Combining social information use and comfort seeking for nest site selection in a cavity-nesting raptor

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Abstract

When selecting a breeding site, individuals can use social information to reduce the uncertainty regarding habitat quality. Individuals of several bird species tend to reuse nests previously occupied by conspecific or heterospecific competitors but the proximate mechanisms underlying this behaviour remain unclear. Reoccupying nests previously used by competitors could result from individuals copying competitors' choices (the 'social information' hypothesis). Alternatively, it could allow individuals to fulfil their need for a soft nest substrate (e.g. by improving thermal insulation or reducing egg breakage risks) at low costs, regardless of previous occupancy (the 'comfort' hypothesis). Here, we aimed to determine which of these non-mutually exclusive mechanisms triggered the preference for old conspecific nest material in a secondary cavity-nesting raptor that does not add lining material to its nests, the lesser kestrel, *Falco naumanni*. Using an experimental design forcing settling lesser kestrels to choose between two adjacent nestboxes containing different substrates, we detected a strong preference for soft substrates (peat moss or old conspecific or European roller, *Coracias garrulus*, nest material) over coarse mineral substrate, especially when the soft substrate also provided social information about previous nest use by a competitor. Despite the apparent absence of preference when directly comparing settlement patterns in soft substrates with and without social information, early settling individuals favoured the substrate with social information, while late settling ones favoured the substrate without social information. This could reflect intraspecific competition avoidance by late arriving individuals that may be competitively inferior to early arriving ones. This hypothesis is supported by a later laying date of young breeders in our population. Our findings suggest that both comfort seeking and social information use explain the preference for previously used nest cavities, and that nest site choices may depend on individual competitive abilities and experience.

Keywords: cavity nesting, conspecific attraction, double-box, *Falco naumanni*, informed decision, lesser kestrel, nestbox choice experiment, nest reuse, nest substrate, old nest material

Introduction

Choosing where to breed is a decision with important fitness consequences. Indeed, it determines the abiotic and biotic conditions that breeding individuals and their progeny will have to deal with, sometimes for long periods of time (e.g. the availability of resources, shelters, exposure to predators, parasites; Danchin et al. 2008). Collecting reliable cues on habitat quality thus enables breeding individuals to reduce uncertainty regarding the consequences of this crucial decision (Schmidt, Dall, & van Gils, 2010). In particular, individuals can use personal information, collected through their own experience with the breeding environment (e.g. habitat quality, past reproduction), and/or social information, collected by cueing on the presence, success and decisions of conspecific or heterospecific competitors (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Danchin, Giraldeau, Valone, & Wagner, 2004; Seppänen, Forsman, Mönkkönen, & Thomson, 2007; Valone, 2007).

Social information available for breeding site selection is diverse and may be used at different spatial (e.g. competitor's density in an area, Forsman et al. 2008; reproductive success in a patch, Boulinier et al. 2008; presence in a specific site, Kivelä et al. 2014) and temporal scales (e.g. cues from the previous breeding season, Doligez et al. 2002; from prebreeding, Rushing et al. 2015; from ongoing breeding, Forsman et al. 2012). For secondary cavity-nesting birds, the presence of old nest material can be a particularly important source of information (reviewed in Mazgajski 2007, e.g. Loukola et al. 2014). Indeed, old nests will remain in cavities across breeding seasons unless removed, making this cue accessible not only to philopatric individuals but also to immigrants and yearlings, which may lack information and previous experience with that specific breeding site (e.g. Doligez, Pärt, Danchin, Clobert, & Gustafsson, 2004; Parejo, White, & Danchin, 2007). While old nest material does not convey precise quantitative information on the breeding success of its previous owner, it can nevertheless provide qualitative cues on past success (e.g. flattened nest material, faeces, unhatched eggs; Erckmann et al. 1990) and on past predation events (e.g. predator's urine or faeces and egg fragments, Tolvanen et al., 2018). Accordingly, such proof of previous occupancy has been proposed to be used as a source of information in several bird species (e.g. Gergely, Mészáros, Szabad, & Székely, 2009; Hoi, Krištín, Valera, & Hoi, 2012; Loukola et al., 2014; Mingju et al., 2019; Podofillini et al., 2018; Sumasgutner, Vasko, Varjonen, & Korpimäki, 2014), triggering either attraction or avoidance depending on the species and on the environmental or social context (see Mazgajski, 2007).

The proximate mechanisms triggering attraction to, or avoidance of, old nest material can be diverse, but their experimental identification was not the focus of previous studies. Four hypotheses have been proposed to explain why individuals should actively prefer or avoid nesting on top of old nest material (reviewed in Mazgajski, 2007). First, the presence of old nest material shows that competitors, either conspecific or heterospecific, previously selected the site. Individuals may then exploit this source of information and copy competitors with the same resource needs, especially when they have only poor, outdated or no personal information regarding habitat quality. The presence of old nest material can thus be a valuable source of information for migratory species which are highly constrained in their reproduction timing and can save prospecting time at the onset of the breeding season by using social cues (e.g. Ringhofer & Hasegawa, 2014; Rushing et al., 2015). Second, reoccupying old nests might be favoured as it can reduce nest-building effort or improve the thermal insulating properties of the nest (e.g. Loukola et al., 2014; Mainwaring, Hartley, Lambrechts, & Deeming, 2014; Mazgajski, 2007). This might again be particularly important for species that are highly time constrained (e.g. migrants, Loukola et al., 2014), but also for species that do not add lining material to their nest (e.g. the European kestrel, *Falco tinnunculus*, Mingju et al. 2019). Third, in contrast, individuals may avoid nesting on top of old nest material due to the higher risk of infection by ectoparasites and pathogens surviving in nest material across years (Rendell & Verbeek, 1996), and to avoid infection by ectoparasitic flies seeking out hosts (Tomás, Ruiz-Castellano, Ruiz-Rodríguez, & Soler, 2020). Moreover, avoidance might also be selected for when reoccupying an old nest entails a higher risk of predation (e.g. if the superposition of nest material brings the parents or offspring closer to the nest entrance, Wesolowski, 2002; or if predators revisit sites that were previously occupied by prey, Otterbeck et al., 2019; Sorace et al., 2004). Finally, competition avoidance may also explain why individuals avoid previously occupied nest sites: they may, for example, favour niche space previously unused by competitors (Forsman et al., 2014) or nest sites without potentially current nesting competitors (Loukola et al., 2014). A further possibility is that reusing old nest material could passively result from individuals independently sampling the environment and using cues other than nest contents to identify nesting sites of higher quality (e.g. based on sun exposure, safety from potential predators, etc.), which will lead to accumulation of nest material through successive breeding attempts. Yet, if individuals actively choose a nesting site for its content, determining the proximate reasons behind these choices will contribute significantly to our understanding of the patterns of nest site selection in birds. Disentangling the roles of different drivers of preference versus avoidance of old nests requires rigorous experiments in natural settings, but few such experiments have been conducted.

Here, we aimed to disentangle the use of social information from the search for a ‘comfortable’, soft and insulating substrate by investigating nest site selection in relation to the presence of old nest remains in the lesser kestrel, *Falco naumanni*. Lesser kestrels are migratory, colonial and secondary cavity-nesting raptors. Similar to other colonial birds (Evans, Votier, & Dall, 2016), lesser kestrels may rely on social information for both foraging (suggested in Cecere et al., 2018) and breeding site selection (Aparicio, Bonal, & Muñoz, 2007). They strongly prefer breeding in nest sites with conspecific old nest remains (organic matter composed of faeces, pellets and prey remains) than in clean nest sites (with mineral substrate; Negro and Hiraldo 1993, Podofillini et al. 2018). Yet, the underlying proximate mechanisms driving this behaviour are unclear. Indeed, previous studies could not disentangle whether the preference for previously used nest cavities resulted from the use of social information (hereafter called the ‘social information’ hypothesis) and/or from the need for a soft nest substrate (hereafter called the ‘comfort’ hypothesis), reducing the risk of egg breakage and/or ensuring better thermal insulation (to buffer against cold spells early in the breeding season and/or high temperatures late in the season, which can reach detrimental levels for the nestlings inside the cavity; Campobello, Lindström, Di Maggio, & Sarà, 2017; Catry, Franco, & Sutherland, 2011).

