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Research article

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

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Spatial segregation of foraging areas among conspecifics breeding in neighbouring colonies has been observed in several colonial vertebrates and is assumed to originate from competition and information use. Segregation between foraging individuals breeding in different parts of a same colony 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. To shed light on the processes (namely competition and memory) driving small-scale spatial segregation of foraging areas in colonial species, we used empirical data and developed an individual based model (IBM). By GPS tracking lesser kestrels *Falco naumanni* breeding in an urban area and foraging in the surrounding farmland, we found that foraging areas of individuals nesting in two close-by (ca 600 m) roof terraces (i.e. nest clusters) were significantly spatially segregated. Individuals from different nest clusters showed different departure bearings and encountered different habitats but showed similar fitness traits. Individuals from the same cluster did not seem to follow conspecifics when leaving for a foraging trip. The IBM, based on data from seven roof terraces, showed that such collective spatial segregation does not necessitate social information use: personal information and memory may be sufficient to mechanistically explain intra-colony segregation of foraging areas. Besides, there was a clear distance-dependent segregation: individuals from distant clusters segregated more, matching what is observed at large spatial scales (i.e. among neighbouring colonies). Our results do not question the fact that colonial species may use social information during foraging or that colonies can act as information centres. Instead, they suggest that within-colony foraging range spatial segregation, arising from simple mechanisms not necessarily involving

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information sharing, might be widespread in colonial systems. These results thus further challenge the long-standing view that colonies should be regarded as single cohesive entities.

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 is tightly associated with colony size, acting not only within colonies but also at a multi-colony scale (Cairns 1989), and may have consequences for population dynamics (Ashmole 1963, Furness and Birkhead 1984). As an ecological response, segregation of foraging areas among individuals from neighbouring 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, the use of social information or other cues exposing the presence of foraging conspecifics may be very limited in some contexts or systems (e.g. in species where the spatial scale of segregation in foraging distribution is much larger than the perception range, or species neither detecting conspecifics over large distances nor cues of foraging activity by conspecifics as they do not significantly modify the environment, like seals while foraging at sea). However, spatial segregation also occurs in these species (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). Far from being contradictory, Wakefield et al. (2013) and Aarts et al. (2021) revealed that density-dependent competition, spatial arrangements and sizes of colonies, together with memorized personal information, play a crucial role in colony-level segregation, which could be further reinforced by socially acquired information, for instance among species foraging in groups or relying on local enhancement at

foraging grounds. Lourie et al. (2021) developed an agent-based model and found that high degrees of memory and/or conformity (i.e. copying the choices of others, here members of the same colony), rather than the density of conspecifics, could lead to spatial partitioning of foraging sites among colonies of frugivorous bats. Their empirical investigation also revealed that memory and to a lesser extent conformity leads to spatial segregation in fruit tree foraging choices in bats. These results again highlighted the complex, intertwined, and varying effects of different processes leading to spatial segregation of foraging areas in colonial species.

All aforementioned empirical and theoretical studies focused on segregation of foraging areas between individuals from neighbouring colonies, separated by large or similar distances compared to foraging movements and by areas where foraging was possible and where spatial segregation emerged (Fig. 1, 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, sometimes spread within a landscape unsuitable for breeding or separated by physical barriers (e.g. rock crevices on the two sides of a promontory, Pereira et al. 2022, Waggitt et al. 2014, or small islets in an archipelago, Morinay et al. 2022; Fig. 1). Whether we call these sub-units 'sub-colonies', 'social units', 'clusters', 'groups', or 'nests aggregates' does not matter from a conceptual point of view, and there is no consensus regarding such terminology in the previous literature. Besides, even in large homogeneous colonies, an important distinction exists between 'between-colony' and 'within-colony' segregation. Within-colony segregation occurs when individuals from distinct sectors of a same colony 1) depart for foraging areas from very close locations compared to the extent of foraging movements, and 2) have departure locations that can be separated by unsuitable areas for foraging. Between-colony segregation instead implies that individuals breeding in distinct colonies depart for foraging areas from distant locations and that suitable foraging areas occur between departure locations (Fig. 1). Hence, individuals breeding in different parts of a same colony have access to a shared foraging area (the 'halo') surrounding the colony, entailing roughly similar travel costs, potentially leading to high levels of competition. We may thus expect strong selective pressures to reduce competition, leading to some behavioural differentiation in individuals nesting in different parts of a colony, such as foraging specialisation (Ramellini et al. 2022), and that minor differences in travel costs between parts of a colony will lead to spatial segregation in such highly competitive settings (Bolton et al. 2019, Fig. 1). Few
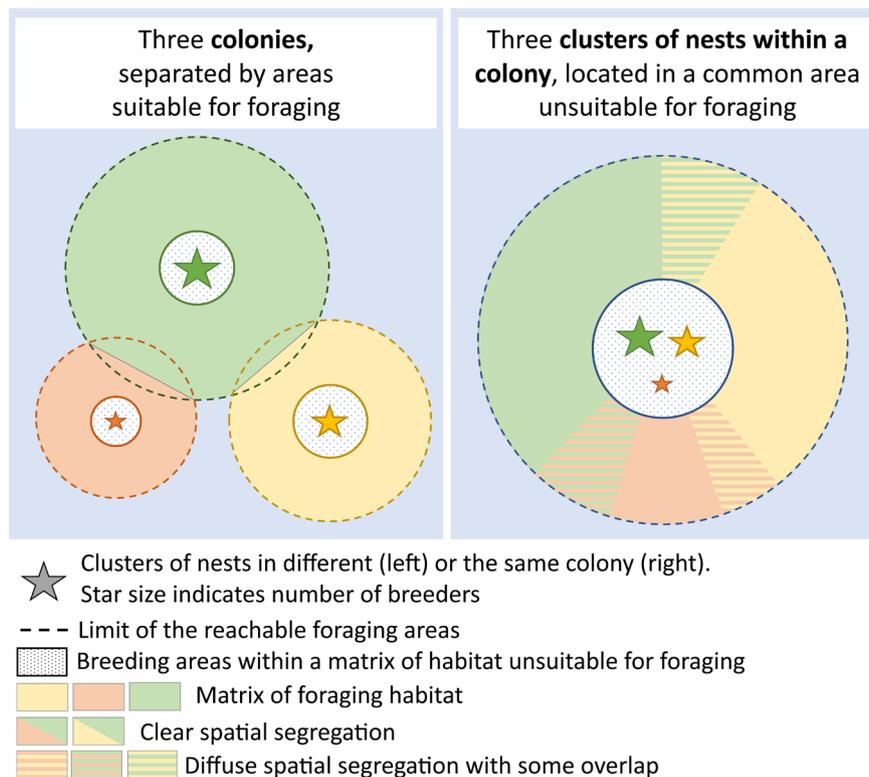
Figure 1. Conceptual differences between 'between-colony' and 'within-colony' spatial segregation during foraging. Unlike nesting sites located within a same colony (right), neighbouring colonies (left) are separated by foraging areas. Distances between colonies are also larger than between nesting sites within a colony, and comparable or higher than distances travelled while foraging. Therefore, clusters of nest sites within a colony share in theory the exact same halo of resources, making the competition for food likely more intense within-colonies than between neighbouring colonies. Yet, nests within a colony are located close to each other and individuals from different clusters of nests or simply different locations within the colony have approximately the same travel costs to reach the same foraging site . We thus expect spatial segregation to be clearer between colonies, and more diffuse within-colonies (i.e. with more overlaps of foraging areas). As the season progresses, we may expect an increase in travel time as resources close to the colony get depleted (Ashmole's halo effect), but this should affect all sectors of a colony and all colonies and is not represented here. This 'between'- and 'within-colony' distinction is relevant from a spatial ecology perspective but could differ in other contexts (e.g. landscape genetics, population dynamics). While this dichotomy is practical for researchers, the distinction between neighbouring colonies and different sectors of the same colony might be, in reality, rather part of a continuum between these two extreme conditions.

empirical studies, largely restricted to marine species, have explored spatial foraging segregation within-colonies compared to between neighbouring colonies (Masello et al. 2010, Bogdanova et al. 2014, Kuhn et al. 2014, Waggitt et al. 2014, Ceia et al. 2015, Sánchez et al. 2018, Pereira et al. 2022, Ito et al. 2021, Morinay et al. 2022). These studies, showing partly contrasting patterns, have not provided any firm conclusion yet on the specific ecological features or processes driving or preventing such segregation. 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 underlie within-colony 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 an individual based model (IBM), applicable not only to our study system but to colonial species more generally.

