Anti-predatory benefits of heterospecific colonial breeding for a predominantly solitary bird

João Gameiro[1*], Aldina M.A. Franco[2], Teresa Catry[3], Jorge M. Palmeirim[1], Inês Catry[4,5,6]

[1]cE3c – Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal

[2]School of Environmental Sciences, University of East Anglia, Norwich, UK

[3]Centro de Estudos do Ambiente e do Mar (CESAM), Departamento de Biologia Animal, Faculdade de Ciências da Universidade de Lisboa, Lisbon, Portugal

[4]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal

[5]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, 1349-017 Lisboa, Portugal

[6]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal

*jgameiro92@gmail.com

Predation risk profoundly shapes how animals behave and is one of the main forces driving the formation or maintenance of groups. For some species, group living may be facultative, and individuals may live solitarily or aggregate with conspecifics or heterospecifics, but the advantages of each strategy are still poorly known. Here, we investigated whether a predominantly solitary breeding species, the European roller *Coracias garrulus*, acquires anti-predatory benefits from nesting in mixed-species colonies dominated by lesser kestrels *Falco* *naumanni*. We compared the risk-taking behaviour of solitary rollers and rollers breeding in colonies by conducting two sets of experiments. Firstly, we investigated rollers' latency to resume incubation when presented with a novel object, and secondly assessed their latency to resume chick provisioning and their investment in mobbing behaviour towards a predator model. We additionally compared the breeding performance and nest predation rate of rollers in each social context (solitary vs colonial) using data from 300 breeding attempts across six years. We found that rollers breeding in colonies returned to their nests sooner during the presentation of both the novel object and the predator model and attacked the predator model less frequently than solitary rollers, suggesting they can use heterospecifics as cues in deciding whether is safe to return to their nests. In addition, rollers in colonies suffered less nest predation than solitary ones, but this did not translate into a higher productivity. Future studies should investigate whether breeding in colonies provide other advantages to rollers, such as increased adult survival or fitness.

Keywords: anti-predatory behaviour; facilitation; group-living; mixed-species colonies; predation; protective nesting associations

Predation is a major driving force in the evolutionary history of animals, influencing their behaviour and affecting their fitness (Lima & Dill 1990; Quinn & Ueta 2008; Inbánez-Álamo et al. 2015; Graham & Shutler 2019). In addition to the lethal effects of failing to escape a predator, animals may experience non-lethal effects when responding to predation risk, by redirecting time and energy from other fitness-enhancing activities such as mating, feeding, or caring for offspring (Lima & Dill 1990; Frid & Dill 2002; Cresswell 2008). Because anti-predatory strategies are costly, behaviours used by animals to evade predators are plastic and require individuals to successfully identify real threats (Frid & Dill 2002; Crane & Ferrari 2017). One way to do so is by being fearful to novel, risky stimuli, i.e., being neophobic (Cran & Ferrari 2017; Crane et al. 2020). As at the individual level, all cues from predators and non-predators are novel during the first encounter, a frightened response to new stimuli is a safe strategy to learn about real predators (Brown et al. 2013; Crane & Ferrari 2017).

Anti-predatory behaviour may also be influenced by the presence of nearby individuals, and predation is often considered an important factor in the evolution of sociality, influencing the structure and dynamics of communities (Lima & Dill 1990; Uetz et al. 2002; Varela et al. 2007; Lehtonen & Jaatinen 2016; Crane et al. 2020). Living in groups increases prey conspicuousness (Varela et al. 2007) but may reduce predation risk through increased efficiency in predator detection and deterrence, or simply through dilution effects (Brown & Hoogland 1986; Arroyo et al. 2001; Hass & Valenzuela 2001; Beauchamp 2008; Lehtonen & Jaatinen 2016). Individuals in groups may detect predators earlier as total time spent in vigilance increases with group size, while reducing the need for individual investment (Brown & Hoogland 1986; Beauchamp 2008; LaBarge et al. 2021). Similarly, individuals in groups engaged in mobbing – where animals harass, distract, or confuse an approaching predator by lunging or calling towards it – should face lower individual predation risk than those mobbing solitarily, whilst maintaining or increasing mobbing effectiveness (Brown & Hoogland 1986; Arroyo et al. 2001; Krams et al. 2009).

Mixed-species groups are common across many taxa and may enhance anti-predatory benefits more than single-species assemblages (Stensland et al. 2003; Sridhar & Guttal 2018; Boulay et al. 2019; Goodale et al. 2020). This may occur because species have different sensory or behaviour capabilities; for example, individuals may aggregate with more vigilant, vocal, or aggressive species that are more effective at driving predators off (Quinn & Ueta, 2008; Sharpe et al. 2010; Campobello et al. 2012; Goodale et al. 2019; Gabel et al. 2021). Additionally, because niche overlap is highest among conspecifics, aggregating with other species may alleviate the costs associated with intraspecific competition (Sridhar & Guttal, 2018; but see Gaglio et al. 2018; Catry & Catry 2019). Lastly, for some species, e.g., those living solitary or in small groups, achieving a group large enough to provide anti-predatory benefits may only be possible by aggregating with heterospecifics (Semeniuk & Dill 2006; Goodale et al. 2019, 2020). Whether to live solitarily, in single, or in mixed groups may depend on localized adaptations to specific ecological conditions such as habitat structure or predation pressure (Wagner et al. 2000; Quinn & Ueda 2008; Marino 2010; Murthy et al. 2015; Liu et al. 2020). However, how predation risk favours one strategy over the other remains poorly studied.

In birds, mixed-species groups often occur as mixed-species colonies, where birds concentrate on highly dense breeding sites. Colonies are particularly susceptible to predation, as they are fixed in space and are more conspicuous through visual, acoustic, or olfactory cues (Rolland et al. 1998; Varela et al. 2007). In this study, we investigate whether a typically solitary bird species, the European roller *Coracias garrulus* (hereafter roller), acquires anti-predatory benefits from nesting in lesser kestrels *Falco naumanni* colonies. Both species are long-distance migrants, wintering mostly in sub-Saharan Africa and breeding in the Western Palearctic (Finch et al. 2015; Sarà et al. 2019), and share similar dietary and nesting requirements in their South European breeding grounds (Catry et al. 2009, 2016, 2019; Birdlife International, 2021). Previous studies on solitary rollers found that they avoided areas with higher predation risk but did not alter parental care in the presence of a predator model (Parejo & Avilés 2011; Expósito-Granados et al. 2016). On the other hand, lesser kestrels are known for their marked mobbing behaviour and have been described as the protector species in nesting associations with red-billed coughs *Pyrrhocorax pyrhocorax* (Blanco & Tella 1997) and jackdaws *Corvus monedula* (Campobello et al. 2012). In southern Portugal, rollers can be found breeding both solitarily and in association with mixed-species colonies dominated by lesser kestrels (Catry et al. 2009; Gameiro et al. 2020). We conducted behavioural experiments examining the risk-taking behaviour towards a novel object and towards a predator model in rollers breeding solitarily and rollers breeding in mixed-species colonies. In addition, we investigated whether potential benefits from each social breeding strategy (solitary vs colonial) translate into lower nest predation rates and higher breeding success. We expect the presence and behaviour of neighbouring lesser kestrels would inform rollers on whether returning to the nest is safe, regulating rollers investment in nest-defensive behaviours (Seppänen et al. 2007; Quinn & Ueta 2008; Campobello et al. 2012). If nesting in colonies provides direct anti-predatory benefits, we predict rollers breeding in colonies to have lower predation rates and higher productivity.

