parental care phase data subset.

Sex-based differences in daily nest attendance

A fitted Generalized Additive Mixed Model (GAMM) with a binomial family was used to model nest attendance (0 or 1) during the incubation phase as a function of sex, time of day, day of the year, and individual identity. This model was used to quantify nest attendance probability across a 24-hour cycle and determine differences between females and males during incubation phase. The smooth effect of time of day (decimal hour) was modelled separately for each sex, and a separate smooth term for day of the year (Julian day) captured potential seasonal patterns during incubation. This model allows to estimate nonlinear relationships between the explanatory variables, time of day and day of the year, as well as the phase and the binary response variables (attending or not attending the nest).

A circular buffer of 10-meter radius was created around each nest to define spatial zones for nest attendance during incubation. For each GPS fix, it was determined if the point fell within the nest buffer with st_within (Pebesma & Bivand, 2023; version 1.0.19) to generate a binary attendance variable (1 = inside the nest buffer; 0 = outside the nest buffer). To have a temporal standardization of observations, timestamps were converted to decimal hours to support continuous time modelling. To allow phase-specific modeling of attendance patterns, the dataset was separated according to the breeding phase of incubation. A binomial GAMM model with a logit link was fitted using the ‘gam’ function of the package ‘mgcv’ (Wood, 2011; version 1.9.1) using the sex as a fixed effect. For the smooth term, it was included (i) the hour of day, that interacts with sex to analyse sex-specific daily patters, and (ii) a separate smooth term for the day of the year (Julian day), that accounts for potential seasonal variation in nest attendance across the incubation period. Random intercepts were also applied for each bird to account for potential individual variation. GAMMs were built for incubation data. The overall model fit was assessed using summary statistics and diagnostic checks. ROC curves were used to evaluate model discrimination ability and computed Area Under the Curve (AUC).

Results

The breeding season considered a total of 28 individuals, 15 were females and 13 were males. From these 28 tagged Stone-curlews a total of 91 nests were monitored (41 associated to females and 50 associated to males). However, for the nest data subset, the 28 Stone-curlews were filtered to the ones that had successful nests, which reduced the sample down to 11 Stone-Curlews (six females and five males). Out of these 11 Stone-curlews, there were 12 nests on this spatial scale. For the incubation phase, there was a total of 20 Stone-curlews with successful incubation, 10 females and 10 males. In the incubation spatial scale there were 32 nests (13 associated to females and 19 associated to males). The parental care phase was the same number of Stone-curlews as the spatial scale nests which were 11 Stone-curlews and 12 nests (see Table 1).

Table 1. Summary of the number of birds and nests per data subset including its respective definition.

Data subset		Definition	Number of birds (F + M)	Number of nests
Breeding season		Locations from the full breeding season	28 (15 + 13)	91
Nests		Locations only from nests that succeeded in both incubation and parental care phases	11 (6 + 5)	12
Phase	**Incubation**	Locations only during successful incubation phase	20 (10 + 10)	32
	Parental care	Locations only during successful parental care phase	11 (6 + 5)	12

Sex-based differences core and home-range area size

When considering the whole breeding period, mean core area (50% kernel) was 20.21 ± 22.83 ha for females (n = 22) and 17.46 ± 15.82 ha for males (n = 23), while home-range area (95% kernel) was 89.62 ± 173.27 and 82.59 ± 113.97 for females and males, respectively. There were no significant differences between females and males on mean core area (Mann-Whitney test: W = 503, p = 0.60) and home-ranges (Mann-Whitney test: W = 1414, p = 0.59), although females tend to have bigger areas than males (see Table 2, Figure 5).

Table 2. Summary of all values and statistical tests (Mann-Whitney test) performed for the core area (50% probability kernel) and home-range area (95% probability kernel) calculated by the Brownian Bridge Movement Model (BBMM) during the three data subsets.

BBMM probability kernel (%)	Data subset		Sex	Mean ± SD (ha)	W	*p*
50	Breeding season		F	20.21 ± 22.83	503	0.60
			M	17.46 ± 15.82		
	Nest		F	18.57 ± 22.35	16	0.62
			M	14.46 ± 11.89		
	Phase	Incubation	F	22.58 ± 30.33	258	0.50
			M	14.73 ± 18.40		
		Parental care	F	13.32 ± 15.91	50	0.20
			M	8.33 ± 12.21		
95	Breeding season		F	89.62 ± 173.27	1414	0.59
			M	82.59 ± 113.97		
	Nest		F	74.71 ± 199.96	40	0.19
			M	85.50 ± 82.90		
	Phase	Incubation	F	94.49 ± 186.42	487	0.60
			M	86.38 ± 123.26		
		Parental care	F	80.40 ± 207.19	36	0.32
			M	69.37 ± 97.38		