To test whether the ‘comfort’ and/or the ‘social information’ hypotheses explain the preference for previously used nests, we performed a set of experiments whereby we made lesser kestrel pairs choose between adjacent paired nestboxes (hereafter called ‘dyads’) containing different substrates. The paired nestboxes were lined with specific combinations of four substrates, which differed in the degree of softness and/or social information content: (1) old lesser kestrel nest material from previous breeding seasons (soft and providing social information); (2) old nest material from the European roller, *Coracias garrulus*, a sympatric cavity-nesting species (soft and providing social information from a competitor); (3) peat moss (soft but not providing social information); and (4) mineral substrate (gravel; coarse and not providing social information), which mimics the substrate normally found in cavities that have not been previously occupied by breeding lesser kestrels.

According to the ‘comfort’ hypothesis, we expected lesser kestrels to prefer nesting in boxes with soft substrates over those with coarse material, regardless of the social information content of the soft substrates. According to the ‘social information’ hypothesis, we expected lesser kestrels to prefer nesting in boxes with the soft substrate that contained social information (i.e. signs of previous breeding attempts) over those with a soft substrate without social information (i.e. peat moss). These two hypotheses are non-mutually exclusive and could result in the overall preference of nest substrates providing both comfort and social information. To better understand the mechanisms underlying, and the consequences of, nest site preferences, we compared the frequency of settlements in nestboxes with different substrates, as well as the settlement timing and proxies of reproductive investment and output (clutch size, hatching success) of pairs breeding on different substrates.

Methods

Study site and species

The experiments were conducted in a large (ca. 1,000 pairs) colony of lesser kestrels (Matera, southern Italy; 40°40’N, 16°36’E) during four breeding seasons (April-July 2016-2019). The lesser kestrel is a small (ca. 120 g), migratory and colonial raptor, which generally breeds on human infrastructures and forages in the countryside surrounding the colony (Cecere et al., 2020), feeding mainly on invertebrates, lizards and small mammals (Rodríguez, Tapia, Kieny, & Bustamante, 2010). Adults reach breeding areas in February-March (Sarà et al., 2019), and start laying eggs between late April and early May. Females lay three to five eggs (single brooded), which are incubated for approximately 30 days. They are secondary-cavity nesters, breeding in rocky cavities, roof tiles of old buildings or ruins, and readily settle in artificial nestboxes. Breeding pairs do not add any nest lining material (Cramp 1998). However, over the years, organic material (mostly prey remains, such as insect elytra and other chitinous parts, small mammal fur and bones, regurgitated pellets and faeces) accumulate in occupied cavities. Lesser kestrels have been found to prefer nesting in cavities containing such organic substrate resulting from previous breeding attempts (Cramp, 1998; Negro & Hiraldo, 1993). We relied on nestboxes, made of refractory bricks (external size: 30 × 37 cm and 30 cm high) and closed at both ends by wooden panels, which have been provided at the periphery of roof terraces since 2008 – 2010. The front panel had a 65 mm diameter entrance hole (see Podofillini et al., 2018 for details).

Nestboxes were checked two to three times per week from late April to mid-May and up to five times until July to monitor reproductive parameters (laying date, clutch size, hatching date, number of nestlings; see Podofillini et al. 2018 for details on the visiting rate). Adults were captured by hand in the nest, identified or ringed if not previously ringed with a unique alphanumeric metal ring on one leg and a unique alphanumeric colour ring on the other leg, and released back to the nest. Some individuals were identified from the alphanumeric colour ring without handling them.

Experimental design

By monitoring non-experimental nestboxes, we could confirm that lesser kestrels prefer nesting in nestboxes that were previously occupied (see Results and Negro & Hiraldo, 1993; Podofillini et al., 2018). To determine the proximate mechanisms underlying this preference, we aimed to make lesser kestrels choose one of two types of substrates for breeding. We therefore organized 80 nestboxes in 40 dyads (i.e. two adjacent nestboxes), which were separated from other dyads by at least 2 m. Within a dyad, the two nestboxes contained different substrates (Fig. 1). This double-box design allowed us to control for any microenvironmental effects on lesser kestrels' breeding site choice (e.g. sun exposure or direction of the nestbox) and to make sure that they always had an equal opportunity to settle on each tested treatment.

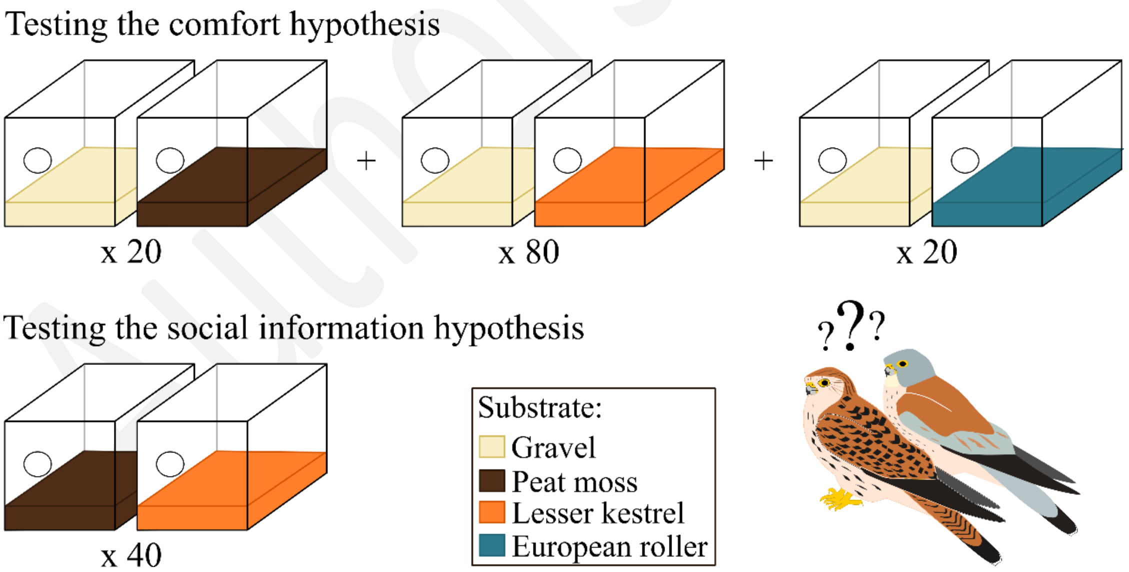

Figure 1. Design of the double-box experiments testing the comfort and social information hypotheses in lesser kestrels. In 4 years, different substrates were provided in nestboxes, which were arranged in 40 dyads. To test the comfort hypothesis, old lesser kestrel nest material was paired with gravel in 2016 (40 dyads), 2017 (20 dyads) and 2018 (20 dyads); old European roller nest material and peat moss were paired with gravel in 2017 and 2018, respectively (20 dyads each). To test the social information hypothesis, old lesser kestrel nest material was paired with peat moss in 2019 (40 dyads). The total number of dyads of each type is given below each represented dyad.

