Within-colony segregation of foraging areas: from patterns to processes

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Abstract

Spatial segregation of foraging areas among conspecifics breeding in different colonies has been observed in several colonial vertebrates and is assumed to originate from competition and information use. Segregation between sub-groups of foraging animals from the same colony (hereafter sub-colonies) has comparatively received limited attention, even though it may have strong impacts on colony structure and individual fitness, and thus on population dynamics of colonial species. Here we (1) used empirical data on a colonial bird and (2) developed an Individual Based Model (IBM) to shed light on the processes driving small-scale spatial segregation of foraging areas. Through the IBM, we tested whether memory and competition alone, without social information use, could explain the observed patterns of spatial segregation. By GPS tracking breeding lesser kestrels (*Falco naumanni*), we found that foraging areas of individuals breeding in two distinct sub-colonies within a large colony were significantly spatially segregated. Individuals from the two sub-colonies showed different departure bearings and encountered different habitats but did not differ in any fitness- or dispersal-related trait. Yet, individuals from a same sub-colony did not seem to follow departing or returning individuals when leaving for a foraging trip. The IBM showed that such collective spatial segregation does not necessitate any social information use to emerge: personal information and memory may be sufficient to mechanistically explain intra-colony segregation of foraging areas. Our results do not question the fact that colonies act as information centres, and that individuals may rely on social information for foraging. Instead, they suggest that within-colony spatial dynamics, arising from simple mechanisms not involving information sharing, might be widespread in colonial systems. While colonies have long been thought as single cohesive entities, we call for a careful generalisation of foraging data collected over a spatially limited part of colonies.

Keywords: central-place foraging, colonial, competitive exclusion, home-range, spatial overlap, Individual-Based Model, lesser kestrel, memory

Introduction

Colonial vertebrates often aggregate in high densities and this may lead to strong competition when foraging on shared grounds off the colony (Danchin and Wagner, 1997). Such foraging competition shapes, and in turn is affected by, colony size and population dynamics (Ashmole, 1963; Furness and Birkhead, 1984), acting not only within colonies but also at a multi-colony scale (Cairns, 1989). As an ecological response, segregation of foraging areas among individuals from different colonies is widespread (Bolton et al., 2019; Wakefield et al., 2013) and has been very frequently reported among avian taxa (79% of seabirds, reviewed in Bolton et al. 2019, but also raptors: Cecere et al. 2018) and mammals (e.g. bats: Dawo et al., 2013, fur seals: Kuhn et al., 2014). Such spatial segregation is thought to originate from the increasing depletion of resources around colonies, combined with density-dependent competition between colonies sharing part of their foraging grounds (the density-dependent Ashmole's halo effect: Ashmole, 1963; Lewis et al., 2001; Weber et al., 2021; and the Density-Dependent Hinterland Model: Cairns, 1989; Wakefield et al., 2013).

While these ultimate causes of spatial segregation have been well studied, several individual- and population- level proximate mechanisms have been proposed to foster such segregation. For example, the combined use of personally and socially acquired information at both colony and foraging grounds was shown to be essential in driving inter-colony spatial segregation in a highly social, group-foraging seabird exploiting ecologically dynamic landscapes with limited predictability of resources (Wakefield et al., 2013). Yet, depending on the species' ecology, social information use may not always be possible (e.g., species not

foraging in groups or not detecting conspecifics over large distances, like seals) or advantageous, for example because preys are small and unaggregated, and thus not shareable. However, spatial segregation also occurs in these species (e.g. Kuhn et al., 2014). A recent model found that memorized personal information, without any use of social information, can lead to spatial segregation between colonies (Aarts et al., 2021; confirmed empirically in bats foraging in fruit trees, Lourie et al., 2021). Far from being contradictory, Wakefield et al. (2013) and Aarts et al. (2021) reveal that density-dependent competition, spatial arrangements and sizes of colonies, together with memorized personal information play a critical role in colony-segregation, which could be further reinforced by socially acquired information, for instance among species foraging in groups.

All aforementioned empirical and theoretical studies focused on segregation between neighbouring colonies, separated by areas where foraging was possible and where spatial segregation emerged (see also Ainley et al., 2004). Whether the same mechanisms trigger spatial segregation during foraging at smaller spatial scales, for example within-colonies, remains an open question. Indeed, when colonies are large enough, they rarely constitute a cohesive entity but are rather split into smaller homogeneous sub-units (hereafter, sub-colonies), sometimes separated by physical barriers (e.g. rock crevices on the two sides of a promontory, Pereira et al., 2022; Waggitt et al., 2014). Ecologically, an important distinction to be made between colony- and sub-colony-scale segregation is that foraging individuals from distinct sub-colonies depart from very close locations without any foraging opportunities in-between. As a result, individuals breeding in different sub-colonies in theory deplete the same ‘halo’ of resources around the colony and share the same travel costs (considering an even distribution of resources around the colony). The physically reachable foraging areas should then completely overlap between sub-colonies, leading to even stronger competition than between neighbouring colonies. We may thus expect some population-level behavioural

response in individuals from different sub-colonies with respect to intra-colony competition, like spatial segregation of foraging grounds (Bolton et al., 2019). Few empirical studies, largely restricted to marine species, have explored spatial foraging segregation within-colonies compared to between neighbouring colonies (Masello et al., 2010a; Bogdanova et al., 2014; Kuhn et al., 2014; Waggitt et al., 2014; Ceia et al., 2015; Sánchez et al., 2018; Ito et al., 2020; Morinay et al., 2022; Pereira et al., 2022). These studies, showing partly contrasting patterns, have not provided any firm conclusion yet as whether this phenomenon is widespread at this smaller scale. This current lack of knowledge calls for (1) further empirical work in other species with different ecological features and (2) theoretical mechanistic approaches.

Here, we aimed to assess which mechanisms might underlie small-scale spatial segregation of foraging areas, and which individual and populational consequences such segregation may have, by (1) using empirical data on a colonial bird species and (2) developing a general Individual Based Model (IBM), applicable not only to our study system but to other colonial species more generally.

To provide empirical evidence of spatial segregation, we used tracking data from 690 foraging trips performed by 45 lesser kestrels *Falco naumanni* breeding in two distinct sub-colonies of a large colony (ca. 1,000 pairs) located about 600 m apart in an old town (i.e. without any foraging possibilities between them). The lesser kestrel is an ideal candidate to address questions related to spatial segregation of foraging grounds. It is a colonial and migratory raptor that feeds on patchily distributed and ephemeral preys (invertebrates, lizards, and small rodents Catry et al., 2016, Di Maggio et al., 2018) in heterogeneous and relatively temporally dynamic farmland habitats. The relative uncertainty faced by individuals arriving from migration and foraging in such habitat should favour the use of personal, or socially acquired, information (Evans et al., 2016; Riotte-Lambert and Matthiopoulos, 2020). This,

combined with the high conspecific density they experience throughout the breeding season, may lead to segregation of exploited areas (Wakefield et al., 2013; Aarts et al., 2021), which was actually detected between neighbouring colonies (Cecere et al., 2018; see also Figure 1). Given previous evidence in other systems, we tested whether lesser kestrels spatially segregate also at the sub-colony level. Given that lesser kestrels are non-territorial during foraging and have been shown to use social information obtained at the colony in some contexts (nest site selection, Aparicio et al., 2007; Morinay et al., 2021; antipredator vigilance, Campobello et al., 2012), and are known to sometimes forage in groups (typically in patches with ephemeral and high prey density, in fields being ploughed), we might expect them to also use foraging social information obtained at the colony, by eavesdropping on the departure or return bearings of other sub-colony members. We first tested whether members of the two sub-colonies differed in the bearing taken when departing on foraging trips, and then compared the bearings taken by individuals when departing the sub-colonies to those of concomitantly departing and returning individuals.

To better understand the population and individual consequences that between-sub-colony segregation might have, we tested the following hypotheses with the empirical data. Segregation could lead members of the two sub-colonies to encounter different habitat types and quality (as in Assandri et al., 2022 between colonies), which, in turn, may lead members of one sub-colony to forage further or spend more energy while foraging, and have ultimately different reproductive success (e.g. effect of foraging tactic on energy expenditure and nestling mass increase; Cecere et al., 2020). If sub-colonies indeed differ in the advantages they confer, we expect a non-random assortment of individuals among these sub-colonies (e.g., the sub-colony conferring advantages hosting more philopatric, maybe more experienced individuals, with better competitive abilities enabling them to secure a breeding site in the best sub-colony).

Finally, to address which mechanisms might lead to spatial segregation between sub-colonies, we used an IBM approach (Aarts et al., 2021) and tested whether competition for limited food resources and the use of memorized personal knowledge might suffice for spatial segregation of foraging areas to emerge at this small scale.

Materials and methods

Study species and site

Lesser kestrels are medium-size (ca. 120 g) secondary cavity nesters and usually breed below roof tiles of ruins or old buildings, in rocky cavities, but readily accept nestboxes. These raptors reach their European breeding grounds in February/March (Sarà et al., 2019) and females start laying between late April and early May (usually 3-5 eggs). During the 28-day incubation and 35 to 40-day nestling-rearing periods, partners share nest attendance and rearing duties.

Lesser kestrels are non-territorial on foraging grounds and forage mostly alone, but they are also seen sometimes foraging in groups, especially when exploiting rich resources patches (typically following ploughing tractors, which overall constitutes stochastic events, Inês Catry et al., 2014). The use of social information either at foraging grounds (local enhancement) or at the colony (following behaviour) has not been shown yet in this species. However, lesser kestrels use social information in other contexts. In particular, they rely on the colony breeding success for settlement decisions (yearlings avoiding the competition while older ones prefer sites with high past reproductive success, Aparicio et al., 2007). Moreover, early breeders tend to favour nest sites containing cues of previous breeding events, while late, usually young, breeders tend to avoid such cues (Morinay et al., 2021). We may thus expect lesser kestrels to use other social cues at the colony, like eavesdropping on departure or return bearing of neighbours (Boyd et al., 2016). Besides, with the observed

state-dependent use of social information for breeding site selection (Morinay et al., 2021), we could expect, in our case, that if one sub-colony is more attractive, it may be favoured by some specific phenotypes.

The study was conducted in 2016-2018 and 2020 in the city of Matera (southern Italy), hosting ca. 1,000 lesser kestrel pairs. Up to 274 nestboxes were positioned on seven roof terraces of public buildings between 2010 and 2016. Nestboxes were oriented in all directions, on roof terraces that dominated or equalled surrounding buildings. The majority of nestboxes are visible to all breeders on each roof terraces. Every spring since 2016, we checked nestboxes every 2 to 5 days to record the occupancy, laying date, clutch size, hatching date, brood size, and nestling survival up to ca. 14 days after hatching. While foraging, breeders from our study site are fully segregated from those breeding in the two nearby and similarly large colonies (Figure 1).

GPS deployment

Tracking data were gathered from 45 individuals breeding on two roof terraces, referred to here as 'Genio' and 'Provincia', which we used as names for sub-colonies. Birds were captured in the nestbox during late incubation or early nestling-rearing stage and equipped with high resolution Axy-Trek biologgers (TechnoSmArt Europe, Rome, Italy) for 2 to 6 days, simultaneously within year. None of the birds was tagged more than once. On two occasions, both parents of a pair were tracked (i.e., 4 birds among the 45 tagged). The biologger was deployed on the back of the bird using a Teflon wing-harness (for more details see Cecere et al. 2020). Loggers recorded GPS positions (1 fix/min) and tri-axial acceleration (25 Hz). To save battery power, the GPS recorded data from 05:00 to 21:00 (local time) and started recording only from the day after deployment.

Captures, handling and tagging were carried out by the Istituto Nazionale per la Protezione e la Ricerca Ambientale (ISPRA) in accordance with ongoing regulations and ethical practices (authorisation by the Law 157/1992 [Art. 4(1) and Art. 7(5)]). The loggers and the harness weighed between 5.0 and 7.2 g, corresponding on average to 4.4 ± 0.7 % (range: 2.8-3.7 %) of individual body mass (144 ± 14 SD g, range: 115-178 g). Even though the tracking period was short, such deployment can have both short and long term consequences for individual's life history and behavioural traits, and in particular for foraging trip duration (Bodey et al., 2018). We could not compare foraging trip duration of tagged and untagged individuals, but, if foraging trips were indeed lengthened, we shall not expect any sub-colony specific effect of the tagging procedure. Besides, loggers' deployment led to no short-term reproductive consequences: tagged individuals had similar nestling survival to untagged individuals (survival of nestlings to 14 days after hatching estimated in 2016-2018: 79% with a tagged parent vs. 77% with untagged parents; $\chi^2_1 = 0.37$, $p = 0.55$). Among the 45 tagged individuals, we could detect 18 individuals (40%) breeding in monitored nestboxes the following year, which matches the rate of annual adult re-sightings within these sub-colonies (43%; sampling period: 2016-2021).

Spatial data pre-processing

Except when mentioned otherwise, all analyses were performed in R v.4.1.1 (R Development Core Team, 2021). Foraging trips were manually identified, and implausible positions excluded, in ESRI ArcMap 10.2.1, following Cecere et al. (2020). A foraging trip was considered as a track starting and ending within 50 m of the nest or night roosting sites. For foraging trips that already started before the loggers turned-on in the morning, we only retained trips for which the first position was within 2 km of the nest. As we aimed to

197 determine spatial segregation during foraging, we discarded locations unlikely to represent
198 foraging activities. In particular, we discarded trips not heading towards rural surroundings
199 but instead involving urban areas only (typically trips between the nest and roosting places).
200 For trips identified as proper foraging trips, we also removed any GPS position located in
201 urban areas. Urban areas were identified based on the Corine Land Cover 2012 habitat
202 classification, hereafter CLC12 (codes 111 and 112, https://land.copernicus.eu/pan-
203 european/corine-land-cover/clc-2012). To further focus on foraging activities, we also
204 discarded positions corresponding to relocation phases between distant foraging locations or
205 between a foraging location and the colony. To identify these "relocation" positions, we used
206 Expectation Minimization binary Clustering algorithm with the *EMbC R* package (Garriga et
207 al., 2019; similarly to Cecere et al., 2020). This procedure relies on GPS data to attribute one
208 of four behaviours to each GPS positions based on velocity and turning angle data. This
209 allowed us to distinguish relocation positions, which, consecutively, build trajectories with
210 low turning angles at high speed, from intensive search (high turning angles at low speed),
211 extensive search (high turning angles at high speed), and perching (low turning angles at low
212 speed; Cecere et al., 2020).