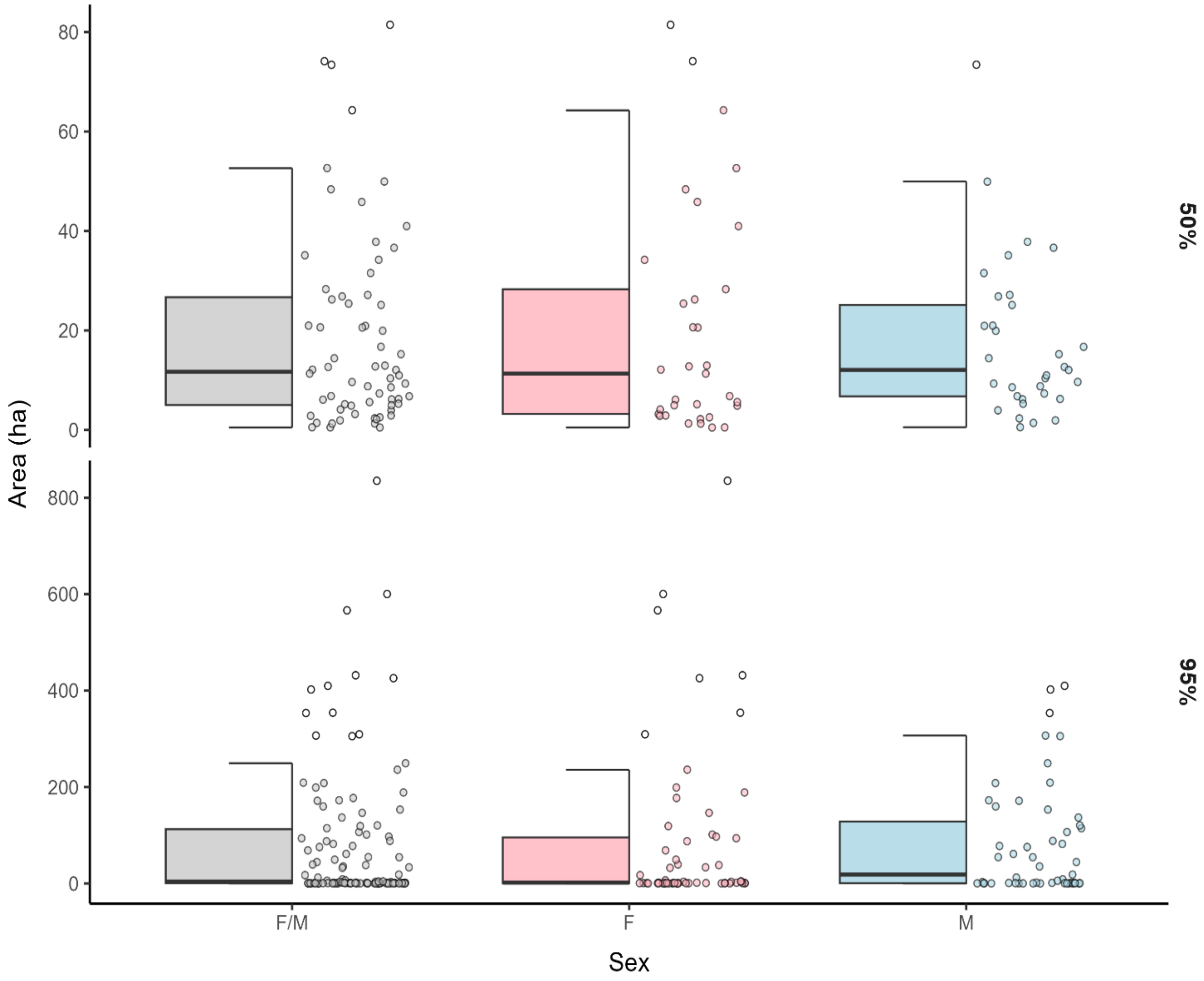

Figure 5. Differences in the core area (50%, upper panel) and home-range (95%, lower panel) size (ha) between females and males during the breeding season (2021 – 2024), calculated by the Brownian Bridge Movement Model (BBMM). Data was pooled for all years as there were no differences in area among years (Annex 2). The graphic is represented in the left by a boxplot, in the right by jittered points. The black bar represents the median. The F/M represents all females and males together; F means female and M means male (50%: n(F) = 33, n(M) = 33, N = 66; 95%: n(F) = 59, n(M) = 51, N = 110).

When considering the nest data subset, mean core area (50% kernel) was 18.57 ± 22.35 ha for females (n = 7) and 14.46 ± 11.89 ha for males (n = 5) and the home-range area (95% kernel) was 74.71 ± 199.96 ha for females and was 85.50 ± 82.90 ha for males (see Table 2, Figure 6). These differences were not statistically significant, with no differences between females and males in mean core area (Mann-Whitney test: W = 16, *p* = 0.62) and home-range area (Mann-Whitney test: W = 40, *p* = 0.19).

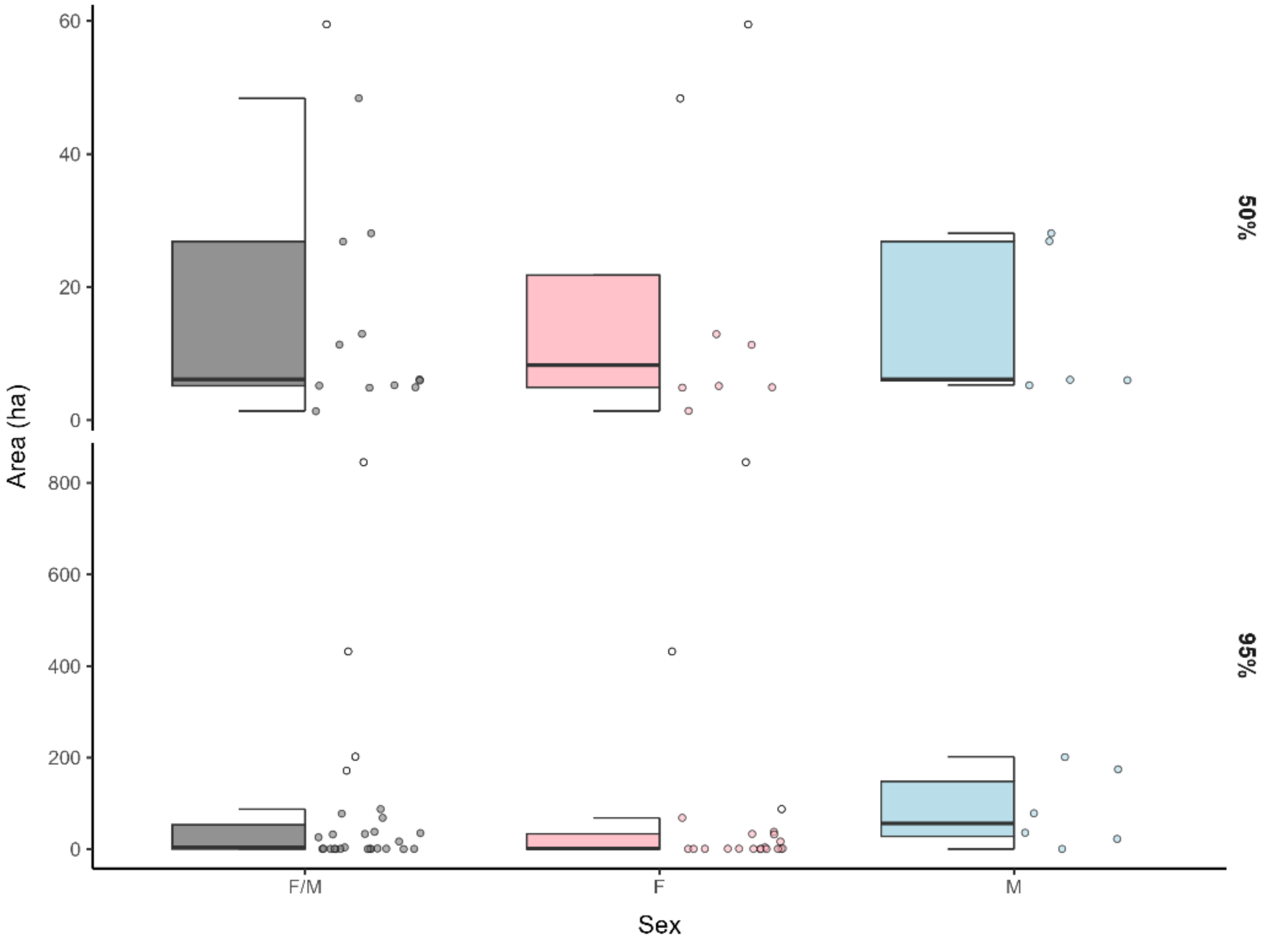

Figure 6. Differences in the core area (50%, upper panel) and home-range (95%, lower panel) between females and males during the nest (incubation and parental care periods), calculated by the Brownian Bridge Movement Model (BBMM). The graphic is represented in the left by a boxplot, in the right by jittered points. The black bar represents the median. The F/M represents all females and males together; F means female and M means male (50%: n(F) = 8, n(M) = 5, N = 13; 95%: n(F) = 21, n(M) = 6, N = 27).