METHODS

Study area and species

This study was conducted in the Special Protection Area (SPA) of Castro Verde, Southeast Portugal (37°43′N, 7°57′W). With ca. 85 000 ha, this is one of the most important strongholds for many endangered farmland birds in Western Europe (Moreira et al. 2007), hosting more than 80% of the Portuguese populations of rollers and lesser kestrels (Catry et al. 2009, 2011; Gameiro et al. 2020). The landscape is dominated by extensive dry cereal cultivation, fallows and grasslands used for livestock, and patches of orchards, vineyards, and small afforestations (Moreira et al. 2007). Here, rollers and lesser kestrels – two secondary-cavity nesting species– nest in cavities of abandoned farmland buildings or artificial breeding structures build in the scope of conservation programs targeting the recovery of lesser kestrels since 2000 (Catry et al. 2009; Catry et al. 2011; Gameiro et al. 2020). Artificial nests include nest-boxes, clay pots, and breeding walls and towers with up to 90 cavities (Catry et al. 2009).

Lesser kestrels arrive to the breeding grounds in early February and typically lay in April-May. Both sexes participate in incubation and chick rearing. Incubation lasts ca. 28 days and chicks fledge at 36 (del Hoyo et al. 2001a). Rollers arrive at the breeding grounds in mid-April and laying usually occurs in May-June. Both sexes engage in incubation and chick rearing. Incubation takes ca. 20 days and chicks fledge at 20-25 days (Del Hoyo et al. 2001b). Rollers can breed in isolated nests (isolated cavities in farmhouses or in nest-boxes placed on trees or telephone poles), or within mixed colonies, with up to four roller pairs per colony. Lesser kestrel colonies range from two to 80 breeding pairs. Other species can also be found breeding in these mixed-species colonies, including common kestrel *Falco tinnunculus*, barn owl *Tyto alba*, little owl *Athene noctua*, jackdaw *Corvus monedula*, spotless starling *Sturnus* *unicolor*, and feral pigeon *Columba livia* (Catry & Catry 2019). These species do not significantly contribute to the communal defence, and so attention was given only to lesser kestrels (see results). Potential nest/adult predators in the area include carrion crow (*Corvus corone*), Eurasian magpie (*Pica pica*), barn owl (*Tyto alba*), ladder and Monpellier snake (*Zamenis scalaris* and *Malpolon monspessulanus*, respectively), weasel (*Mustela nivalis*), garden dormhouse (*Eliomys quercinus*), and rats (*Rattus* sp.).

Data collection

From 2017 to 2019, two sets of experiments were conducted to compare risk-taking behaviour in rollers breeding solitarily and rollers breeding in mixed-species during the incubation and chick-rearing periods.

Risk-taking behaviour towards a novel object during incubation

This experiment, aiming to describe the latency of rollers to resume incubation during the presentation of a novel object (neophobia), was conducted in 2017 and 2018, by selecting rollers pairs at early incubation stage. One person (observer) slowly approached a nest until the incubating roller escaped, placed a *GoPro Hero 4 session* camera (novel object; Fig. S1) 10cm from the nest entrance, and abandoned the area after 15min since the roller left the nest (to standardize the period of human disturbance across all nests). The experiment was carried out for further 90 minutes, after which the observer returned to recover the object. Flight initiation distance was not measured as it was not possible to approach the nest in a linear transect in all sites due to landscape variability, namely the presence of different structures such as walls or fences in the approach line. Latency to resume incubation was determined by analysing the camera videos, and measured as the time, in minutes, it took one of the parents to enter the nest. A total of 75 roller pairs were tested across 35 breeding sites, of which 27 were solitary (8 in 2017 and 19 in 2018) and 48 were in colonies (25 in 2017 and 23 in 2018). Rollers that failed to return to the nest during the experiment were attributed a latency of 90 minutes (15 pairs, 20%).

Risk-taking behaviour towards a predator model during chick-rearing

This experiment, aiming at investigating risk-taking behaviour and nest defence by rollers in the presence of a potential predator, was conducted in 2019. A crow-like model was presented to simulate a carrion crow *Corvus corone*, a potential egg/nestling predator in the area. Previous pilot experiments tested other predator models, including common magpie *Pica pica*, barn owl *Tyto alba*, and Montpellier's snake *Malpolon monspessulanus*, but they were not perceived as a threat (personal observation, data not shown).

Experiments were conducted when nestlings were approximately 15 days old and consisted of three sequential phases: (1) pre-demonstration, a control period before the predator model presentation (30min); (2) demonstration, during which the predator model was presented (20min); and (3) post-demonstration, after removing the predator model (40min). During the pre-demonstration phase, we recorded the provisioning rate (number of times a roller entered its nest) through direct observation, starting from the first nest entrance event, to ensure parents were actively feeding their nestlings. After the pre-demonstration phase, the crow model was placed ca. 1m above the focal nest entrance (usually on the roof or wall crevice), and the parental behaviour was recorded using a camera (*GoPro Hero 4 session*) placed on the floor at 10-15m from the nest to monitor the behaviour of birds in a wide range (Fig. S1).

Video recordings were analysed to determine: (1) rollers' latency to return to the nest-site, measured as the time elapsed until the first time a roller perched on the structure, fed their nestlings, or attacked the predator model, (2) the number of provisioning events, and (3) the number of attacks against the predator model. During the post-demonstration, we measured the time elapsed until rollers resume chick provisioning and registered the number of provisioning events. All observation and recordings were conducted when the observer was positioned >200m from the nest (inside a car), ensuring that it was not disturbing the birds. Each experiment lasted 90mins and was performed for a total of 33 roller pairs, of which 12 were solitary and 21 were in colonies.

No experiment resulted in nest abandonment from rollers.

Breeding parameters and nest predation rate

From 2014 to 2019, 298 roller nests across 52 breeding sites (mean nests per year = 50, min = 42, max = 55), of which 88 were solitary and 210 bred within mixed-species colonies, were visited weekly to record laying date, clutch size, and productivity (number of fledged chicks per breeding attempt). Nests that lost eggs and/or nestlings with clear signs of predation such as broken eggs or dead chicks with injuries in the nest/floor were recorded as being predated.

All field work involving bird monitoring and experiments was approved by the Instituto de Conservação da Natureza e Florestas (ICNF).

Data analysis

Influence of social context in risk-taking behaviour towards a novel object

The latency of rollers to resume incubation during a neophobia event was investigated using a Gamma General Linear Mixed Model (GLMM) with latency (in minutes) as the response variable, social context (solitary vs colonial) and laying date (Julian date, days) as explanatory variables, and site ID as random factors. Year was not included in the model was there was no difference in roller's response between years (w_{74} = 597, P = 0.306). Laying date was used to control for individual traits/experience, under the assumption that early breeders are older, more experienced individuals and more risk prone (Verhulst & Nilsson 2008; Brommer et al. 2014; Winkler 2016; Poblete et al. 2021). A log-link was used as data had a right-skewed distribution.

Influence of social context in risk-taking behaviour towards a predator

We first confirmed that the crow model was perceived as a threat, as rollers avoided feeding their nestlings during the predator demonstration phase (Kruskal-Wallis on the provisioning rate among the three stages of the experiment: χ^2_2= 45.563, P < 0.001) (Fig. 1).