213 We obtained tracking data corresponding to 690 foraging trips from 45 individuals (13
214 individuals in 2016, 12 in 2017, 11 in 2018, 9 in 2020). The sex ratio of tracked individuals
215 was relatively balanced (20 females vs. 25 males; Table S1). These 690 foraging trips were
216 evenly distributed between the two sub-colonies (327 trips by 16 individuals for Genio, 364
217 trips by 29 individuals for Provincia), despite some year-specific differences. See Table S1
218 for detailed numbers of individuals, average sampling duration per individuals, and total
219 number of foraging trips considered per sub-colony and year.

220 To test for spatial segregation during foraging between the two sub-colonies, we first
221 ensured that movements of tagged individuals were representative of the sub-colony using

Lascelles et al. (2016) representativeness algorithm: for each sub-colony, we randomly selected from 1 to N-1 individuals and estimated how many of the GPS locations from the non-selected individuals overlapped with the individual 95% KDE of the selected individuals. We replicated this procedure 100 times for each selected sample size. The two representativeness curves we obtained indicate that the 16 individuals tagged in Genio and the 29 individuals tagged in Provincia were well representative of their sub-colony (Figure S1), reinforcing the idea that the slight difference in sample size between sub-colonies should not affect the results.

Spatial segregation of home ranges

To test for spatial segregation between members of the two sub-colonies, we used the randomization method described in Cecere et al. (2018). We calculated the Utilization Distribution Overlap Index (UDOI) between all pairs of the 45 individuals based on their 95% fixed Kernel Density Estimate (KDE - R package '*adehabitatHR',* (Calenge, 2006) applied to individual locations (excluding relocations; see above). For KDEs, here and below, we always used the reference bandwidth '*href*' as smoothing factor to ensure the best fit of kernels for each individual data, and the same grid cell size (a 23 × 23 km grid with a cell size of 200 m). We reported the UDOIs in a 45 × 45 matrix (entries of the matrix were the 45 tracked individuals). We estimated the point biserial correlation between the upper parts of this UDOI matrix and a 45 × 45 binary 'membership' matrix describing whether the two individuals were breeding in the same sub-colony (0) or a different sub-colony (1; the reference used with the *biserial.cor* function from *ltm* package; Rizopoulos, 2006). We expected birds from the same sub-colony to have more overlapping UDs than birds from different sub-colonies, i.e., we expected a negative and lower than random correlation between these two matrices. To

statistically test this deviation from random, we used a randomisation procedure: we rotated individual sets of positions around the sub-colony 10,000 times, to produce null distributions not influenced by interspecific competition or habitat selection. Next, the calculations like those for the observed GPS locations were repeated for the rotated locations. The resulting null-distribution of correlations was used to compare with the observed correlation for the true GPS locations to derive *p*-values (with an α risk of 0.05, Cecere et al., 2018).

We finally ensured that we did not confound sub-colony and year effects by pooling data from different years, meaning that individual KDEs did no overlap more within than between years. We used the same methodology as above, except that we compared the overlap of KDEs within and between years, for each sub-colony separately.

Departure bearing from the colony

Given lesser kestrels flying behaviour and relatively low-rising buildings in the Matera city, we did not expect the birds to be affected by any physical obstacle when leaving the sub-colony. Individuals bearing when departing or returning to the colony should thus provide reliable information on their foraging sites (as shown in Figure S3).

To test whether a potential spatial segregation of foraging grounds may originate from decisions made at the colony, we compared the departure bearings taken by individuals from Genio to those taken by individuals from Provincia sub-colony. For each foraging trip, we retrieved the bearing of the first GPS position after 500 m of travelling from the colony. We chose 500 m as this rather small distance (smaller than the distance separating the two sub-colonies) corresponds to the threshold distance after which the bearing seemed to stabilize (see Figure S3). To ensure comparability, the departure location at the colony was the exact location between the two sub-colonies. We only retained trips starting at the sub-colony (i.e.,

we removed trips that started before the GPS turned on in the morning, where individuals were already further than 200 m from their sub-colony at the start of recording). To test the effect of the sub-colony on the departure bearing (circular variable) while controlling for individual repeated measures, we relied on a Bayesian statistical approach. Indeed, unlike the frequentist framework, Bayesian inferences enable to perform circular analyses with random effects (here individual identity; Cremers and Klugkist, 2018). We thus fitted a circular mixed effect regression model with 10,000 iterations, a burn-in of 100, a lag of 3 and a seed of 101, to allow the convergence of the chains (visual inspection; function *bpnme* from the *bpnreg* package; Cremers, 2020).

At a finer temporal scale, segregation between sub-colonies could result from social information gained at the nesting site, by eavesdropping on departing or returning individuals (Weimerskirch et al., 2010; Boyd et al., 2016), or through synchronous departures. Individuals from the same sub-colony would thus tend to take departure bearings similar to the bearings of returning or departing individuals at similar times. To test these two possibilities, we compared, for each trip, the bearing taken when leaving the sub-colony to the bearings taken by other members of the sub-colony tracked concurrently either when (1) leaving or (2) returning to the colony. Reagarding (1), to compare departure bearings, we selected, for each trip, all the trips performed by individuals from the same sub-colony and retained only those which were initiated within 35 minutes (half the average foraging trip duration here). A wide-enough time window was necessary as the aim was to test whether bearings were more similar for trips closer in time. We also performed this analysis for a 20- and 50-minutes time-window, and results were overall similar (see Results). We calculated the absolute difference in the departure bearings from the sub-colony (degrees) for each pair of temporally close foraging trips. We fitted this variable in a Generalized Linear Mixed effects Model (GLMM with Gamma distribution; *glmer* from the *'lmerTest'* R package,

Kuznetsova et al., 2017) with the absolute departure time difference between the focal pair of trips and the distance between the nestboxes of the focal individuals as fixed (scaled) covariates. Indeed, we may expect individuals breeding closer to each other (or partners as this is the case for two breeding pairs with both partners tagged) to share, inadvertently or intentionally, more information than individuals breeding further away. We initially included individual and foraging trip identifiers as random terms but remove them as they explained no significant proportion of variance (singular fit). Regarding (2), to compare a departure bearing (first location within 500 m of the colony) with the bearing taken by individuals returning to the colony (last location within 500 m of the colony), we used an approach similar to (1). We then fitted the difference between the departure and returning bearings with a similar LMM, analogously to (1).

Population- and individual-level consequences

If foraging individuals from each sub-colony show spatially distinct foraging areas, we can expect sub-colony differences in exploited foraging habitats, which may translate in sub-colony differences in reproductive success. We could also expect birds from the two sub-colonies to show differences in philopatry and survival, for instance if between-colony differences in the average phenotypic quality of individuals exist. Higher quality individuals may thus survive better and be more philopatric to a given sub-colony over the years. We thus tested whether individuals from the two sub-colonies differed in a range of intrinsic and behavioural variables: type of habitat encountered, foraging trip duration, size of daily used foraging area, and energy expenditure while foraging, with different (generalized) linear mixed effects models. Based on the long-term monitoring of the population (see Table 1 for the large sample sizes), we also tested whether individuals breeding in the two sub-colonies

differed in their body condition (measured here by Scaled Mass Index, SMI; see Podofillini et al., 2019), offspring's growth rates and breeding success (measured here by the number of fledglings). With the same large dataset, we tested whether the two sub-colonies differed in their age composition (≤ 2 years old versus ≥ 3 years old), survival and dispersal behaviour of breeders (philopatric vs. immigrant, Capture-Mark-Recapture (CMR) model based on 333 breeding event by 346 individuals). See Text S1 for methodological details.

Individual-Based Model

To determine whether the combination of competition for resources and the use of personal information, through individual-level memory, could explain sub-colony segregation during foraging, we implemented an IBM, based on Aarts et al. (2021). The model and its parameters are described in detail in Text S2, yet we provide here a comprehensive summary. We relied on empirical data for seven sub-colonies monitored for 5 years. These sub-colonies, encompassing ca. 350 breeding individuals (approximatively one fifth of the whole lesser kestrel population breeding in Matera city), are the largest and main aggregates of nesting sites in Matera city, other sites being more scattered. Differently from Aarts et al. (2021), we used the true arrangement of the seven sub-colonies and their average number of breeding pairs. We provided the simulated lesser kestrels with a 24 × 24 km grid (1 ha cells) centered on breeding sites containing patchily distributed prey items (between 3 and 7 prey items/ha, reflecting the expected prey density available for one fifth of the lesser kestrel breeding population; Rodriguez & Bustamante, 2008). Modelled lesser kestrels were hypothesized to possess a map of expected food resources for each cell, and to update this knowledge while foraging and exploring the environment. A foraging trip consisted of an individual leaving the sub-colony towards the cell with the highest anticipated intake rate, similarly to Aarts et al.

(2021). Once there, it would detect prey density in a radius of 300 m around this first target cell. If resources within this 300 m-wide area were too limited (i.e., if the time required for successful hunting would exceed a certain threshold, here 30 min, which approximates the average duration of the foraging phases of lesser kestrels' trips, 38 min (SD 43.60, Ramellini pers. comm., from the empirical GPS data), the individual would continue its travel by selecting the next best expected area (at least 600 m apart). Once the individual successfully foraged, it returned to its sub-colony. For the first round, all individuals departed from the sub-colony within a 3-min time-window. After this first trip, each continued to forage for 14 h/d, for 40 d. We did not explicitly model self-maintenance foraging here as this was implicitly included through a parametrization of maximum foraging and trip duration based on empirical data (i.e. it could have occurred concurrently, and is in any case minimal to the amount of food provided to nestlings on a daily basis). The food resource progressively got depleted as the season progressed but was partially replenished each night.

In this main scenario, individuals could retain information on all visited patches (unlimited memory). On average, individuals remembered the prey content of 3214 ± 346 SD patches. To test the effect of knowledge and memory abilities on segregation, we implemented alternative models (Table 1), whereby: (1) individuals had a limited memory (remembered 0, 50, 100, 500 or 5000 visited patches), or (2) individuals were omniscient regarding resource distribution and abundance. When memory size is low, we would expect individuals to keep visiting the closest patches (despite being empty) and lose time in exploring depleted patches at the close vicinity of the colony, instead of going further away to pristine patches. We thus expected that spatial segregation will increase with memory size, as individuals would remember (and avoid) patches in the immediate surroundings of the colony and tend to explore and forage in patches right ahead but further and further away from their sub-colony. As an extreme case of knowledge acquisition, when individuals are omniscient to

368 the current prey density, we expect them to perfectly segregate, foraging in the most
369 rewarding yet closer patches compared to their sub-colony location. To test the effect of
370 between-sub-colony competition on spatial segregation, we implemented each of the 6 models
371 (perfect memory, limited memory with 4 different levels, and omniscient) without
372 competition: we simulated sub-colony as if they were alone in the colony (this led to
373 simulating 7 times each of these 6 models, one for each sub-colony; see Text S2). We
374 expected that when individuals are not subject to competition between sub-colonies, they
375 would forage all around the colony. We thus ended up with 12 models, including a null model
376 (memory of 0 and no competition).

377 For each model, we drew maps of foraging locations and estimated overlap index
378 (here UDOI) between each pair of sub-colonies (see Text S2). For the main scenario
379 (unlimited memory), we tested whether more distant sub-colonies would segregate more
380 strongly by testing the correlation between the UDOI matrix and a matrix of geographic
381 distances between sub-colonies (Mantel test using the *mantel.rtest* function, from the R
382 package *ade4*; Dray & Dufour, 2007). We also compared a range of parameters depending on
383 the memory size and the presence/absence of competition: trip duration, distance travelled,
384 and the proportion of unsuccessful trip (i.e., trips lasting 5 h, corresponding to events when
385 individuals went back to their nest without food). We expected that individuals without poor
386 memory abilities to perform longer trips, closer to the colony, and more likely to be
387 unsuccessful as they will forget that patches at the vicinity of the colony have been depleted.
388 We also expected that individuals with perfect knowledge of their prey field and/or not
389 exposed to between-sub-colony competition to perform more efficient foraging trips (shorter,
390 further away, and successful).

391

Results

Spatial segregation and departure bearing

Individual home ranges were significantly segregated between the two sub-colonies (Figures 2a and S4): the value of the observed correlation r_{obs} between the individual 95% KDE overlap and the sub-colony membership felt within the 5% lowest values of random correlations (r_{obs} = -0.04, p = 0.04, Figure S5). For both Genio and Provincia, there was no difference in overlaps between KDEs from the same or different years (p > 0.16; Figure S6). The observed sub-colony difference in home ranges should thus not be due to yearly differences in foraging site selection.

The departure bearing was different between sub-colonies (intercept: -116.4° ± 10.0 SD [-136.5; -97.0]; sub-colony effect: 127.9° ± 6.5 SD [116.1; 141.5]; Genio being the reference). Individuals from Genio tended to head south-west when leaving the nesting site, while individuals from Provincia tended to head south-east (Figure 2). Yet, for members of a same sub-colony, trips did not have more similar departure bearings when they were initiated closer in time (within a 35-min time-window: estimate = -0.00 ± 0.00 SE, t = -0.49, p = 0.63, N = 83). In other words, there was no evidence that individuals from the same sub-colony left collectively the colony site to forage in the same region. Results with a 20-min and 50-min time-window for the bearing comparison were similar (20-min: t = -1.42, p = 0.16, N = 48; 50-min: t = -1.55, p = 0.12, N = 125). Similarly, individuals did not seem to copy the direction taken by returning individuals (within a 35-min time-window: estimate = -0.00 ± 0.00 SE, t = -0.54, p = 0.59, N = 135; 20-min: t = 0.73, p = 0.47, N = 89; 50-min: t = 0.27, p = 0.79, N = 194). The difference between departure and returning bearings increased with the time elapsed between the two considered trips (with a 35-min time window: estimate = 0.003 ± 0.001 SE, t=2.02, p = 0.05; 50-min: t=2.24, p = 0.03; but this did not hold with a 20-min

time-window: t = 1.42, p = 0.16). A similar but weaker trend was observed for difference in bearings between two departures (35-min time window: estimate = 0.004 ± 0.003 SE, t=1.72, p = 0.09; 50-min: t=1.96, p = 0.05; but this also did not hold with a 20-min time-window: t = 1.06, p = 0.30).

