

Original Article

Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed-species colonies

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In mixed-species assemblages, antipredator benefits for a timid species nesting close to a more pugnacious one are often reported. Advantages for the protected species are usually manifested in terms of higher reproductive success than conspecifics nesting remote to the protector species. Whether the protector species also accrues any benefit remains untested, and the species-specific behavioral traits underlying enhanced reproductive output in mixed-species associations remain poorly documented. We studied associations between lesser kestrels (*Falco naumanni*) and jackdaws (*Corvus monedula*) nesting in rural buildings in the Gela Plain (Italy). We tested for interspecific interactions of jackdaws and lesser kestrels by comparing single- and mixed-species colonies in terms of: 1) vigilance, nest attendance, and intra- and interspecific interference and 2) defensive responses shown by each species when confronted with potential predators or competitors. In both species, nesting in mixed associations was accompanied by decreased vigilance. Diminished vigilance, however, was associated with decreased defensive effort for lesser kestrels, whereas jackdaws increased alarm calling, but only in small colonies. Our results reveal a reciprocal influence on behavior of lesser kestrels and jackdaws nesting within the same colony, whereby both species experience decreased energetic expenditures associated with vigilance, but only lesser kestrels appear to benefit via reduced nest defense effort. We discuss our results in light of the possible asymmetrical information transfer triggered by a common set of nest predators that favors the exchange of interspecific information regarding predator detection and defense. *Key words*: antipredator behavior, *Corvus monedula*, *Falco naumanni*, information transfer, interspecific interactions, mutualism, predator protection, vigilance. [*Behav Ecol*]

INTRODUCTION

The aggregation of different species to form a species assemblage can provide foraging and/or antipredator benefits for one or more of the species involved (Seppänen et al. 2007). In particular, enhanced access to food and predator detection and deterrence are benefits that favor the formation of mixed-species associations (Stensland et al. 2003; Quinn and Ueta 2008; Goodale et al. 2010). These same benefits, however, accrue where conspecifics aggregate together, and thus serve as selective forces favoring the evolution and maintenance of coloniality (Clark and Mangel 1984; Caro 2005; Campobello and Hare 2007). Where conspecifics aggregate, however, benefits are, at least in part, offset by increased competition for food, mates, and/or nest sites (Fitzgibbon 1990; Serrano and Tella 2007). Reduced niche overlap among aggregations of allospecifics allows the benefits of large group size to accrue without increasing intraspecific competition (Waser 1984).

Where members of multiple species aggregate together, foraging and antipredator benefits derive not only from a group size effect but also from complementary characteristics that each species brings to the assemblage (Phelps et al. 2007). Recently, interspecific information transfer has been consid-

ered to be a tool at the disposal of each species comprising a mixed-species assemblage, which can improve resource exploitation and predator avoidance, and thus influence the community structure (Goodale et al. 2010). In that each species contributes their own unique morphological, ecological, and behavioral adaptations to an assemblage, however, interspecific exchanges may involve information or attributes that would not be available in a single-species group (Fitzgibbon 1990). For example, the complementary tactics of badgers (*Taxidea taxus*) and coyotes (*Canis latrans*) hunting Uinta ground squirrels (*Urocitellus armatus*) enhance the predatory efficiency of both species (Cahalane 1950; Minta et al. 1992). Improved predator detection has also been documented for cowtail stingray (*Pastinachus sephen*) that rest closer to the whipray (*Himantura uarnak*), a species with more sensitive mechanoreceptors, and hence an enhanced ability to detect approaching predators (Semeniuk and Dill 2006).

Except among primates (Stensland et al. 2003), detailed studies documenting behavioral changes of species within mixed-species groups have been rare. In birds, mixed-species assemblages often occur in the form of multispecies nesting associations (Quinn and Ueta 2008), which provide pronounced antipredator benefits (Quinn et al. 2003). A timid species nesting close to a more pugnacious one will derive the predator-deterrent benefit of the size or aggressiveness of its neighbor for its own nests (Richardson and Bolen 1999). Evidence that less-protected species enjoy reduced predation by nesting close to a protector abounds (Ueta 1994; Quinn and Kokorev 2002), though few studies have elucidated the

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fitness payoff for the apparent protector (Sergio et al. 2004). Furthermore, whether species-specific behavioral traits provide information to all species comprising the mixed associations and thus underlie these benefits remains untested (Krause et al. 2009). To better understand the adaptive mechanisms promoting the evolution and maintenance of mixed-species assemblages, research must go beyond the identification of costs and benefits to the parties involved (Stensland et al. 2003; Goodale et al. 2010).