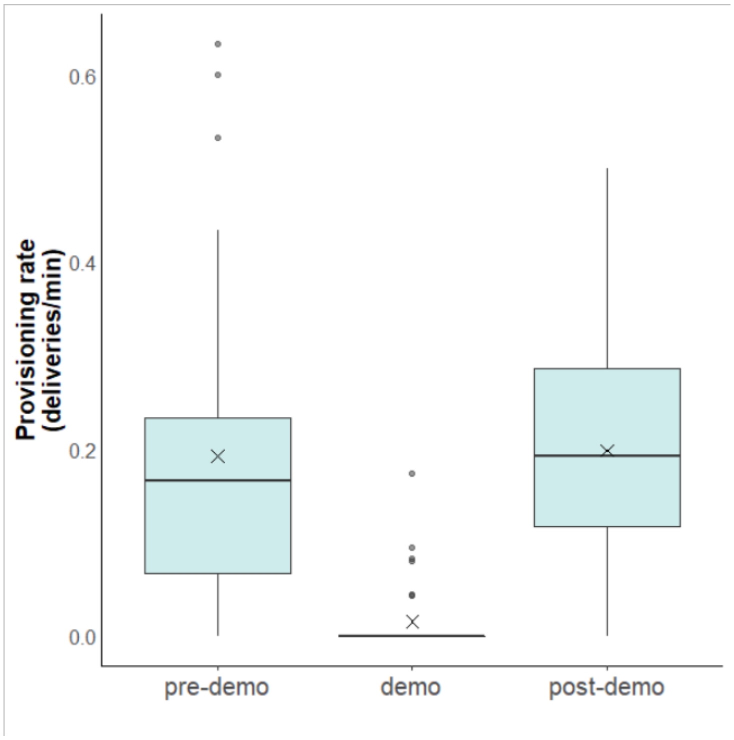

Figure 1: Chick provisioning rate during each phase of the predator (carrion crow) presentation experiment: pre-demonstration (pre-demo) – before placing the predator model; demonstration (demo) – during predator presentation; post-demonstration (post-demo) – after removing the predator model. Data from 33 roller pairs.

Latency to return to the nest-site during the predator demonstration and latency to resume chick feeding during the post-demonstration were investigated through log-Gamma Generalized Linear Models (GLMs) with latency (in minutes) as the response variable and breeding social context (solitary vs colonial) and laying date as predictors. Roller attack rate during predator demonstration was investigated through a zero-inflation log-Poisson GLM, using number of attacks as the response variable, with duration of the experiment as an offset and breeding social context (solitary vs colonial) and laying date as explanatory variables. To further investigate the influence of the number of lesser kestrels on roller's behaviour during the predator exposure experiment, we run the same set of GLM models for rollers breeding in colonies, using the number of lesser kestrel pairs and laying date as explanatory variables.

Breeding parameters and nest predation

To examine how breeding parameters and nest predation varied between solitary rollers and rollers breeding in colonies, four GLMMs were used, using social context and laying date as explanatory variables, and year (2014 to 2019) and site ID as random factors. A binomial distribution was used for the predation rate model, a normal distribution for the laying date model, and Poisson distributions for the clutch size and productivity models. Predation (0 or 1) was additionally used as an explanatory variable for the productivity model.

Despite recent ringing efforts in the area, we lacked sufficient marked rollers to control for individual variation. Alternatively, because rollers are expected to show relatively high nest fidelity, breeding site ID (structure hosting individual roller nests or lesser kestrel colonies) was used as a random factor to address the non-independence of measures between years (Schwartz et al 2021; Valera & Václac 2021).

All continuous variables were centred and scaled prior to analysis. All analysis were conducted with R software 3.6.1 (R Core Team, 2016).

RESULTS

Influence of social context in risk-taking behavior towards a novel object

Latency to resume incubation during the neophobia event was significantly lower for rollers in colonies and decreased with increasing laying date. Solitary rollers took, on average, 55.2 ±

30.3 min to resume incubation, while rollers in colonies took 31.0 ± 26.9 min (Table 1, Fig. 2).

Table 1: Parameters of log-Gamma GLM investigating the effect of social breeding context (solitary vs colonial rollers) on roller's latency to resume incubation during the presentation of a novel object (GoPro camera), using site ID as a random factor. Data from 75 roller pairs across 35 breeding sites (27 solitary and 48 in colonies) sampled during in 2017 and 2018.

Effect	Variance (SD)	Estimate	SE	Z-value	P-value
Site ID	0.244 (0.494)				
Intercept [solitary]		**3.953**	**0.192**	**20.563**	**< 0.001**
Breeding context [Colonial]		**-0.824**	**0.249**	**-3.307**	**0.001**
Laying date		**-0.312**	**0.088**	**-3.551**	**< 0.001**

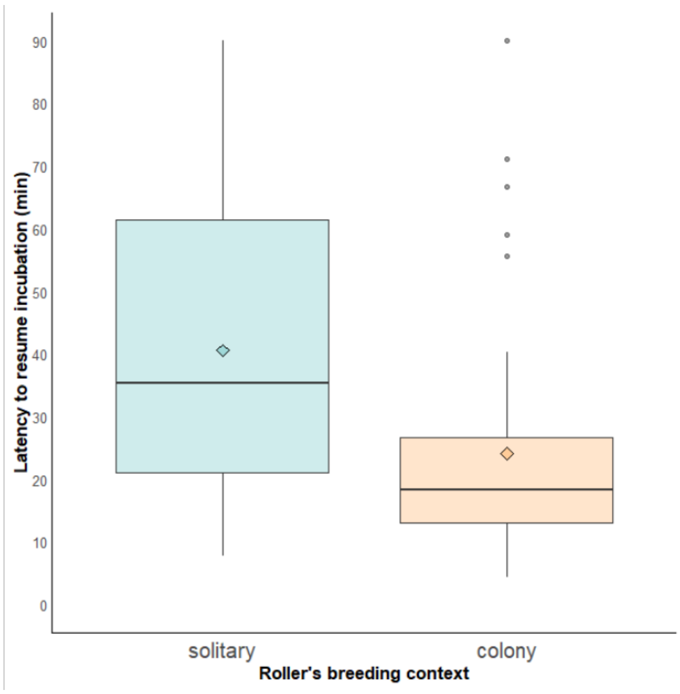

Figure 2: Latency to resume incubation during the neophobia experiment (presentation of a novel object – GoPro camera) in solitary rollers (solitary) and rollers breeding in lesser kestrel colonies (colony). Middle, lower and upper hinges of the boxplot correspond to the median, 25th and 75th percentiles, respectively, and whiskers and individual dots correspond to the range. Diamonds correspond to the mean. Data from 75 roller pairs (27 solitary and 48 in colonies) sampled during the breeding seasons of 2017 and 2018.

Influence of social context in risk-taking behavior towards a predator model

Twenty (60.6%) out of the 33 roller pairs tested returned to the nest-site during the predator demonstration phase (either by perching, entering the nest, or attacking the crow), taking on average 14.2 min to return (solitary: mean = 15.2, min = 4.2, max = 20; colonial: mean = 13.5, min = 1.1, max = 20). Roller's latency to return was not influenced by neither laying date or social context (solitary vs colonial, Table 2). Rollers attacked the predator model at an average rate of 0.21 attacks/min (solitary: mean = 0.25, min = 0, max = 1.2; colonial: mean = 0.19, min = 0, max = 2.04). Attack rate was influenced by laying date, with early breeders attacking the predator model more often, but not by the breeding social context (Table 2). After removing the predator model (post-demonstration), early breeding rollers tended to resume chick provisioning sooner, but this effect was not significant (Table 2).