To test the comfort hypothesis, one nestbox of each dyad in 2016–2018 contained gravel, while the paired nestbox contained either remains from an old lesser kestrel nest (*N* = 80 dyads), remains from an old European roller nest (*N* = 20 dyads) or peat moss (*N* = 20 dyads; Fig. 1). We aimed to provide lesser kestrels with generally suitable substrates, on top of which reproduction was feasible, thereby investigating preferences between contrasting but nevertheless suitable alternatives. Thus, gravel was chosen as a coarse mineral substrate similar to what can be found in cavities commonly occupied by lesser kestrels (e.g. when breeding in rock cavities or decaying buildings). The data from the first experimental year, when paired nestboxes contained old lesser kestrel nest material or gravel (40 dyads), have already been used in a previous publication with a focus on reproductive success and consequences for nestling fitness (Podofillini et al., 2018). We chose European roller because this species is also a secondary-cavity nester, it breeds in sympatry with lesser kestrels (BirdLife International, 2020) and both species can occupy the same nest sites (Catry & Catry, 2019). European rollers and lesser kestrels therefore share the same resource needs in terms of nesting sites, which is a prerequisite for social information use (Seppänen et al., 2007). European rollers do not nest in the city of Matera and, therefore, lesser kestrels did not directly compete with European rollers for access to our experimental nestboxes. Even though European roller nests may not be recognized as such by breeding lesser kestrels lacking experience with this competitor, they nevertheless convey clear information on past occupancy by another bird species as they contain fragments of eggshells, feathers, pellets and prey remains that clearly differ in appearance from those of lesser kestrels (to the human eye at least).

Providing peat moss versus gravel substrates allowed us to directly test the comfort hypothesis. The sole comparison between old conspecific/heterospecific nest material and gravel did not allow us to directly distinguish between the comfort and social information hypotheses, but it did allow us to confirm that either of them was valid. In addition, by combining data from 2016 to 2018, we could compare the relative overall preference for different substrates, providing some support for the comfort or (conspecific and/or heterospecific) social information hypothesis (Table 1). To formally test the social information hypothesis, one nestbox of each dyad in 2019 contained remains from an old lesser kestrel nest while the paired nestbox contained peat moss (*N* = 40 dyads; Fig. 1, Table 1).

Table 1. Predictions regarding the preferences of nest substrates across the four experimental designs and the corresponding tested hypotheses

Dyad type	Year (*N*)	Main predictions and hypotheses tested	Secondary predictions and hypotheses tested when combining 2016-2018
LK vs GV	2016 (40) 2017 (20) 2018 (20)	LK > GV: comfort and/or social information hypotheses	If LK = RL > PT > GV: social information hypothesis prevails; yet, comfort hypothesis also valid If LK > RL = PT > GV: conspecific social information hypothesis prevails; heterospecific nest only providing a soft and insulating substrate
RL vs GV	2017 (20)	RL > GV: comfort and/or social information hypotheses	
PT vs GV	2018 (20)	PT > GV: comfort hypothesis PT = GV, while LK > GV: support for the social information hypothesis	
LK vs PT	2019 (40)	LK = PT: comfort hypothesis LK > PT: social information hypothesis	

LK: old lesser kestrel nest material; GV: gravel, RL: old European roller nest material; PT: peat moss; '>' indicates a greater preference for one substrate; '=' indicates an equal preference. Predictions and the tested hypotheses when combining data from 2016 to 2018 are also shown. *N*: number of experimental dyads.

A nestbox was considered as chosen when egg laying began (i.e. at least one freshly laid egg was found during nest checks). We ensured that all choices were made when the kestrels had an equal opportunity to choose between both substrates within a dyad. Given the closeness of nestboxes within dyads, in the vast majority of cases a single pair settled per dyad. When two females laid eggs in both nestboxes of one dyad, we only considered the choice of the first settled female (based on laying date) to avoid including choices made without having both options available (this was the case for *N* = 14 dyads over 145 dyads occupied across 4 years, i.e. 10% of the occupied dyads, with either complete clutches in both nestboxes of one dyad, *N* = 11 dyads, or a complete clutch in the first occupied nestbox and an incomplete clutch, with one or two unhatched eggs, in the other nestbox for *N* = 3 dyads). Pairs settling in nestboxes where the adjacent paired box was already occupied were almost exclusively (13 of 14 pairs) the latest pairs to settle on the roof terraces. In one case, both nestboxes were occupied on the same day in 2016 (same laying date), and data from this dyad were removed from analyses. Overall, we analysed 108 nestbox choices when testing the comfort hypothesis and 36 choices when testing the social information hypothesis. As females may sometimes lay one egg in a cavity and lay the rest of the clutch in a different one, we ensured that all results remained qualitatively unchanged when considering only nestboxes that were effectively used for breeding (i.e. where at least three eggs were laid or, if only one or two eggs were laid, where at least one of them successfully hatched; see all models output in Tables A1 and A2).

Overall, 76% of adults breeding in our experimental nestboxes could be captured/identified (*N* = 64 individuals in 2016, 52 in 2017, 30 in 2018 and 65 in 2019). There is thus a risk that we considered the same unidentified individuals several times when pooling choices made in 2016–2018 when testing the comfort hypothesis. We verified that results remained qualitatively unchanged when analysing each breeding season separately (Fig. A1). Among the identified breeders, none were recaptured in different nestboxes the same year, and 27 individuals were recaptured in experimental nestboxes across years (23 individuals captured in 2 years, three captured in 3 years, one captured in 4 years). All results remained qualitatively unchanged when considering only the choices made by ringed individuals on their first breeding attempt in our experimental nestboxes (i.e. individuals naïve to the experimental set-up; *N* = 82 choices for the comfort hypothesis testing; *N* = 32 choices for the social information hypothesis testing; details not shown).

Each year in February, before lesser kestrels' arrival from African nonbreeding areas, old substrates were collected and all nestboxes were carefully emptied and cleaned. Then, the new substrates were prepared and distributed among experimental nestboxes to set up the experiments. To create a substrate indicating previous occupancy by lesser kestrels, we vigorously mixed the collected old lesser kestrel nest material and manually broke down large aggregates of organic matter, to obtain a homogeneous mixture of pellets, faeces, prey remains and small eggshell fragments, which we eventually distributed among the designated experimental nestboxes. In 2017, we collected old European roller nest material (composed of species-specific organic material and remains of prey items, as well as sand, pine needles and shells) from nestboxes located in another study area (Tuscany, Central Italy) and treated it similarly to the lesser kestrel nest material. As gravel substrate, we used a coarse (grain size ca. 5–15 mm) crushed carbonate rock gravel, simulating a substrate potentially occurring in natural rocky breeding cavities. For peat moss, we used commercially available sphagnum dry peat moss, normally used for home gardening. We fully renewed gravel and peat moss substrates every year, substituting them with new material if needed or reusing the old material when intact. We standardized the thickness of substrates among nestboxes (ca. 5 cm material).