First, to provide empirical evidence of spatial segregation, we used GPS tracking data from 690 foraging trips performed by 45 lesser kestrels *Falco naumanni* breeding in two distinct parts of a large colony (ca 1000 pairs). The lesser kestrel is an ideal candidate to address questions related to spatial segregation of foraging areas. It is a colonial raptor that feeds on patchily distributed and relatively ephemeral preys (invertebrates, lizards, and small rodents Catry et al. 2016, Di Maggio et al. 2018, although likely not as ephemeral as seascapes experienced by colonial seabirds) in heterogeneous and highly temporally dynamic farmland habitats surrounding colony sites (Morganti et al. 2021). A former study also showed that their resources can get depleted around their colonies, if the density of foraging individuals is high enough, as the season progresses (Bonal and Aparicio 2008). The location of the two study sub-units, which were characterized by clusters of nestboxes positioned on distinct roof terraces spaced ca 600 m apart in an old town (Podofillini et al. 2018), implies that there are no suitable foraging grounds between

them (as in Fig. 1b), because lesser kestrels do not forage in urban areas (Cecere et al. 2020). Besides, lesser kestrels from this colony forage at much greater distances outside of the colony (The relative uncertainty faced by individuals arriving from migration and foraging in such farmland 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 of the study species (Cecere et al. 2018, Fig. 2). Given previous evidence in other systems and based on GPS-tracking data from 45 individuals belonging to these two nest clusters, we first tested whether lesser kestrels spatially segregate also at a small-spatial scale, i.e. within-colony.

Second, we tested whether individuals from the two nest clusters differed in the bearing taken when departing on foraging trips, and then compared the bearings taken by individuals when leaving the nesting site to those of concomitantly departing and returning individuals. Indeed, lesser kestrels are non-territorial during foraging, 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; Morganti et al. 2021, Cioccarelli et al. 2022). Hence, we might expect them to use foraging social information obtained at the colony, by eavesdropping on the departure or return bearings of neighbouring breeders.

Third, to better understand the population- and individual-level consequences of within-colony segregation, we tested the following hypotheses with either the GPS-tracking data or fitness-related information obtained for the two nest clusters. Segregation could lead individuals breeding in different parts of a colony to encounter habitats differing in types and quality (Assandri et al. 2022), which, in turn, may lead individuals from a given cluster to forage further or spend more energy while foraging, eventually leading to differences in reproductive success (e.g. effect of foraging tactic on energy expenditure and nestling mass increase; Cecere et al. 2020, Genovart et al. 2003, Fayet et al. 2020 at the within-colony level) or adult survival rate (Genovart et al. 2018, Vincenzi et al. 2016). If breeding in different parts of a colony indeed makes a difference in the advantages it confers, we may expect a non-random distribution of individuals within the colony (e.g. parts of the colony conferring advantages hosting more experienced individuals, with better competitive abilities enabling them to secure a breeding site
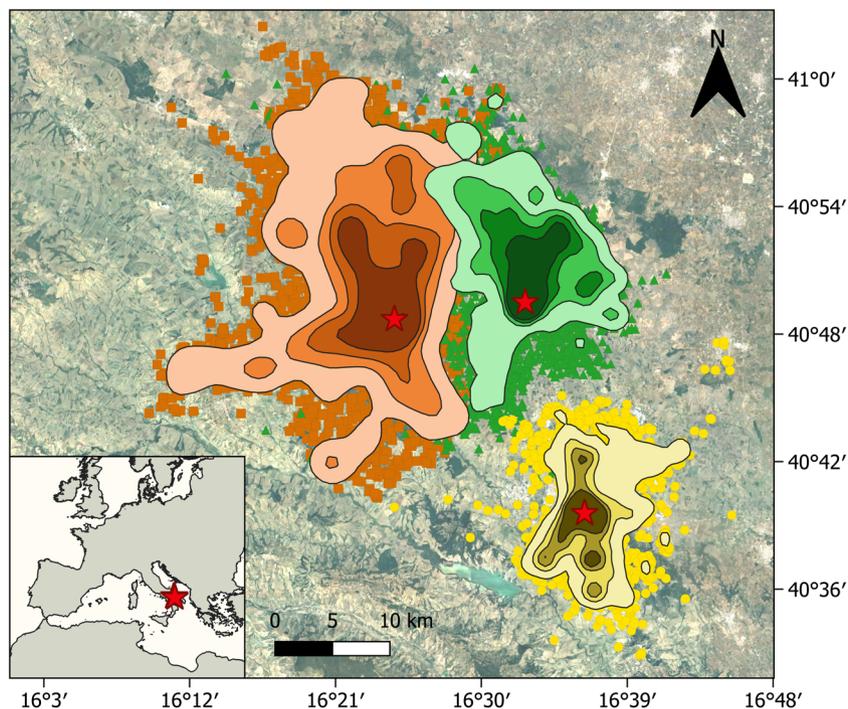

Figure 2. Spatial segregation during foraging by lesser kestrels breeding in three large neighbouring colonies: Matera (south-east, yellow shades, round symbols), Gravina in Puglia (north-west, orange shades, square symbols), and Altamura (north-east, green shades, triangle symbols). The three colonies host ca 800–1000 breeding pairs each (La Gioia et al. 2017). 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 recording positions every 15 min (Cecere et al. 2018). In Matera, 13 individuals were equipped with GPS-UHF devices in 2019 (i.e. a different sample of birds compared to analyses of within-colony spatial segregation). In Gravina in Puglia and Altamura, 9 and 9 individuals respectively were equipped in 2016 and 8 and 15 individuals respectively in 2017. Red stars denote the location of each colony.

in the best parts of the colony), as expected from patterns observed both among- (Spottiswoode 2007) and within-colonies (Genovart et al. 2003).

Finally, to address which mechanisms might lead to spatial segregation within 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.

Material and methods

Study species and site

Lesser kestrels are medium-size (146 g on average in our population) secondary cavity nesters which usually breed under 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 (Ramellini et al. 2022).

Lesser kestrels are non-territorial on foraging grounds and forage mostly alone, but sometimes they also congregate on foraging grounds, especially when exploiting rich resource patches (typically flushing of insects upon mechanical harvesting of cereals, which overall constitute stochastic events, Catry et al. 2014). The use of social information either at foraging grounds (local enhancement) or at the colony site (following behaviour) has not been previously documented 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 avoid competition while older individuals 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 (Aparicio et al. 2007, Morinay et al. 2021), we could expect, in our case, that if one part of the colony is more attractive, it may be favoured by some specific phenotypes.

The study was conducted from 2016 to 2020 in the city of Matera (southern Italy), hosting ca 1000 lesser kestrel pairs (La Gioia et al. 2017) in ca 2.5 km^2 (most of them within the inner part of the city, i.e. a 0.6 km^2 area). Up to 274 nestboxes were positioned on seven roof terraces of public buildings between 2010 and 2018 (Podofillini et al. 2018, 2019). Roof terraces constitute clusters of nest boxes located very close to each other within a city (i.e. a non-foraging area) and separated from other roof terraces by sites unsuitable for breeding (e.g. streets). Distances between the seven studied roof terraces

(mean = 0.6 ± 0.4 SD km, range from 0.1 to 1.4 km) were an order of magnitude less than the distances that lesser kestrels breeding in Matera travel when foraging (mean = 5.6 ± 2.5 SD km, range from 0.9 to 17.8 km). Roof terraces constitute specific units embedded within a network of such units in the city and, in that respect they both 1) present specificities independent of other roofs (e.g. in terms of information exchange possibilities) and 2) still maintain close interactions with individuals nesting on other roof terraces. For instance, we know that lesser kestrels use very local social information for nest site selection (Morinay et al. 2021), but they also interact with nesters of other roof terraces, as they share the same roosting sites at night (Supporting information).