Table 2: Parameters of GLMs investigating the effect of social breeding context (solitary vs colonial) and laying date on roller's risk-taking behaviour during the presentation of a predator (crow model). Significant effects displayed in bold. Data from 33 roller pairs (12 solitary and 21 in colonies) sampled during the breeding season of 2019.

Effect	Estimate	SE	Z-value	p-value

Demonstration phase				
Latency to return to nest-site				
Intercept [solitary]	**2.786**	**0.154**	**18.135**	**<0.001**
Laying date	0.044	0.094	0.468	0.643
Social context [colonial]	-0.087	0.193	-0.453	0.654
Attack rate				
Count model				
Intercept [solitary]	**-0.750**	**0.137**	**-5.477**	**<0.001**
Laying date	**-0.595**	**0.086**	**-6.893**	**<0.001**
Social context [colonial]	-0.184	0.160	-1.152	0.249
Zero-inflation model				
Intercept [solitary]	0.339	0.588	0.576	0.564
Laying date	-0.081	0.361	-0.226	0.821
Social context [colonial]	-0.062	0.737	-0.084	0.933
Post-demonstration phase				
Latency to resume chick provisioning				
Intercept [solitary]	**2.966**	**0.151**	**19.593**	**<0.001**
Laying date	0.222	0.123	1.808	0.081
Social context [colonial]	-0.029	0.251	-0.117	0.908

When considering only rollers breeding in colonies, latency to return to the nest-site and attack rate decreased significantly with increasing colony size, i.e., the number of lesser kestrel pairs (Table 3). Early breeders also attacked more frequently than late breeders, and rollers in larger colonies tended to resume chick provisioning sooner than rollers in smaller colonies, although this effect was not significant (*P* = 0.078; Table 3).

Table 3: Parameters of GLMs investigating the effect of colony size (number of lesser kestrel pairs) and laying date on roller's risk-taking during the presentation of a predator (crow model). Significant effects displayed in bold. Data from 21 roller pairs sampled during the breeding season of 2019.

Effect	Estimate	SE	Z-value	P-value
Demonstration phase				
Latency to return to nest-site				
Intercept	**2.644**	**0.132**	**19.982**	**<0.001**
Laying date	0.070	0.136	0.514	0.613
Colony size	**-0.397**	**-2.924**	**-2.924**	**0.009**
Attack rate				
Count model				
Intercept	**-0.888**	**0.136**	**-6.539**	**<0.001**
Laying date	**-0.555**	**0.139**	**-3.981**	**<0.001**
Colony size	**-0.345**	**0.135**	**-2.558**	**0.011**
Zero-inflation model				
Intercept	0.312	0.515	0.607	0.544
Laying date	-0.107	0.563	-0.191	0.849
Colony size	-0.142	0.766	-1.097	0.057

Post-demonstration phase				
Latency to resume chick provisioning				
Intercept	*2.921*	*0.162*	*17.992*	*<0.001*
Laying date	0.298	0.167	1.789	0.090
Colony size	-0.311	0.167	-1.868	0.078

Does nesting in colonies increases breeding performance?

Laying date and clutch size were similar between solitary rollers and rollers breeding in lesser kestrel colonies, and clutch size decreased significantly with increasing laying date (Fig. 3; Table S1). Predation of roller nests was significantly lower in colonies compared to solitary nests, and it was not influenced by laying date (Table S1). Predation occurred in 23.3% of solitary nests and in 10.3% of nests in colonies (Fig. 3). Roller productivity (number of fledging chicks per breeding attempt) decreased significantly with increasing laying date and was lower in nests where predation was recorded, but did not differ with roller breeding social context (Table S1).

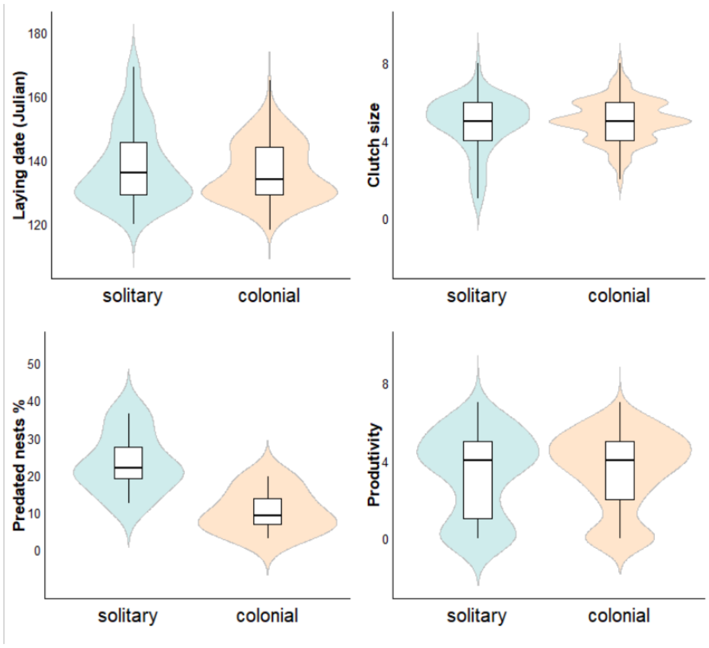

Figure 3: Reproductive parameters and proportion of predated nests amongst solitary rollers (solitary) and rollers breeding in lesser kestrel colonies (colonial). Middle, lower and upper hinges of the boxplot correspond to the median, 25th and 75th percentiles, respectively, and whiskers and individual dots correspond to the range. Diamonds correspond to the mean. Productivity was calculated as the number of chicks fledged per breeding attempt. Data from 298 roller pairs monitored from 2014 to 2019 (88 solitary, 210 colonies).

DISCUSSION

Living in groups may offer protection from predators, particularly when assembled individuals belong to various species that differ in their capacities to be vigilant or aggressive, or because grouping with conspecifics alone is insufficient to produce anti-predatory benefits (Sridhar & Guttal, 2018; Goodale et al. 2020). This study provides a clear example of a protective nesting association (Richardson & Bolen 1999; Quinn & Ueta 2008; Rocha et al. 2016; Burgas et al. 2021), documenting a solitary breeding species, the European roller, gaining direct anti-predatory benefits from nesting within mixed-species colonies dominated by lesser kestrels.

Influence of social context on roller's neophobia

During the presentation of a novel object, rollers breeding in colonies resumed incubation almost twice as fast as solitary rollers. A novel stimulus such as an unrecognizable object (or sound or smell), may be perceived as a potential predation threat, and so a fearful reaction may be a plastic, adaptative strategy to avoid a potential deadly encounter (Brown et al. 2013; Crane & Ferrari 2017). Nesting near lesser kestrels may help rollers perceive the threat-level of a novel stimuli and assess whether it is safe to return to their nests by picking up cues from the responses of their heterospecific neighbours (Seppänen et al. 2007; Goodale et al. 2010; Crane et al. 2020). Lesser kestrels always arrived sooner to the colony (on average 7.1 min sooner than rollers), which could have facilitated the return of rollers to their nests (Rasolofoniaina et al. 2021). Solitary rollers, on the other hand, have no neighbours to which acquire information from, and so might need more time to perceive the actual risk from the novel stimuli by themselves. By returning faster to the nest-site, rollers in colonies can reduce egg's exposure to predators or adverse physical conditions (e.g., hot temperatures), while simultaneously increasing incubation time (Frid & Dill 2002).