We randomized the attribution of each substrate treatment within a dyad in the first year and each dyad type within terraces in 2017. In following years, nest content types were systematically switched within dyads: a nestbox containing gravel or old lesser kestrel nest material did not contain the same substrate the following year. Similarly, dyad types were switched across dyads between 2017 and 2018: a dyad of old lesser kestrel nest material versus gravel in 2017 contained gravel versus peat moss in 2018. Lesser kestrels are highly philopatric at the colony scale (57% natal philopatry and 72% breeding philopatry; Negro et al. 1997, Serrano et al. 2001), and at the subcolony scale (91% breeding philopatry to the roof terrace in Matera in 2016 – 2020, Morinay et al. n.d.). Yet, philopatry should have a minimal impact on our experimental design because the fidelity to the nestbox is low in this population (only 7%, Morinay et al. n.d.). Here, among the 27 identified individuals that bred for several years in our experimental nestboxes, only six (22%) bred in the same dyad and only one in the same nestbox. Nevertheless, the initial randomization and subsequent switching allowed us to remain conservative in regard to potential individual site fidelity. In addition, it allowed us to test two additional hypotheses: (1) the use of the previous occupancy as a source of social information at the nestbox level (i.e. whether individuals remember and select nestboxes that they have seen occupied in the previous year, irrespective of their current content), and (2) the independent sampling of the nest site's quality by individuals, leading to the recurrent occupancy of some 'high-quality' dyads, irrespective of their content (i.e. whether a specific dyad was systematically preferred across years, because of its orientation or sun exposure, for example).

Ethical note

Capture, handling and tagging procedures were conducted by the Italian Institute for Environmental Protection and Research (ISPRA), under the authorization of Law 157/1992 [Art. 4(1) and Art. 7(5)], which regulates activities on wild bird and mammal species in Italy. Field and handling procedures were also conducted in line with the ASAB/ABS guidelines for the treatment of animals in behavioural research. To minimize disturbance at the colony, nestbox monitoring was conducted two to three times per week early in the season and a maximum of five times in total after individuals had laid eggs (to detect clutch size, hatching date and hatching success). Breeding adults were captured/identified on the nest during incubation and early chick-rearing periods, when the chances of successfully capturing adults in the nest are maximized (Soravia, Cecere, & Rubolini, 2021). To minimize disturbance of the colony and allow partners to provision nestlings, ringing was conducted out of the roof terraces. Adults rearing nestlings were processed and usually released within 15 min to allow them to rapidly resume nestling provisioning.

Statistical analyses

We first aimed at assessing whether lesser kestrels could (1) simply occupy previously occupied nestboxes, irrespective of their content, and/or (2) independently agree on the higher intrinsic quality of specific sites (dyad) on the terraces by relying on cues other than the substrate. We thus fitted three separate generalized linear models (GLMs) investigating whether the occupancy of (1) a single (i.e. nondyadic) nestbox, (2) a nestbox paired in a dyad or (3) a dyad (i.e. the occupation of at least one nestbox in the dyad) was predicted by occupancy in the previous year, while including year as a random intercept effect (data from 2017–2020 for all monitored single nestboxes for (1), and from 2017–2019 for all experimental nestboxes for (2) and (3), as systematic monitoring began in 2016).

To test the comfort hypothesis, we determined whether the probability of choosing a soft over a coarse substrate differed from chance. We thus fitted a binomial GLM, with the choice of a soft substrate as the response variable (0 when choosing gravel, 1 when choosing soft substrate, i.e. peat moss, old lesser kestrel or European roller nest material; model based on the data from 2016–2018). As the comfort and social information hypotheses are nonexclusive, we also expected the preference for soft substrates to be more pronounced within dyads presenting social information (i.e. dyads with old lesser kestrel or European roller nest material treatment in either nestbox). We initially included as a single fixed factor the type of dyad (three-level factor, i.e. whether gravel was paired with peat moss, old lesser kestrel nest material or old European roller nest material). This, however, led to convergence issues as there was no settlement on gravel when the alternative was old European roller nest material. We thus eventually included as predictor a two-level factor describing whether the dyad presented social information (coded 1) or not (coded 0). We ensured that results remained unchanged when fully excluding dyads with European roller nest material.

To test the social information hypothesis, we fitted an intercept-only binomial GLM with the choice of a soft substrate containing social information (0 when choosing peat moss, 1 when choosing old lesser kestrel nest material, based on the data from 2019) as the response variable.

Then, we tested whether individual timing of reproduction (laying date) and proxies of reproductive success (clutch size, hatching success) varied according to the chosen substrate. Since Podofillini et al. (2018) only found an effect of the nest substrate (either old lesser kestrel nest material or gravel, in 2016) on lesser kestrels' hatching success and no effect on chick growth and survival, we only monitored the hatching success in the subsequent years of this experiment.

We fitted separate models for the experiments aiming at testing the comfort (2016–2018) and the social information hypotheses (2019). We retained incomplete clutches (probably nests deserted during egg laying) for the models fitting the laying date and clutch size (see Tables A1 and A2 for quantitatively similar results without these nests), but we removed them for the model fitting hatching success.

For testing the effects of a soft substrate (2016–2018 data) on laying date (calculated relative to the first egg laid in the considered breeding season), clutch size, hatching success (number of eggs hatched over total number of eggs in each clutch), we fitted linear mixed (LMMs) or generalized linear mixed models (GLMMs) with the chosen substrate type as a predictor (four-level factor) and the type of dyad per year (e.g. ‘lesser kestrel versus gravel in 2018’) as a random factor. If the random effect variance could not be estimated (singular fit), we removed this term from the models. We relied on LMM for laying date and on binomial GLMM (events/trials syntax and accounting for overdispersion) for hatching success. For clutch size, we initially fitted an LMM, but removed the random effect as it explained no variance. Owing to the distribution of this variable (count), we then fitted a simple linear model, relying on a permutation test for assessing significance (see below). For testing differences in laying date, clutch size and hatching success between soft substrates with and without social information (2019 data), we used the same approach as described above, but relied on linear models/GLMs (i.e. without random effects).

Some substrate contrasts (except lesser kestrel nest material versus gravel) were only provided in a single breeding season, and by pooling data from 2016–2018 we may have blurred year-specific effects. Hence, we further ensured that this had minimal impacts on our results by showing year-specific preferences (Fig. A1) and repeating the analyses of laying date, clutch size and hatching success for each dyad type (see Results). The latter, however, was not feasible for dyads of European roller nest material versus gravel, as no individuals chose to lay eggs on gravel in this case (Fig. A1).

As we found a difference in laying dates between substrates (see Results), we tested whether it could reflect an age effect, i.e. whether late breeders (with late laying dates) were likely to be younger individuals. We categorized age of breeders as young (1–2 years old) and old (>2 years old). We considered 2-year-old breeders as ‘young’ because lesser kestrels mostly breed for the first time at this age, although some 1-year-old individuals may settle and attempt breeding (Cramp 1998, this study). Thanks to the intensive ringing of adults and nestlings in the study area since 2016, we could assign age class to many individuals recaptured in successive years, while we also relied on plumage criteria for males (typical yearling plumage, Baker, 1993). We could obtain laying date information for 35 young (10 females and 25 males) and 181 old individuals (47 females and 134 males; *N* = 144 breeding events overall). We eventually modelled the within-year laying date (days elapsed from the first egg laid each year) with an LMM including age, sex and their interaction as covariates, and individual identity as a random effect.

All statistical analyses were performed with R 4.0.0 (R Core Team, 2020). LMMs and GLMMs were fitted with the lmer and glmer R functions, respectively (‘lme4’ R package, Bates, Maechler, Bolker, & Walker, 2015). Permutation tests of linear models were performed with the lmperm function (5000 permutations; ‘permuco’ R package; Frossard & Renaud, 2019). Models’ fit was assessed by visual inspections of residuals versus predicted and fitted values. The fit of models with binomial distribution errors was assessed with ROC curves and AUC values (Robin et al., 2011).