Nestboxes were oriented in all directions, on roof terraces that dominated or equalled surrounding buildings. Nestboxes were placed ca 2 to 6 m away from the closest nestbox, and the majority of nestboxes are visible to all breeders on each roof terrace. 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 (Podofillini et al. 2018, 2019). Assessing nestling survival after this age (at age 20 days approximately) and before fledging is not possible as nestlings wander around their nestbox and may occupy nests other than their own (Romano et al. 2022). Breeding density is high in the monitored roof terraces (80% of the nest boxes occupied on average over four years and all seven roof terraces, ranging from 75 to 94% in the core roof terraces; see the Supporting information for a detailed description of breeder density per year and roof terrace). While foraging, breeders from our study sites in Matera city are fully segregated from those breeding in the two nearby and similarly large colonies in the cities of Gravina and Altamura (Fig. 2). Exchange of individuals among these three colonies seems extremely rare (only one natal dispersal event across colonies, among 37 recruitment events detected and 1636 nestling and 882 adults ringed since we started ringing in 2016; note that ringing effort has been more extensive in Matera).

GPS deployment

Tracking data were gathered from 45 individuals breeding in 2016–2018 and 2020 on two roof terraces, referred to here as 'Genio' (40°39′53.8″N, 16°36′13.7″E) and 'Provincia' (40°39′44.9″N, 16°36′34.5″E). Birds were captured in the nestbox during late incubation or early nestling-rearing stage and equipped with high resolution Axy-Trek biologgers (TechnoSmArt Europe) 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-loop 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 $4.4\% \pm 0.7$ (range: 2.8–5.7%) of individual body mass (144 g $\pm$ 14 SD, range: 115–178 g). Even though the tracking period was short (4.5 days $\pm$ 2.3 SD on average, ranging from 3 to 6 days usually, except for one individuals that we could only recapture 18 days after deployment), such deployment can have both short- and long-term consequences for individual's life history and behavioural traits, and in particular concerning 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 would not expect any roof terrace-specific effect of the tagging procedure. A former study performed on largely the same dataset showed that different loads caused by tags deployed on individuals with different body mass had no effect on the observed foraging behaviour (Cecere et al. 2020). 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 versus 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 roof terraces (43%; sampling period: 2016–2021). Furthermore, tagging did not affect adult body condition (Ramellini et al. 2022).

Spatial data pre-processing

Except when mentioned otherwise, all analyses were performed in R ver. 4.1.1 (www.r-project.org). Foraging trips were visually identified, and implausible positions (unrealistically high travel speed) excluded, in ESRI ArcMap ver. 10.2.1, following Cecere et al. (2020). A foraging trip was considered as a track starting and ending within 50 m from the nest or night roosting sites. For foraging trips that started before the loggers turned-on at 05:00 h, we only retained trips for which the first position was within 2 km from the nest. As we aimed to determine spatial segregation during foraging, we discarded locations unlikely to represent foraging activities. In particular, we discarded trips not heading towards rural surroundings but instead involving urban areas only (typically trips between the nest and roosting places). For trips identified as foraging trips, we also removed any GPS position located in urban areas. Urban areas were identified based on the Corine Land Cover 2012 habitat classification, hereafter CLC12 (codes 111 and 112, https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012). To further focus on foraging activities, we also discarded positions corresponding to relocation phases between distant foraging locations or between a foraging location and the colony. To identify these 'relocation' positions, we used

expectation-maximization binary clustering algorithm with the 'EMbC' R package (www.r-project.org, Garriga et al. 2019, similarly to Cecere et al. 2020). This procedure relies on GPS data to attribute one of four behaviours to each GPS position based on speed and turning angle data. This allowed us to distinguish relocation positions, which, consecutively, build trajectories with low turning angles at high speed, from intensive search (high turning angles at low speed), extensive search (high turning angles at high speed), and perching (low turning angles at low speed; Cecere et al. 2020).

We obtained tracking data corresponding to 690 foraging trips from 45 individuals (13 individuals in 2016, 12 in 2017, 11 in 2018, 9 in 2020; Supporting information). These 690 foraging trips were evenly distributed between the two roof terraces (327 trips for Genio, 364 trips for Provincia), despite some year-specific differences. Yet, there were more tagged individuals in Provincia (N = 29) than in Genio (N = 16), but we accounted for individual identity in statistical analyses (below). The sex ratio of tracked individuals was relatively balanced (6 females and 10 males in Genio, 14 females and 15 males in Provincia; Supporting information). See the Supporting information for details regarding the number of individuals, tracking duration per individual, and total number of foraging trips considered per roof terrace and year.

To test for spatial segregation during foraging between birds from the two roof terraces, we first ensured that movements of tagged individuals were representative of a given roof terrace using Lascelles et al. (2016) representativeness algorithm: for each roof terrace, 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 95% kernel density estimate (KDE) of each selected individual. 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 nest cluster (Supporting information), reinforcing the idea that the slight difference in sample size between roof terraces should not affect the results.

Spatial segregation of foraging areas

To test for spatial segregation of foraging areas between birds breeding in the two roof terraces, 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% KDE (R package 'adehabitatHR', Calenge 2006) applied to individual locations (excluding relocations). For KDEs, here and below, we always used the same grid cell size (a 23 × 23 km grid with a cell size of 200 m) and the reference bandwidth *href* as smoothing factor to ensure the best fit of kernels for each individual data (mean $\pm$ SD values of *href* and their range for the 16 individuals in Genio: 747 $\pm$ 402 (range: 274–1809); for the 29 individuals in Provincia: 671 $\pm$ 350 (range: 74–1934)). 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 triangular parts of this UDOI matrix and a 45×45 binary 'membership' matrix describing whether the two individuals were breeding in the same roof terrace (0) or in two different roof terraces (1; the reference used with the *biserial.cor* function from 'ltm' package; Rizopoulos 2006). We expected birds from the same roof terrace to have more overlapping UDs than birds from different roof terraces, 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 GPS locations around the roof terrace centroid 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 compared to 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 roof terrace and year effects by pooling data from different years, meaning that individual KDEs did not 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 roof terrace separately.

Foraging trip departure bearing

Since lesser kestrels can fly high above the Matera city old town, where buildings are relatively low, we did not expect the birds to be affected by any physical obstacle when leaving the nesting site. Individuals bearing when departing or returning to the colony should thus provide reliable information on the foraging areas (Supporting information).

To test whether a potential spatial segregation of foraging areas may originate from decisions made at the nesting site, we compared the departure bearings taken by individuals from Genio with those taken by individuals from Provincia. 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 roof terraces) corresponds to the threshold distance after which the bearing seemed to stabilize (Supporting information). To ensure comparability, we considered the departure location at the colony not to be each roof terraces, but the centroid of the two roof terraces instead. We only retained trips starting at the nesting site (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 nesting site at the start of recording). To test the effect of the nesting site 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 10000 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 roof terraces 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 roof terrace 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 nesting site to the bearings taken by other nesters of the roof terrace tracked concomitantly either when 1) leaving or 2) returning to the colony. Clearly our approach has its limitations as we could only track a small proportion of individuals from the same roof terrace concurrently. Regarding 1), to compare departure bearings, we selected, for each trip, all the trips performed by individuals from the same roof terrace and retained only those that were initiated within 35 min (half the average foraging trip duration here) before the focal trip. 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-min time-window, and results were overall similar. We calculated the absolute difference in the departure bearings from the roof terraces (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 one breeding pairs with both partners tagged concurrently) to share, inadvertently or intentionally, more information than individuals breeding further away. We initially included both individual identities and both foraging trip identifiers as random terms but removed them as they explained no significant proportion of variance (i.e. singular fit). Regarding 2), to compare a departure bearing (first location over 500 m from the colony) with the bearing taken by individuals returning to the colony (last location over 500 m from the colony), we used an approach similar to 1). We then fitted a GLMM (Gamma distribution) to the difference between the departure and returning bearings, analogously to 1).