Influence of social context on roller's nest defensive behaviour

During the presentation of a predator model, there were no differences in risk-taking behaviour between solitary and colonial rollers: latency to return to the nest during predator demonstration, attack rate against the predator model, and latency to resume chick provisioning after predator removal were similar across both social contexts.

Mobbing behaviour is a common group defence strategy in many taxa and serves the dual function of (1) alerting con- and heterospecific neighbours about the presence of a threat (Goodale et al. 2010; Campobello et al. 2012; Dutour et al. 2017), and (2) recruiting them to participate in the communal defence, decreasing the individual energy investment and risk of getting caught by a predator through dilution or selfish-herd effects (Brown & Hoogland 1986; Arroyo et al. 2001; Krams et al. 2009; Lehtonnen & Jaatinen 2016). It follows that the more individuals participating in mobbing, the higher the success of deterring the predator, so an effective mobbing event may only be achieved at a certain group size (Krams et al. 2009). In our study, lesser kestrel mobbing behaviour was only noticeable in larger colonies (> 25 breeding pairs), peaking at a rate of 25 attacks/minute (Fig. S2), and recruiting common kestrels, jackdaws and one Montagu's harrier not breeding in the colonies. This may explain why the effect of social context on roller's risk-taking behaviour was only significant when distinguishing rollers breeding in different sized colonies, rather than just the solitary vs colonial dichotomy. Roller's mobbing intensity decreased with increasing colony size, strongly suggesting that rollers benefit from the aggressive behaviour of their heterospecifics by reducing their investment and risk in defensive duties. Similar patterns were described for colonial or semi-colonial species (Arroyo et al. 2001; Krams et al. 2009), or when comparing solitary and colonial species (Brown & Hoogland 1986), but has never been described for a solitary species breeding in association with a colonial heterospecific.

Other factors influencing roller's risk-taking behaviour

Rollers' risk-taking behaviour, both towards a novel object and a predator, was also influenced by laying date, with early breeders generally (but not always) performing better than late breeders. In birds, early breeders are often older or more experienced individuals, selecting higher quality breeding areas, having higher reproductive success, and being more risk prone (Verhulst & Nilsson 2008; Brommer et al. 2014; Winkler 2016; Poblete et al. 2021). Our data, from six consecutive breeding seasons, showed that early breeding rollers laid more eggs and had higher productivity (number of fledging chicks) than late breeders. More experienced individuals may be better at picking up cues from their surroundings, which includes perceiving the presence and behaviour of neighbours or predators (Verhulst & Nilsson 2008; Graham & Shutler 2019). This may explain why early breeding rollers in our study showed improved risk-taking responses by attacking the predator model more frequently and likely resuming chick provisioning earlier after predator removal, a similar result to what was reported for other bird species (Brommer et al. 2014; Poblete et al. 2021). However, our neophobia experiment revealed that early breeders took more time to resume incubation than late breeders, contradicting this hypothesis. Rollers are single-brooded, so losing a clutch later in the season may compromise breeding for that year (Tilgar & Kikas 2009; Ghalambor et al. 2013). It is possible that the motivation to incubate for late breeders surpasses the risk of approaching a novel stimulus that may or may not end up as a real danger, as opposed to rollers presented with a predator model that is perceived as a larger threat (Brown et al. 2013; Crane & Ferrari 2017).

In addition to the social context and timing of breeding, there are other factors that may have influenced roller's risk-taking behaviour that were not addressed in this study. Current brood value is expected to regulate parental investment, with parents taking higher risks when they have more offspring or when the probability of that offspring surviving increases, i.e., in older broods (Tilgar & Kikas 2008; Graham & Shutler 2019). Although we controlled for brood age, by testing rollers at similar development stages, we could not disentangle the effects of brood size from laying date due to their high correlation. Personality traits, i.e., consistent individual variation in behaviour across different contexts (Biro & Stamps 2008; Brommer et al. 2014; Santos et al. 2015), may also shape individual risk-taking behaviour, but these were not investigated in this study. Brood value or individual behavioural differences may have been responsible for some of the observed variability in roller's response and could help explain the lack of social context effect on roller's likelihood to attack the predator models, or the time it took for rollers to resume chick provisioning after predator removal.

Implications of coloniality for a solitary breeding species

Predation is one of the strongest selective forces in nature, shaping life-history traits and the structure and dynamics of communities (Cresswell 2008; Quinn & Ueta 2008; Ibáñez-Álamo et al. 2015; Crane & Ferrari 2017). If rollers acquire direct anti-predatory benefits from breeding near lesser kestrels, one of the possible outcomes of such benefits would be to have higher productivity, as a result of higher nestling survival due to lower predation levels. However, data from near 300 breeding events across six consecutive breeding seasons show no differences in laying date, clutch size, or productivity between rollers breeding in different social contexts, suggesting there are no evident reproductive advantages of nesting within colonies. The anti-predatory advantages of nesting within colonies may be offset by costs typically inherent to group living and could explain the similar productivity levels between solitary and colonial rollers (Wagner et al. 2000; Semeniuk & Dill 2005; Gaglio et al. 2018; Catry & Catry 2019; Goodale et al. 2020). The niche similarity between rollers and lesser kestrels (preying on similar resources or avoiding the same predator) may increase the value of interspecific social information and facilitate the formation of mixed-species groups, but it may also increase the potential for interspecific competition, particularly when breeding at high densities (Parejo et al. 2005; Seppänen et al. 2007; Sridhar & Guttal 2018; Goodale et al, 2020). The two species are known to largely overlap in their trophic resources (Catry et al. 2016, 2019; Gameiro et al. submitted), and previous studies on these mixed-species colonies have reported higher parasitic burden on colonies with increasing number of lesser kestrels (Gameiro et al. 2021), all of which may reduce offspring fitness and breeding success.

On the other hand, both lethal and non-lethal effects of predation may impact animals beyond their reproductive output. Parents may be killed or become impaired while defending a nest, or may exhaust their energy in anti-predatory behaviours potentially affecting their own fitness or survival in future reproductive attempts (Creel & Christianson 2008; Cresswell 2008; Oteyza et al. 2021). Even if not providing clear reproductive advantages, the protection provided by lesser kestrels in mixed colonies against predators may still result in an adaptive breeding strategy for rollers. Further studies should investigate whether breeding in mixed-species colonies provide other advantages to rollers.

ACKNOWLEDGEMENTS

This work was supported by Fundação para a Ciência e a Tecnologia (FCT) through grants to cE3c (UIBD/00329/2020), CESAM (UIDO/50017/2020 and UIDP/50017/2020), and InBIO (UID/BIA/50027/2013). JG was supported by a FCT doctoral grant (PD/BD/128366/2017); IC and TC by FCT contracts (DL57/2016/CP1440/CT0023 and IF/00694/2015, respectively); and AF by a Natural Environment Research Council (NERC) standard grant (NE/K006312/1).