Population- and individual-level consequences

The composition of habitats encountered by tracked lesser kestrels differed between the two sub-colonies. Individuals from Genio encountered mostly arable lands (70% of encountered habitats), while individuals from Provincia also encountered to a significant extent grasslands and wooded areas (43% of encountered habitats overall; Figure S7). There was no significant sub-colony difference in individuals' trip duration, size of daily used area, or daily energy expenditure during foraging trips (Overall Dynamic Body Acceleration ODBA) (Table 1). Based on the long-term monitoring of this population, we observed no sub-colony difference in breeders' SMI and no overall sub-colony differences in nestlings' body mass or number of fledglings (Table 1). Yet, nestlings from Provincia had a slightly higher growth rate than those from Genio, as shown by the effect of nestlings' age by sub-colony interaction on nestlings' body mass (0.74 ± 0.23 SE, $t = 3.429$, $p < 0.001$; Figure S8). The age-composition was similar between sub-colonies (Table 1). Neither survival nor philopatry probabilities differed between sub-colonies (Tables S2-S3 for the output of the CMR approach).

Individual-Based Model

Based on 40 d simulations with 350 individuals breeding in 7 sub-colonies and remembering any visited cell, a clear segregation among the most distant sub-colonies emerged, while this segregation was less marked between close-by sub-colonies (Figures 3, 4). This segregation

by distance pattern was valid for all scenarios including between-sub-colony competition (all p-values < 0.03; not calculated for the omniscient scenario with UDOI values based on 50% KDE as all overlaps were zero).

Scenarios with a certain level of memorial capacity (> memorized 500 cells) seemed to be the most realistic scenarios (Figures S9 and S10). Indeed, when individuals had poor memorial capacities, foraging trips were extremely long, very close to the colony, and were often unsuccessful, which is highly unlikely in nature (Figures S9 and S10). Contrarily, with good memorial capacities, individuals performed mostly successful trips, which duration was similar to the one observed in our empirical data (Figure S9).

When considering segregation of core foraging areas (UDOI based on 50%), segregation of foraging grounds was much lower in the absence than in the presence of between-sub-colony competition (for all memory types except no memory, Figure 5a). This was less marked when considering segregation of home range (UDOI based on 95% KDE) as these likely encompass more areas in the close vicinity of the colony. Comparing scenarios with different memory capabilities (from 0 to 500, and all cells remembered), segregation increased with memory size (Figure 5), up to a certain threshold where it may have been detrimental to remember too many cells (>5,000 cells). Indeed, when an individual remembers all visited cells, it will avoid remembered sites that have been depleted and not return to them even though replenishment occurred and that they are thus close and of high quality. Spatial segregation was almost absolute when the simulated individuals were omniscient regarding food availability and individuals competed with members of other sub-colonies (Figures 5 and S9-S11). Contrarily, when individuals did not compete among sub-colonies, overlap was the greatest when individuals were omniscient (Figures 5 and S10).

Discussion

In recent years, a growing body of literature now complemented by the present study demonstrated that spatial segregation occurs between neighbouring sectors of a same colony. Here, spatial segregation of foraging areas occurred between lesser kestrels breeding in different sub-colonies while foraging in the rural landscape outside the colony. This segregation originated from different bearings taken when leaving the sub-colonies. Individuals breeding in Genio headed on average south-west and encountered mostly arable lands, while the ones breeding in Provincia headed on average south-east and encountered a mixture of arable land and more natural, less managed landscapes (grasslands and wooded areas). Yet, these differences in habitats did not yield to any marked consequences for individual fitness or sub-colony composition. Detailed analysis of departure and return bearings did not provide any evidence for collective departure for foraging or sharing of foraging information at the breeding site among birds of the same sub-colony. Our IBM showed that when individuals from different sub-colonies compete for food, they tend to segregate during foraging more than expected in the absence of competition, even more so when they have a good memory of the visited patches. Both our empirical and theoretical results concur to the fact that the observed small-scale spatial segregation of foraging areas in lesser kestrels is less likely to originate from social information use than from competition and memory use combined.

Spatial segregation: a pattern across scales

Regardless of the geographical and even taxonomic scales ecologists are looking at it, spatial segregation of foraging grounds seems to be the norm in many colonial systems. At the large scale, between neighbouring colonies, occurrences of such segregation were shown in various taxa and have been previously extensively reviewed (Bolton et al., 2019). At a smaller scale,

between sub-colonies or very close colonies, there is an obvious and likely artificial bias towards studies on marine species (seabirds: Bogdanova et al., 2014; Ceia et al., 2015; Hipfner et al., 2007; Ito et al., 2020; Masello et al., 2010; Morinay et al., 2022; Pereira et al., 2022; Sánchez et al., 2018; and one sea mammal: Kuhn et al., 2014), except for this present study on a terrestrial raptor. Despite the more limiting, yet expanding, number of studies conducted at this small scale, we suggest that spatial segregation of foraging grounds could be widespread as the same mechanisms seem to act at all scales. We have to slightly nuance here because, this pattern seems to be distance-dependent, both at the colony (Aarts et al., 2021) and sub-colony scale (this study, both the empirical and modelling part): (sub-)colonies that are very close to each other overlap more in their foraging areas. We may thus expect to observe no segregation if we compare foraging areas of individuals breeding at very close locations (e.g., 50 m in Waggitt et al., 2014)Our results thus confirm, for sub-colonies, the existence of a pattern that has long been theorized and empirically shown at the colony level.

Underlying processes

The segregation pattern emerging from our IBM was strikingly similar to the one originating from the empirical data (comparing Figures 2 and 3). We showed that the use of social information is not necessarily required for spatial segregation to emerge between the foraging distributions of lesser kestrels' sub-colonies. Individual-level memory of visited patches, and the fact that individuals compete and tend to minimize travelling and foraging costs (thus following the Optimal Foraging Theory, Charnov, 1978) could cause the observed spatial segregation of foragers belonging to different sub-colonies (Figures 2, 3 and 5). This extends Aarts et al. (2021) results, which showed on a larger spatial scale that personal memory combined with indirect competition can lead to the segregation of the foraging grounds of

513 different colonies. Other previous models, yet on non-colonial central place foragers, have
514 also confirmed this idea: personal memory can lead to foraging segregation between
515 competing individuals (Riotte-Lambert et al. 2015; Dubois et al., 2021).

516 Given the strong competition for food resources among individuals from a same
517 colony, it is not surprising that the same mechanisms trigger among- and within-colony
518 spatial segregation of foragers. Yet, these results contrast with those of Wakefield et al.
519 (2013), who found that both social information collected at the colony and through local
520 enhancement are required, in addition to memory, to originate spatial segregation between
521 colonies (see Aarts et al., 2021 for a discussion of this discrepancy). Here, the segregation of
522 sub-colonies may simply be the result of individuals of the same sub-colonies progressively
523 acquiring similar knowledge of the environment, through personal experience and memory.
524 First, same-sub-colony individuals make similar decisions (going to the closest resource
525 patches, which implies taking roughly similar departure bearings), progressively expanding
526 the sub-colony foraging ground as resources get depleted. Then, when individuals encounter
527 resources patches that are already part of another sub-colony's foraging ground, these patches
528 appear of lesser quality as already depleted, and are thus avoided. The sub-colony thus
529 expands in another direction, to maintain a given intake rate. This sequence of processes has
530 been suggested for several seabird species (e.g. tufted puffins, Hipfner et al., 2007; Cory's
531 shearwater, Ceia et al., 2015). This parsimonious explanation does not necessitate any
532 territoriality, voluntary avoidance of conspecifics, social learning or cultural evolution of
533 foraging site (Wakefield et al., 2013) and is concordant with spatial segregation in colonial
534 species which do not have access to social information outside of the colony (e.g. seals,
535 Robson et al., 2004).

536

Social information use

While colonial breeding can provide benefits in terms of enhanced access to information in various contexts (e.g. predators, nesting site quality, Danchin & Wagner, 1997; Evans et al., 2016), an inherent cost of living at high densities is an increased competition for resources. These costs and benefits likely vary depending on the species ecology and its prey spatio-temporal distribution. For instance, for colonial breeders with observable conspecifics feeding on patchily distributed and ephemeral prey, the selective advantage of exploiting social information could be strong (as in northern gannets, Wakefield et al., 2013). However, as soon as there is some temporal persistence in foraging patch quality, the knowledge holder might prioritize personal information (memory) on the short term, and be reluctant to share this information with others. However, since successful foraging is an information that cannot be easily hidden when breeding close to each other, individuals may still be prone to follow experienced and successful individuals departing from the colony.

Empirical evidence for colonies acting as information centres is scarce: only few studies have confirmed that birds actually obtain information regarding food at the colony (Courbin et al., 2020; Harel et al., 2017; Thiebault et al., 2014; Weimerskirch et al., 2010). Here we failed to provide such evidence in lesser kestrels and instead showed that the spatial segregation pattern can solely result from competition and individual memory. Similarly to northern gannets (Waggitt et al., 2014), lesser kestrels did not seem to follow each other when leaving their sub-colony: there was no specific synchrony in bearing taken when leaving the breeding site between breeders from the same - compared to a different- sub-colony. However, to properly test social information use with GPS data, a much larger sample of individuals tagged at the exact same period would be required. We cannot rule out that lesser kestrels benefit from social information for foraging, as it is the case when selecting breeding sites (Aparicio et al., 2007; Morinay et al., 2021), engaging in predator vigilance (Campobello

et al., 2012), or when detecting large aggregates of conspecifics in superabundant but ephemeral resource patches (Catry et al., 2014). However, in our foraging context, we expect social information use to happen away from the colony by copying or avoiding, rather than at the colony.

Conclusion

We suggest that spatial segregation of foraging areas among sub-colonies is more widespread than currently presumed and originates from simple rules (optimal foraging in the presence of competitors and memorial capacities). By considering a colony as a cohesive entity, we may currently be overlooking important within-colony variability regarding habitat selection but also their intrinsic consequences (e.g., individual fitness). Unfortunately, field ecologists are often highly constrained to which parts of a colony they can access and study (e.g., seabirds in cliffs), and in that respect, our lesser kestrel colony is ideal. We recommend, whenever possible to study different units of a colony or, if technically impossible, to take care when deriving conclusions regarding foraging behaviour as it may have radical consequences on our understanding of the colony functioning, dynamic and behaviour, and - when applicable - on conservation actions to be implemented at foraging grounds.

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Conflict of interest

Authors declare no conflict of interests.

Figures and Tables

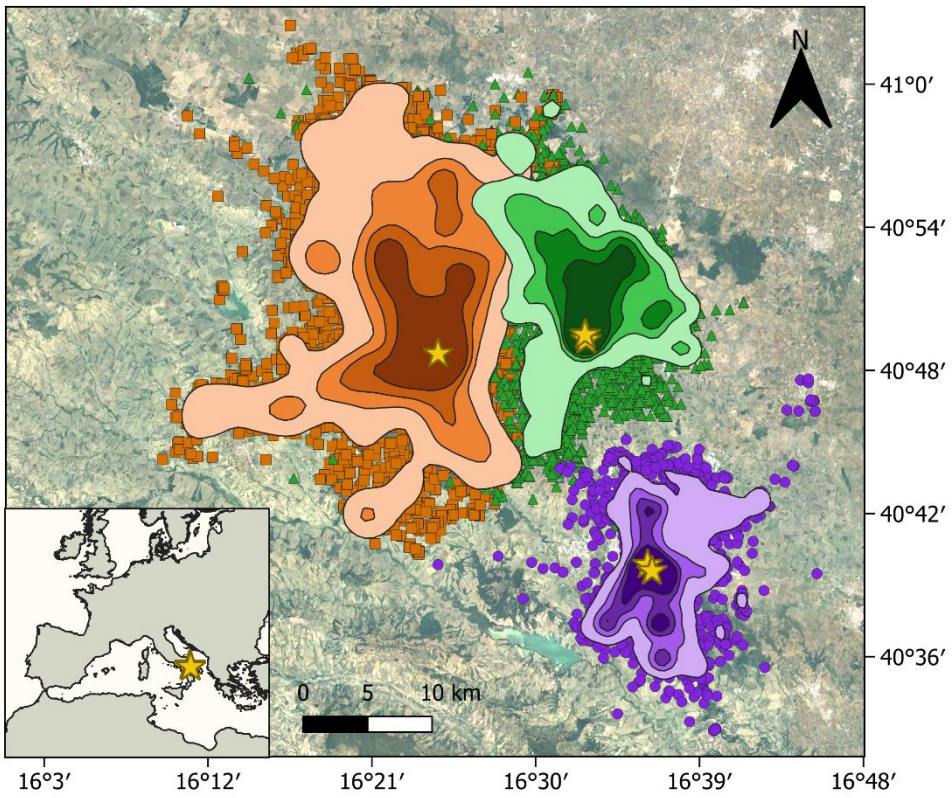
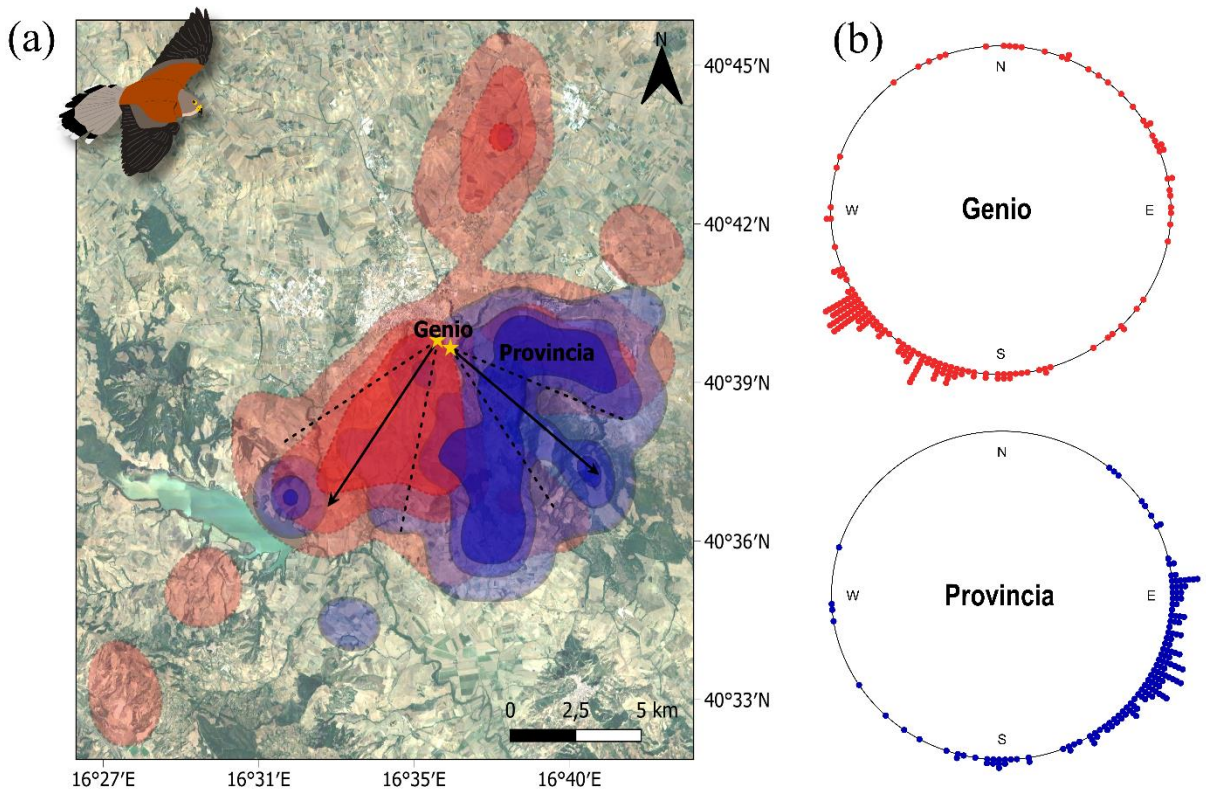