Results

Effect of previous occupancy

From the monitoring of single nestboxes since 2016, we confirmed that a nestbox was more likely to be occupied if it was already occupied in the previous year (nonexperimental nestboxes only; estimate ± SE = 1.09 ± 0.25, Z = 4.35, *P* < 0.001, *N* = 495 breeding attempts between 2017 and 2020). When considering only dyadic nestboxes, a nestbox was more likely to be occupied if it was not occupied in the previous year (estimate ± SE = -1.06 ± 0.27, *Z* = -3.95, *P* < 0.001, *N* = 240 breeding events), a result related to our systematic swapping of substrates within dyads among years (see Methods). In addition, the occupancy of at least one nestbox in a dyad did not depend on the occupancy of this dyad in the previous year (estimate ± SE = 0.70 ± 0.85, *Z* = 0.82, *P* = 0.41, *N* = 120 breeding events).

The comfort hypothesis

The probability of choosing a soft versus a coarse substrate was higher than expected by chance (Fig. 2; estimate ± SE of the intercept for the null model = 2.67 ± 0.39, *Z* = 6.83, *P* < 0.001).

The preference for soft substrates was particularly pronounced for individuals settling on substrates providing social information (old lesser kestrel or European roller nest material) compared to individuals settling on soft substrates not providing social information (peat moss; effect of the presence of social information within the dyad, Table A1). Lesser kestrels preferred old European roller nest material over gravel (in 100% of the cases), but the extent of this preference was not significantly different from that of old lesser kestrel nest material (Fig. A1). Nevertheless, the preference for a soft substrate providing social information versus a soft substrate not providing social information was similar when excluding dyads with old European roller nest material (estimate ± SE = 2.04 ± 0.83, $Z = 2.47$, $P = 0.014$). The preference for old lesser kestrel nest material versus gravel was highly consistent across years (Fig. A1).

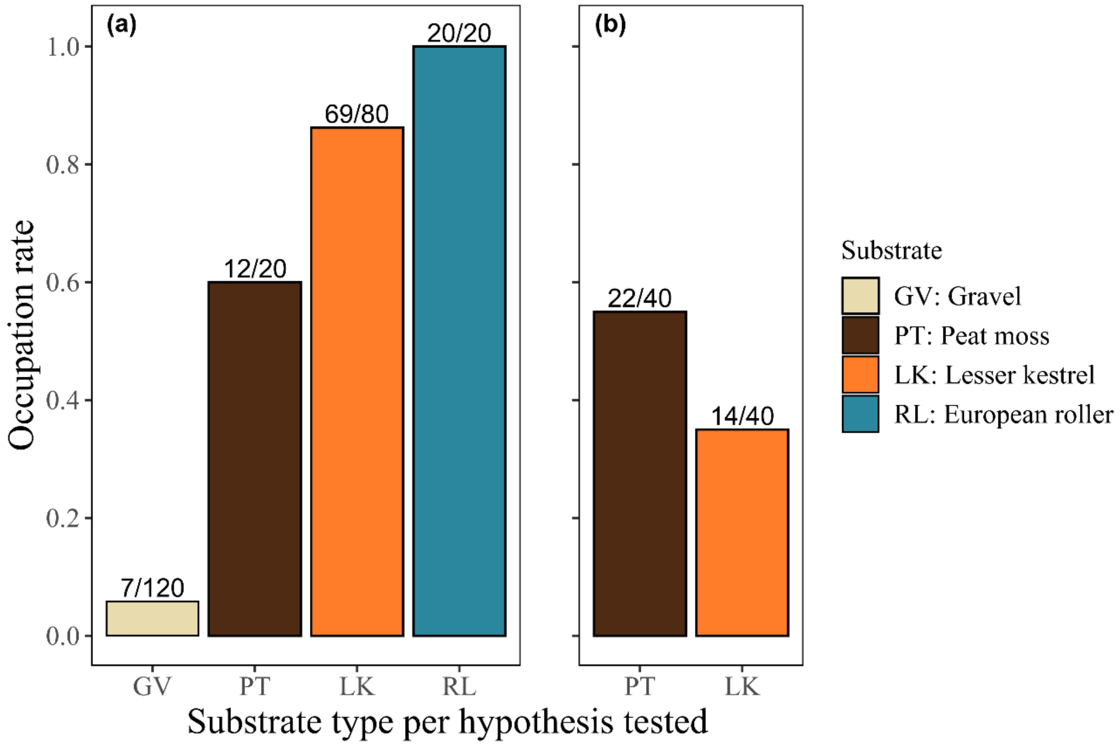

Figure 2. Occupation rate of each substrate type when testing (a) the comfort hypothesis and (b) the social information hypothesis. All occupations on gravel were pooled for illustrative purposes (see Fig. A1 for more detailed representation). The proportion of nestboxes occupied over the total number of dyads of each type is given above each bar.

There was no difference in laying dates between substrate types when the three soft substrates were paired with the coarse one (gravel; $|t| < 0.98$). This lack of difference in settlement timing was observed irrespective of whether the soft substrate presented social information or not (Tables 2 and A1).

Pairs settling on old lesser kestrel or European roller nest material laid more eggs than those settling on gravel (old lesser kestrel nest material: mean ± SE = 4.32 ± 0.10; old European roller nest material: mean ± SE = 4.45 ± 0.19; gravel: 3.57 ± 0.32; Table A1). There was no difference in clutch size between pairs settled on peat moss versus gravel (peat moss: mean ± SE = 4.33 ± 0.24; Table A1). Yet, these differences in clutch sizes did not hold when excluding deserted nests (Table A1).

Comparisons of laying dates and clutch sizes among substrates were similar when considering each type of dyad separately (details not shown). There was no difference in hatching success between substrate types (Table A1). However, when considering dyads of old lesser kestrel nest material versus gravel only, pairs settled on old conspecific nest material had a significantly higher hatching success (73%) than those settled on gravel (25%; estimate ± SE = 1.89 ± 0.85, $Z = 2.24$, $P = 0.025$). There was no difference in hatching success between substrates when considering dyads of peat moss versus gravel only (83% on average; details not shown).

The social information hypothesis

When individuals had the choice of either peat moss or old lesser kestrel nest material, there was no overall preference for a soft substrate with or without social information (Table A2). However, laying date differed between the two soft substrates: females occupying nestboxes with social information laid eggs earlier (23 May on average), while females occupying nestboxes providing only comfort laid eggs a week later (lesser kestrel versus peat moss: Fig. 3, Tables 2 and A2). There was no difference in clutch size (|Table A2) or hatching success (Table A2) between soft substrates.

Linking settlement timing and individual age

Laying date differed between young and old breeders (estimate ± SE = -8.95 ± 2.06, $t_{213} = -4.35$, $P < 0.001$): young individuals laid eggs later (marginal mean ± SE = 22.44 ± 1.92) than old ones (marginal mean ± SE = 13.49 ± 0.92; nonsignificant age*sex interaction was removed from the model; $t_{212} = -1.47$, $P = 0.14$). Including age in the 2019 laying date model testing the effect of the chosen substrate did not yield useful results as only two young individuals were found (versus 27 old individuals), both of which bred on peat moss.