Author contribution

JG: Conceptualization; Methodology; Investigation; Formal Analysis; Writing – Original Draft; Writing – Review and Editing. AF: Conceptualization; Writing – Review and editing. TC: Conceptualization; Methodology; Investigation; Writing – Review and Editing. JP: Writing – Review and Editing; IC: Conceptualization; Methodology; Investigation; Writing – Review and Editing

REFERENCES

Arroyo B, Mougeot F, Bretagnolle V. 2001. Colonial breeding and nest defence in Montagu's harrier (Circus pygargus). Behavioral Ecology and Sociobiology 50: 109-115. Doi:10.1007/s002650100342.

Beauchamp G. 2008. What is the magnitude of the group-size effect on vigilance? Behavioral Ecology 19: 1361-1368. Doi:10.1093/beheco/arn096.

Birdlife international. 2021. IUCN Red List for birds. Downloaded from http://www.birdlife.org on 04/06/2021.

Biro PA, Stamps JA. 2008. Are animal personality traits linked to life-history productivity? Trends in Ecology and Evolution 23: 361–368. Doi:10.1016/j.tree.2008.04.003.

Blanco G, Tella JL. 1997. Protective association and breeding advantage of choughs in lesser kestrel colonies. Animal Behaviour 54: 335-342. Doi:10.1006/anbe.1996.0465.

Boulay J, Aubernon C, Ruxton GD, Hédoin V, Deneubourg JL, Charabidzé D. 2019. Mixed-species aggregations in arthropods. Insect Science 26: 2-19. Doi:10.1111/1744-7917.12502.

Brommer JE, Karell P, Ahola K, Karstinen T. 2014. Residual correlations, and not individual properties, determine a nest defence boldness syndrome. Behavioral Ecology 25(4): 802-812. Doi:10.1093/beheco/aru057.

Brown CR, Hoogland JL. 1986. Risk in mobbing for solitary and colonial swallows. Animal Behaviour 34: 1319-1323.

Brown GE, Ferrari MCO, Elvidge CK, Ramnarine I, Chivers DP. 2013. Phenotypically plastic neophobia: a response to variable predation risk. Proceedings of the Royal Society B: Biological Sciences 280: 20122712. Doi:10.1098/rspb.2012.2712.

Burgas D, Ovaskainen O, Blanchet FG, Byholm P. 2021. The ghost of the hawk: top predator shaping bird communities in space and time. Frontiers in Ecology and Evolution 9: 1-7. Doi:10.3389/fevo.2021.638039.

Campobello D, Sarà M, Hare JF. 2012. Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies. Behavioral Ecology 23(2): 425-433. Doi:10.1093/beheco/arr207.

Catry I, Alcazar R, Franco AMA, Sutherland WJ. 2009. Identifying the effectiveness and constraints of conservation interventions: A case study of the endangered lesser kestrel. Biological Conservation 142: 2782-2791. Doi:10.1016/j.biocon.2009.07.011.

Catry I, Catry T, Alho M, Franco AMA, Moreira F. 2016. Sexual and parente-offsrping dietary segregation in a colonial raptor as revealed by stable isotopes. Journal of Zoology 299: 57-67. Doi:10.1111/jzo.12324.

Catry I, Sampaio A, Silva MC, Moreira F, Franco AMA, Catry T. 2019. Combining stable isotope analysis and conventional techniques to improve knowledge of the diet of the European roller Coracias garrulus. Ibis 161: 272-285 Doi:10.1111/ibi.12625.

Catry I, Silva JP, Cardoso A, Martins A, Delgado A, Sanches AR, Santos A, Estanque B, Cruz CM, Pacheco C, Leitão D, Pereira E, Matilde E, Moital F, Romba F, Sequeira N, Monteiro P, Rocha P, Correia R, Alcazar, R, Cangarato R, Heleno R, Catry T, Silva T, Ferro T. 2011. Distribution and population trends of the European Roller in pseudo-steppe areas of Portugal: results from a census in sixteen SPAs and IBAs. Airo 21: 3-14.

Catry T, Catry I. 2019. Nest-site provisioning re-shapes species interactions within bird assemblages. Ibis 161: 699-704. Doi:10.1111/ibi.12731.

Crane AL, Brown GE, Chivers DP, Ferrari MCO. 2020. An ecological framework of neophobia: from cells to organisms to populations. Biological Reviews 95: 218-231. Doi:10.1111/brv.12560.

Crane AL, Ferrari MCO. 2017. Patterns of predator neophobia: a meta-analytic review. Proceedings of the Royal Society B: Biological Sciences 284: 20170583. Doi:10.1098/rspb.2017.0583.

Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23(4): 194-201. Doi:10.1016/j.tree.2007.12.004.

Cresswell W. 2008. Non-lethal effects of predation in birds. Ibis 150: 3-17. Doi:10.1111/j.1474-919X.2007.00793.x.

del Hoyo J, Elliott A, Sargatal J. 2001a. Handbook of the birds of the world, Vol 2. New World Vultures to Guineafowl. Barcelona, Lynx Edn.

del Hoyo J, Elliott A, Sargatal J. 2001b Handbook of the birds of the world, Vol 6. Mousebirds to Hornbills. Barcelona, Lynx Edn.

Dutour M, Léna JP, Lengagne T. 2017. Mobbing calls: a signal transcending species boundaries. Animal Behaviour 131: 3-11. Doi:10.1016/j.anbehav.2017.07.004.

Expósito-Granados M, Parejo D, Avilés JM. 2016. Sex-specific parental care in response to predation risk in the European roller, Coracias garrulus. Ethology 122: 72-79. Doi:10.1111/eth.12444.

Finch T, Saunders P, Avilés JM, Bermejo A, Catry I, de la Puente J, Emmenegger T, Mardega I, Mayet P, Parejo D, Račinskis E, Rodríguez-Ruiz J, Sackl P, Schwartz T, Tiefenbach M, Valera F, Hewson C, Franco AMA, Butler SJ. 2015. A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. Diversity and Distributions 21: 1051-1062. Doi:10.1111/ddi.12345.

Frid A, Dill L. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1): 2-17.

Gabel W, Frederick P, Zabala J. 2021. Alligator presence influences colony site selection of long-legged wading birds through large scale facilitative nest protector relationship. Scientific Reports 11: 1-12. Doi:10.1038/s41598-020-80185-5.

Gaglio D, Sherley RB, Cook TR, Ryan PG, Flower T. 2018. The costs of kleptoparasitism: a study of mixed-species seabird colonies. Behavioral Ecology 29(4): 939-947. Doi:10.1093/beheco/ary050.

Gameiro J, Franco AMA, Catry T, Palmeirim JM, Catry I. 2020. Long-term persistence of conservation-reliant species: Challenges and opportunities. Biological Conservation 243: 1-10. Doi:10.1016/j.biocon.2020.108452.

Gameiro J, Veiga J, Valera F, Palmeirim JM, Catry I. 2021. Influence of colony traits on ectoparasite infestation in birds breeding in mixed-species colonies. Parasitology: 1-9. Doi:10.1017/S0031182021000470.

Ghalambor CK, Peluc SI, Martin TE. 2013. Plasticity of parental care under the risk of predation: how much should parents reduce care? Biology Letters 9: 1-4. Doi:10.1098/rsbl.2013.0154.

Graham KF, Shutler D. 2019. How robust are risk-taking associations in incubating birds? A test and a review. Behavioral Ecology and Sociobiology 73(79): 1-9. Doi:10.1007/s00265-019-2692-x.