Finally, during incubation the mean core area (50% kernel) was 22.58 ± 30.33 ha and 14.73 ± 18.40 ha for females (n = 13) and males (n = 19), respectively. Regarding the home-range area (95% kernel), females had 94.49 ± 186.42 ha and males had 86.38 ± 123.26 ha (see Table 2, Figure 7). The incubation phase did not have significant differences between females and males in the mean core area and home-range area as well (Mann-Whitney test: W = 258, *p* = 0.50 and W = 487, *p* = 0.60, respectively). Regarding the parental care phase, females had a mean core area of 13.32 ± 15.91 ha (n = 7) and males had 8.33 ± 12.21 ha (n = 5), whereas in the home-range area, the mean was 80.40 ± 207.19 and was 69.37 ± 97.38 for females and males, respectively (see Table 2, Figure 7). This phase also did not have significant differences between females and males in the mean core areas (Mann-Whitney test: W = 50, *p* = 0.20) and home-range areas (Mann-Whitney test: W = 36, *p* = 0.32).

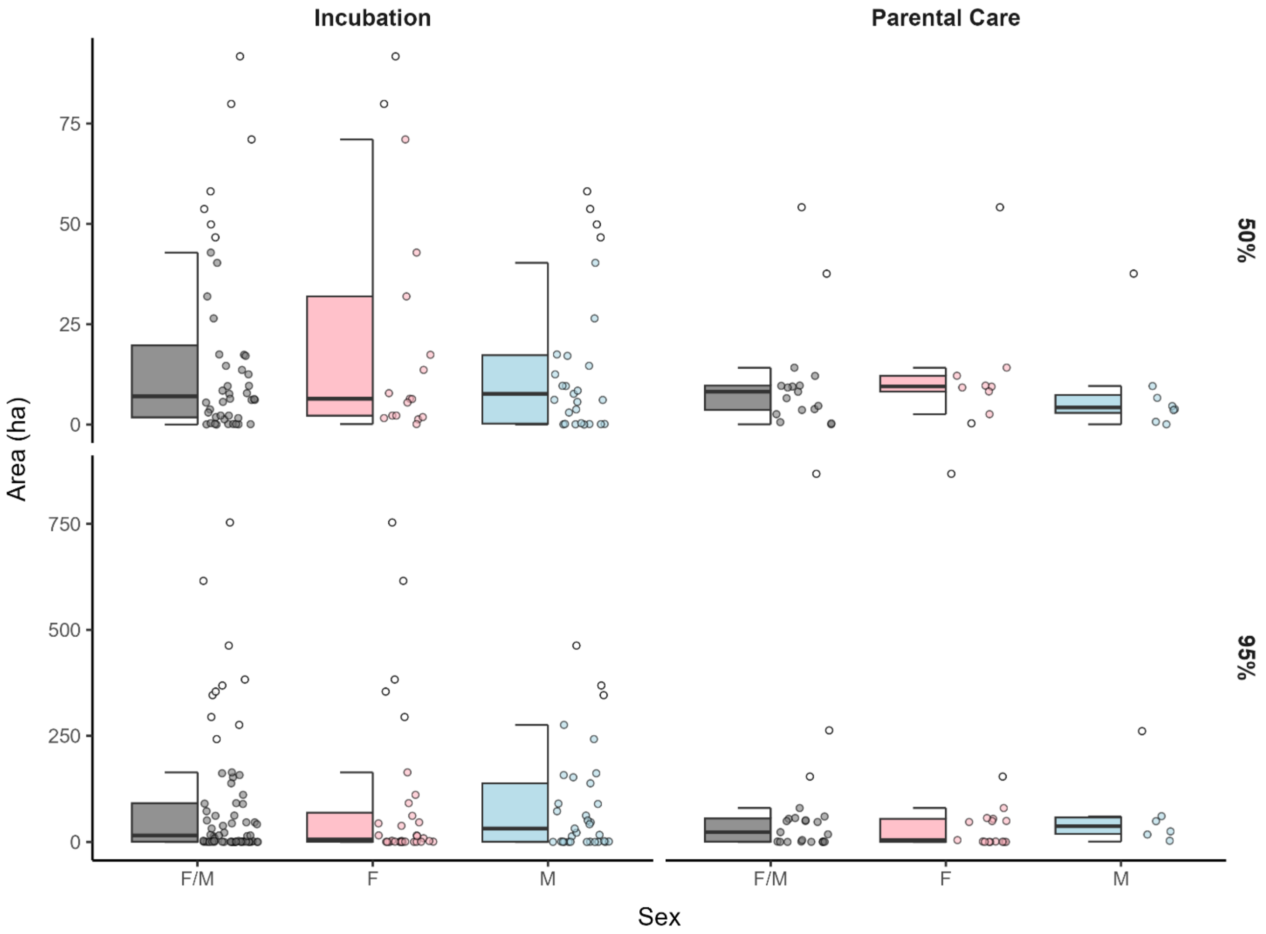

Figure 7. Differences in the core area (50%, upper panel) and home-range (95%, lower panel) between females and males during the incubation (left panel) and parental care phase, (right panel) calculated by the Brownian Bridge Movement Model (BBMM). The graphic is represented in the left by a boxplot, in the right by jittered points. The black bar represents the median. The F/M represents all females and males together; F means female and M means male (Incubation, 50%: n(F) = 17, n(M) = 27, N = 44; 95%: n(F) = 32, n(M) = 33, N = 65; Parental care, 50%: n(F) = 9, n(M) = 8, N = 17; 95%: n(F) = 17, n(M) = 6, N = 23).

Sex-based differences in movement centrality based on distance to the nest

When addressing the whole breeding season, females had a mean of MD of 2462.59 ± 14469.47m and males had 239.61 ± 500.64m (see Table 3). There were no registered significant differences between females and males (Mann-Whitney test: W = 1144, *p* = 0.34). The statistical analysis was performed with all data values, but to better show the visual representation through the graphic, it excluded four outliers that biased the visual results (Annex 1). When excluding the outliers, the MD range of females and males did not have a large difference compared to the mean MD when not excluding the outliers. However, the individual variation of females is slighter larger than males (Figure 8).

Table 3. Summary of all values and statistical tests (Mann-Whitney test and Student's t-test) for the three data subsets calculated by the mean distance of all GPS locations (MD).

