

Lesser kestrels of the same colony do not overwinter together

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Abstract

Migratory connectivity describes the linkage between breeding and nonbreeding sites, having major ecological implications in birds: 1 season influence the success of an individual or a population in the following season. Most studies on migratory connectivity have used large-scale approaches, often considering regional populations, but fine-scale studies are also necessary to understand colony connectivity. The lesser kestrel *Falco naumanni*, an insectivorous migratory raptor which form colonies during the breeding period, was considered to have strong connectivity based on regional populations. However, no small-scale studies on migratory connectivity have been conducted. Therefore, we GPS (Global Positioning System)-tracked 40 adult lesser kestrels from 15 different Spanish breeding colonies, estimating the overlap index between home ranges and the distance between their centroids. It was found that lesser kestrels from the same breeding colony placed their nonbreeding areas at 347 ± 281 km (mean \pm standard deviation) away from each other (range = 23–990), and their home ranges overlapped by $38.4 \pm 23.6\%$. No differences between intra-colony and inter-colony metrics were found, which suggests that lesser kestrels from the same breeding cluster do not overwinter together, but they spread out and mixed independently of the colony belonging throughout the nonbreeding range of the species. Ultimately, this study highlights the importance of performing connectivity studies using fine-scale approaches.

Key words: *Falco naumanni*, GPS telemetry, migratory connectivity, nonbreeding, raptor, spatial ecology, wintering.

Migratory birds divide the annual cycle between 2 areas separated by hundreds or thousands of kilometers (breeding and nonbreeding grounds), usually under different environmental conditions and selective pressures, with respect to food distribution and abundance, rearing constraints, competition, etc. (Urios et al. 2017; López-López et al. 2021; Urios and García-Macía 2022). The movements of migratory birds are determined by a complex set of environmental drivers which often differs between breeding and nonbreeding areas. This entails several ecological implications regarding foraging habits, aggregation patterns, home range sizes, etc.

In this context, migratory connectivity is defined as the degree of linkage between breeding and nonbreeding sites via the trajectories of individual migrants (Webster et al. 2002; Boulet and Norris 2006; Bauer et al. 2016). On the one hand, “low connectivity” occurs when individuals from the same breeding population are widely spread throughout the nonbreeding range of the species, mixing with individuals from other breeding populations (Webster et al. 2002; Dias et al. 2012). On the other hand, “strong connectivity” occurs when most individuals from 1 breeding population migrate to the same nonbreeding ground (Webster et al. 2002; Guilherme et al. 2022). Migratory connectivity follows a continuum, so populations usually lie between those 2 ends. Therefore, both

“low” and “strong” connectivity have been reported in several taxa, including raptors and Passeriformes (Lemke et al. 2013; Finch et al. 2017). Advances in the last decades in remote tracking, analysis of molecular genetic markers, and chemical isotopes have offered new insights in the study of migratory connectivity.

Connectivity patterns have ecological and evolutionary consequences in birds. Populations with low connectivity may contain more variation for migratory behavior (i.e., timing and direction). Furthermore, birds widely spreading throughout the nonbreeding range must face different selective pressures due to the variety of winter locations. On the other hand, populations with strong connectivity will face similar selective pressures and may contain less behavioral variation, leading populations to acquire more local and specific adaptations. Ultimately, on an evolutionary scale, connectivity patterns could lead to speciation processes (Webster et al. 2002). Although low connectivity may facilitate rapid range shifts in response to climate change, populations with wide spreading may not find optimal wintering habitats (Finch et al. 2017). Studying connectivity patterns is fundamental to understanding population dynamics and providing good management keys to species conservation. Processes in 1 season influence the success of an individual in the following season, that is,

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seasonal carry-over effects may affect population dynamics (Harrison et al. 2010). For example, winter survival may determine breeding densities and reproductive success, and winter survival is influenced, in part, by events that occurred in the previous breeding season (Fretwell 1972).