Goodale E, Beauchamp G, Magrath RD, Nieh JC, Rxuton GD. 2010. Interspecific information transfer influences animal community structure. Trends in Ecology and Evolution 25: 354-361. Doi:10.1016/j.tree.2010.01.002.

Goodale E, Ruxton, GD, Beauchamp, G. 2019. Predator eavesdropping in a mixed-species environment: how prey species may use grouping, confusion, and the cocktail party effect to reduce predator detection. Frontiers in Ecology and Evolution 7: 1-9. Doi:10.3389/fevo.2019.00141.

Goodale E, Sridhar H, Sieving KE, Bangal P, Colorado GJ, Farine DR, Heymann EW, Jones HH, Krams I, Martínez AE, Montaño-Centellas F, Muñoz J, Srinivasan U, Theo A, Shanker K. 2020. Mixed- company: a framework for understanding the composition and organization of mixed-species animal groups. Biological Reviews 95: 889-910. Doi:10.1111/brv.12591.

Hass CC, Valenzuela D. 2002. Anti-predator benefits of group living in white-nosed coatis (Nasua narica). Behavioral Ecology and Sociobiology 51: 570-578. Doi:10.1007/s00265-002-0463-5.

Ibáñez-Álamo JD, Magrath RD, Oteyza JC, Chalfoun AD, Haff TM, Schmidt KA, Thomson RI, Martin TE. 2015. Nest predation research: recent findings and future perspectives. Journal of Ornithology 156: 247-262. Doi:10.1007/s10336-015-1207-4.

Johnson FR, McNaughton EJ, Shelley CD, Blumstein DT. 2003. Mechanisms of heterospecific recognition in avian mobbing calls. Australian Journal of Zoology 51: 577-585. Doi:10.1071/ZO03031.

Krams I, Bērziņš A, Krama T. 2009. Group effect in nest defence behaviour of breeding pied flycatchers, Ficedula hypoleuca. Animal Behaviour 77: 513-517. Doi:10.1016/j.anbehav.2008.11.007.

LaBarge LR, Allan ATL, Berman CM, Hill RA, Margulis SW. 2021. Extent of threat detection depends on predator type and behavioural context in wild samango monkey groups. Behavioral Ecology and Sociobiology 75(13): 1-12. Doi:10.1007/s00265-020-02959-1.

Lehtonen J, Jaatinen J. 2016. Safety in numbers: the dilution effect and other drivers of group life in the face of danger. Behavioral Ecology and Sociobiology 70: 449-458. Doi:10.1007/s00265-016-2075-5.

Lima S, Dill L. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68(4): 619-640. Doi:10.1139/z90-092.

Liu M, Chan SF, Rubenstein DR, Sun SJ, Chen BF, Shen SF. 2020. Ecological transitions in grouping benefits explains the paradox of environmental quality and sociality. American Naturalist 195(5): 818-832. https://doi.org/10.1086/708185.

Magrath RD, Haff TM, Fallow PM, Radford A. 2015. Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biological Reviews 90: 560-586. Doi:10.1111/brv.12122.

Marino A. 2010. Costs and benefits of sociality differ between female guanacos living in contrasting ecological conditions. Ethology 116: 999-1010. DOI:10.1111/j.1439-0310.2010.01812.x.

Moreira F, Leitão PJ, Morgado R, Alcazar R, Cardoso A, Carrapato C, Delgado A, Geraldes P, Gordinho L, Henriques I, Lecoq M, Leitão D, Marques AT, Pedroso R, Prego I, Reino L, Rocha P, Tomé R, Osborne PE. 2007. Spatial distribution patterns, habitat correlates and population estimates of steppe birds in Castro Verde. Airo 17: 5-30.

Murthy A, Sharma M, Amith-Kumar UR, Isvaran K. 2015. Groups constrain the use of risky habitat by individuals: a new cost to sociality. Animal Behaviour 113: 167-175. DOI:10.1016/j.anbehav.2015.12.027.

Oteyza JC, Mouton JC, Martin TE. 2021. Adult survival probability and body size affect parental risk-taking across latitudes. Ecology Letters 24: 20-26. Doi:10.1111/ele.13615.

Parejo D, Avilés JM. 2011. Predation risk determines breeding territory choice in a Mediterranean cavity-nesting bird community. Oecologia 165: 185-191. Doi:10.1007/s00442-010-1723-0.

Parejo D, Danchin É, Avilés JM. 2005. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? Behavioral Ecology 16: 96-105. Doi:10.1093/beheco/arh136.

Poblete Y, Botero-Delgadillo E, Espíndola-Hernández Vásquez RA. 2021. Risk-taking behaviour relates to timing of breeding in a sub-Antarctic rainforest bird. Ibis: 1-12. Doi:10.1111/ibi.12941.

Quinn JL, Ueta M. 2008. Protective nesting associations in birds. Ibis 150: 146-167. Doi:10.1111/j.1474-919X.2008.00823.x.

R Core Team. 2016. A Language and environment for statistical computing. Retrieved from Vienna: R Foundation for statistical computing website: https://cran.rproject.org/

Rasolofoniaina BN, Kappeler PM, Fichtel C. 2021. Neophobia and social facilitation in narrow-striped mongooses. Animal Cognition 24: 165-175. Doi:10.1007/s10071-020-01429-5.

Richardson DS, Bolen GM. 1999. A nesting association between semi-colonial Bullock's orioles and yellow-billed magpies: evidence for the predator protection hypothesis. Behavioral Ecology and Sociobiology 46: 373-380. Doi:10.1007/s002650050632.

Rocha AD, Fonseca D, Masero JA, Ramos JA. 2016. Coastal saltpans are a good alternative breeding habitat for Kentish plover Charadrius alexandrines when umbrella species are present. Journal of Avian Biology 47: 824.833. Doi:10.1111/jav.00883.

Rolland C, Danchin É, de Fraipont M. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. American Naturalist 151(6): 514-529. Doi:10.1086/286137.

Santos CD, Cramer JF, Pârâu LG, Wikelski M, Dechmann DKN. 2015. Personality and morphological traits affect pigeon survival from raptor attacks. Scientific Reports 5: 1-8. Doi:10.1038/srep15490.

Sarà M, Bondi S, Bermejo A, Bourgeois M, Bouzin M, Bustamante J, de la Puente J, Evangelidis A, Frassanito A, Fulco E, Giglio G, Gradev G, Griggio M, López-Ricaurte L, Kordopatis P, Marin S, Martínez J, Mascara R, Mellone U, Pellegrino SC, Pilard P, Podofilini S, Romero M, Gustin M, Saulnier N, Serra L, Sfougaris A, Urios V, Visceglia M, Vlachopoulos K, Zanca L, Cecere JG, Rubolini D. 2019. Broad-front migration leads to strong migratory connectivity in the lesser kestrel (Falco naumanni). Journal of Biogeography 46(12): 2663-2677. Doi:10.1111/jbi.13713.

Schwartz T, Besnard A, Avilés JM, Górski A, Kiss O, Parejo D, Račinskis E, Šniaukšta L, Šniaukštienė M, Szkeres O, Catry I. 2021. Geographical variation in pace-of-life in a long-distance migratory bird: implications for population management. Oecologia 197: 167-178. https://doi.org/10.1007/s00442-021-05012-8.

Semeniuk CAD, Dill MD. 2005. Cost/benefit analysis of group and solitary resting in the cowtail stingray, Pastinachus sephen. Behavioral Ecology 16: 417-426. Doi:10.1093/beheco/ari005.