Figure 1. Spatial segregation during foraging by lesser kestrels breeding in three large neighbouring colonies: Matera (south-east, purple shades, round symbols), Gravina di Puglia (north-west, orange shades, square symbols), and Altamura (north-east, green shades, triangle symbols). The three colonies host ca. 800-1,000 breeding pairs each. The polygons (from dark to light shades) represent the contours of the 50%, 65%, 80% and 95% colony-specific Kernel Density Estimates (KDE). GPS positions come from 54 individuals tracked for the entire nestling-rearing stage (on average 27 days ± 11 SD) with solar-driven, remote-downloading GPS-UHF loggers (NanoFix GEO + RF, PathTrack Ltd., UK) recording positions every 15 minutes. In Matera, 13 individuals were equipped in 2019 (i.e., a different sample of birds compared to subsequent analyses focusing on 2016-2018 and 2020, but see Fig. S1). In Gravina di Puglia and Altamura, 9 and 9 individuals respectively were equipped in 2016 and 8 and 15 individuals respectively in 2017. Stars locate each colony.



778

779 **Figure 2. Sub-colony home-ranges and bearing of breeding birds when departing for**
780 **foraging trips from the sub-colonies Genio (red, dashed contours) and Provincia (blue,**
781 **solid contours).** (a) Bearings are provided as sub-colony posterior means (arrows) along with
782 their 95% High Posterior Density intervals (dashed lines). For illustrative purpose, we provide
783 KDEs estimated at the sub-colony level, excluding relocations: from light to darker shades,
784 95%, 75% and 50% KDEs. (b) Distribution of each trip bearing, for trips that departed from
785 the sub-colony (distance of the first recorded GPS position below 200 m) and measured from
786 the sub-colony to the first GPS position after having travelled 500 m. Note that the sub-colony
787 Genio is located 600 m North-West of the sub-colony Provincia but considering the middle of
788 both sub-colony locations as anchoring location for bearing calculation led to strictly similar
789 patterns.

790

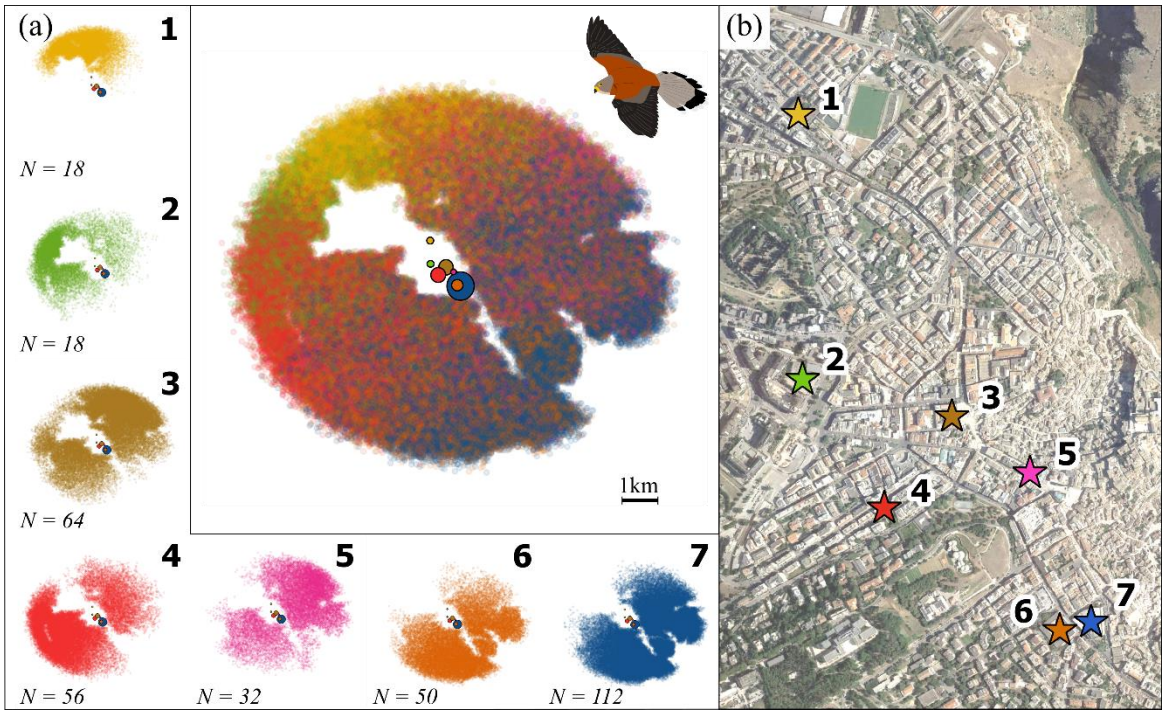
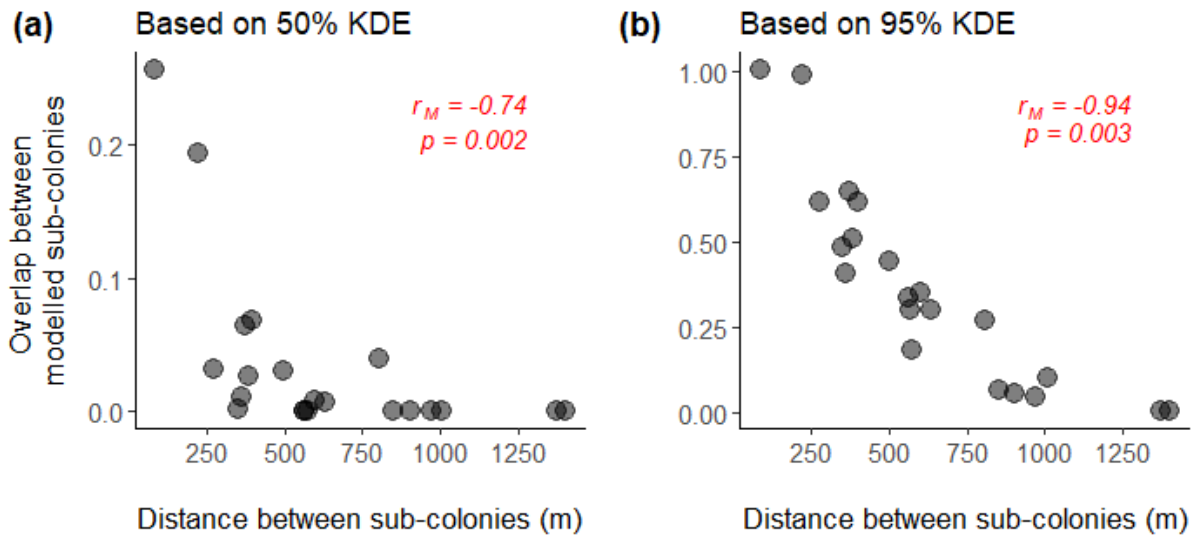


Figure 3. Foraging events of the 350 modelled lesser kestrels, (a) represented together and split per sub-colony (a, 1-7). *N* below each miniature refers to the average number of breeders in each sub-colony used in the IBM, based on the monitoring of this colony since 2016. (b) The true location of each sub-colony in Matera is also provided. Sub-colonies are represented in different colours, and dots are foraging events. Larger opaque circles correspond to the sub-colony locations, and their sizes to the number of breeders they host (see Text S2 for details).



800

801 **Figure 4. Greater segregation of modelled foraging grounds (as measured by decreasing**
802 **overlap) between more distant sub-colonies.** Segregation is especially high (small UDOI
803 value) between sub-colonies that are distant by more than 1,250 m. The scenario considered
804 here is with unlimited memory, yet results remain qualitatively similar (negative correlation)
805 with other scenarios. In the IBM, the seven sub-colonies were arranged according to their
806 actual geographical coordinates (see Figure 3). Overlap values correspond to UDOI.
807 Correlations derived from a Mantel test and their associated p-values are provided for each
808 simulation type. Each point corresponds to a pair of sub-colonies compared.

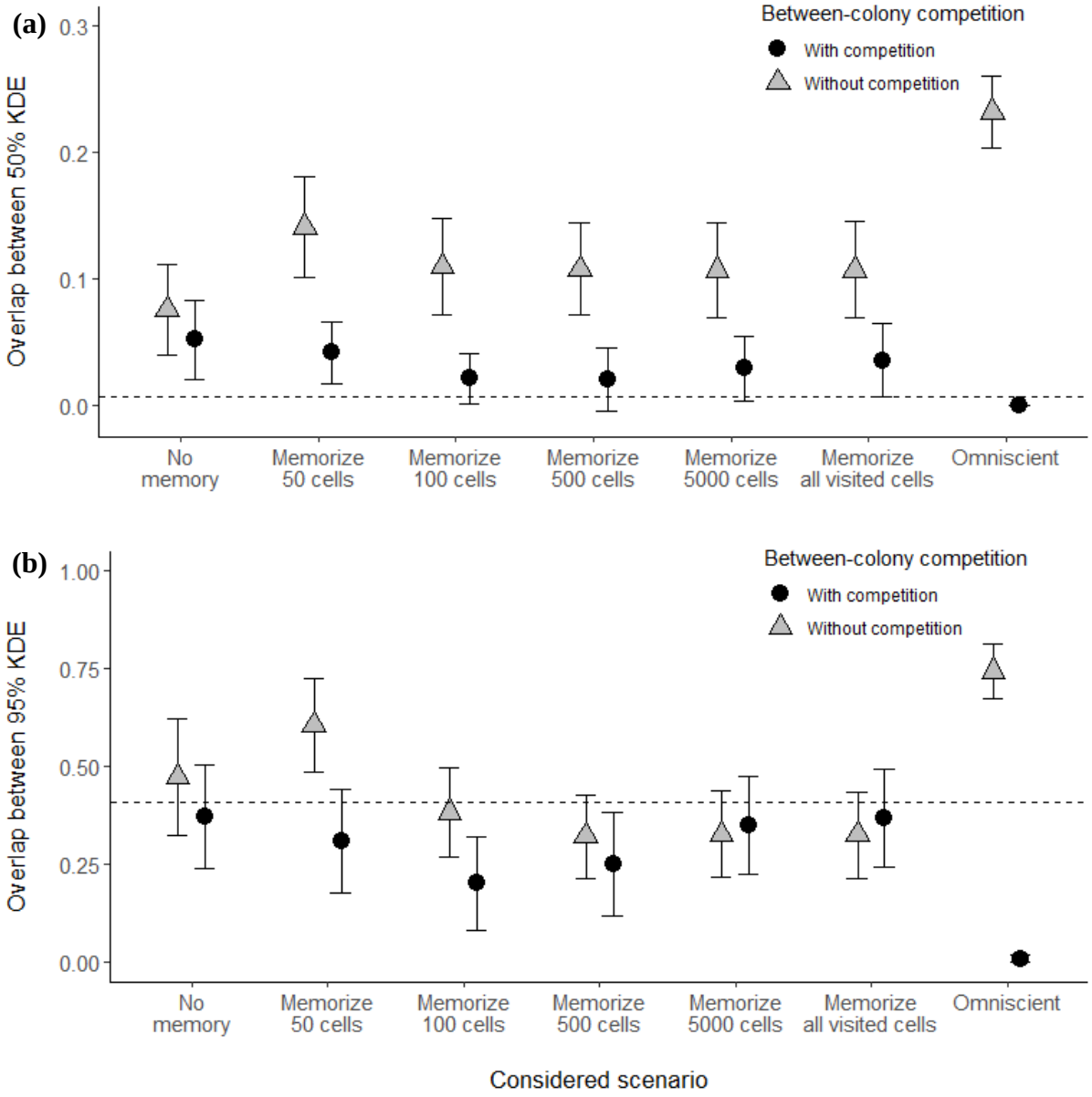


Figure 5. UDOI values between (a) 50% and (b) 95% KDE obtained from the simulated data for all modelled scenarios, both with (black circle) and without (grey triangle) competition for food resources between sub-colonies. The dashed lines correspond to the value obtained from our empirical data (from overlap between KDE derived at the sub-colony level).

Table 1. Sub-colony differences in foraging trip characteristics, breeders' and nestlings' traits. The unit of each variable is given in parenthesis. We also provide the mean, standard deviation, and sample sizes for each variable and sub-colony, and, when available, the associated statistic and *p*-values (not available for the Bayesian mixed circular regression of the bearing). Values in bold are significantly different between the two sub-colonies. Circular SDs were calculated using the '*circular*' R package (Agostinelli and Lund, 2017).