Individual- and population-level consequences of spatial segregation

If foraging individuals from different roof terraces show spatially distinct foraging areas, they will most likely encounter different habitats, which may translate into both individual and nesting-site-level consequences. We thus first tested whether individuals from the two roof terraces differed in the type of habitat they encountered while foraging.

Given the striking difference observed, we further investigated whether individuals from the two roof terraces may adapt their foraging behaviour to these differences in encountered habitats , and which consequences this may have for the breeders themselves and their progeny. Based on the spatial data, we thus tested whether individuals from the two roof terraces differed in a range of intrinsic and behavioural variables: foraging trip duration, size of daily used foraging area, and energy expenditure while foraging (overall dynamic body acceleration [ODBA], Wilson et al. 2006). Based on the general monitoring of the population (i.e. from 2016 to 2020, see Table 1 for sample sizes), we tested whether individuals breeding in the two roof terraces differed in their body condition (measured here by the scaled mass index, SMI; see Podofillini et al. 2019), as well as in nestling's body mass, growth rates and survival (measured here by the number of nestlings reaching 14 days of age). If breeders from one roof terrace tend to forage in higher quality sites, resulting in higher reproductive success, this roof terrace may attract higher quality breeders. We may thus expect that the age-composition of the roof terrace would differ, young individuals (i.e. naïve, unexperienced, and possibly subordinate) being less likely to breed in the higher-quality nesting site. Therefore, with the same general monitoring dataset, we tested whether the two roof terraces differed in the age composition of breeding individuals, i.e. in their propensity to host young ($\leq$ 2-year-old) or older ($\geq$ 3-year-old) breeders (note that most lesser kestrels reproduce for the first time when 2-years old; Catry et al.

2017, Morinay et al. 2021). For all these analyses, we fitted different mixed models (GLMMs and LMMs). Details on variable estimation and all models' specifications are provided in the Supporting information.

Finally, we may also expect birds from different roof terraces to show differences in survival, for instance if differences in habitats encountered have such fitness consequences, or if between-roof terrace differences in the average phenotypic quality of individuals exist. Higher quality individuals may thus survive better and select the best nesting site over the years. We then tested whether breeders from the two roof terraces differed in their interannual survival using a capture–mark–recapture (CMR) approach based on 599 capture events of 383 individuals. See the Supporting information for details on variable estimation and models' specifications.

Individual-based model

With their IBM, Aarts et al. (2021) showed that the combination of competition for resources and the use of personal information, through individual-level memory, could explain segregation of foraging ranges between neighbouring colonies. To determine whether the same mechanisms could also explain foraging segregation at the roof terrace level, we also implemented an IBM (with different memory capacities, with or without competition), simulating foraging breeders during the nest-rearing period, by adapting Aarts et al. (2021)'s model to the roof terrace level and our study system (e.g.

Table 1. Roof terrace differences in foraging trip characteristics, nestlings' and breeders' traits. The unit of each variable is given in parenthesis. We also provide the mean, standard deviation (or standard error when mentioned), and sample sizes for each variable and roof terrace, and, when available, the associated statistic and p-values (not available for the Bayesian mixed circular regression of the bearing). Circular SDs were calculated using the 'circular' R package (Agostinelli and Lund 2017). Variables in bold are significantly different between the two roof terraces. 'breed.' and 'ind.' refer to the number of breeding events and unique individuals respectively. *obtained from the 3rd best-fitting CMR model indicating a difference in survival probability between the two roof terraces; this was not supported by the other two best-fitting models.

| Variable	Mean ± SD for the two roof terraces (Sample size)		Statistic	p-value
	Genio	Provincia		
Individual bearing (°)	−146.61 ± 1.14	122.27 ± 0.72	−	−
	171 trips, 15 ind.	*152 trips, 24 ind.*		
Individual size of daily used area (ha)	75.10 ± 70.31	41.99 ± 30.17	$t=-0.78$	0.45
	25 days, 10 ind.	*23 days, 15 ind.*		
Individual daily ODBA (g)	0.29 ± 0.13	0.29 ± 0.13	$t=0.28$	0.78
	51 days, 14 ind.	*90 days, 29 ind.*		
Individual trip duration (min)	71.50 ± 64.15	68.56 ± 62.35	$t=-0.52$	0.61
	153 trips, 15 ind.	*139 trips, 23 ind.*		
Individual breeders' SMI (g, std. by sex)	−0.07 ± 1.00	0.04 ± 1.00	$t=0.92$	0.36
	153 breed., 129 ind.	*302 breed., 235 ind.*		
Nestling body mass (g)	41.53 ± 25.12	43.59 ± 28.76	$t=0.80$	0.43
	90 nestlings	*144 nestlings*		
Nestling survival per nest (nb.)	2.80 ± 0.93	2.65 ± 0.96	$W=2177$	0.40
	49 nests	*82 nests*		
Nestling growth rate on average (g day⁻¹)	6.28	7.02	$t=3.43$	< 0.001
	90 nestlings	*144 nestlings*		
Age composition (prop. of old breeders)	0.79	0.75	$z=0.10$	0.92
	48 breed., 35 ind.	*95 breed., 70 ind.*		
Adult's survival probability*	0.56 ± 0.05 SE	0.63 ± 0.04 SE	−	−
	133 ind.	*250 ind.*		
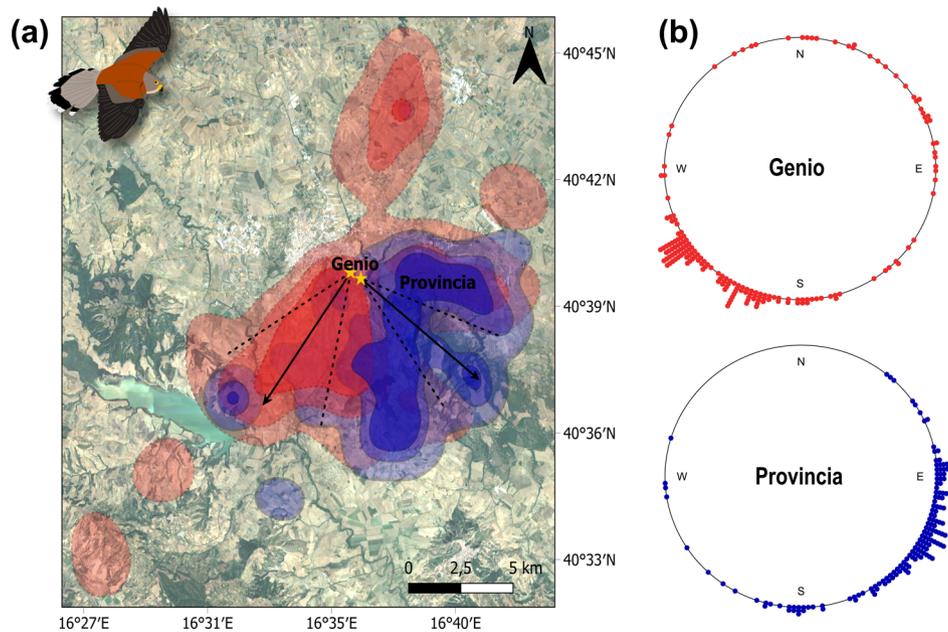
Figure 3. Home-ranges and bearing of breeding birds when departing for foraging trips from the roof terraces Genio (red, dashed contours) and Provincia (blue, solid contours). Both roof terraces are located in the larger colony of Matera (the southern-most colony in Fig. 1). (a) Bearings are provided as posterior means (arrows) along with their 95% High Posterior Density intervals (dashed lines). For illustrative purpose, we provide KDEs estimated when combining all locations from breeders in each roof terrace, excluding relocations: from light to darker shades, 95, 75 and 50% KDEs. See the Supporting information for individual level 95% KDEs. (b) Distribution of each trip bearing, for trips that departed from the roof terrace (distance of the first recorded GPS position below 200 m) and measured from the roof terrace to the first GPS position after having travelled 500 m. Note that Genio is located 600 m north-west of Provincia but considering the middle of both roof terrace locations as anchoring location for bearing calculation led to strictly similar patterns.

specific prey density and distribution, specific predator density and roof terrace localisation, a predator feeding on few/one prey item at a time, and moving between prey patches when hunting time becomes too long). All parts of the model algorithm differing from Aarts et al. (2021) and our model parameters are described in detail in the Supporting information, yet we provide here a comprehensive summary of the key features specific to our model.