The scale approach may be important in migratory connectivity studies because it may lead to different results. Most studies on migratory connectivity have used large-scale approaches (Finch et al., 2017; Sarà et al. 2019; Studds et al. 2021; Guilherme et al. 2022), often considering regional populations as sample unit. However, fine-scale approaches using colonies are also necessary (Finch et al. 2017; Bracey et al. 2018). For example, it has been reported that the lesser kestrel *Falco naumanni*, an insectivorous raptor widely distributed among the Palearctic, shows a strong migratory connectivity: Iberian birds migrate to western Sahel, Balkan birds chiefly to central-eastern Sahel, and Italian ones to eastern Sahel (Sarà et al. 2019). This was expected because this species forms colonies and individuals highly aggregate during the breeding season, even respecting the boundaries of the neighboring colonies (Di Maggio et al. 2013; Cecere et al. 2018). However, this large-scale approach may not respond to several questions: no flocking behavior has been reported in the species during post-breeding migration and the composition of communal roosts in the Sahel are larger (often hundreds of individuals; BirdLife International 2023) than breeding colonies in Europe (often a few tens; Bustamante et al. 2020). Therefore, communal roosts are probably the result of mixed aggregations between individuals from different colonies. Fine-scale approaches are necessary to study the destinations and nonbreeding areas of colony members and the selective pressures they face, which may ultimately lead to a better understanding of the population dynamics of the colonies, differences in the number of individuals returning to their colonies, or the reproductive success of the colonies in the following season.

We GPS-tracked 40 adult lesser kestrels from 15 Spanish breeding colonies in order to study the migratory connectivity and aggregation patterns of individuals from the same breeding colony during the nonbreeding period in West Africa. The main objective of this study was to analyze the migratory connectivity of the lesser kestrels, a long-distance migrant raptor, using a colony-scale approach. To do this, we explored differences between colonies in phenology metrics and home range sizes and estimated the intra- and inter-colony overlap index and distances. Based on previous large-scale studies (Sarà et al. 2019), it was expected high connectivity in the species, but we hypothesize that this connectivity will change on a smaller scale.

Materials and Methods

Study species

The lesser kestrel (*Falco naumanni* Fleischer, 1818; Falconidae) is a small migratory raptor with a large geographical range in Eurasia and Africa. Their breeding populations extend from Central Asia to the Mediterranean region (Bijleveld 1974; Cramp and Simmons 1980; Ortego 2016; GBIF 2022). Individuals from the Eastern Palearctic usually use a longer eastern migratory route to spend the winter in East and South Africa (Ferguson-Lees and Christie 2001), while birds from the Western Palearctic follow a shorter western migratory route across the Mediterranean Sea (Sarà et

al. 2019), to reach their nonbreeding grounds in sub-Saharan Africa. The lesser kestrel is essentially insectivorous and sometimes feeds on small mammals and reptiles (Rodríguez et al. 2006, Rodríguez et al. 2010). This species prefers open areas like steppes (Atienza and Tella 2004), but it is also linked to urban environments and human constructions, where they often nest (Ortego 2016). It is a gregarious bird that usually forms colonies of dozens of pairs during the breeding season (Bustamante et al. 2021).

Globally, the lesser kestrel is considered as “Least Concern” because their entire population is currently “stable,” with 80,000–134,000 mature individuals (IUCN 2021). However, it has been considered “vulnerable” in Spain since the 1990s (Bustamante et al. 2021). In this country, around 10,000 breeding pairs have been estimated, distributed throughout more than 2,000 colonies and isolated breeding areas (Arroyo and García 2007, Bustamante et al. 2020).

Tagging and sample size

Forty adult lesser kestrels (21 females and 19 males) tagged at 15 different colonies in Spain provided data on nonbreeding movements after returning to their breeding colony (Table 1 and Figure 1). We obtained data for 55 nonbreeding seasons between 2016 and 2021 (Supplementary Table S1).

The 15 colonies included 2.7 ± 1.4 individuals tagged on average (range = 1–5): Pinto (5), Perales del Río (4), T0rrejón de Velasco (4), Navalcarnero (4), Villalpando (4), Palma del Condado (4), Doñana National Park (3), Baena (2), Castelló de Empuries (2), Tarancón (2), Villares del Saz (2), La Almarcha (1), Can Viure (1), Fraga (1), and Arganda del Rey (1).