Data subset		Sex	Mean ± SD (m)	W	t	*p*
Breeding season		F	2462.59 ± 14469.47	1144	-	0.34
		M	239.61 ± 500.64			
Nest		F	197.99 ± 123.68	-	- 0.83	0.43
		M	262.66 ± 147.65			
Phase	**Incubation**	F	138.08 ± 97.76	104	-	0.47
		M	136.30 ± 69.41			
	Parental care	F	255.89 ± 155.28	-	-1.07	0.31
		M	368.34 ± 210.73			

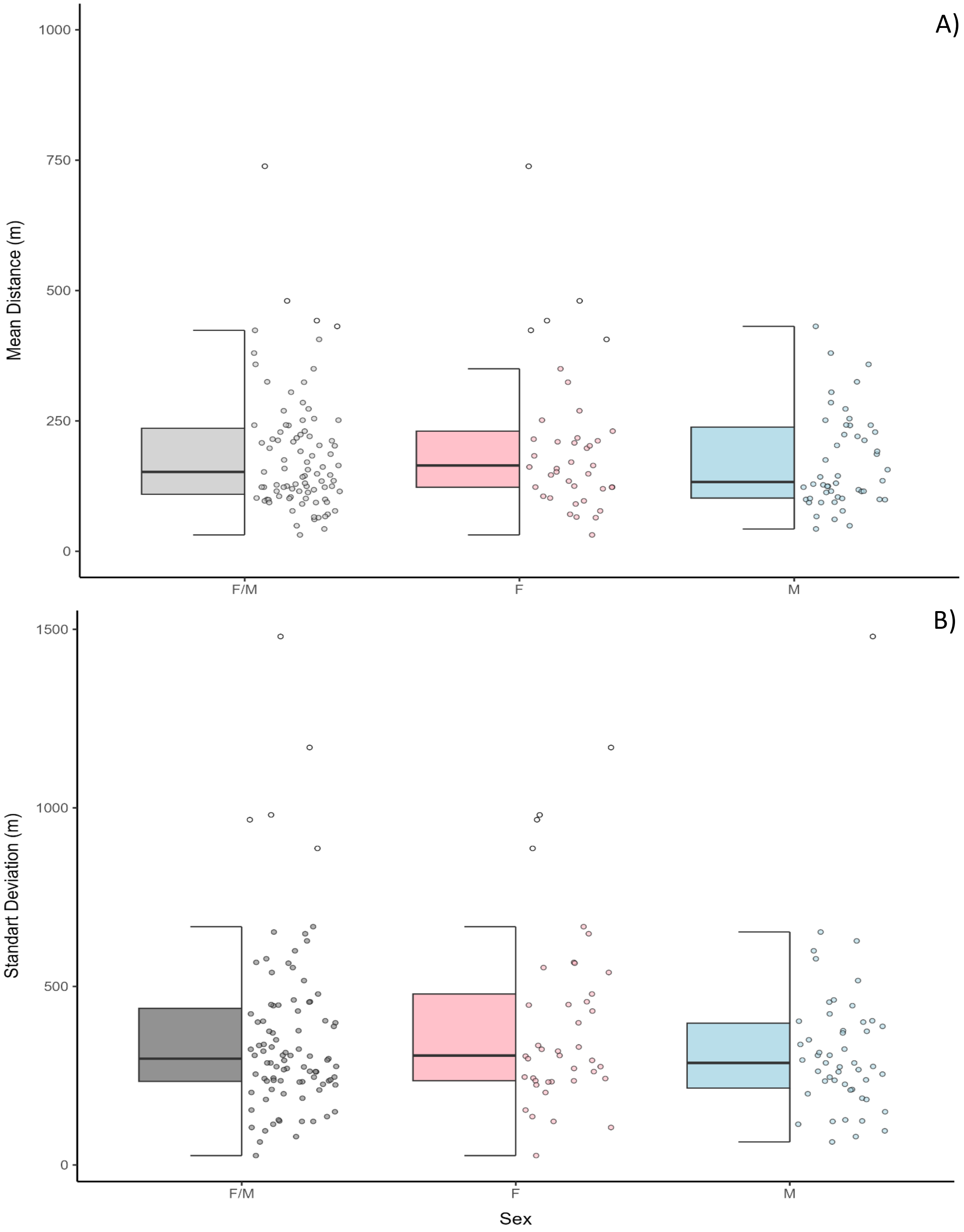

Figure 8. A) Differences between females and males in the breeding season (2021 – 2024) calculated by the mean distance of all GPS locations (MD). Data was pooled for all years as there were no differences in area among years (Annex 3). The graphic is represented in the left by a boxplot, in the right by jittered points. The black bar represents the median. The F/M represents all females and males together; F means female and M means male (n(F) = 41, n(M) = 50, N = 91). B) Standard deviation (SD) in the breeding season (2021 - 2024) of the mean distance of all GPS locations (MD).

Regarding the nest, females had a mean of the MD of 197.99 ± 123.68m and males had a mean of 262.66 ± 147.65m (see Table 3). This spatial scale also did not have significant differences (Student's t-test: t = - 0.83, *p* = 0.43), but males had a larger mean of MD than females. This is also confirmed by the graphic representation that showed that males had a larger median and larger MD range than females. There was no large difference in the individual variation between females and males (Figure 9).