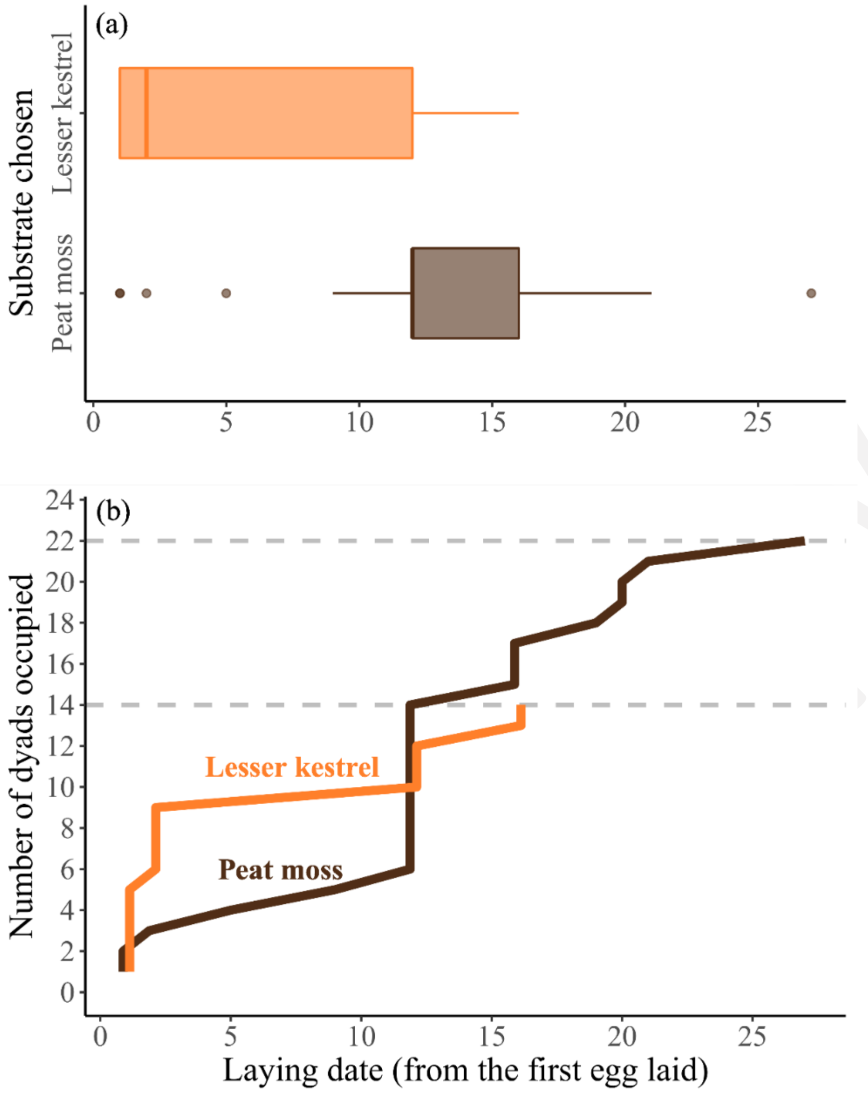

Figure 3. Settlement timing within dyads testing the social information hypothesis, when old lesser kestrel nest material (orange) was paired with peat moss (brown). (a) Distribution of laying date according to the chosen substrate. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers. (b) Temporal variation in the cumulative number of dyads occupied according to the chosen substrate. Overall, 36 of 40 experimental dyads were occupied in this experiment (2019). Within dyads, the nestbox containing peat moss was chosen in 22 of 36 dyads, and the nestbox containing old lesser kestrel nest remains was chosen in 14 of 36 dyads (dashed lines). Laying date is expressed in days elapsed since the day when the first egg was laid among all experimental dyads.

Table 2. Laying date of pairs breeding in nestboxes with different nest substrates, when testing the comfort and social information hypotheses

Substrate type	Mean ± SD (*N*)
Test of the comfort hypothesis (2016–2018)	
Gravel	13.57 ± 6.37 (7)
Lesser kestrel	12.78 ± 6.93 (69)
European roller	9.70 ± 4.58 (20)
Peat moss	11.83 ± 6.53 (12)
Test of the social information hypothesis (2019)	
Lesser kestrel	5.79 ± 6.18 (14)
Peat moss	12.78 ± 6.61 (22)

Mean laying date is calculated as days elapsed since the day when the first egg was laid in each year among all experimental nests.

Discussion

By means of a double-box experiment, we showed that lesser kestrels strongly prefer to nest on top of comfortable soft substrates, clearly avoiding coarse mineral substrate. In addition, lesser kestrels seemed to use social cues to select breeding sites: the preference for soft substrates over gravel was more pronounced when the soft substrate also provided conspecific (as shown in Podofillini et al., 2018) or heterospecific social information. When formally testing the social information hypothesis, we found that peat moss and old conspecific nest material were chosen equally. The absence of an overall preference between different soft substrates with or without conspecific cues is in line with a previous experiment carried out in a different cavity-nesting species that does not add nest lining material, the Eurasian hoopoe, *Upupa epops* (Díaz-Lora et al., 2019). Yet, we showed that the apparent absence of preference for old lesser kestrel nest material at the population level was the result of a temporal difference in preference for both substrates: early breeders favoured nesting on top of old conspecific nest material while late breeders favoured nesting on peat moss and actively avoided old conspecific nests. Such temporal shifts in preference were not observed when gravel was paired with a soft substrate (Table 2). In addition, we showed that lesser kestrels did not use the actual presence of breeders in a specific nestbox of a dyad in the previous year as a source of social information for the settlement decision, nor did they systematically prefer specific nesting sites (here dyads). These results suggest that lesser kestrels collect and use currently available social cues informing on past competitor occupancy (here nest content) for decision making, thereby supporting previous evidence on breeding site selection and reproductive timing in this species (Serrano et al. 2001, 2004, Serrano and Tella 2003, Aparicio et al. 2007).

Our results are in line with studies of other bird species showing a greater and/or earlier occupancy of cavities containing old nest material compared to empty cavities (e.g. eastern bluebirds, *Sialia sialis*, Davis, Kalisz, & Wells, 1994; pied flycatchers, *Ficedula hypoleuca*, Olsson & Allander, 1995; burrowing owls, *Athene cunicularia*, Riding & Belthoff, 2015; European kestrels, Mingju et al., 2019, Sumasgutner, Vasko, Varjonen, & Korpimäki, 2014; reviewed in Mazgajski 2007). Choosing a soft substrate for species that do not add any lining material may be selected for if it reduces the risk of egg breakage, improves the insulation of the cavity and/or is a source of beneficial bacterial strains (Díaz-Lora et al., 2019; Mazgajski, 2007). We did not find any clear difference in hatching success between treatments, except when only retaining dyads of old lesser kestrel nest material versus gravel, which is in line with earlier findings suggesting that reusing nests improves incubation efficiency (including nondyadic nests, Podofillini et al. 2018). Yet, the strength of the selective advantage provided by nesting on soft and insulating nest material likely varies among years and environmental conditions (e.g. cold/wet versus warm/dry seasons), as shown by the effect of extreme climatic events on reproductive success (Marcelino et al., 2020) and by the annual variation in hatching and fledging success (Sarà, Campobello, & Zanca, 2012) in this species. By combining results from different years and treatment types, we may have blurred year-specific differences in hatching success. Indeed, some contrasts between treatments were only provided for single years (except the comparison of old lesser kestrel nest remains and gravel; Table 1). Our results are thus subject to specific conditions each year. Based on the monitoring of all nestboxes, laying dates were globally earlier in 2018 and later in 2019 than in other years, while clutch size was similar among years, and hatching success was lower in 2016 than in other years (Table A3). Yet, the rejection of the coarse substrate was clear in all years, and the preference for old lesser kestrel nest material was highly consistent across years, despite these slight differences in phenology. We thus believe that combining years should not have strongly affected our results, which was further corroborated by year-specific tests (Fig. A1).