Lesser kestrels were captured at the breeding colony, usually during courtship while roosting near the nest. After capture, individuals were ringed, weighed (mean = 146 g; $n = 40$), and measured. The sex was determined by morphological characteristics, given the sexual dimorphism of the species (Cade and Digby 1982). A GPS-biologger transmitter was attached to the back of each individual by a back-pack harness tied with Teflon ribbon, designed to allow its release after a few years of monitoring. All the transmitters were Nano-GPS from PathTrack (Leeds, UK) model NanoFix GEO+RF (weigh = ~ 4g, less than 5% of birds' weight), thus complying with the recommended standard (Kenward 2001).

Biologgers provided GPS fixes every 15 min to 1 h from dawn to dusk during the nonbreeding season and downloaded data to a base located at the breeding colony. Some biologgers provided locations 24 h a day from February to October, but night locations were excluded. Only kestrels that migrated back to the breeding colony provided data on nonbreeding movements. Locations were filtered at a homogeneous 1-h frequency to avoid bias in subsequent calculations, allowing deviations up to 20 min. Locations were transformed to UTM (Universal Transverse Mercator) coordinates.

Analysis of movement-related variables

We determined arrival to and departure from the nonbreeding grounds based on marked shifts in daily distances and interruptions in migration latitudinal displacements (Lopez-Ricaurte et al. 2021). Therefore, arrival to the nonbreeding ground was established when the individual abruptly stopped the latitudinal displacement and reduced daily traveled distances, and vice versa.

Table 1 Metadata of the 40 lesser kestrels tagged with Solar GPS biologgers. Sex, age, colony (province), and beginning/end of tracking of each individual are shown

ID	Age	Sex	Colony (Spanish province)	Beginning of tracking	End of tracking
16639	Adult	Male	Baena (Córdoba)	2017	2018
16643	Adult	Female	Baena (Córdoba)	2017	2019
16687	Adult	Female	Castelló de Empuries (Gerona)	2017	2018
16688	Adult	Male	Castelló de Empuries (Gerona)	2017	2019
17281	Adult	Female	Tarancón (Cuenca)	2018	2019
17292	Adult	Female	Tarancón (Cuenca)	2018	2019
17240	Adult	Male	Villares del Saz (Cuenca)	2018	2019
17245	Adult	Female	Villares del Saz (Cuenca)	2018	2019
17288	Adult	Female	La Almarcha (Cuenca)	2017	2019
16690	Adult	Male	Can Viure (Barcelona)	2017	2019
16611	Adult	Male	Fraga (Huesca)	2016	2019
17235	Adult	Male	Arganda del Rey (Madrid)	2018	2019
16127	Adult	Male	Perales del Río (Madrid)	2017	2019
16137	Adult	Male	Perales del Río (Madrid)	2017	2020
17256	Adult	Female	Perales del Río (Madrid)	2018	2019
17261	Adult	Male	Perales del Río (Madrid)	2018	2019
16275	Adult	Female	Pinto (Madrid)	2017	2018
16212	Adult	Male	Pinto (Madrid)	2016	2017
17239	Adult	Female	Pinto (Madrid)	2018	2019
17237	Adult	Male	Pinto (Madrid)	2018	2020
17241	Adult	Female	Pinto (Madrid)	2019	2020
17250	Adult	Male	Torrejón de Velasco (Madrid)	2018	2020
17251	Adult	Male	Torrejón de Velasco (Madrid)	2018	2019
17253	Adult	Male	Torrejón de Velasco (Madrid)	2018	2019
17254	Adult	Male	Torrejón de Velasco (Madrid)	2018	2020
17278	Adult	Female	Navalcarnero (Madrid)	2018	2020
17280	Adult	Female	Navalcarnero (Madrid)	2018	2019
17282	Adult	Female	Navalcarnero (Madrid)	2018	2019
17262	Adult	Female	Navalcarnero (Madrid)	2018	2019
16679	Adult	Female	Villalpando (Zamora)	2017	2019
16661	Adult	Female	Villalpando (Zamora)	2017	2018
16584	Adult	Female	Villalpando (Zamora)	2017	2018
16616	Adult	Female	Villalpando (Zamora)	2017	2017
17195	Adult	Male	Espacio Natural de Doñana (Sevilla)	2018	2019
17199	Adult	Female	Espacio Natural de Doñana (Sevilla)	2018	2019
17218	Adult	Male	Espacio Natural de Doñana (Sevilla)	2018	2019
17210	Adult	Male	Silo de la Palma del Condado (Huelva)	2018	2019
17214	Adult	Female	Silo de la Palma del Condado (Huelva)	2018	2019
17215	Adult	Female	Silo de la Palma del Condado (Huelva)	2018	2019
17219	Adult	Male	Silo de la Palma del Condado (Huelva)	2018	2019