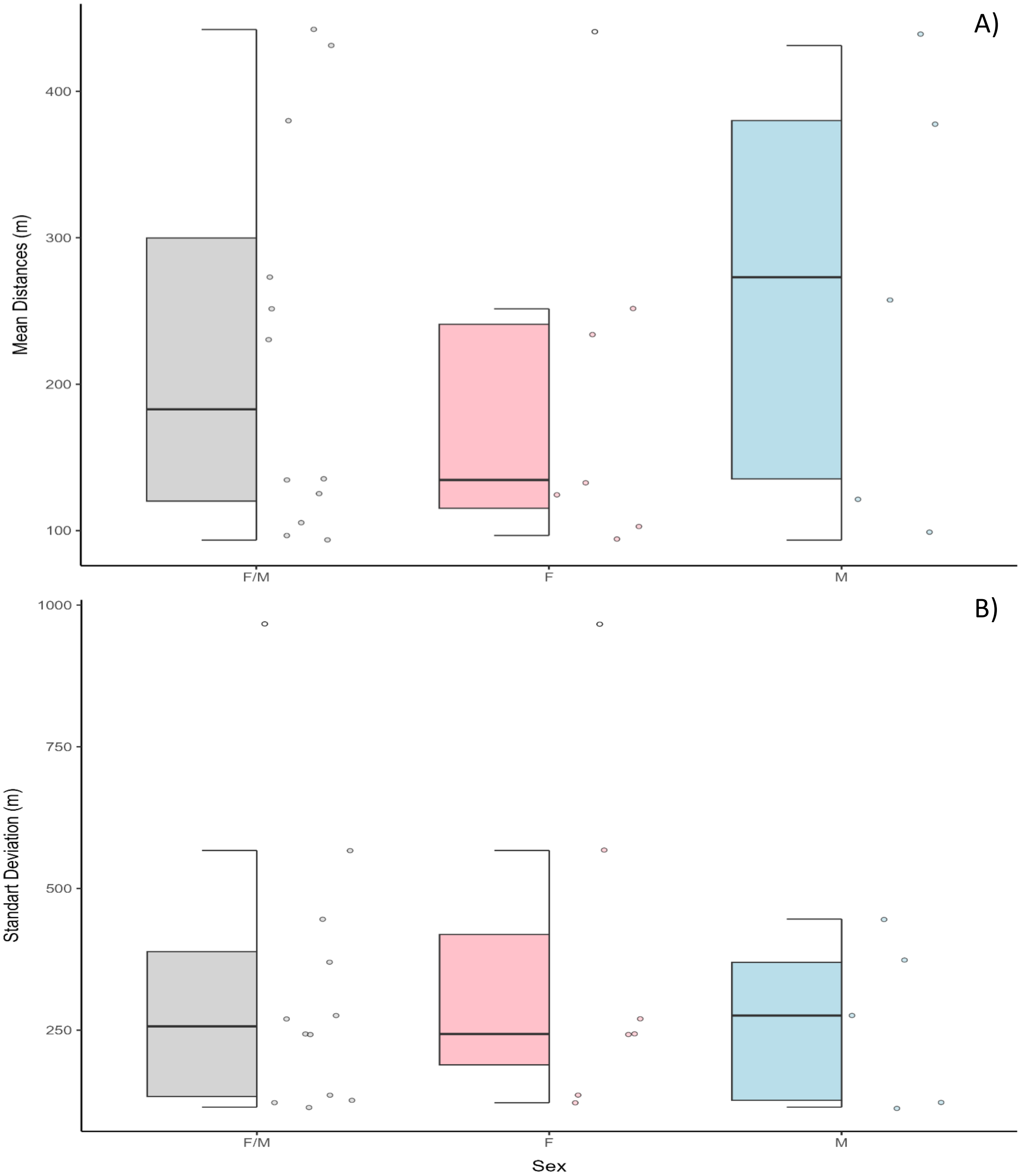

Figure 9. A) Differences between females and males in the nest (incubation and parental care phase) calculated by the mean distance of all GPS locations (MD). The graphic is represented in the left by a boxplot in the right by jittered points. The F/M represents all females and males together; F means female and M means male (n(F) = 7, n(M) = 5, N = 12). B) Standard deviation (SD) in the nest (incubation and parental care phase) of the mean distance of all GPS locations (MD).

At last, in the incubation phase, the females had a mean of 138.08 ± 97.76m and the males had a mean of 136.30 ± 69.41m (see Table 3). There were no significant differences between females and males (Mann-Whitney test: W = 104, *p* = 0.47). In the graphic representation it is visible that females have a larger range of MD compared to males, however, the mean of MD of females and males is only larger by 2m. The individual variation is also slighter bigger for females (Figure 8). In the parental care phase, females had a mean of 255.89 ± 155.28m, whereas males had 368.34 ± 210.73m (see Table 3). This phase also didn't have significant differences between females and males (Student's t-test: t = -1.07, *p* = 0.31). Compared to the incubation phase, the parental care phase had larger MDs on both females and males as it also proved by the graphic representation. The individual variation of females and males has a slighter larger range for males (Figure 10).

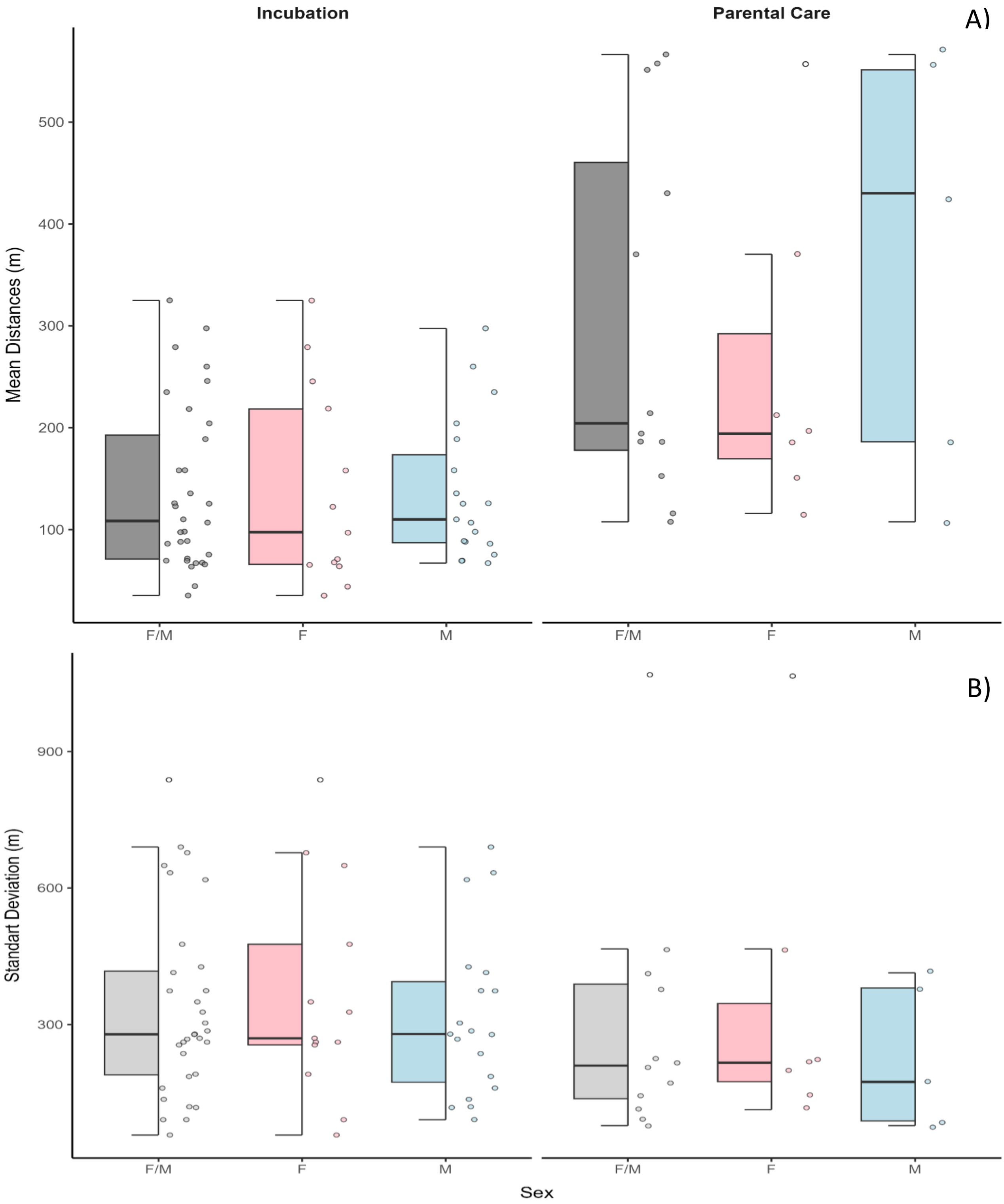

Figure 10. A) Differences between females and males in the incubation and parental care phase calculated by the mean distance of all GPS locations (MD). The graphic is represented in the left by a boxplot, in the right by jittered points. The F/M represents all females and males together; F means female and M means male (Incubation, n(F) = 13, n(M) = 19, N = 32; Parental care, n(F) = 7, n(M) = 5, N = 12). B) Standard deviation (SD) in the incubation and parental care phase of the mean distance of all GPS locations (MD).