The apparent absence of reproductive success differences between nest substrates also contrasts with results reported in Sarà et al. (2012), which showed that the natural presence of old nest material positively predicted nestling survival. Yet, in such previous unmanipulated settings, good quality sites providing increased reproductive success are more likely to be occupied and thus accumulate old nest remains across years. The strength of our experimental design lies in double-boxes with randomized treatments, allowing us to reliably decouple the conspecific preference for a given nest material from the natural quality and potential fitness payoffs of a specific nest site (e.g. centrality in the colony, orientation and sunlight exposure of the nestbox).

The presence of old nests is known to act as a social cue for settlement decisions, for example by informing on the availability of suitable sites (a form of conspecific attraction, e.g. in Eurasian penduline tits, *Remiz pendulinus*, selecting trees with old nests, Gergely et al. 2009) or sites with low predation pressure (e.g. barn swallows, *Hirundo rustica*, preferring sites with numerous undamaged nests, Ringhofer and Hasegawa 2014). Sites with old nest material might thus be preferentially favoured by individuals and consequently occupied first, as shown in our study as well as in other species (e.g. pied flycatchers, Olsson and Allander 1995; European kestrels, Sumasgutner et al. 2014). In addition, nestboxes without cues from previous occupation (but with a soft substrate) were not simply occupied later by default, because the double-box experimental design allowed us to always keep both treatments available for individual choice. Instead, soft substrates without social cues were actively preferred by later birds, suggesting that both early and late birds detect and use the social cue provided by old conspecific nest material, but to make opposite settlement decisions.

This temporal difference in preferences can originate from different mechanisms. First, competition avoidance may explain why late breeders avoid nesting on old nest material. Indeed, competition for nest sites, especially in man-made environments where cavities are scarce, can be high in lesser kestrel colonies (e.g. in Portuguese urban versus rural areas, Franco, Marques, & Sutherland, 2005) and the availability of nest sites is known to be a key limiting factor for the breeding of secondary-cavity nesters (Newton, 1994). In Matera, between 60 and 97% of the nestboxes are occupied every year (Morinay et al. n.d.), suggesting that competition for the best nest sites could be high in this population (e.g. peripheral sites, with the optimal sunlight exposure/microclimate, Sarà et al. 2012; sites with old nest material, Podofillini et al. 2018 and this study). In our population, young breeders start laying ca. 9 days later than old ones, similarly to other lesser kestrel populations, where late breeders are either young individuals (Catry, Moreira, Alcazar, Rocha, & Catry, 2017) or immigrants (Serrano, Tella, Donázar, & Pomarol, 2003). Late breeders are thus likely to be less experienced and less competitive than early arriving philopatric conspecifics. Old nest material could thus be preferred by experienced individuals but avoided by inexperienced ones if settling in a site that appears of good quality (i.e. previously selected by conspecifics) implies competitive costs, like increased territorial defence or conflicts with competitive neighbours and prospectors. In general, such a pattern could result either from the active selection of lower quality sites by less competitive individuals or from their eviction from good quality sites (as suggested in failed or first-time breeding male collared flycatchers, *Ficedula albicollis*, Doligez, Danchin, Clobert, & Gustafsson, 1999; Doligez et al., 2004). Here, we showed that late breeders actively and preferentially selected sites without cues from past breeding attempts even when another soft substrate with social cues was equally available.

Second, nestboxes with old nest material might have appeared to late-arriving individuals to be currently occupied, explaining why they settled in the nearby nestbox. To avoid conflicting with earlier, already settled birds, late breeders may indeed select (1) a dyad without attending competitors, and (2) within the dyad, the nestbox that appears unoccupied. This possible explanation is supported by the fact that individuals laid eggs later in 2019 than in previous years (Table A3). Thus, the absence of temporal patterns in the other years (in particular in 2018 between old lesser kestrel nest material and peat moss) might have simply been because settlement occurred earlier, when none of the nestboxes containing old nest material was perceived as recently occupied.

Finally, nestboxes with old nest material that were still unoccupied late in the season might have been perceived as recently deserted, hence potentially as poor-quality breeding sites.

Contrary to what was suggested as a reason for active rejection of old nest material (Mazgajski, 2007), parasite avoidance is not likely to have shaped the observed rejection of old lesser kestrel nest material late in the season. Indeed, Podofillini et al. (2018) showed that ectoparasite load (haematophagous flies, *Carnus hemapterus*, developing and sometimes overwintering in old nest material; Valera, Casas-Crivillé, & Calero-Torralbo, 2006) was lower in late than early broods, and that there was no difference in ectoparasite load of nestlings reared in nestboxes containing gravel or old lesser kestrel nest material (after 3 days of age). Fully ruling out a role for nest ectoparasites, however, would require assessing ectoparasite load in nestlings reared on peat moss.

Determining whether late breeders tend to prevent risks of competition, or simply avoid breeding on already occupied or recently deserted nests, would require further experimental tests. Yet, regardless of the actual mechanism explaining the temporal shift in substrate preference in 2019, our results reveal that both early and late breeders perceived this difference in nest material and used this cue to make their settlement decision.

How lesser kestrels used social information (here, the presence of old nest material) for settlement decisions seemed to depend on their own competitive abilities. To assess competition level and select their breeding site in accordance with their own competitive abilities or experience, lesser kestrels could be expected to rely on other social cues, like the aggressiveness of competitors or the apparent quality of neighbours. This has, for example, been shown in male wood warblers, *Phylloscopus sibilatrix*, which copy the settlement choice of low-quality conspecifics (Szymkowiak, Thomson, & Kuczyński, 2016), and in female collared flycatchers, which eavesdrop on competitors' songs to select a breeding site according to their own aggressiveness (Morinay, Forsman, & Doligez, 2020). Identifying social cues used by lesser kestrels needs further experimental investigations, at both conspecific and heterospecific levels. Our results suggest that lesser kestrels also exploit heterospecific social cues, as old European roller nest material was selected in all cases when paired with the coarse substrate. This could reflect the active preference for a soft substrate of a competitor sharing the same resource needs in terms of breeding sites but implying lower competitive pressure. Alternatively, the intrinsic properties of European roller nests may be simply better than the other soft substrates, leading to a preferred settlement on them, irrespective of the social information they may convey. In rural areas, European rollers and lesser kestrels are known to breed in sympatry, sometimes occupying the same old buildings or ruins (Catry & Catry, 2019). Yet, as European rollers do not breed in the urban context of the study colony, whether lesser kestrels recognized heterospecific nest material as such remains to be empirically shown. In addition, the European roller is dominant over the lesser kestrel (Catry, Alcazar, Franco, & Sutherland, 2009). Therefore, our results could differ if the experiments were conducted in areas where European rollers and lesser kestrels compete for nesting space: lesser kestrels can be expected to avoid nesting on top of European roller nest material if other 'safe'/comfortable sites are available. It is also possible that in our study only the most experienced/dominant lesser kestrels occupied nestboxes with these old European roller nests. The measurement of traits informing on individual dominance or competitive ability towards heterospecifics would be required to confirm this possibility.

To conclude, we showed that lesser kestrels favour comfortable soft nest substrates when choosing a nest site but may also exploit social information to either select or avoid sites previously occupied by conspecifics, probably as a side-effect of competition for nest sites in this colonial secondary cavity-nesting raptor. As this species is currently the subject of large-scale conservation actions in Europe, often involving providing large numbers of nestboxes (Gameiro, Franco, Catry, Palmeirim, & Catry, 2020; Iñigo & Barov, 2010), our results bring important insights on the mechanisms underlying nest site selection in this species. In particular, adding or keeping old nest material in some artificial nest sites and providing soft substrates like peat moss in others should considerably improve nest site attraction for both early and late (possibly young or immigrant) breeders and should be widely adopted in nestbox provisioning programmes.