Variable	**Sub-colony mean ± SD** *(Sample size)*		***Statistic***	***p-value***
	Genio	**Provincia**		
Individual bearing *(°)*	**-146.61 ± 1.14** *171 trips, 15 ind.*	**122.27 ± 0.72** *152 trips, 24 ind.*	**-**	**-**
Individual size of daily used area *(ha)*	75.10 ± 70.31 *25 days, 10 ind.*	41.99 ± 30.17 *23 days, 15 ind.*	t = -0.78	p = 0.45
Individual daily ODBA *(g)*	0.29 ± 0.13 *51 days, 14 ind.*	0.29 ± 0.13 *90 days, 29 ind.*	t = 0.28	p = 0.78
Individual trip duration *(min)*	71.50 ± 64.15 *153 trips, 15 ind.*	68.56 ± 62.35 *139 trips, 23 ind.*	t = -0.52	p = 0.61
Individual breeders' SMI *(g, std. by sex)*	-0.07 ± 1.00 *153 breed., 129 ind.*	0.04 ± 1.00 *302 breed., 235 ind.*	t = 0.92	p = 0.36
Nestling body mass *(g)*	41.53 ± 25.12 *90 nestlings*	43.59 ± 28.76 *144 nestlings*	t = 0.80	p = 0.43
Nestling survival per nest *(nb.)*	2.80 ± 0.93 *49 nests*	2.65 ± 0.96 *82 nests*	W = 2177	p = 0.40
Sub-colony age composition *(prop. of old breeders)*	0.73 *59 breed., 44 ind.*	0.76 *138 breed., 89 ind.*	z =0.10	p = 0.92

Supplementary Material

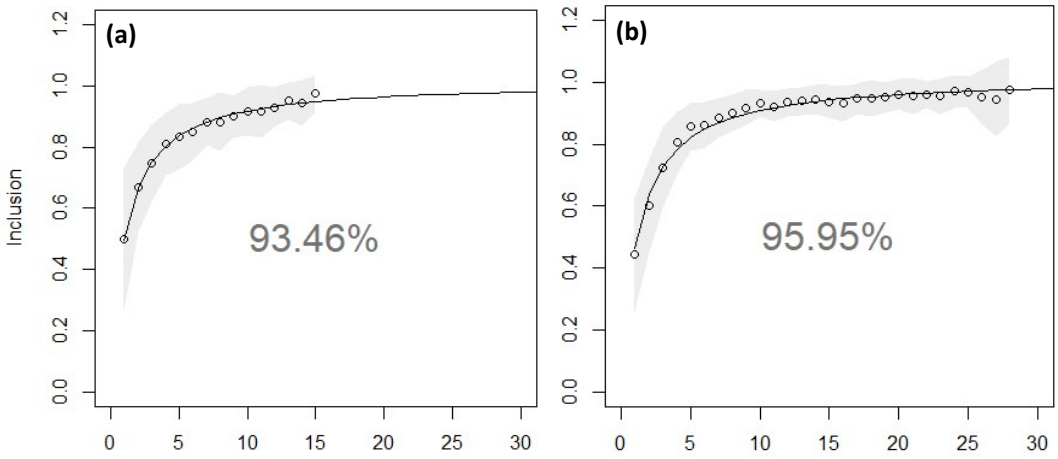


Figure S1. Representativeness curve for (a) Genio and (b) Provincia sub-colonies. The curves represent the inclusion of out-of-sample GPS positions from the 95% kernel density estimates of the sampled GPS positions, the sample size being comprised between 1 and N-1 (N=16 for Genio and 29 for Provincia) individuals. The solid lines represent the nonlinear regression lines, and the shaded areas correspond to the variability among the 100 draws for each sample size. Representativeness values (written in grey) were estimated from the asymptote of the linear regressions. Procedure based on Lascelles et al. (2016).

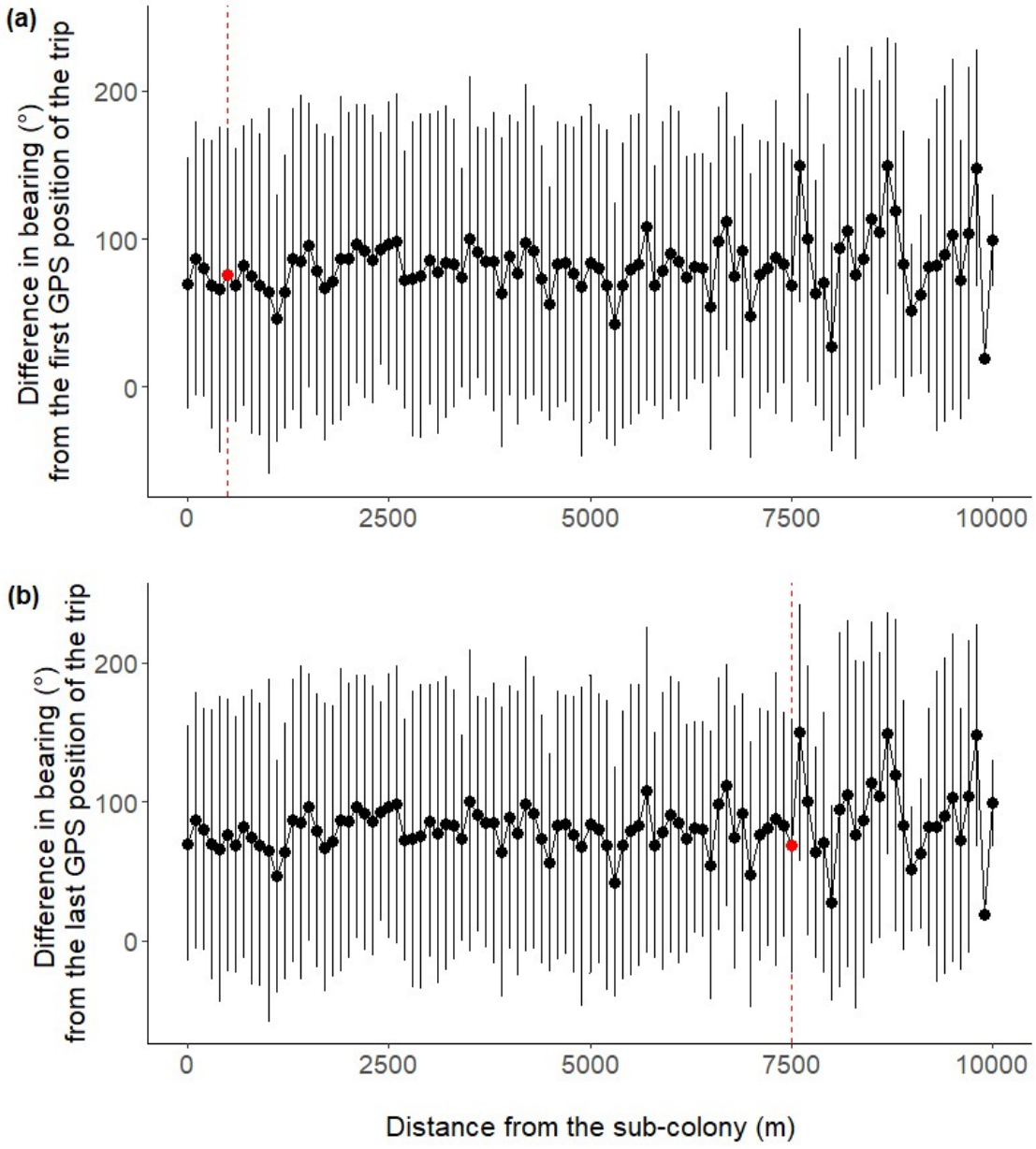


Figure S3. (a) Stabilisation of bearings after 500m travelling off the sub-colony and (b) evidence of relatively directed flights for individuals returning to the sub-colony. Dots correspond to the average difference, across foraging trips, between (a) the first and subsequent GPS positions of a trip or (b) the last and previous GPS positions of a trip. GPS positions were classified in categories of distances to the sub-colony (each 100 m). The red dot and vertical dashed line highlight (a) 500 m, a distance after which the difference in bearing between the first and each other positions seems to stabilise, or (b) 7500m a distance from which there is no drastic distance dependent change in orientation. Vertical solid lines delimit the mean ± SD.

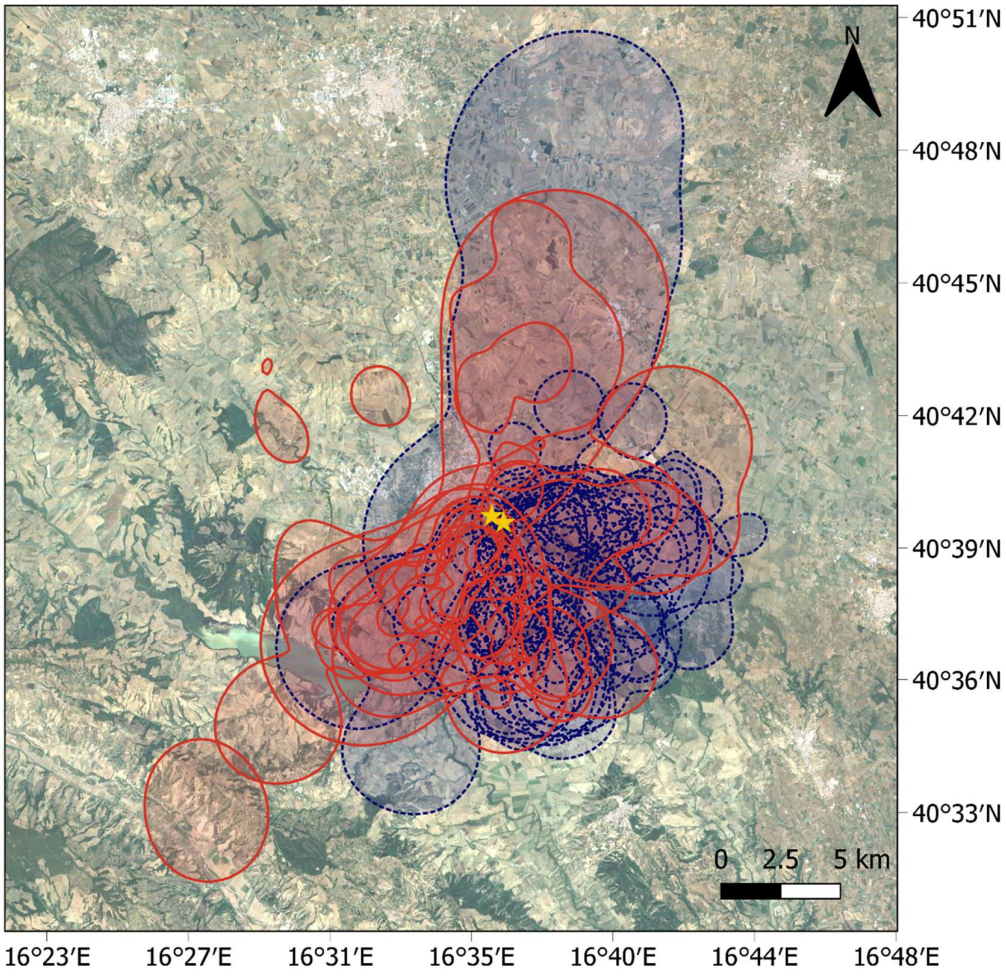
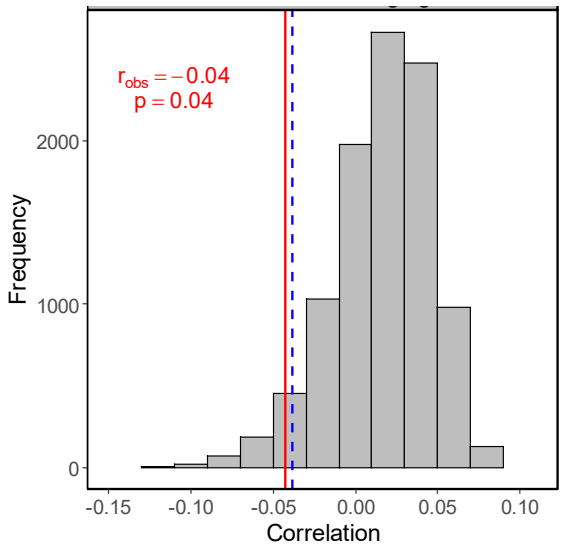


Figure S6. Contours of all individual 95% KDEs. Individuals from Genio are represented in red (solid lines, sub-colony at the north-west) and individuals from Provincia are represented in blue (dashed lines, sub-colony at the south-east). Sub-colonies are identified by stars.



27

28 **Figure S5. Testing spatial segregation between sub-colonies.** We show the observed point
29 biserial correlation (red line) and frequency of random correlations (grey bars) between the
30 upper parts of the matrix of overlap between individual 95% KDE and the sub-colony
31 membership matrix. The dashed blue line indicates the limit of the 5% lowest value of the
32 10,000 random correlations. The sub-colony membership matrix comprises zeros when
33 individuals belong to the same sub-colony and ones otherwise. A low value of observed
34 correlation compared to the random ones means that individuals from the two sub-colonies
35 segregate during their foraging trips.

36

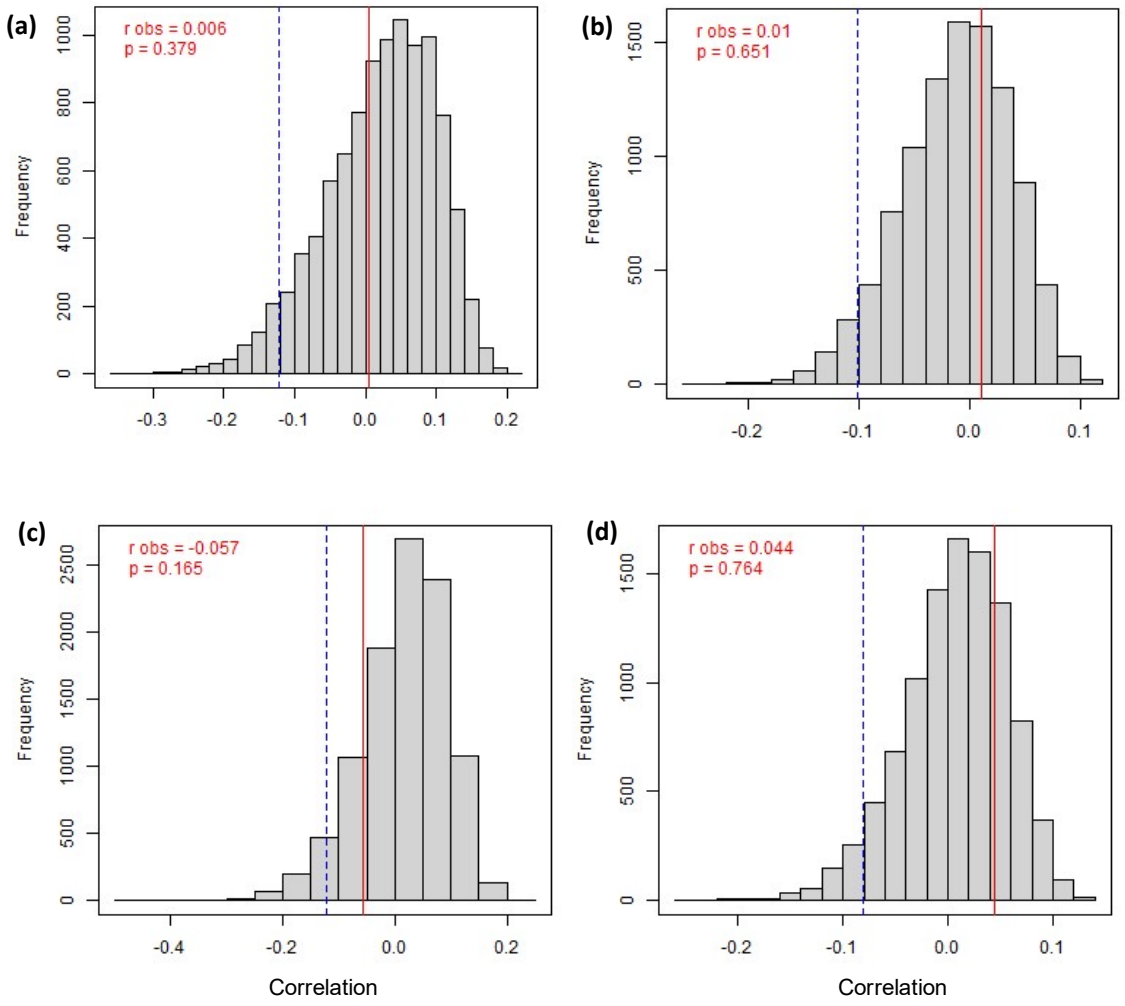


Figure S6. Observed (red line) and random (grey bars) correlations between the matrix of overlap between individual 50% KDE (a,b) or 95% KDE (c,d) and the year matrix. Values were computed for Genio (a,c) and Provincia (b,d) sub-colonies. Dashed blue lines indicate the limit of the 5% lowest values of the 10,000 random correlations. We used the same randomization method as used to test spatial segregation, but estimated point biserial correlations between the upper parts of a matrix of kernel overlap and a 45x45 binary 'year' matrix describing whether individuals were tagged the same year (0) or different years (1). A high value of observed correlation, falling within the 95% of random correlations, thus means that individuals tagged the same year did not overlap more than individuals tagged in different years.