Sex-based differences in daily nest attendance

Both females and males showed significant non-linear temporal patterns in nest attendance across the day (for females: edf = 8.65, *p* < 0.001; for males: edf = 8.40, *p* < 0.001), with higher probabilities of nest visitation during daytime compared to night-time for both sexes (see Table 4, Figure 9). Through the visual representation of the GAMM model, it is visible that females tend to have a probability of nest attendance higher than males during the day hours (7:00 – 21:00). In contrary to what happens at night, in which males seem to have a higher probability than females on being in the nest (Figure 9). The parametric effect of sex remained non-significant (*p* = 0.89), suggesting no overall linear difference between sexes when controlling for time and season dependent effects. There was also a significant seasonal effect (edf = 8.868, *p* < 0.001), indicating variation in nest attendance probability across the breeding season. The random effect of individual identity was highly significant (edf = 24.83, *p* < 0.001), highlighting substantial individual variability in nest attendance behaviour. The model explained 6.14% of the deviance. Diagnostic checks confirmed adequate smoothing (k-index ≈ 0.99), indicating sufficient spline complexity. The incubation model achieved an AUC of 0.66, indicating a moderate ability to distinguish nest attendance presence or absence (see Table 4).

Table 4. Summary of the GAMM model values regarding bird nest attendance during the incubation phase.

		Estimate standard deviation	**Z value**	**Edf**	**Qui square**	***p***	**Deviance explained**	**k-index**	**AUC**
Fixed effect	Intercept	- 0.43	-1.91	-	-	0.06	-	-	-
	Sex (F vs. M)	- 0.05	-0.14	-	-	0.89	-	-	-
Fixed effect (Splines)	Hour of day (F)	-	-	7.84	1774.7	< 0.001	-	-	-
	Hour of day (M)	-	-	7.13	676.5	< 0.001	-	-	-
	Julian day			8.87	149.2	< 0.001	-	-	-
Random effect	Bird ID	-	-	24.83	1343.4	< 0.001	-	-	-
Quality of adjustment	-	-	-		-	-	6.14%	-	-
Model diagnosis	-	-	-	-	-	-	-	> 0.9	-
Predictive capacity	-	-	-	-	-	-	-	-	0.66

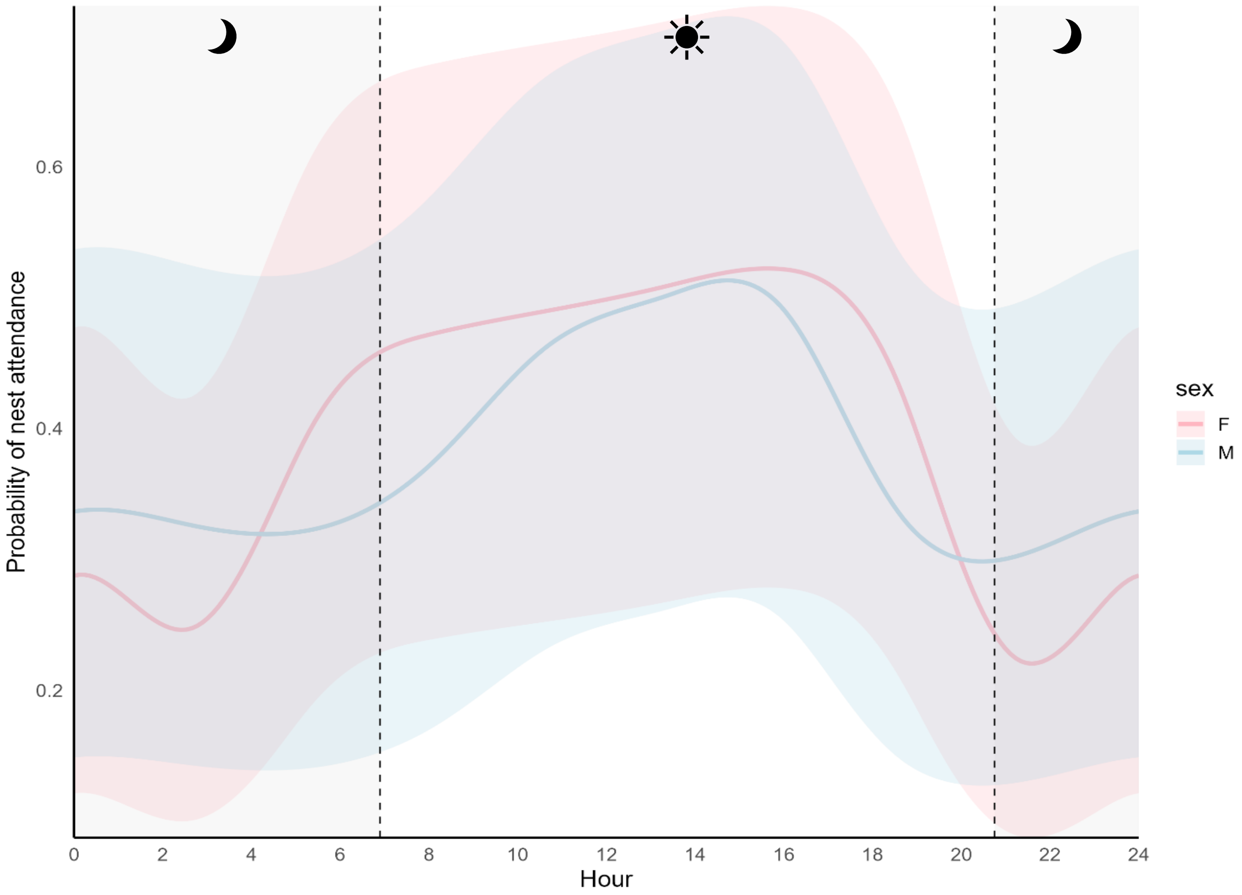

Figure 11. Sex-specific cyclic GAMM predictions of nest attendance across the 24-hour period during incubation (binomial family, logit link). Solid curves show fitted smooths of hour of day by sex and shaded bands are pointwise 95% confidence intervals. Vertical dashed lines mark the daytime boundaries used in the analysis, and light-grey rectangles indicate night-time (☽). Predictions are shown on the probability scale (back-transformed from the logit), representing population-level effects (individual random effect set to zero) with day of year held constant (n(F) = 16810, n(M) = 21597, n(nest) = 89, n(trackid) = 27, N = 38407).