We relied on empirical data from seven roof terraces monitored for several years (Supporting information, Fig. 4b). These roof terraces, 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. Altogether, the seven roof terraces constitute a natural continuum of breeding location clusters within the colony, and this allowed us to also infer on the impact of inter-nesting site distances on the segregation level. Therefore, differently from Aarts et al. (2021), we used the true spatial arrangement of the seven roof terraces and their average number of breeding pairs.

We provided the simulated lesser kestrels with a 24 × 24 km grid (1 ha cells) centred on breeding sites containing patchily distributed prey items (between 3 and 7 prey items ha^{-1}, reflecting the expected prey density available for one fifth of the lesser kestrel breeding population; Rodriguez and Bustamante 2008). Similarly to Aarts et al. (2021), modelled individuals 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 roof terrace towards the cell with the highest anticipated intake rate. Contrary 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 from the empirical GPS data; Ramellini et al. 2022), 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 roof terrace before engaging in a new trip. If the entire foraging trip time exceeded a limit (here 5 h, see Supporting information) and the individual did not manage to capture a prey, it would return from this unsuccessful trip to its roof terrace and engage in a new trip. For the first round, all individuals departed from the roof terrace within a 3 min time-window. After this first trip, each continued to forage for 14 h day^{-1}, for 40 days. 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 compared to the amount of food provided to nestlings on a daily basis).
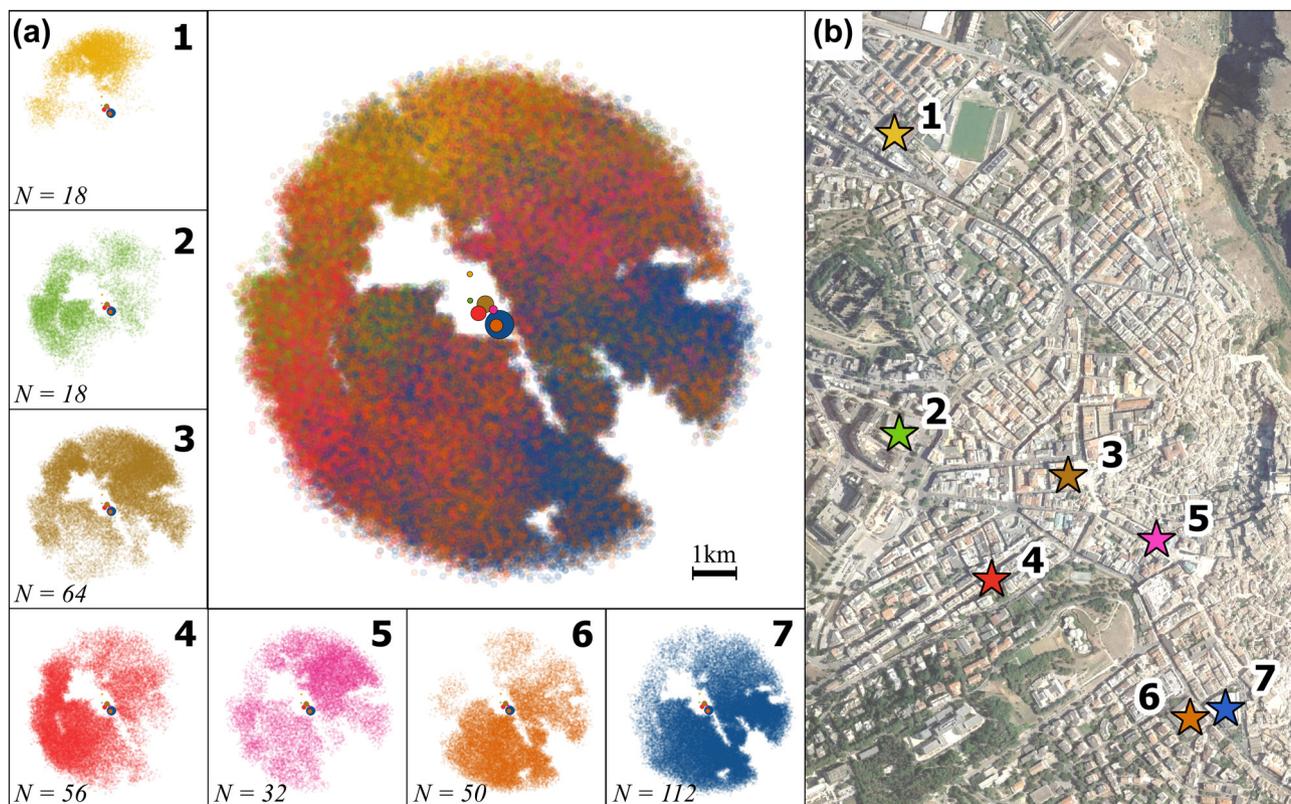
Figure 4. Foraging events of the 350 modelled lesser kestrels, (a) represented together and split per roof terrace (a, 1–7; 4 being Genio and 7 Provincia). *N* below each miniature refers to the average number of breeders in each roof terrace used in the IBM, based on the monitoring data collected since 2016. (b) Actual location of each roof terrace in Matera (stars). Roof terraces are represented in different colours, and dots are foraging events. Larger opaque circles in (a) correspond to the roof terrace locations, and their size is proportional to the number of breeders they host (see the Supporting information for details).

The food resource progressively got depleted as the season progressed but was partially replenished each night.

In the 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 (Supporting information), 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 was low, we expected individuals to keep visiting the closest patches (despite being empty) and waste time by exploring depleted patches at the close vicinity of the colony, instead of going further away to pristine patches. We thus expected that spatial segregation would 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 more distant, high-quality patches. As an extreme case of knowledge acquisition, when individuals were omniscient to the current prey density, we expected them to perfectly segregate, foraging in the most rewarding patches closer to their own roof terrace compared to any other roof terrace. To test the effect of between-roof terrace competition on spatial

segregation, we also implemented each of the six models (perfect memory, limited memory with four different levels, and omniscient) without competition: we simulated roof terrace as if they were alone in the colony (this led to simulating seven times each of these six models, one for each roof terrace). Comparing models with and without competition allowed us to test whether the spatial segregation could simply be an artifact of individuals reaching the closest foraging areas and always heading in that direction (i.e. right ahead, outside of the colony) or whether between-roof terrace competition actually forced individuals to move and forage in that preferential direction. We expected that when individuals were not subjected to competition between roof terraces, they would forage all around the colony. We thus ended up with 12 models, including a null model (memory of 0 and no competition).

For each model, we drew maps of foraging locations and estimated the overlap index of these foraging locations (here UDOI) between each pair of roof terraces, using both 50 and 95% KDEs (Supporting information). For the main scenario (unlimited memory), we tested whether more distant roof terraces would segregate more strongly by testing the correlation between the UDOI matrix and a matrix of geographic distances between roof terraces (Mantel test using the *mantel.*

rtest function, from the R package 'ade4', Dray and Dufour 2007). We also compared a range of parameters depending on the memory size and the presence/absence of competition: trip duration, distance travelled, and the proportion of unsuccessful trip (i.e. trips lasting 5 h, corresponding to events when individuals went back to their nest without food, which corresponds to a very unrealistic scenario in a natural context of an individual undergoing rearing duties and should never or very rarely occur in models best fitting natural settings). We expected individuals with poor memory abilities to perform longer-lasting trips, closer to the colony, and be more likely to be unsuccessful as they would forget that patches in the vicinity of the colony have been depleted. We also expected that individuals with perfect knowledge of their prey distribution would perform more efficient foraging trips (shorter, further away as prey get depleted at the vicinity of the colony, and successful). Finally, we expected individuals not exposed to among-roof terrace competition to remain closer to the colony as prey depletion would be less intense.