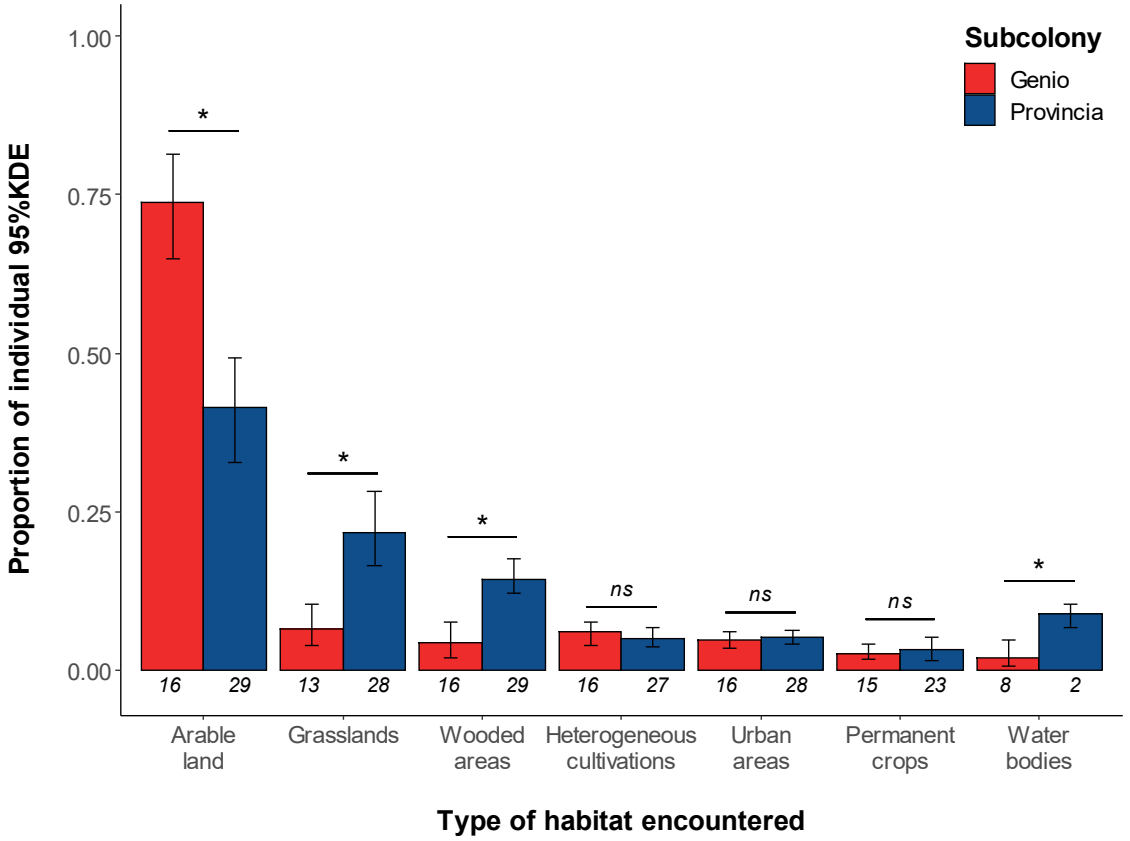


Figure S7. Proportion of habitat types encountered by lesser kestrels from the two sub-colonies during foraging trips (Genio, left bars; Provincia, right bars). Each bar indicates the predicted mean and associated 95% CI estimated by bootstrapping. Stars and 'ns' indicate significant and non-significant sub-colony differences respectively. Number of individuals encompassing each habitat type in its home-range is given below each bar. Note that the difference in water bodies encountered between individuals from Genio and Provincia is based on a very small sample.

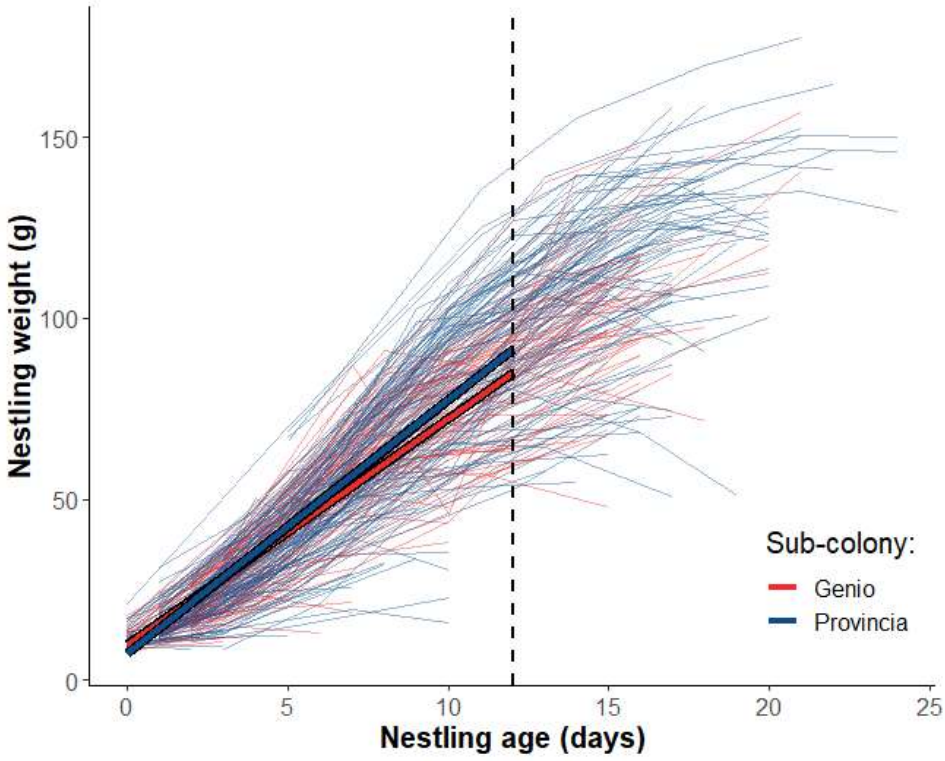


Figure S8. Nestlings' growth curves for both Genio and Provincia sub-colonies. Curves are drawn from data collected in 2016-2018 on 260 nestlings from 53 nests. The vertical dashed line indicates the limit of 12 days, before which the growth is linear. Fitted slopes of nestlings' growth for the period 0-12 days for both sub-colonies are represented on top of the curves (extracted from the fitted linear mixed model, see main text).

Table S1. Sample sizes described by year, sex, and sub-colony ('Genio' or 'Provincia'). We provide here the number of GPS-tagged individuals included in the analyses, the mean individual sampling duration, and the total number of foraging trips considered.

Year	Subcolony	Number of individuals	Mean sampling duration (± SE) in hours / individual	Total number of foraging trips
2016	Genio	2 (0♀ - 2♂)	58.0 ±25.7	35
	Provincia	11 (4♀ - 7♂)	52.8 ±7.6	75
2017	Genio	6 (1♀ - 5♂)	82.4 ±8.4	112
	Provincia	6 (2♀ - 4♂)	53.5 ±3.9	57
2018	Genio	4 (2♀ - 2♂)	57.7 ±19.9	70
	Provincia	7 (4♀ - 3♂)	73.7 ±11.3	140
2020	Genio	4 (3♀ - 1♂)	94.0 ±9.9	110
	Provincia	5 (4♀ - 1♂)	54.9 ±10.4	92
All years	Genio	16 (6♀ - 10♂)	76.2 ±7.3	327
	Provincia	29 (14♀ - 15♂)	58.5 ±4.5	364

Table S2. Models testing for alternative hypotheses regarding recapture (p, considered as a cue of philopatry) and survival (Φ) probabilities, considering different subgroups of adult breeding lesser kestrels over 5 years. Models are ranked according to increasing AICc values. M: male, F: female; G: Genio sub-colony; P: Provincia sub-colony. Akaike Information Criterion (AICc here). For each model, the tested hypothesis is expressed between brackets. (.): no differences between any group; (P+G): differences between sub-colonies; (M+F): difference between sexes; (GM+GF+PM+PF): differences between sub-colonies and sexes; (t): differences between years. Effective sample size: 216 individuals.

Ranking	Model notation	Model explanation	AICc	ΔAICc	Model Likelihood	Nb of estimated parameters
1	p(t)Φ(.)	Recapture probability only changes with time; Survival probability is constant over time sexes and sub-colonies.	361.49	0.00	1.00	4
2	p(t)Φ(t)	Recapture and Survival probability only change with time.	363.28	1.79	0.41	5
3	p(t)Φ(M+F)	Recapture probability only changes with time; Survival probability differs between males and females.	363.37	1.87	0.39	5
4	p(t)Φ(G+P)	Recapture probability only changes with time; Survival differs between the sub-colonies Genio and Provincia.	363.59	2.10	0.35	5
5	p(M+F)*t)Φ(.)	Recapture probability changes with time and between sexes; Survival probability is constant over time sexes and sub-colonies.	367.38	5.89	0.05	7
6	p(t)Φ(GM+GF+PM+PF)	Recapture probability only changes with time; Survival differs between sub-colonies of Genio and Provicncia as well as between sexes.	367.40	5.91	0.05	7
7	p(G+P)*t)Φ(.)	Recapture probability changes with time and between sub-colonies; Survival probability is constant over time sexes and sub-colonies.	367.84	6.35	0.04	7
8	p(.)Φ(.)	Recapture probability and survival are constant over time, sexes and sub-colonies.	368.01	6.52	0.04	2
9	p((M+F)*t)+Φ(M+F)	Recapture probability changes with time and between sexes; Survival probability idiferrs between sexs.	369.24	7.75	0.02	8
10	p(t)+Φ((M+F)*t)	Recapture probability changes with time. Survival probability changes with time and between males and females.	369.49	8.00	0.02	8

Table S2 (suite). Models testing for alternative hypotheses regarding recapture (p, considered as a cue of philopatry) and survival (Φ) probabilities, considering different subgroups of adult breeding lesser kestrels over 5 years. Models are ranked according to increasing AICc values. M: male, F: female; G: Genio sub-colony; P: Provincia sub-colony. Akaike Information Criterion (AICc here). For each model, the tested hypothesis is expressed between brackets. (.): no differences between any group; (P+G): differences between sub-colonies; (M+F): difference between sexes; (GM+GF+PM+PF): differences between sub-colonies and sexes; (t): differences between years. Effective sample size: 216 individuals.

Ranking	Model notation	Model explanation	AICc	ΔAICc	Model Likelihood	Nb of estimated parameters
11	p((G+P)*t)Φ(M+F)	Recapture probability changes with time and between Genio and Provincia; Survival probability differs between males and females.	369.77	8.28	0.02	8
12	p(.)Φ(M+F)	Recapture probability is constant; Survival probability differs bewteen males and females.	369.84	8.35	0.02	3
13	p(M+F)Φ(.)	Recapture probability differs between sexes; Survival probability is constant over time sexes and sub-colonies.	369.98	8.49	0.01	3
14	p((G+P)*t)Φ(G+P)	Recapture probability changes with time and between Genio and Provincia; Survival probability differs between the sub-colonies of Genio and Provincia	370.00	8.51	0.01	8
15	p(G+P)Φ(.)	Recapture probability differs between sub-colonies; Survival probability is constant over time sexes and sub-colonies.	370.06	8.57	0.01	3
16	p(M+F)Φ(M+F)	Recapture and survival probabilities are constant in time but differ between males and females.	371.91	10.42	0.01	4
17	p(G+P)Φ(G+P)	Recapture and survival probabilities are constant in time and between sexes but differ between the two sub-colonies.	372.14	10.65	0.00	4
18	p((G+P)*t)Φ(GM+GF+PM+PF)	Recapture probability changes with time and between Genio and Provincia; Survival differs between sub-colonies of Genio and Provicncia as well as between sexes.	373.92	12.43	0.00	10
19	p(GM+GF+PM+PF)Φ(M+F)	Recapture probability is constant in time but changes betwen sexes and sub-colonies; Survival probability differs between sexes.	376.12	14.62	0.00	6

Table S3. Parameter estimations for the three best-ranking equivalent models from the CMR analysis (see Table S2). *p*: recapture probability. Φ = survival probability, M: male, F: female

Model Ranking	Parameter	Estimate	SE	Confidence Intervals (95%)	
				Lower	Upper
1	*p* (2016 to 2017)	0.450	0.000	0.450	0.450
	p (2017 to 2018)	0.301	0.094	0.152	0.509
	p (2018 to 2019)	0.720	0.089	0.520	0.860
	p (2019 to 2020)	0.634	0.093	0.441	0.793
	Φ	0.679	0.060	0.551	0.785
2	*p* (2016 to 2017)	0.450	164.068	0.000	1.000
	p (2017 to 2018)	0.324	0.107	0.156	0.555
	p (2018 to 2019)	0.708	0.094	0.499	0.855
	p (2019 to 2020)	0.655	145.916	0.000	1.000
	Φ (2016 to 2017)	0.450	564.022	0.000	1.000
	Φ (2017 to 2018)	0.617	0.123	0.367	0.817
	Φ (2018 to 2019)	0.720	0.097	0.500	0.869
	Φ (2019 to 2020)	0.655	145.901	0.000	1.000
3	*p* (2016 to 2017)	0.450	457.553	0.000	1.000
	p (2017 to 2018)	0.302	0.094	0.153	0.510
	p (2018 to 2019)	0.721	0.089	0.520	0.860
	p (2019 to 2020)	0.638	0.094	0.442	0.797
	Φ (Males)	0.653	0.082	0.481	0.793
	Φ (Females)	0.692	0.067	0.549	0.806

Text S1. Empirical investigations of correlates of foraging spatial segregation

Foraging spatial segregation could originate from, or conversely result in, individuals from different sub-colonies (i) encountering and foraging in different habitats and (ii) performing differently during their foraging trips. For example, individuals from one sub-colony could be performing short trips, to targeted grassland areas, and spending less energy on a daily basis, while individuals from the other colony would mostly perform long foraging trips to extended arable land and show higher energy expenditure. In accordance, we tested whether individuals from the two sub-colonies (1) encountered different habitat types, (2) showed different duration of foraging trips, (2) used a different spatial extent of foraging areas on a daily basis, and (4) showed different energy expenditure while foraging. To test whether a significant segregation and differences in habitat encountered could result in different reproductive success between sub-colonies, we tested whether nestlings hatched in the two sub-colonies showed (5) different growth rates or body conditions and (6) survival (up to 14 days).