Discussion

This study investigated whether sex-based differences occur in the spatial use and breeding behaviour of the Stone-curlew, a steppe bird species without sexual dimorphism. The results showed no significant differences between females and males across the three data subsets analysed for space use, nor in daily nest attendance throughout a 24-hour period. These findings agree with previous work with a similar sample size, which also examined day and night patterns, but based on direct observation of individuals. For example, Green et al. (2000) reported that both sexes share incubation duties with equally frequent changeovers. Although the sample size in this study was limited and not sufficient to fully represent space use and nest attendance at the population level, it provided unprecedented detail that was only possible when using movement data from GPS-tagged individuals, that are consistent with those of the previous study referred above.

The absence of sex-based differences in both space use and nest attendance suggests that females and males of Stone-curlews have similar roles during the incubation and chick rearing. This may be explained by habitat characteristics and predation pressure, as the species breeds in open grasslands that have high nest predation risk. Therefore, sharing duties probably enhances nest defence, increasing nestlings' survival rates (Caccamo et al., 2011; Tepavac, 2020). Another explanation is that both sexes are equally engaged in foraging and chick provisioning, as food resources may be scattered and require some effort to obtain. Thus, cooperation between pair members is needed to ensure appropriate feeding of both adults and offspring. Additionally, Stone-curlews exhibit diurnal and nocturnal activity patterns, which means that both sexes need to contribute to foraging and nest defence at different times of day, making shared responsibilities extremely important (Caccamo et al., 2011; Hawkes et al., 2021). This pattern was confirmed by the nest attendance results of this study, as females and males showed almost the same probability of attending the nest during both day and night. However, they were noticeably more absent from the nest at night. This behaviour may be explained by their nocturnal foraging habits, which lead them to spend more time away from the nest (Caccamo et al., 2011; Hawkes et al., 2021). This may be also related to the fact that the Stone-curlew is monomorphic, meaning that both females and males have similar ecological roles and physiological capacities. Such similarity may also explain the comparable sizes of home-ranges, core areas and centrality, reinforcing the evidence that both sexes select the same habitats and resources (Green et al., 2000).

While nest attendance has been addressed in some studies of steppe birds, sex-based differences in space use has received far less attention. Most available research on steppe birds during the breeding season focuses on species assemblages, habitat selection and community structure. These studies generally emphasize the influence of environmental factors, interspecific competition or habitat structure (Delgado & Moreira, 2000; Andryushchenko, 2022; Barrero et al., 2023; Oñate et al., 2023; Han et al., 2025) but rarely examine sex-specific area use. Even though no sex-based differences were detected, the results provide valuable insight into Stone-curlew space use during the breeding season. From a conservation perspective, this suggests that management measures do not need to be sex-specific but should instead focus on the spatial requirements of the species as a whole. Regarding nest centrality, this study also found no significant difference between females and males in distance to the nest during incubation and parental care phases. However, males appeared to move slightly further away during parental care. This behaviour is not well documented in the literature, where it is more commonly reported that male parental involvement increases after hatching, particularly in feeding and brooding (Evens et al., 2024). One possible explanation for the present finding is that males may range further to access higher-quality feeding grounds, whereas females remain closer to the nest and offspring, perhaps prioritizing nest and chick protection. This remains speculative, and further research is needed to clarify these patterns. More detailed tracking, ideally complemented by camera trapping, could help disentangle whether these differences are related to chick behaviour or parental roles. Although some researchers suggest that Stone-curlew chicks may leave the nest area soon after hatching, evidence is limited. The only previous study addressing this, Green et al. (2000), reported that chicks rarely moved more than 100 m from the nest and most activity occurred within 1 km of either the nest or chick locations. Data from the present study are consistent with these findings. Nest centrality was lower in parental care than during incubation, while the BBMM remained within a similar size range in both phases. This suggests that chicks might move with the parents in the parental care phase.

Interestingly, this monomorphic steppe bird exhibits behaviours that differ markedly from other sympatric steppe species. Unlike the Stone-curlew, the Little Bustard *Tetrax tetrax* exhibits clear sexual dimorphism. This results in females and males selecting different microhabitats during the breeding season, as females prefer sites with more cover and vegetation for better nest concealment and predator avoidance and males prefer open areas with short vegetation that maximize visibility for courtship displays (Silva et al., 2017). This clear difference in habitat use translates into very clear nest attendance patterns by both sexes. Females are associated to nest sites, while males occupy display territories distant from nesting females (Morales et al., 2008). A similar pattern is seen in the Great Bustard *Otis tarda* that is highly sexually dimorphic, with males much larger than females. During the breeding season, males and females use space differently. Males gather at *leks* to perform courtship displays and compete for mates, leaving these sites soon after mating (Alonso et al., 2000; Morales et al., 2000). Contrary to females that remain in the breeding sites to incubate the eggs and tend to the chicks, showing exclusive maternal care (Cramp & Simmons 1980; Martín, 2001). The pin-tailed sandgrouse *Pterocles alchata* and the black-bellied sandgrouse *Pterocles orientalis* are also ground-nesting steppe birds (del Hoyo et al., 1997; De Juana, 1997). However, in these species, incubation is clearly divided: females attend the nest during the day, while males typically incubate from dusk until mid-morning (De Juana, 1997). In contrast, Stone-curlews show no such temporal partitioning, as both sexes incubate during day and night. The only subtle difference observed is that males tend to incubate more frequently at night, while females incubate more during the day. The model used to describe these patterns explained 6.14% of the deviance, which is common in behavioural studies due to inherently large individual and temporal variability. Nevertheless, incorporating additional variables such as temperature, vegetation structure and food availability, together with accelerometer data, could help refine behavioural interpretations and refine model accuracy.

Although this study contributes to filling gaps about the Stone-curlew breeding behaviour, it also has some limitations. As mentioned above, the sample size was small and may not fully represent the species' breeding behaviour at population level. Even so, considering the logistics it evolves to tag and track wild birds, the study sample is not so small as it requires a great amount of time and resources. Thus, as this is a bird tracking study, this number is not so small, although ideally having a larger sample size is preferred (Lindberg & Walker, 2007; Soanes et al., 2013; Soanes et al., 2014). Moreover, information on both sexes from the same nest was lacking. Collecting such data would allow assessment of pair-level behaviour rather than examining females and males separately. Further studies should increase the sample size and ensure data collection from breeding pairs of the same nest for a better understanding of the sex-specific breeding behaviour. This would also allow to study the space overlap between pair members, who may have home-ranges and core areas of similar size, but exploit different sectors around the nest. This distinction is important because different areas around the nest may vary in resource availability and threats. Finally, future research should not only consider space use but also habitat use to better understand the characteristics of the breeding habitat.