We estimated home ranges (95% Kernel Density Estimator, KDE) and core areas (50% KDE) using all GPS fixes of each individual and year using *adeHabitat* R library (Calenge 2006). We used the *ad hoc* method to estimate the smoothing parameter (Schuler et al. 2014). The centroids of 95% KDE were estimated using QGIS 3.16.6.

In order to explore the influence of sex and colony in the movement metrics, a series of generalized linear mixed models were performed using the *lme4* package in R (Bates et al. 2015). Onset and end of nonbreeding period (day of the year), home ranges (95% KDE) and core areas (50% KDE)

were fitted as response variables, while the sex (male/female) and the breeding colony identification were fitted as explanatory variables. All models were run including individual identification as a random effect. AIC model selections were also performed to determine the distribution of the response variables (Gamma, Poisson, or Gaussian). Gamma distributions were selected for home ranges and core areas, while Gaussian distributions were selected for the onset and end of the nonbreeding period. To evaluate the significance in linear mixed effects, ANOVA tests with Kenward-Roger approximations were performed.

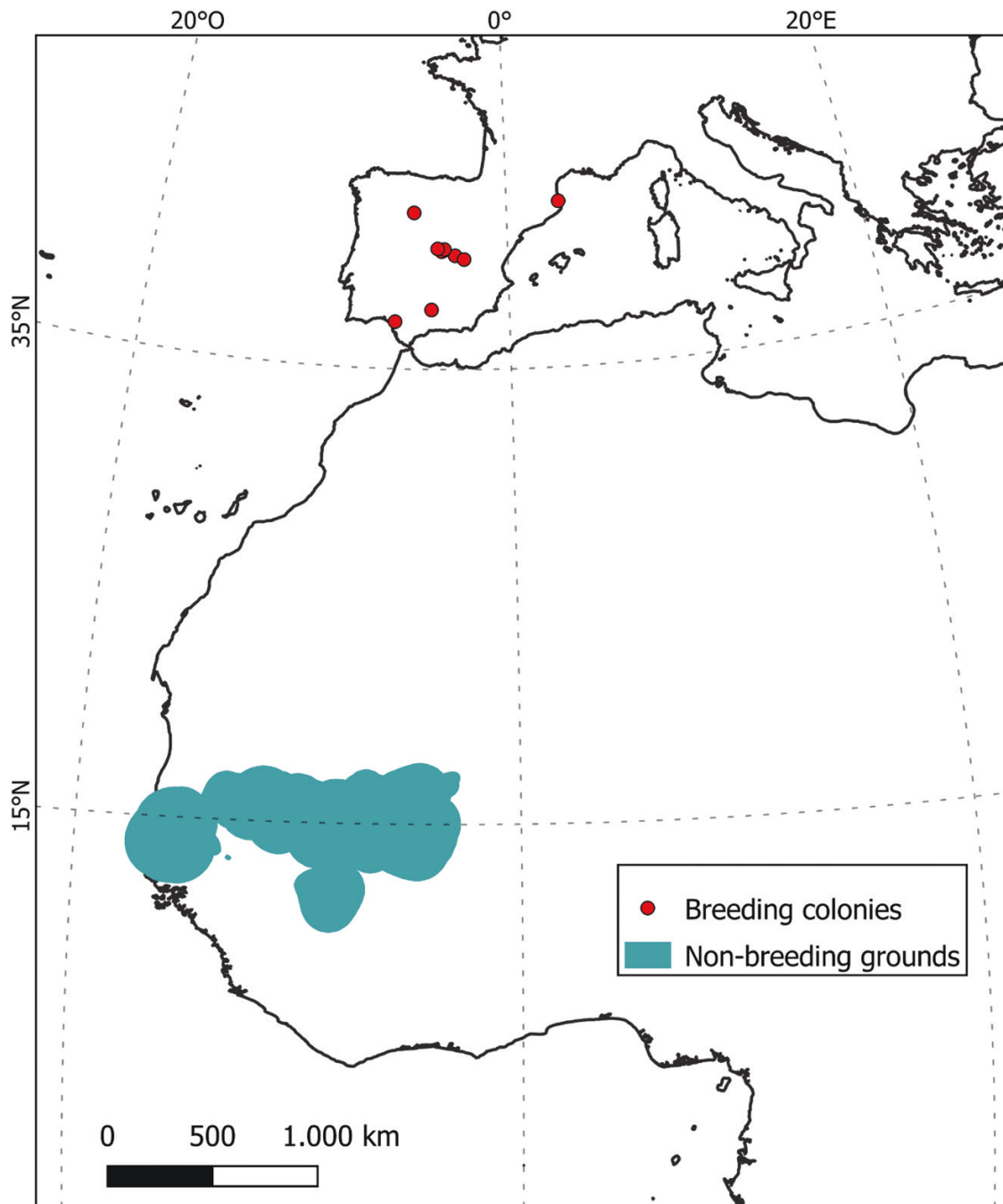


Figure 1 Location of breeding colonies and nonbreeding range in the western Sahel of the 40 lesser kestrels tracked in this study.

Migratory connectivity of the colonies

Two metrics were used to explore the segregation of lesser kestrels throughout their nonbreeding range: home ranges overlaps and distances between home ranges centroids.

Home ranges overlaps were calculated using the function “kerneloverlap” from *adehabitatHR* R library (Fieberg and Kochanny 2005), resulting in a matrix of pairwise comparisons which included the proportion of animal *i*'s home range that is overlapped by animal *j*'s home range (Kernhoan et al. 2001). Overlap values range from 0 (no overlap) to 1 (complete overlap). We calculated the “intra-colony” overlap as the overlap between the home ranges (KDE 95%) of individuals from the same breeding colony during the same year, and the inter-colony overlap as the overlap between home ranges