In relation to these differences, the two sub-colonies could be hosting different phenotypes, which may lead to foraging segregation. We may for example expect experienced, good-quality individuals to aggregate in one, possibly better, breeding site. These individuals may also intrinsically behave differently during foraging, or use different areas than less experience individuals. We then also tested whether the two sub-colonies encompassed individuals (7) with different body condition, (8) of different age classes (9) or with different dispersal status (native vs. immigrant).

Except for the CMR model (see below), all analyses were performed in R v.3.6.3 (R Core Team, 2020). All LMMs were fitted with the function *lmer* from the *'lmerTest'* R package (Kuznetsova et al., 2017). Binomial GLMM fit were assessed with ROC curves and AUC values (*'pROC'* R package, Robin et al. 2011).

Sub-colony differences in encountered habitat

Similarly to Cecere et al. (2018), we considered 7 categories of habitats based on the land use categories of CLC12: arable land (codes 21x), permanent crops (codes 22x), heterogeneous cultivations (codes 24x), grasslands (codes 23x and 321), wooded areas (codes 31x, 322, 323, 324, 33x), urban areas (codes 1x, 12x, including mineral extraction sites coded 131), and water bodies (codes 5xx, 41x). We extracted the proportion of each habitat type within the individual

95% KDEs with the functions *gIntersection* and *gArea* (*'rgeos'* R package, Bivand and Rundel 2020). We analysed these proportions as compositional data and fitted a linear model with isometric log-ratio transformation (*rcomp* data type, '*compositions'* R package, van den Boogaart et al. 2020), including sub-colony identity as a binary covariate.

Sub-colony differences in space use and foraging trips characteristics

We estimated trip duration for all trips that departed and ended within 200 m from the colony. Then, we estimated the size of daily used area for each individual with the *getverticehr* function (from the *'adehabitatHR'* R package, Calenge, 2006; retaining days during which the first foraging trip of the individual started before 6:00 and its last one ended after 17:00 local time, and removing non-foraging relocation positions). Finally, we used the individual daily Overall Dynamic Body Acceleration (ODBA, averaged over all collected values in a day) as a proxy of energy expenditure (Wilson et al., 2006). ODBA was estimated from the tri-axial accelerometer data, by smoothing total acceleration over 1 s and averaging ODBA values during foraging trips over the day (including incomplete days). We $\log_{10}$-transformed all three variables to ensure normality of the residuals, and compared them between sub-colonies with LMMs while also controlling for breeding stage (late incubation vs. early nestling-rearing) and date to account for potential daily meteorological effects. Individual identity was included as a random factor.

Sub-colony differences in nestling performance and adult quality

For these tests, we excluded from the datasets some nests subjected to experiments in 2016 and 2017 (see Costanzo et al., 2020; Podofillini et al., 2019; Soravia, Cecere, & Rubolini, 2021).

In 2016-2018, nestlings were regularly weighed (up to 6 times between hatching and day 20 post-hatching) and their survival monitored as part of another study. We first compared the growth and body condition between nestlings from the two sub-colonies, by fitting the nestling body mass with a LMM, including sub-colony, nestling age and their interaction as covariates, and both individual and nest identity as random factors. We restricted this analysis to measurements taken up to 12 d of age, i.e. when the growth curve was linear (Figure S7). Second, we used the number of alive nestlings in each nest after 14 d as a proxy of reproductive success, and compared it between the two sub-colonies using a Wilcoxon test. Considering survival after 14 d in lesser kestrels is problematic as nestlings tend to wander around their nest,

on the roof terraces, and change nesting site, especially when a perturbation occurs (e.g. field workers walking on the roof). The probability of recapture of nestlings after 14 d in or near their nest is thus not representative of their survival.

To assess breeders' condition from 2016-2020 capture data, we estimated adults' Scaled Mass Index (SMI; following Peig and Green 2009, Podofillini et al. 2019). We fitted SMI values in a LMM with sub-colony identity as a fixed effect and individual identity as a random factor.

Sub-colony differences in adult age

Based on recaptures of ringed breeders (and in two occasions on plumage criteria), we assigned a categorical age (young breeders when ≤ 2 years, old breeders when ≥ 3 years) to 133 individuals breeding in the two sub-colonies of interest (197 breeding events between 2016 and 2020; 40 females and 93 males). To test for difference in age-composition of breeders between the two sub-colonies, we fitted a binomial Generalized Linear Mixed model (GLMM) with age (0 = young breeders, 1 = old breeders) and sub-colony identity as predictors, and individual identity as a random factor.

Sub-colony differences in dispersal: use of a Capture-Mark-Recapture approach

To test for differences in philopatry and immigration rate of breeders between the two sub-colonies, we implemented a Capture-Mark-Recapture (CMR) model in MARK v 9.0 (White & Burnham, 1999). Each individual was attributed to the sub-colony in which it was firstly captured as breeder, discerning between Provincia and Genio. We then built individual capture histories, attributing 1 for each year in which the bird was recaptured at its own sub-colony and 0 for years when this did not occur. Based on AICc, we compared models testing different hypotheses that survival and/or recapture probabilities differed among years (time effect), sexes and/or sub-colonies.

We relied on five encounter occasions (i.e. five reproductive seasons, 2016 to 2020) and 346 individuals divided in four groups according to their sex (F : Female, M : Male) and sub-colony (P : Provincia, G : Genio). We did not include any other individual covariate. In the event matrix, we coded each individual recapture history as 0 (individual not seen breeding/recaptured in its main sub-colony) or 1 (individual seen breeding/recaptured in its main sub-colony; see main text). MARK allowed to model separately the probability of

183 recapture, parameter *p* (which, here, informs on the philopatry) and the 'true' survival (Φ). Of
184 course, it must be stressed that even in CMR framework, permanent desertion of a site cannot
185 be discerned from death. We tested 19 alternative models as presented in Table S2.

186 Goodness-of-fit tests were performed in U-CARE v3.3 (Choquet et al., 2009) following
187 the indications of Choquet et al. (2020). At this step, running the we found a significant
188 'transient' effect in the database (i.e. an excessive number of individuals that were captured
189 only once, potentially biasing the findings of the CMR analysis). To solve this issue and proceed
190 with the analysis, we thus relied on the approach proposed by Pradel et al. (1997), consisting in
191 removing the first capture event of all the individual capture histories. The database was
192 restructured in this sense in U-CARE v3.3. The new database contained an effective sample
193 size of 216 individuals out of the 346 originally available. After the removal of the firs capture
194 events of all the individuals, we obtained non-significant results in the rest of the goodness-of-
195 fit tests that are reccomended by Choquet et al. (2020) (i.e. TEST3.SM, TEST2.CT and
196 TEST2.CL) to verify the assumptions of the Cormack-Jolly-Seber model in presence of
197 transients.

198 There was a very clear and strong effect of time (here 'years') on recapture probability (Table
199 S2), indicating significant differences in recapture probability among different years. This
200 effect is likely due to an increasing number of marked individuals from the first to the fifth
201 study year, but is also likely to be affected by varying weather conditions, eventually
202 influencingthe recapture probabilities among years. Noteworthily, our findings robustly state
203 that recapture probability (*p*, here considered as a proxy of philopatry) did not differ between
204 the sub-colonies of Genio and Provincia, since all the models including this hypothesis - despite
205 of the parametrization of the survival - are ranked far from the best models (Table S2). Estimates
206 of recapture probability varied from a minimum of 30.1% (interval 2017-2018, model 1) to a
207 maximum of 72.1% (interval 2018-2019, model 3), with an overall mean assessed at the 53%.
208 All the three best models coeherently estimated the highest recapture probabilities in the 2018-
209 2019 interval and the lowest in the 2017-2018 interval. Survival probabilities (*Φ*) showed a
210 different pattern from those of recapture probability, since AICc values ranked as equivalent
211 three models (Table S2), assuming respectively (1) a constant survival across years, sexes and
212 sub-colonies, (2) a survival changing only with time and (3) a different survival between males
213 and females. Survival estimates ranged from 72% (interval 2018-2019, model 2) to 45%
214 (interval 2016-2017, model 2) and resulted in 67.9% in model 1. In model 3, in which it is
215 estimated separately for sexes, survival was higher for females.

Text S2. Individual Based Model

The model was adapted from Aarts et al. (2021). Here, we transpose the structure of model description from Aarts et al. (2021) to mention any changes made. See Table S4 for a summary of the key model parameters.

Spatial distribution of sub-colonies and resources

Based on the monitoring of Matera main sub-colonies between 2016 and 2020, we simulated 350 lesser kestrels, distributed among 7 sub-colonies: 18 breeding lesser kestrels in sub-colony n°1, 18 in n°2, 64 in n°3, 56 in n°4 (Genio), 32 in n°5, 50 in n°6, and 112 in n°7 (Provincia). The arrangement of the sub-colonies was fixed and corresponded to their true geographical arrangement in Matera city.

The map of resources was a 240 × 240 grid cell with impenetrable boundaries. Each cell corresponded to an area of 100 × 100 m, simulating 24 km around the average central location among the 7 sub-colonies. Based on the true Corine Land Cover 2021 habitat classification map (https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012), we retrieved for each cell the percentage of unsuitable foraging site (i.e. globally unsuitable sites as considered in the main text [urban, open, and water areas], plus wooded areas which lesser kestrels can fly over, as shown in Figure S6, but in which they do not forage; codes 11x, 12x, 13x, 14x, 244, 31x, 33x, 41x, 42x, 51x, and 52x). If the percentage of unsuitable area exceeded 10% in a cell, we considered this cell as not exploitable by foraging lesser kestrels, and we attributed it 0 prey items, thus precluding lesser kestrels from feeding on it. For the exploitable cells, we attributed a fixed initial number of preys (between 3 and 7), following a uniform distribution.

Lesser kestrels' foraging decisions

Each day, lesser kestrels performed an unlimited number of trips during 14 h, mimicking their diurnal foraging behaviour between 5:00 and 19:00 local time. At the start of the simulation, all individual cognitive / memory maps consisted of 0 prey in unusable cells and 5 prey items in exploitable ones. For each foraging trip, an individual selected the grid cell with the highest anticipated intake rate (similarly to Aarts et al., 2021). More specifically, an individual would minimize the total time expected to spend on a foraging trip which is the sum of the required

travelling time to the cell i, and the expected time required to feed on 1 prey items in that cell, based on the a piori knowledge of the individual:

$$Expected.trip.duration_{expected,i} = Travelling.time_i + Expected.foraging.time_i$$

With:

$$Travelling.time_i = \frac{distance_i}{Movement.speed} \times 2$$

$$Expected.foraging.time_i = \frac{Resource.intake.at.each.trip}{Expected.food.density_i \times intake.rate.parameter}$$

$distance_i$ being the distance (in multiples of 100m) between the considered cell and the sub-colony, and the $expected.food.density_i$ being the expected prey content of the cell, according to the individual a priori, knowledge or memory. See Table S4 for details on the other parameters.

The value of expected trip duration was calculated for each cell, and averaged at 0.1 (i.e. 6 minutes). The cells with the minimum value were selected, and one of them was picked at random. Contrary to Aarts et al. (2021), once the individual reached this first cell, it detected prey abundance in this and all nearby cells within a 300 m radius. It then selected the best cell among these 29 perceived ones. The true time needed to forage in this selected cell was drawn from a gamma distribution:

$$\Gamma\left(k = Resource\ intake\ at\ each\ trip, \theta = {}^{1}/_{food_i \times intake.rate.parameter}\right)$$

with $food_i$ being the number of prey really resent in the cell i.

If the true time needed to forage was greater than a threshold (0.5 h), the individual would move to the next cell with the highest anticipated intake rate and at least 600 m far and will continue with the same decision rules. Conversely, if the true time needed to forage was lower than the 0.5 h threshold, the individual would hunt 1 prey and come back to the colony to deliver the food item to its nestlings. The true prey content of the exploited cell was then reduced by 1 prey.

If the cell was fully depleted, we considered that its resource content was 0.01 prey items, to enable replenishment the following night (see Equation 1). If the total time of the foraging trip exceeded 5 hours, the individual returned to its nest without food. For simplicity, we did not consider daytime rest at the sub-colony: individuals engaged in the next foraging trip immediately after finishing the preceding one. No exploration was considered in the model.

Lesser kestrels travelling speed was set to 23km/h, based on the empirical GPS data for outward and inward travel.