Overall, understanding how Stone-curlews use space during breeding and how far they range from their nests provides essential insights for conservation. Such information contributes to broader knowledge of steppe bird ecology and can inform general habitat management strategies to support ground-nesting species (Moreno et al., 2010; Sanz-Pérez et al., 2019; Sanz-Pérez et al., 2021; Revilla-Martín et al., 2023). Ground-nesting birds are also highly vulnerable to predation, particularly during incubation and chick-rearing and maintaining open steppe vegetation can reduce predation risk and facilitate parental nest attendance (Hofer et al., 2025). Furthermore, the ongoing conversion of steppe land to agriculture and intensive grazing reduces nest site availability and may disrupt parental behaviour, ultimately lowering breeding success (Posadas-Leal et al., 2010; Han et al., 2025). Safeguarding breeding habitats and promoting land-use practices that sustain suitable steppe conditions will therefore be crucial to ensure reproductive success and the long-term persistence of the species.

Conclusion

This study provides new insights into the ecology of a cryptic and elusive steppe bird, that so far this information has been scarce. While our results suggest no sex-based differences in spatial use or nest attendance, further research with larger sample sizes, extended multi-year tracking, and broader environmental contexts is necessary to confirm these patterns. Ultimately, advancing this knowledge will not only clarify sex-specific strategies but also strengthen conservation planning for the Stone-curlew and other steppe-specialists birds.

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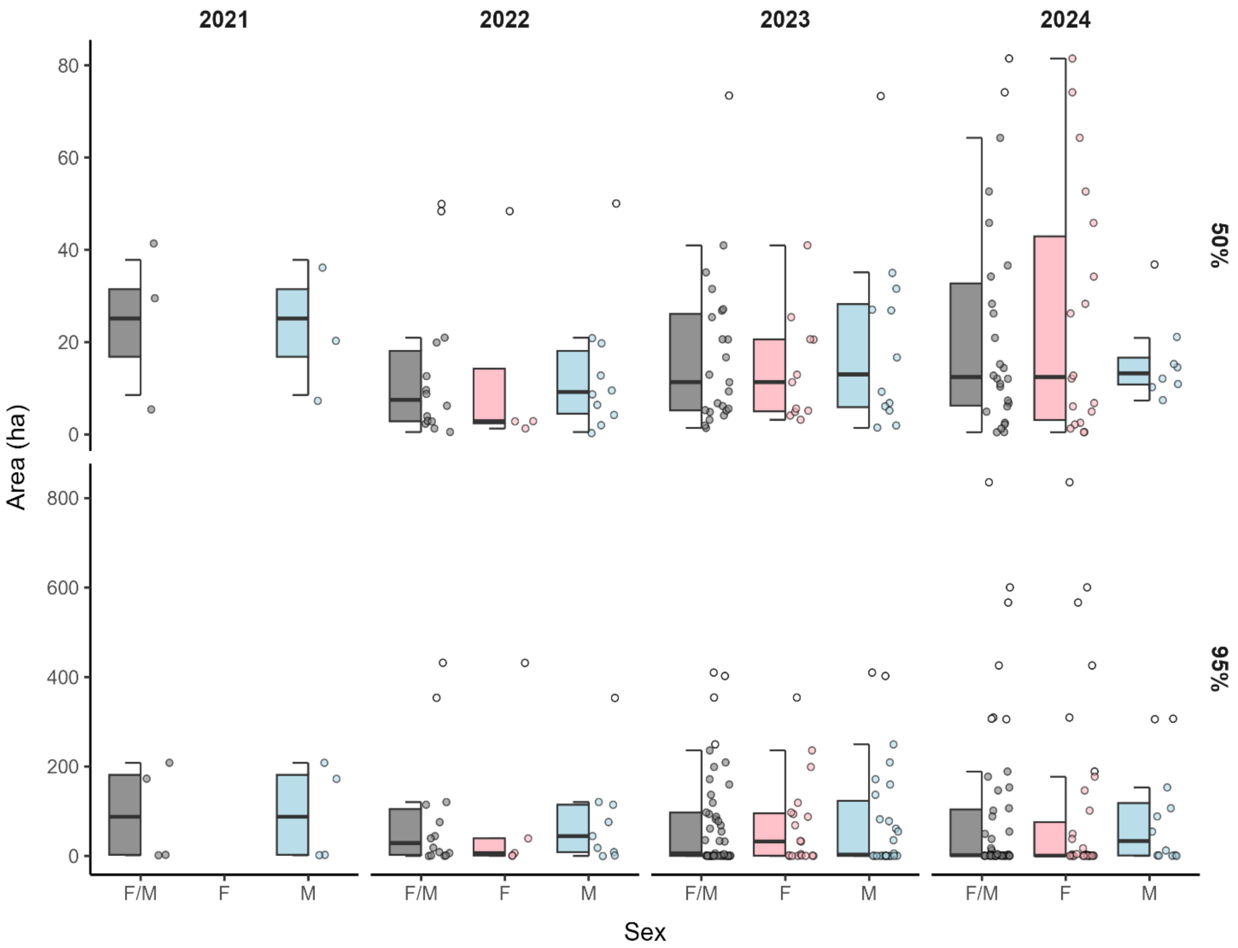
Annex

Annex 1. Outliers excluded from the graphic of the breeding season of mean distances of all GPS locations (MD).

Nest id	Year	Mean distance (m)	Standard deviation	Sex
N3_jesus	2024	92848.60	292.82	F
N2_roberto	2023	3652.86	1479.94	M
N1_gonzalo	2023	738.38	1169.10	F
N2_teresa	2024	480.19	886.52	F

Annex 2. Differences in the core area (50%, upper panel) and home-range range area (95%, lower panel) between females and males during the breeding season area (2021 – 2024) calculated by the Brownian Bridge Movement Model (BBMM). The graphic is represented in the left by a boxplot, in the right by jittered points. The black bar represents the median. The F/M represents all females and males together; F means female and M means male (50%: n(F) = 33, n(M) = 33, N = 66; 95%: n(F) = 59, n(M) = 51, N = 110).



Annex 3. Differences between females and males in the breeding season calculated by the mean distance of all GPS locations (MD). The graphic is represented in the left by a boxplot, in the right by jittered points. The black bar represents the median. The F/M represents all females and males together; F means female and M means male (n(F) = 41, n(M) = 50, N = 91).