of individuals from different colonies during the same year ($n =$ Supplementary Table S3). We only used 95% KDE to calculate overlap because 50% KDEs were too small to overlap between them in many cases. In addition, when data for at least 2 complete years were available for the same individual ($n = 9$), we calculated the repeatability of nonbreeding areas as the year-to-year overlap following the previous method.

Distances between home ranges were estimated as the Euclidian distance between their centroids. Similarly to the previous metric, we estimated intra-colony distance (distances between centroids of the home ranges of individuals from the same breeding colony) and inter-colony distance (those of individuals from different breeding colonies). In order to explore the differences between intra-colony

and inter-colony metrics, 2 linear mixed models (LMMs) were performed, testing the normality of their residuals. Overlap (0–1) and distances between centroids were fitted as response variables, while colony relation (intra-colony/inter-colony) was fitted as an explanatory variable. All models were run including colony identification as a random effect.

All statistical analyses were performed with R Software v. 4.0.5. The significance level was established at < 0.05 .

Results

Phenology and home range sizes

The 40 lesser kestrels spent the nonbreeding period in a longitudinal strip of about 1,600 km within the western Sahel (Figure 1). On average, the nonbreeding period lasted 147 ± 27 days, from the last week of August to the last week of January, on average (Table 2 and Supplementary Table S1). The average nonbreeding season range of an individual (95% KDE) was $143,697 \pm 98,048$ km² (range = 5,001–445,393), while the core areas (50% KDE) averaged $29,414 \pm 20,572$ km² (range = 750–96,323; Table 2 and Supplementary Table S1).