Resource renewal

Resources were partially renewed every day (during night-time) to simulate reproduction (for insects) and movements of prey. Similarly to Aarts et al. (2021), we implemented a renewal function for the resource. In our model, it consisted in the resources X, in cell i on day d+1, being replenished based on a certain proportion of the initial prey content of the cell $X_{i,0}$:

$$X_{i,d+1} = X_{i,d} + rX_{i,0}\left(1 - \frac{X_{i,d}}{K}\right) \quad \text{Equation 1}$$

r being the intrinsic replenishment rate (0.2) and *K* being the maximum carrying capacity of the cell (20 prey items), considered homogeneous among all exploitable cells. There was thus heterogeneity in resource dynamics (i.e. in the speed at which each cell replenished), while the maximum carrying capacity *K* was the same for all cells.

Varying information on resource distribution

Individuals could memorise the content of each detected cell (based on the time it would have taken them to feed in the cell, drawn from a gamma distribution, see Aarts et al. (2021)). In our model, it means that individuals memorized at least 29 cells (all the cells within a 300 m radius form the first targeted cell) at each foraging trip (but see the different memory scenarios below).

Different simulation scenarios explored

We considered 3 different scenarios:

1. Good individual memory (as described in the main text) – For the main simulations, we considered that lesser kestrels could remember any visited cells (i.e. up to 240 × 240 cells; not only the immediately reached cell, but the 29 cells within the 300 m radius, see above).

2. Limited individual memory – Lesser kestrels could only remember a limited number of non-empty cells: the N most recently visited (N being set to 0, 50, 100, 500 and 5000), instead of up to 240 × 240 (57 600) in the main simulations (yet the maximum number of cell visited

was usually below 5,000 in practice, result not shown). Individuals then considered the other visited ones as containing 5 prey items (the initial a priori of the individuals for each cell).

3. Omniscient individuals – Lesser kestrels had a perfect knowledge of the true resource map at the time they are foraging.

For each of these scenarios, we run simulations considering 2 competitive contexts:

A. With between sub-colony competition – All sub-colonies were modelled together

B. No between-sub-colony competition – Each sub-colony was modelled alone to remove competition from the other sub-colonies.

Quantifying between-sub-colonies overlap in foraging distribution

Between-sub-colony overlap was calculated to compare the different scenarios. We used the Utilisation Distribution Overlap Index (UDOI; Fieberg and Kochanny 2005) to estimate the spatial overlap between pairs of sub-colonies. To obtain comparable measures with the empirical data, we converted back each position within the matrix to its accurate GPS position, and used *kernelUD* and *kerneloverlaphr* functions to compute the UDOI estimates (similarly to the empirical analysis, see main text; Calenge, 2006).

We assessed whether individuals segregated spatially more than assumed if they could forage uncounstrained around the subcolony by comparing the UDOI values with (A) and without (B) competition for all memory scenarios (1, 2 and 3).

Simulation settings

Simulations started at 5:00 on the first day, and lasted 40 d. At the start of the simulations, all lesser kestrels departed from their sub-colony within 3 minutes (individual starting time drawn from a uniform distribution). We did not consider any burn-in period, because we considered this learning phase as representative of the start of the reproductive period for a migratory species foraging in a dynamic farmland landscape. Yet, considering the first or last 20 days did not change the overall segregation pattern (Figure S11).

Table S4. Key model parameters. Most parameters were kept constant across simulations, except the ones highlighted in bold (memory type and size, and competition level).

Parameter	Value
Environment	
Cell size	1 ha (100 x 100 m)
Grid dimensions	240 x 240 cells (i.e., 24 x 24 km)
Initial resource landscape	- in exploitable sites: 0 prey item - in exploitable sites: $K_i \sim Uniform(3,7)$ *prey items*
Carrying capacity for prey items per cell	20 prey items
Initial ressource lanscape assumed by foraging individuals	- in exploitable sites: 0 prey item - in exploitable sites: 5 prey items
Replenishement rate	0.2
Replenishement interval	once a day (here a day lasts 14 hours, night time not modelled)
Foraging individual	
Resource intake at each trip	1 prey item
Movement speed	23 km/h (here 230 units of "100 m /h")
Intake rate parameter	0.8
Memory type	**Memorize or Omniscient**
Memory size when memorize type	**0, 50, 100, 500, 5000 or all visited cells**
Competition level	**- With competition (all 7 sub-colonies modelled) or** **- No competition (each sub-colony modelled seperately)**
Radius of prey assessment	within 300 m from the reached cell (i.e. 3 cells away)
Threshold time for foraging attempts per cell	0.5 h
Maximum duration of a foraging trip	5 h
Simulation duration	40 d

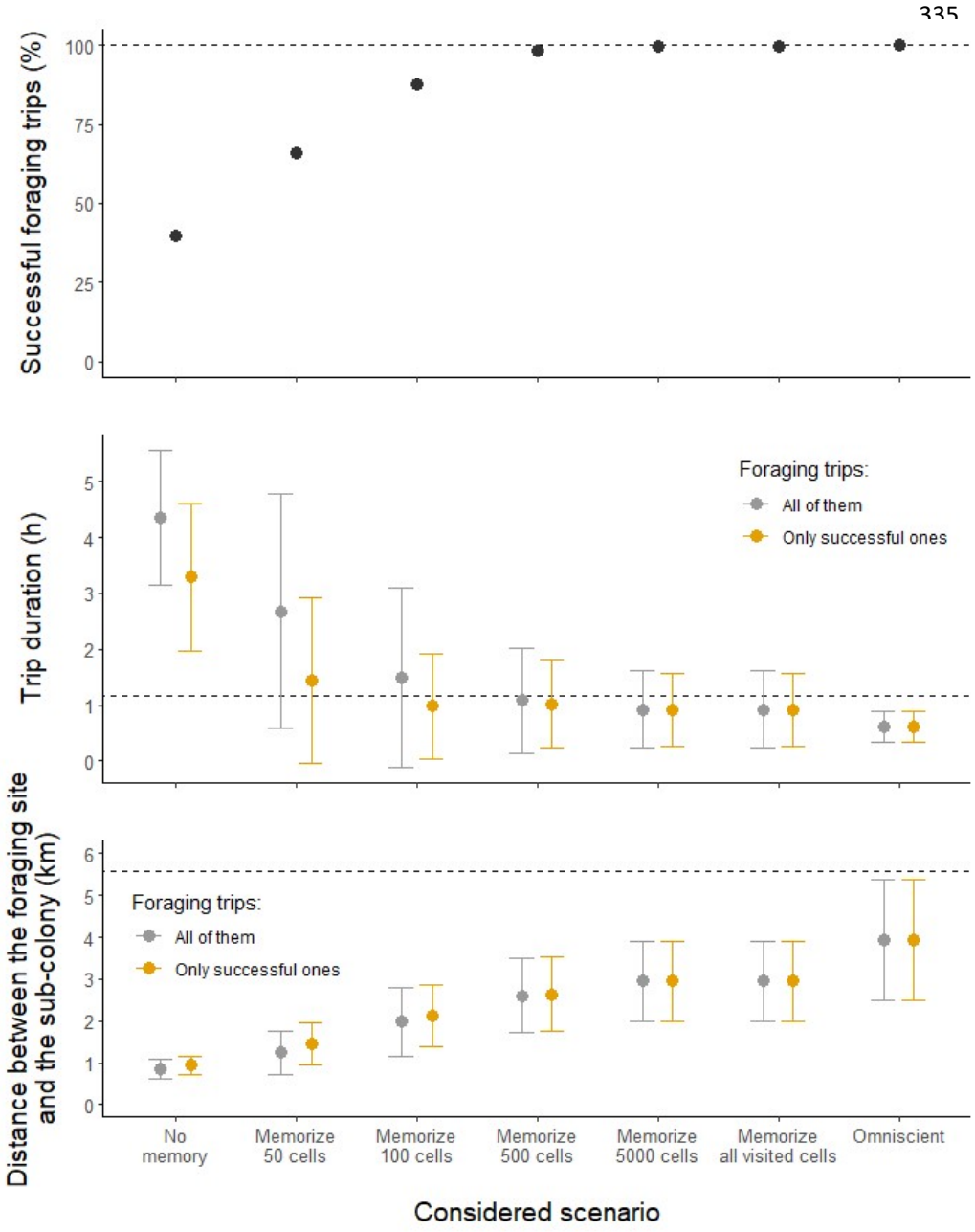


Figure S9. Main foraging trip output metrics for each of the tested scenario, including competition. (a) Percentage of successful foraging trips, i.e., trips during which the bird manage to capture one prey. (b) Mean trip duration and (b) foraging distance from the sub-colony (± SD) considering all foraging trips (grey) or only the successful ones (orange), during which the bird managed to capture one prey. The dashed lines correspond in (a) to the expected level, and in (b) and (c) to the sampled population mean from the GPS data. For (c) we estimated from the GPS data the distance of the furthest point reach, eventhough it may not necessarily correspond to a foraging event during the trip.

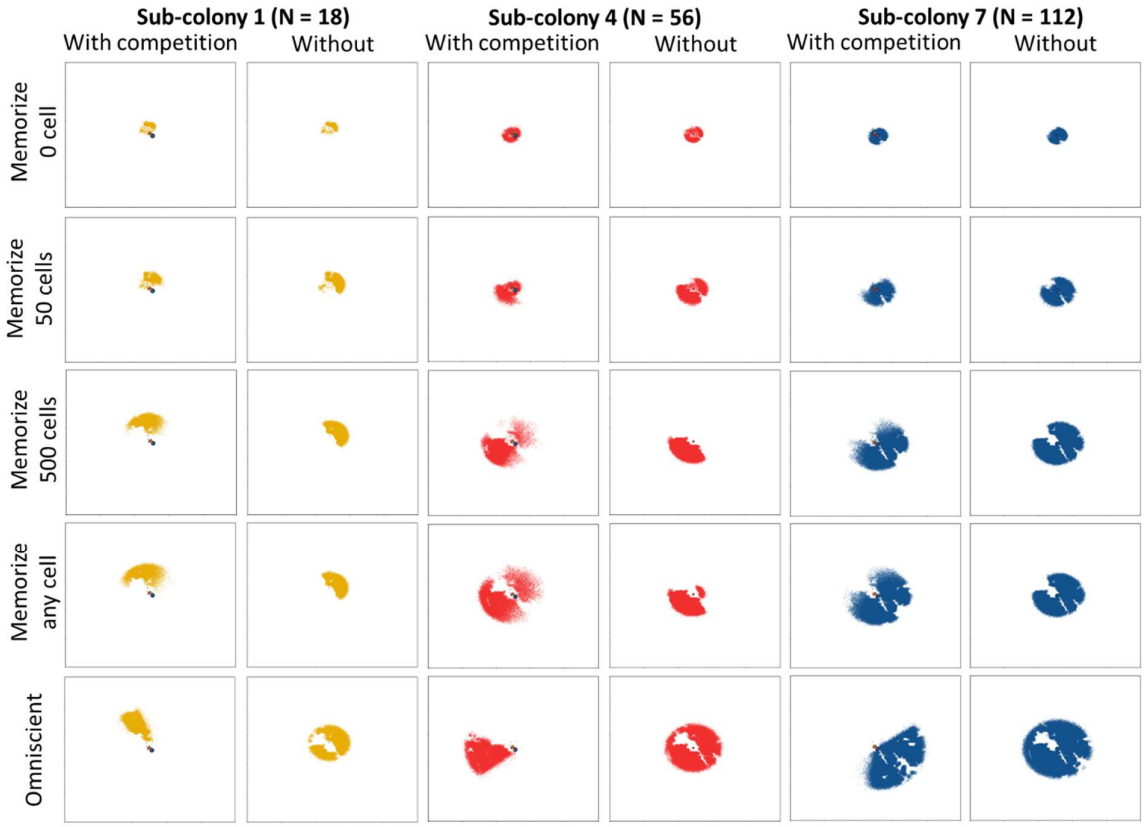


Figure S10. Comparison of foraging events by individuals from sub-colonies 1, 4 (Genio) and 7 (Provincia) for most tested scenarios: with no memory, a limited memory (here 50 and 500 cells memory limit are represented), unlimited memory, and omniscient knowledge of the environment. Foraging events for these scenarios are represented in two contexts: with and without competition. Larger opaque circles in the middle of each plot reflect sub-colony arrangements.

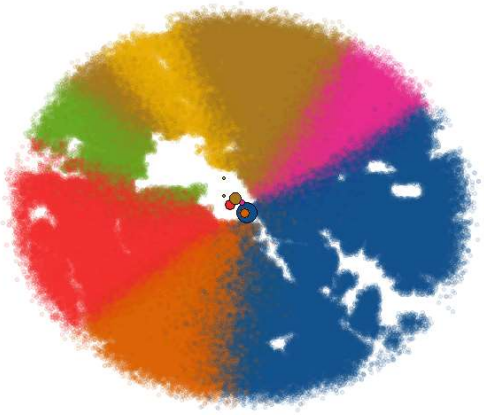


Figure S11. Location of foraging events when all individuals are omniscient regarding prey density. One colour corresponds to one sub-colony, and one dot to one foraging event. Larger opaque circles reflect sub-colony arrangements, and their sizes the number of breeders.

(a) (b)

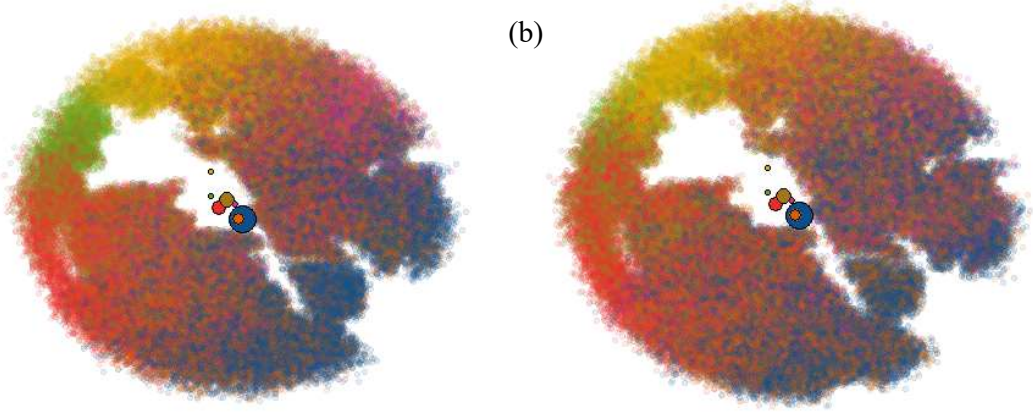


Figure S12. Location of foraging events for (a) the first half and (b) the second half of the simulations. This corresponds to the main scenario, in which individuals compete and can memorize all visited cells. One colour corresponds to one sub-colony, and one dot to one foraging event. Larger opaque circles reflect sub-colony arrangements, and their sizes the number of breeders.

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