Results

Spatial segregation of foraging areas

Individual foraging areas were significantly segregated between the two roof terraces (Fig. 3a, Supporting information): the value of the observed correlation r_{obs} between the individual KDE overlap and the roof terrace membership felt within the 5% lowest values of random correlations ($r_{obs} = -0.04$, p = 0.04, Supporting information). For both Genio and Provincia, there was no difference in overlaps between KDEs from the same or different years (p > 0.16; Supporting information). The observed roof terrace segregation of foraging areas should thus not be due to inter-year differences in foraging site selection.

Foraging trip departure bearings

The departure bearing was different between roof terraces (intercept: $-116.4° \pm 10.0$ SD [-136.5; -97.0]; roof terrace effect: $127.9° \pm 6.5$ 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 (Fig. 3). Yet, for birds from a given roof terrace, trips did not have more similar departure bearings when they were initiated closer in time (within a 35 min time-window: estimate $= -0.002 \pm 0.004$ SE, t $= -0.49$, p $= 0.63$, N $= 83$). In other words, there was no evidence that individuals from the same roof terrace left collectively the nesting site to forage in the same area. Results with a 50 min time-window for the bearing comparison were similar (t $= -1.55$, p $= 0.12$, N $= 125$). We also tested for a 20 min time window, but there were too few pairs of comparable trips to obtain reliable estimates (N $= 48$). Similarly, individuals did not seem to copy the direction taken by returning individuals (within a 35 min time-window: estimate $= -0.001 \pm 0.003$ 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 $= 194$).

There were some indications that the departure and returning bearing were more similar between individuals breeding closer together (for the models considering 35- and 50- min time-windows only, $0.03 \leq p \leq 0.09$ depending on model). However, this effect was independent of the time between the compared trips and may thus be due to the positioning of nests on the roof terrace rather than to 'following' behaviours.

Individual- and population-level consequences of spatial segregation

The composition of habitats in lesser kestrel foraging areas differed between birds breeding on the two roof terraces. Individuals from Genio encountered mostly arable lands (70% of encountered habitats), while individuals from Provincia also encountered substantial proportions of grasslands and wooded areas (43% of encountered habitats overall; Supporting information). There was no significant roof terrace difference in individuals' trip duration, size of daily used area, or daily energy expenditure during foraging trips (Table 1). Based on the multi-year monitoring data, we observed no roof terrace difference in breeders' SMI and no overall roof terrace differences in nestlings' body mass or survival (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 roof terrace interaction on nestlings' body mass (0.74 ± 0.23 SE, $t = 3.429$, p < 0.001; Supporting information). The proportion of younger versus older breeders did not significantly differ between roof terraces; however, it was greater in 2020 than in 2019, likely due to the increasing number of ringed individuals over the years (so an increasing number of old ringed breeders too). There was also no clear difference in adult interannual survival probabilities between the two roof terraces: among the three best-fitting models, the last one found a higher survival probability for individuals breeding in Provincia (mean $\pm$ SE $= 0.63 \pm 0.04$) than those breeding in Genio (0.56 ± 0.05). Yet, these estimates greatly overlap (Tables 1, Supporting information). Hence, a small difference in survival may exist between birds nesting on the two roof terraces, but the current short time series may not allow to detect this effect (see the Supporting information for the output of the CMR models).

Individual-based model

Based on 40 days simulations with 350 individuals breeding in seven roof terraces and remembering any visited cell, a clear segregation among the most distant roof terraces emerged, while this segregation was less marked between close-by roof terraces (Fig. 4−5). This pattern of increasing segregation by distance was valid for all scenarios including between-roof terrace 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 memory capacity (> memorized 500 cells) seemed to be the most realistic (Supporting information). Indeed, when individuals had poor memory
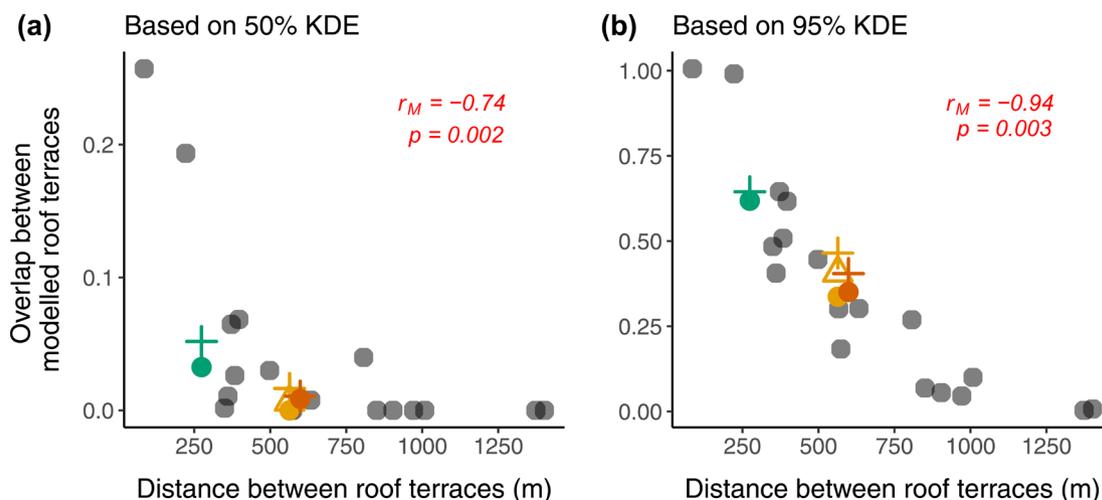
Figure 5. Larger spatial segregation of simulated foraging locations (as measured by decreasing overlap) between more distant roof terraces (points). Overlap values correspond to UDOI, based either on (a) 50% KDEs or (b) 95% KDEs obtained for each roof terrace (with reference bandwidth h_{ref}). Each point corresponds to a pair of roof terraces. Correlations derived from a Mantel test (r_M) and their associated p-values are provided in each panel. Segregation is virtually complete (small UDOI value) between roof terraces that are distant by more than 1250 m. The scenario considered here is with unlimited memory, yet the negative correlation was also observed for the other scenarios. In the IBM, the seven roof terraces were arranged according to their actual geographical coordinates (Fig. 4b). For comparison with empirical data, we highlight three types of UDOI values: Genio versus Provincia (based on Fig. 4b numbering: 4 versus 7; yellow), Genio versus Biblioteca (4 versus 3; green), and Provincia versus Biblioteca (7 versus 3; orange). The triangle corresponds to the overlap index calculated from the empirical data from this manuscript, based on KDEs derived at the roof terrace level (with h_{ref}). Crosses correspond to overlap indices calculated from a combination of empirical data from two types of deployed GPSs (Axi-Trek GPSs as presented in the main text and GPS-UHFs as presented in Fig. 2; KDEs estimated with bandwidth $h_{ad hoc}$; see the Supporting information for details).

capacities, foraging trips were extremely long, very close to the colony, and were often unsuccessful (Supporting information), which is highly unlikely in nature, especially when individuals are provisioning their nestlings as in our simulations. Contrarily, with good memory capacities, individuals performed mostly successful trips, whose durations were similar to the one observed in our empirical data (Supporting information).