No differences between sexes were found in the onset dates (ANOVA P -value = 0.67), end dates ($P = 0.63$), home ranges ($P = 0.22$), or core areas ($P = 0.19$). Likewise, no differences between colonies were found in the onset dates ($P = 0.19$), end dates ($P = 0.31$), home ranges ($P = 0.60$), or core areas ($P = 0.54$).

All but 1 individual (8 out of 9) repeated their nonbreeding areas (95% KDE) in consecutive years (Supplementary Table S3 and Supplementary Figure S1). The year-to-year overlap of those nonbreeding areas was 49 ± 27 % (range = 33–87). Only 1 individual (17,253) shifted completely its nonbreeding area, resulting in zero overlap.

Migratory connectivity of the colonies

Intra-colony home ranges (95% KDE) overlap index averaged 38.8 ± 21.4 % (range = 0–69; Figures 2 and 3 and Supplementary Table S2), while inter-colony overlap index was 35.5 ± 12.5 % (range = 14–50; Figure 3 and Supplementary Table S3). The distance between the centroids of home ranges (95% KDE) of individuals from the same breeding colony averaged 347 ± 281 km (range = 23–990), while those of individuals from different colonies averaged 335 ± 262 km (range = 16–1,067; Figure 3). Differences

between intra-colony and inter-colony metrics were not found (Table 3).

Discussion

This study supports that there is no small-scale migratory connectivity in the lesser kestrels breeding in Spain, according to home range overlaps and distances between them. On the contrary, it is suggested that individuals from the same breeding colony disaggregate during the wintering season in western Africa and communal roosts are composed by birds from different breeding clusters.

Sex and colony belonging did not influence nonbreeding phenology and home range sizes. Lesser kestrels usually showed itinerant behavior during the nonbreeding season and occupied large areas irrespectively of sex and the breeding colony of origin. Indeed, the lesser kestrels occupied larger areas during the nonbreeding period than other raptors in the Sahel and other sub-Saharan regions, such as the lesser spotted eagles (*Aquila pomarina*; Meyburg et al. 2015), the Montagu's harrier (*Circus pygargus*; Limiñana et al. 2012b), the Egyptian vulture (*Neophron percnopterus*; García-Ripollés et al. 2010), and the booted eagle (*Aquila pennata*; Urios et al. 2017). Lesser kestrels usually move along the longitudinal Sahelian strip and occupy several smaller areas (López-Ricaurte et al. 2022), probably motivated by the insectivorous diet of the species and the deteriorating ecological conditions in the Sahel during late winter (Trierweiler et al. 2013): lower food abundances require more intense foraging activity, flight effort and displacements between areas (Schlaich et al. 2016; García-Macía et al. 2022). In fact, grasshopper density was shown to influence the distribution of the lesser kestrel and other insectivorous species in the western Sahel (Augiron et al. 2015). Therefore, the abundance of insects may be the key to understanding the itinerant movements of insectivorous raptors in the Sahel and the large areas occupied by these species. Ultimately, this itinerant behavior and the large areas occupied by the species may also affect migratory connectivity (Fraser et al. 2017).

Our results suggest that there is no small-scale migratory connectivity in the lesser kestrel. The estimated intra-colony overlap and distances were not significantly higher than inter-colony metrics, which suggests that lesser kestrels aggregate irrespectively of colony belonging and share space and resources. Low connectivity has been widely reported in long-distance migrant birds (Finch et al. 2017), including

Table 2 Phenology and movement-related variables during nonbreeding season: onset and end of nonbreeding season, duration, home ranges (95% Kernel Density Estimator, KDE), and core areas (50% KDE). Values are shown as "mean \pm SD (minimum–maximum)," calculated by using mean values of each nonbreeding season. Specific values are shown in Supplementary Table S1

	Onset of nonbreeding period	End of nonbreeding period	Duration of nonbreeding period (days)	Home range (95% KDE, km ²)	Core areas (50% KDE, km ²)
Overall ($n = 55$)	29/08	24/01	147 ± 27	$143,697 \pm 98,048$ (5,001–445,393)	$29,414 \pm 20,572$ (750–96,323)
Male ($n = 30$)	09/09	02/02	146 ± 25	$145,253 \pm 87,939$ (5,001–279,949)	$30,020 \pm 18,709$ (750–58,163)
Female ($n = 25$)	16/08	12/01	149 ± 30	$141,829 \pm 110,811$ (12,770–445,393)	$28,687 \pm 22,983$ (2,764–96,323)