Data availability

Data on the dyad experiment are available here: https://doi.org/10.17632/64w9khbkd6.1

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Appendix

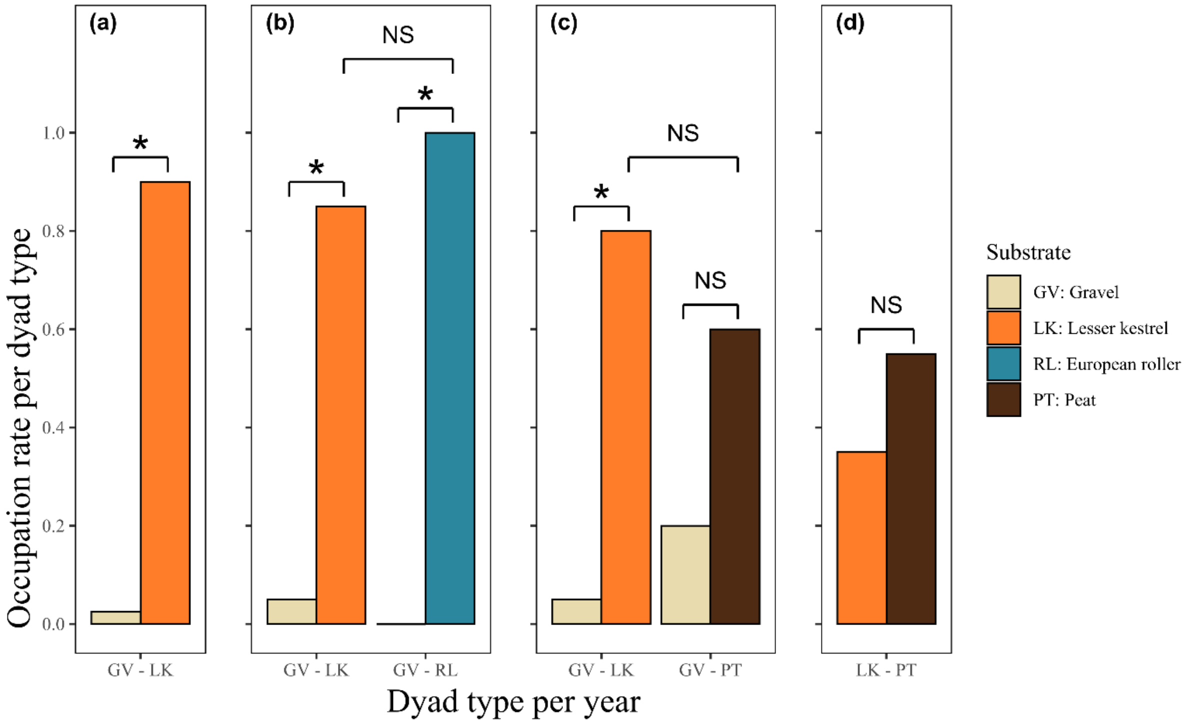

Figure A1. Occupation rate of each type of dyad, categorized by the nest substrate chosen, in (a) 2016, (b) 2017, (c) 2018 and (d) 2019. **P* <0.05, based on results from binomial tests (within dyads) and Fisher tests (across dyads).

Table A1. Output of the statistical models fitted to detect differences between substrate types, when testing the comfort hypothesis (data from 2016–2018)

	All nests				Excluding deserted nests			
	Estimate ± SE	*t*	*Z*	*P*	Estimate ± SE	*t*	*Z*	*P*
Comfortable substrate chosen								
Intercept	1.10 ± 0.58		1.903	0.057	1.10 ± 0.58		1.903	0.057
Social information (1)	2.29 ± 0.82		2.783	0.005	2.67 ± 0.92		2.909	0.004
Laying date								
Intercept	13.76 ± 2.83	4.870			12.63 ± 3.03	4.167		
Substrate (LK)	-1.95 ± 2.88	-0.679			-0.87 ± 3.17	-0.275		
Substrate (RL)	-4.06 ± 4.16	-0.976			-3.42 ± 4.31	-0.794		
Substrate (PT)	-1.48 ± 3.14	-0.473			-0.85 ± 3.14	-0.271		
(1|substrate type per year)	7.44 ± 2.73				7.45 ± 2.73			
Residual variance	37.93 ± 6.16				36.16 ± 6.01			
Clutch size								
Intercept	3.57 ± 0.32	11.178			4.00 ± 0.30	13.298		
Substrate (LK)	0.75 ± 0.34	2.229		0.031	0.35 ± 0.31	1.125		0.267
Substrate (RL)	0.88 ± 0.37	2.367		0.019	0.58 ± 0.35	1.678		0.098
Substrate (PT)	0.76 ± 0.40	1.895		0.062	0.33 ± 0.37	0.905		0.371
Hatching success								
Intercept					0.69 ± 0.67	1.031		0.305
Substrate (LK)					0.28 ± 0.70	0.403		0.688
Substrate (RL)					0.33 ± 0.77	0.428		0.669
Substrate (PT)					1.01 ± 0.90	1.125		0.263

LK: old lesser kestrel nest material; RL: old European roller nest material; PT: peat moss. For the first model, the presence of substrate providing social information was coded as 0 (absence, state of reference) or 1 (presence). The substrate of reference is gravel for all the other models. All nests: *N* = 108 for each model; excluding deserted nests: *N* = 105 for each model.

Table A2. Output of the statistical models fitted to detect differences between substrate types, when testing the social information hypothesis (data from 2019)

	All nests				Excluding deserted nests			
	Estimate ± SE	*t*	*Z*	*P*	Estimate ± SE	*t*	*Z*	*P*
Substrate with social information chosen								
Intercept	-0.45 ± 0.34		-1.32	0.186	0.36 ± 0.35		-1.024	0.306
Laying date								
Intercept	12.77 ± 1.38	9.289		< 0.001	12.10 ± 1.37	8.829		< 0.001
Substrate (LK)	-6.99 ± 2.21	-3.169		0.003	-6.31 ± 2.14	-2.956		0.006
Clutch size								
Intercept	3.59 ± 0.22	16.526			3.80 ± 0.20	19.150		
Substrate (LK)	0.41 ± 0.35	1.174		0.322	0.20 ± 0.31	0.647		0.563
Hatching success								
Intercept					1.54 ± 0.64		2.421	0.016
Substrate (LK)					-0.21 ± 0.81		-0.253	0.800

LK: old lesser kestrel nest material. The substrate of reference is peat moss for all models. All nests: *N* = 36 for each model; excluding deserted nests: *N* = 34, except for hatching success, where *N* = 12. The sample size is low when considering hatching success because only a few eggs hatched on the last visit of the season.

Table A3. Among-year variation in laying date, clutch size and hatching success

	Descriptive statistics	*N*
Laying date		
2016	136 ± 8.58	132
2017	137 ± 6.81	129
2018	128 ± 8.11	143
2019	145 ± 8.24	110
Clutch size		
2016	3.96 ± 1.05	135
2017	4.05 ± 1.03	127
2018	4.05 ± 0.98	151
2019	3.54 ± 1.23	152
Hatching success		
2016	0.61 ± 0.13	135
2017	1.21 ± 0.21	63
2018	1.31 ± 0.15	126
2019	2.01 ± 0.40	33

Descriptive statistics: means ± SD are shown for laying date and clutch size; marginal means ± SE are shown for hatching success. The descriptive statistics for hatching success were obtained from a binomial model fitting the number of successes and failures within a brood as a response variable with year as a categorical predictor, and from the R package ‘emmeans’ (Lenth, 2019). The sample size is low for hatching success in 2019 because only a few eggs hatched on the last visit of the season.