When considering core foraging areas (UDOI based on 50%), segregation of foraging areas was much lower in the absence than in the presence of among- roof terrace competition (for all memory types except no memory, Fig. 6a). This was less marked when considering segregation of larger foraging areas (UDOI based on 95% KDE) as the latter likely encompassed more areas in the close vicinity of the colony. Comparing scenarios with different memory capabilities (from 0 to 5000, and all cells remembered), segregation increased with memory size (Fig. 6), up to a certain threshold (between 500 and 5000 memorized cells) after which it either reaches a plateau (in the absence of competition), or segregation even slightly decreases (in the presence of competition). This could be explained by the fact that when an individual remembers many or all visited cells, it will avoid remembered sites that have been depleted and not return to them even though replenishment occurred, thus exploring wider areas, which may lead to greater overlap. Spatial segregation was almost complete when the simulated individuals were omniscient regarding food availability and individuals competed with nesters of other roof terraces (Fig. 6, Supporting information).

On the contrary, when individuals did not compete among roof terraces, overlap was the greatest when individuals were omniscient (Fig. 6, Supporting information). This is explained by the fact that when individuals did not have to compete with individuals from other roof terraces, they tended to forage all around and closer to the colony (Supporting information). Stronger segregation occurred instead (i.e. individuals foraged in areas more in front of their roof terrace, and possibly further away) when they experienced competition (Fig. 4, Supporting information).

Discussion

In recent years, a growing body of literature has demonstrated that spatial segregation in foraging distribution occurs between individuals from neighbouring sectors of a same colony (Masello et al. 2010, Bogdanova et al. 2014, Kuhn et al. 2014, Waggitt et al. 2014, Ceia et al. 2015, Sánchez et al. 2018, Ito et al. 2021, Morinay et al. 2022, Pereira et al. 2022). Here, lesser kestrels breeding in the same colony but nesting on two different roof terraces (nest clusters) located only 600 m apart, showed partial but significant spatial segregation while foraging kilometres away from the colony. This segregation originated from different bearings taken when leaving roof terraces. Individuals nesting on the Genio roof terrace headed on average south-west and encountered mostly arable lands, while the ones nesting on the Provincia roof terraces headed on average south-east and encountered a mixture of arable land and more natural, less intensively
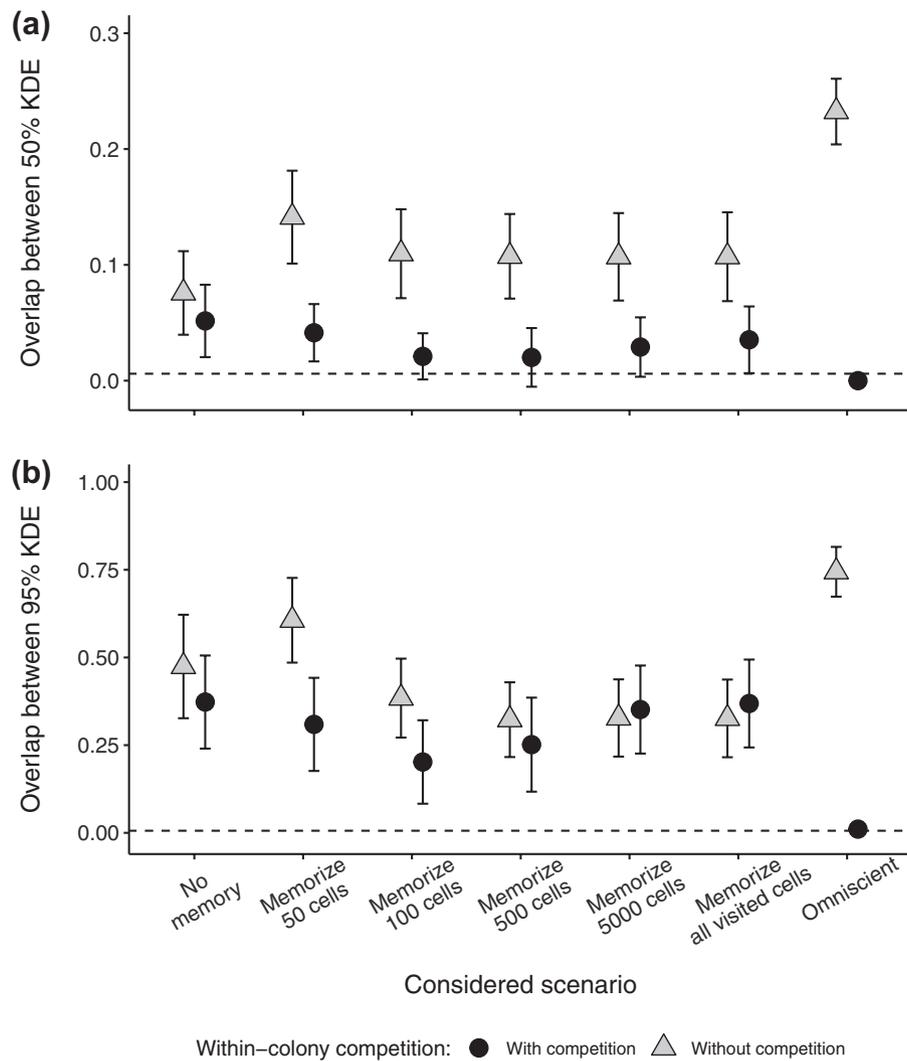
Figure 6. UDOI values obtained from the simulated data for all modelled scenarios, both with (black circle) and without (grey triangle) competition for food resources between roof terraces within the colony. The dashed lines correspond to the value obtained from our empirical data (from overlap between KDEs derived at the roof terrace level).

managed landscapes (grasslands and wooded areas). Yet, these differences in habitats did not lead to any marked roof terrace differences in individual body condition, reproductive success or survival, or in the proportion of younger versus older breeders. Detailed analyses of departure and return bearings did not provide evidence for collective departure for foraging or sharing of foraging information at the nesting site among birds nesting on the same roof terrace. Our IBM showed that when individuals from different roof terraces compete for food and use personal memory, they tend to segregate during foraging more than expected in the absence of competition, despite the proximity of the roof terraces. Spatial segregation increased when they had a good memory of the visited patches and when they were nesting on more distant roof terraces. Both our empirical and theoretical results concur to the fact that the observed spatial segregation of foraging areas between lesser kestrels nesting on different roof terraces is less likely to originate from social information use than from competition and memory use combined.

Spatial segregation of foraging areas: a pattern across scales

Regardless of the geographical scale ecologists are considering, spatial segregation of foraging areas seems to be the norm in many colonial systems. At a large scale, between neighbouring colonies, occurrences of such segregation have been shown in various taxa and have been previously extensively reviewed (Bolton et al. 2019). At a smaller scale, within-colony or very close colonies, there is a clear bias towards studies of marine species (seabirds: Hipfner et al. 2007, Masello et al. 2010, Bogdanova et al. 2014, Ceia et al. 2015, Sánchez et al. 2018, Ito et al. 2021, Morinay et al. 2022, Pereira et al. 2022, and one sea mammal: Kuhn et al. 2014), except for the 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 areas could be widespread as the same mechanisms seem to act both at large and small scales. However, this pattern seems to

be distance-dependent, both at the colony (Aarts et al. 2021) and within-colony scales: we have shown here that birds from roof terraces that are very close to each other overlap more in their foraging areas (Fig. 5). We may thus expect to observe no segregation if we were to compare foraging areas of individuals breeding at even closer locations (e.g. 50 m in Waggitt et al. 2014). Our results thus confirm, at within-colony scale, the existence of a pattern that has long been theorized and empirically shown at the colony level. Besides, it also supports the idea that the practical distinction between sub-units (i.e. roof terraces in our study case) and colonies is actually an almost continuum of more or less clustered nesting locations in which individuals are exposed to a gradient of competition while foraging (Fig. 1).

Underlying processes

The segregation pattern emerging from our IBM was strikingly similar to the one originating from the empirical data (comparing Fig. 3 and 4). We showed that the use of social information is not necessarily required for spatial segregation to emerge between the foraging distributions of lesser kestrels' nest clusters. 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 1976) could cause the observed spatial segregation of foragers from different nest clusters (Fig. 3, 4, 6). This extends Aarts et al. (2021)'s results, which showed on a larger spatial scale that personal memory combined with indirect competition can lead to the segregation of foraging grounds of different colonies. Other previous models, yet on non-colonial central place foragers, have also confirmed this idea: personal memory can lead to foraging segregation between competing individuals (Riotte-Lambert et al. 2015, Dubois et al. 2021).