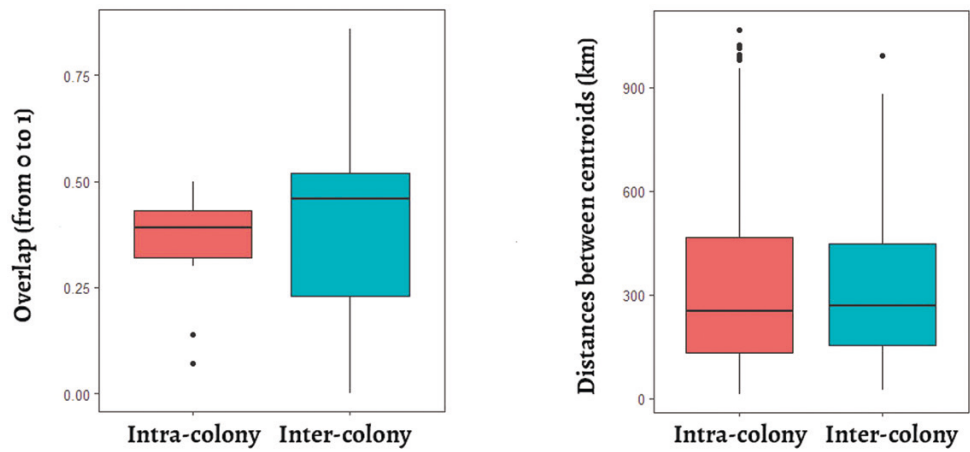


Figure 2 Differences in home range overlaps and distances between their centroids between intra-colony and inter-colony.