Semeniuk CAD, Dill LM. 2006. Anti-predator benefits of mixed-species groups of cowtail stingrays (Pastinachus sephen) and whiprays (Himantura uarnak) at rest. Ethology 112: 33-43. Doi:10.1111/j.1439-0310.2006.01108.x.

Seppänen JT, Forsman JT, Mönkkönen M, Thomson RL. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88(7): 1622-1633. Doi:10.1890/06-1757.1.

Sharpe LL, Joustra AS, Cherry MI. 2010. The presence of an avian co-forager reduces vigilance in a cooperative mammal. Biology Letters 6: 475-477. Doi:10.1098/rsbl.2009.1016.

Sridhar H, Guttal V. 2018. Friendship across species borders: factors that facilitate and constrain heterospecific sociality. Philosophical Transactions of the Royal Society B 373: 20170014. Doi:10.1098/rstb.2017.0014.

Stensland E, Angerbjörn A, Berggren P. 2003. Mixed species groups in mammals. Mammal Reviews 33: 205-223. Doi:10.1046/j.1365-2907.2003.00022.x.

Tilgar V, Kikas K. 2008. Is parental risk taking negatively related to the level of brood reduction? An experiment with pied flycatchers. Animal Behaviour 77: 43-47. Doi:10.1016/j.anbehav.2008.08.027.

Uetz GW, Boyle J, Hiebert CS, Wilcox RS. 2002. Antipredator benefits of group living in colonial web-building spiders: the 'early warning' effect. Animal Behaviour 63: 445-452. Doi:10.1006/anbe.2001.1918.

Valera F, Václav R. 2021. Residency patterns and apparent survival in a cavity-nesting bird: population consequences of nest-box supplementation revealed by a long-term study. Avian Conservation and Ecology 16(2): 8. http://www.ace-eco.org/vol16/iss2/art8/

Varela SAM, Danchin É, Wagner RH. 2007. Does predation select for or against avian coloniality? A comparative analysis. Journal of Evolutionary Biology 20: 1490-1503. Doi:10.1111/j.1420-9101.2007.01334.x.

Verhulst S, Nilsson JÅ. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society B 363: 399-410. Doi:10.1098/rstb.2007.2146.

Wagner RH, Danchin É, Boulinier T, Helfenstein F. 2000. Colonies as byproducts of commodity selection. Behavioral Ecology 11(5): 572-573. Doi:10.1093/beheco/11.5.572.

Winkler DW. 2016. Breeding biology of birds. In Lovetter IJ, Fitzpatrick JW (eds). Handbook of bird Biology. p408-409. Ithaca: The Cornel Lab of Ornithology.

Supplementary material

Figure S1: Example photos of the neophobia and predator experiments: (A) novel object (GoPro Hero 4 session) placed next to nest entrance, (B) frame from video recording of that novel object, and (C) crow-like predator model placed at the top of a nesting structure.

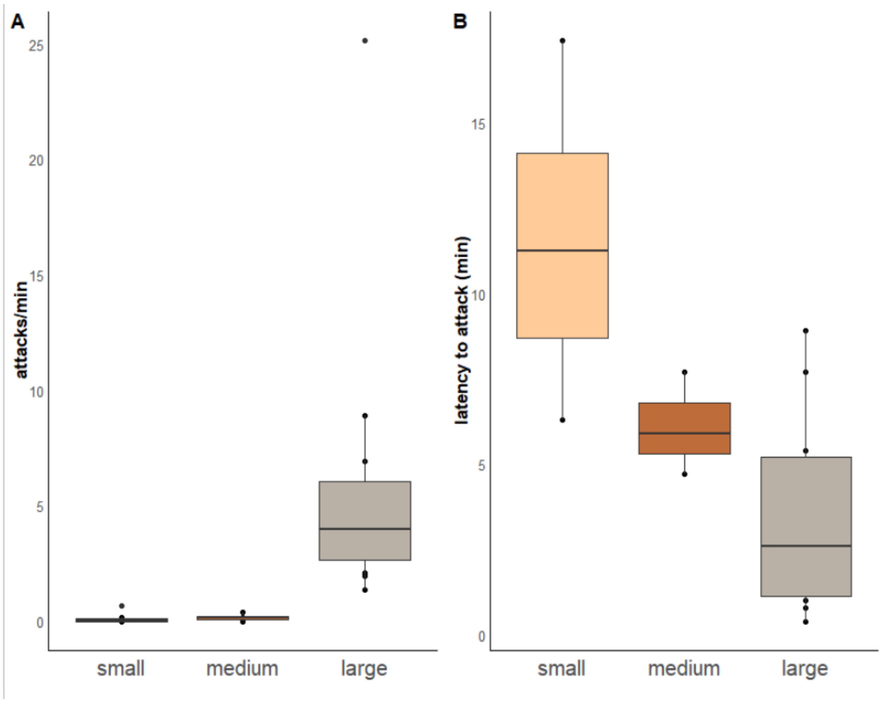

Figure S2: Lesser kestrel mobbing intensity (attacks/min) and latency to initiate mobbing in small (≤10 breeding pairs), medium (11 to 24 bp) and large (≥ 25 bp) lesser kestrel colonies. Mobbing intensity was significantly higher in large than in small or medium colonies ($p < 0.001$ and $p = 0.002$, respectively; Kruskal-Wallis $X^2_2 = 16.96$, p-value < 0.001). Latency to initiate mobbing decrease only significantly from small to large colonies (p-value = 0.002; ANOVA $F_2 = 9.98$, $p = 0.003$).

Table S1: Generalized Linear Mixed Models on reproductive parameters and nest predation rate of rollers breeding solitarily and in mixed-species colonies dominated by (solitary vs colonial). A normal distribution was used for the laying date model, Poisson distributions for the clutch size and productivity models, and binomial distribution for the predation model. Data from 298 breeding attempts across 52 sites from 2014 to 2019 (88 solitary, 210 in colonies)

Effect	Variance (SD)	Estimate	SE	Z-value	p-value
Laying date					
Site ID	14.350 (3.788)				
Year	6.340 (2.518)				
Intercept [solitary]		**137.532**	**1.656**	**83.054**	**<0.001**
Social context [colonial]		-0.407	1.542	-0.264	0.792
Clutch size					
Site ID	0.000 (0.000)				
Year	0.000 (0.000)				
Intercept [solitary]		**1.590**	**0.051**	**30.998**	**<0.001**
Social context [colonial]		0.009	0.061	0.153	0.878
Laying date		**-0.118**	**0.029**	**-4.022**	**<0.001**
Nest Predation					
Site ID	0.300 (0.548)				
Year	0.000 (0.000)				
Intercept [solitary]		**-1.194**	**0.311**	**-3.835**	**<0.001**
Social context [colonial]		**-0.933**	**0.382**	**-2.442**	**0.015**
Laying date		0.200	0.170	1.181	0.238
Productivity					
Site ID	0.000 (0.000)				
Year	0.008 (0.091)				
Intercept [solitary]		**1.421**	**0.076**	**18.590**	**<0.001**

Social context [colonial]	-0.085	0.077	-1.106	0.269
Laying date	**-0.130**	**0.038**	**-3.433**	**0.001**
Nest predation [yes, no]	**-2.212**	**0.227**	**-9.350**	**<0.001**