Given the strong competition for food resources among individuals from a same colony, it is not surprising that the same mechanisms trigger among- and within-colony spatial segregation of foragers. Yet, these results contrast with those of Wakefield et al. (2013), who found that both social information collected at the colony and through local enhancement are required, in addition to memory, to lead to spatial segregation between colonies (Aarts et al. 2021 for a discussion of this discrepancy). Here, the segregation of birds from different nest clusters may simply be the result of individuals from the same nest cluster progressively acquiring similar knowledge of the environment, through personal experience and memory. When individuals encounter resource patches that have been depleted (either by individuals from the same or another cluster), such patches will appear of lower quality and should thus be avoided. However, individuals from the same nest cluster make similar decisions: going to the closest resource patches, which implies taking roughly similar departure bearings. This has two major consequences. By leaving towards roughly the same direction, individuals will encounter patches depleted by other individuals from the same nest cluster and progressively expand their foraging range as

resources get depleted (following the Ashmole's halo effect; Ashmole 1963). Concurrently, resource patches nearby are also depleted by individuals from other clusters. Hence, to maintain a given intake rate, individuals from a given cluster will have to expand their foraging ground further away from the neighbouring nest cluster, while foraging in other directions may be prevented owing to the strong competition with birds from other nest clusters. Accordingly, in the absence of between-nest cluster competition, lesser kestrels tend to indeed forage all around their own nest cluster (Supporting information). This sequence of processes has been proposed to explain spatial segregation of foraging areas in several seabird species (e.g. tufted puffins, Hipfner et al. 2007, Cory's shearwater, Ceia et al. 2015). This parsimonious explanation does not necessitate any territoriality, voluntary avoidance of conspecifics, social learning or cultural evolution of foraging site (Wakefield et al. 2013) and is concordant with spatial segregation in colonial species which do not have (or have only limited) access to social information outside of the colony (e.g. seals, Robson et al. 2004).

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 and Wagner 1997, Evans et al. 2016), an inherent cost of living at high densities is an increased competition for resources. In our study colony, lesser kestrels breed at high densities (ca 1000 breeding pairs, most of them concentrated in the inner part of the city, i.e. a 0.6 km² area) and competition for breeding sites seems high ($\geq$ 80% of the nestboxes occupied in the most studies roof terraces across years; Supporting information). Competition for food resources in the foraging areas is thus expected to be high (as suggested by much broader home ranges compared to smaller colony sites; Cecere et al. 2018), which implies both that lesser kestrels must gain substantial benefits from living close by (as shown by the use of social information for breeding site selection in this population, Morinay et al. 2021; or predator vigilance effect in other populations, Campobello et al. 2012) and that they should behaviourally respond to such high competition while foraging (present study).

The costs and benefits of breeding in colonies likely vary depending on the species' ecology and the spatio-temporal distribution of prey. 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, or in several bats species, Egert-Berg et al. 2018). 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 (Afshar et al. 2015) and may suffer from sharing this information with others (Barbier and Watson 2016). However, since successful foraging is an information that cannot be easily hidden when breeding close to each other (Evans et al. 2016),

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: few studies have confirmed that birds actually obtain, at the colony, information regarding food (Weimerskirch et al. 2010, Thiebault et al. 2014, Harel et al. 2017, Jones et al. 2018, Courbin et al. 2020). Here we failed to provide such evidence in lesser kestrels. Similarly to northern gannets (Waggitt et al. 2014), lesser kestrels did not seem to follow each other when leaving their roof terrace: there was no synchrony in bearing taken when leaving the nesting site between individuals from the same roof terrace. However, to properly test social information use with GPS data, a much larger sample of individuals tracked simultaneously would be needed. Here, we relied on few individuals tagged at the same time in comparison to the number of breeders per roof terrace. We thus cannot completely rule out that individuals may follow one another, or that lesser kestrels benefit in other ways from social information, as it is the case when selecting nest sites (Aparicio et al. 2007, Morinay et al. 2021), engaging in predator vigilance (Campobello et al. 2012), or detecting large aggregates of conspecifics in superabundant but ephemeral resource patches (Catry et al. 2014). However, in our foraging context, we would rather expect social information use to happen away from the colony by copying or avoiding each other, rather than at the colony.

Individual- and populational-level consequences of spatial segregation

Spatial segregation of foraging areas originates from individual responses to high density-dependent competition with breeders of nearby nest clusters (or colonies) and should enable individuals to maintain a given intake rate despite these ecological constrains. Accordingly, besides a slight difference in nestling growth rate, we could not detect any significant difference in energetic costs or proxies of reproductive success between individuals from the two roof terraces. Spatial segregation of foraging areas could thus be simply a by-product of resource depletion and competition avoidance at the individual level, without necessarily any marked individual's fitness or populational consequences. Here, lesser kestrels from the two roof terraces presumably experienced qualitatively similar foraging areas, despite using different foraging habitats. A similar pattern was observed in Cory's shearwaters: individuals from different sectors of the same colonies moved across different types of habitats but fed in similar ones in terms of physical and biological properties (Ceia et al. 2015). Moreover, we found no or weak differences in adult quality or survival among individuals from the two roof terraces. This contradicts previous studies both at the colony and within-colony level showing differences in parental investment, reproductive success or survival, which could be related to differences in individual quality among colonies or different sectors of the same colony (Rodway et al. 1998, Genovart et al. 2003, 2018, Serrano et al. 2005, Spottiswoode 2007, Fayet et al. 2020). A possible explanation for our findings is that Genio

and Provincia are both hosting high quality individuals compared to other parts of the colony. The high occupation rate of nestboxes of both roof terraces (as well as in the other main roof terraces) is in line with this hypothesis (Supporting information). We also cannot rule out that any observed difference is the result of intrinsic differences in the quality of the nesting site. For instance, the slight difference in nestling growth rate between nestlings from Genio and Provincia could also result from varying exposure of nestboxes to heat (e.g. differences in shading; Corregidor-Castro et al. unpubl.).

Conclusion

We suggest that within-colony spatial segregation of foraging areas is not restricted to marine species feeding on highly ephemeral prey patches and could thus be more widespread than currently presumed. We also suggest that such small-scale segregation originates from simple rules (optimal foraging in the presence of competitors and memory 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 specific 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, care should be taken 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.

Author contributions

Jennifer Morinay: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Funding acquisition (supporting); Investigation (equal); Methodology

(equal); Project administration (supporting); Resources (supporting); Software (equal); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Louise Riotte-Lambert**: Formal analysis (supporting); Methodology (equal); Software (equal); Validation (equal); Writing – review and editing (supporting). **Geert Aarts**: Methodology (equal); Software (equal); Validation (equal); Writing – review and editing (supporting). **Federico De Pascalis**: Data curation (supporting); Investigation (equal); Project administration (supporting); Writing – review and editing (supporting). **Simona Imperio**: Formal analysis (supporting); Software (equal); Writing – review and editing (supporting). **Michelangelo Morganti**: Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Writing – review and editing (supporting). **Carlo Catoni**: Investigation (equal); Resources (equal); Writing – review and editing (supporting). **Giacomo Assandri**: Data curation (supporting); Validation (supporting); Writing – review and editing (supporting). **Samuele Ramellini**: Validation (equal); Writing – review and editing (supporting). **Diego Rubolini**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (supporting). **Jacopo G. Cecere**: Conceptualization (equal); Data curation (lead); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (supporting).

Data availability statement

Data are available from Movebank (Movebank ID 1984558612) (Morinay et al. 2023). R Code used to test spatial segregation between sub-colonies is in the Supporting information.

Supporting information

The Supporting information associated with this article is available with the online version.

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