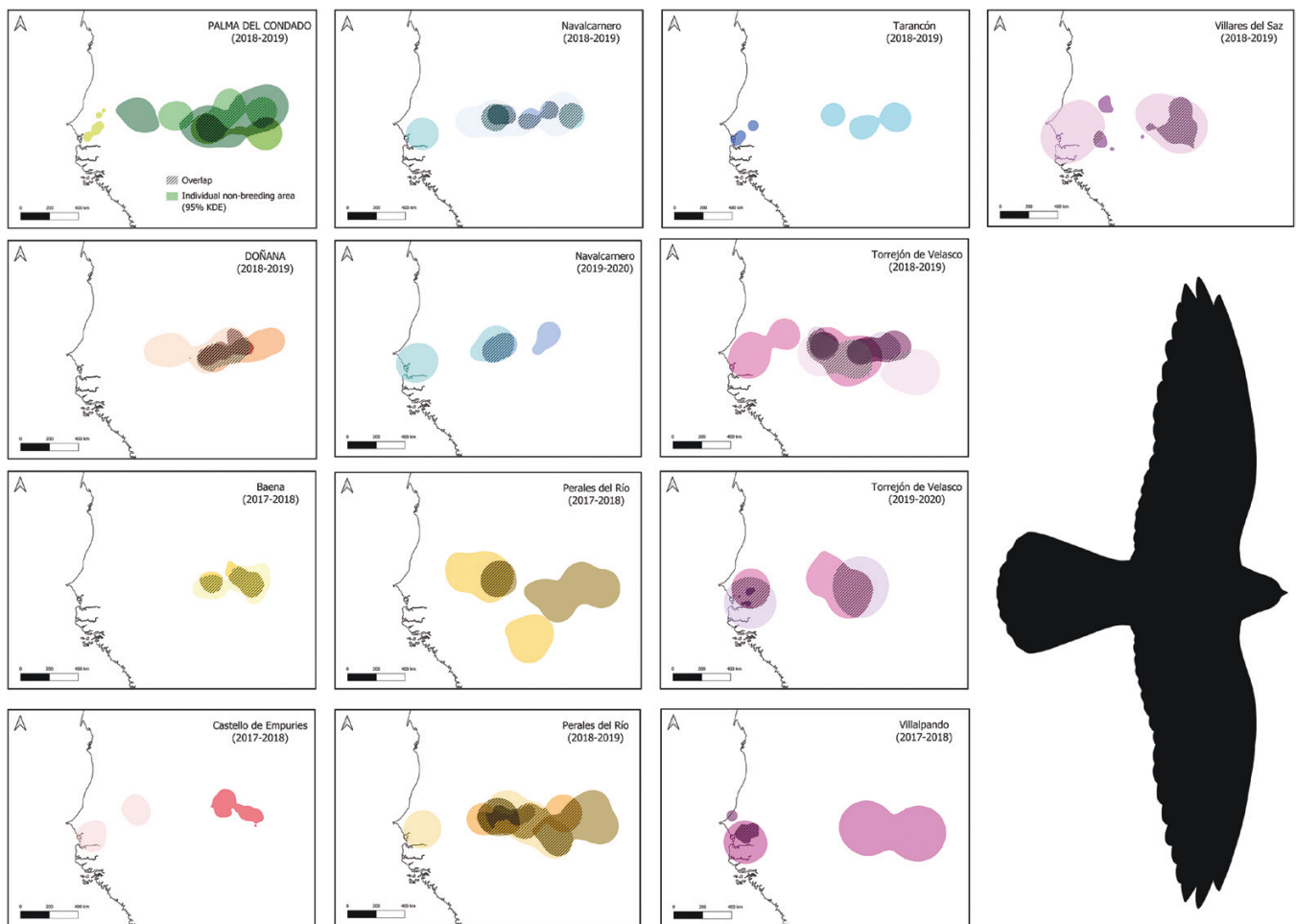


Figure 3 Overlap of nonbreeding areas of individuals from the same breeding colony. Each panel represents the overlapping of the members of the colony during a single nonbreeding period. Each individual nonbreeding area is represented in a different color.

Table 3. LMMs coefficients for explanatory variable (colonial relation) used to explain home ranges overlap and distances between them for the 40 lesser kestrels wintering in western Sahel. SE = Standard error; P = P-value. Significant values are highlighted in bold

Variable	Home ranges overlap (0-1)				Distances between centroids (km)			
	Estimate	SE	Degrees of freedom	P	Estimate	SE	Degrees of freedom	P
(Intercept)	0.351	0.055	15.64	<0.001	366.10	61.02	15.42	<0.001
Intra-colony	0.029	0.064	13.48	0.66	63.00	68.82	0.92	0.48

other insectivorous birds that overwinter in the Sahel, such as the Montagu's harrier (Limiñana et al. 2012a).

However, Sarà et al. (2019) reported strong connectivity for lesser kestrels, but using a population-scale approach. Therefore, the species may show strong connectivity at large scales, but not at a small one. Probably, belonging to the same breeding cluster does not affect the behavior out of the breeding season and large-scale connectivity results from the efficiency of the migratory routes selected by the different regional populations. Low connectivity was expected in the colonies because the ecological and reproductive constraints during the nonbreeding period are very different from those during the breeding season (Urios and García-Macía 2022). Without being tied to a nest and a colony, lesser kestrels are able to optimize landscape exploration and forage independently of their breeding partners. Thus, the itinerant behavior of the species during the nonbreeding season, triggered by the deteriorating environmental conditions, may be the most efficient strategy during this period, when individuals prioritize the search for the best foraging areas and are mixed with other individuals irrespective of colony belonging.

The high spreading degree in the Sahel might also respond to habitat loss and fragmentation, forcing individuals to separate their foraging areas to avoid competition (Curtis 2005). Further studies should explore how the changing environmental conditions in the Sahel affect the selection of nonbreeding areas by the species. In the case of the lesser kestrel, despite its itinerant behavior, its fidelity to the same nonbreeding areas may have negative implications on its foraging activity.

In conclusion, our study suggests that there may be large-scale migratory connectivity in the lesser kestrel (Sarà et al. 2019), but not a small-scale one, with colonies belonging to the same breeding cluster in Iberia mixing among them within the wintering grounds.

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Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

Conflict of Interest

The authors declare no conflict of interest.

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