In this study, we investigated the nesting association between lesser kestrels (*Falco naumanni*) and jackdaws (*Corvus monedula*) breeding in the Gela Plain (Italy), both in single- and mixed-species colonies. Lesser kestrels have been identified as the protector species of red-billed choughs (*Pyrrhocorax pyrrhocorax*), in that the nesting success of choughs nesting with lesser kestrels is greater than those nesting solitarily (Blanco and Tella 1997). The mechanism underlying that benefit, however, remains undocumented in that neither the vigilance at the colony nor the antipredator responses of choughs or lesser kestrels in the single- versus mixed-species colonies have been recorded. Furthermore, it is unclear whether lesser kestrels that are party to an association with choughs experience enhanced, unchanged, or diminished fitness. As with choughs, lesser kestrels share a variety of potential egg, nestling, fledgling, and adult predators with jackdaws (Blanco and Tella 1997). Lesser kestrels are skillful flyers (Cramp 1980), whereas jackdaws, like other corvids, have a particularly rich vocal repertoire (Cramp and Perrins 1993). Both of these elements may serve to enhance vigilance and thus facilitate both predator detection and deterrence (Goodale and Kotagama 2005, 2008; Campobello and Sealy 2010, 2011).

In addition to the complementary nature of their antipredator adaptations, species joining a large multispecies assemblage rather than a like-sized group of conspecifics may benefit via the dilution of intraspecific competition (Fitzgibbon 1990). This may be especially true for jackdaws where both predation and intraspecific interference contribute significantly to nest failure (Röell 1978). Nest site competition among jackdaws is fierce, as males without a nest hole have no opportunity to mate with females (Henderson et al. 2000). Like lesser kestrels, jackdaws are cavity nesters, though they leave ample nest habitat for lesser kestrels where mixed-species colonies occur (Forero et al. 1996). Jackdaws, however, are described as opportunists and scavengers and, in some cases, feed almost exclusively on eggs and nestlings (Cramp and Perrins 1993), although jackdaw predation on lesser kestrel nests is rare (Forero et al. 1996).

We explored the effect of nesting in multispecies assemblages on vigilance and defense responses of jackdaws and lesser kestrels by comparing the behaviors of each species nesting in single- versus mixed-species colonies. We focused initially on colony vigilance, nest attendance, and intra- and interspecific interference. Second, we presented taxidermically prepared models in order to quantify the defensive response shown by each species when confronted with potential predators or competitors in both single- and mixed-species colonies. In contrasting responses of birds in single- and mixed-species associations, we also considered the different number of individuals nesting within each colony, so that the effects of colony size and association type on the vigilance and defensive responses of each species could be disentangled.

MATERIALS AND METHODS

From April to July 2009, we collected observations and conducted experiments at 16 colonies: 5 including lesser kestrels only (hereafter, LK single), 5 with jackdaws only (JD single), and 6 that were mixed-species colonies with both lesser kestrels (LK mixed) and jackdaws (JD mixed) nesting.

Study area

The study area was the “Biviere e Piana di Gela” (Italy; 37°01'N, 14°20'E; hereafter Gela Plain), a roughly 450 km² area 200 m above sea level, 80% covered by cereal, leguminous, and artichoke cultivations (Mascara and Sarà 2006). The rest of the area contains pasture and garigue vegetation, predominantly graminaceous plants, rosemary (*Rosmarinus officinalis*), juniper (*Juniperus communis*, *J. oxycedrus*, and *J. phoenicea*), and rock samphire (*Crithmun maritimum*). Several farmhouses and rural buildings have been built in the area since the 1950s, but most of those are now abandoned. They are of different sizes and maintenance status, from ruins made of small walls to 2-level mansions with several rooms, cellars, and outbuildings. In addition to the crevices in the walls, the roofs of these structures are covered by overlapping rows of saddle-shaped tiles offering both lesser kestrels and jackdaws numerous cavities in which to raise their offspring (Mascara and Sarà 2006).

Colony and nest observations

From 8 to 25 April 2009, we conducted preliminary observations of lesser kestrels and jackdaws at the colonies to delineate the behavioral variables and the experimental sets to be used in subsequent observations and model presentations. We did not include data from these preliminary observations in our analyses. Starting on 26 April 2009, at each colony, we conducted 4–9 observation sessions at 3 randomized time periods of the day (AM: 0800–1200 h Central Eastern Time (CET), noon: 1200–1600 h CET, and PM: 1600–2000 h CET). We employed scan and all-occurrence sampling during 5 min intervals for a total of 20 min of observation (Martin and Bateson 1986) during each observation session, starting 10 min after we had retreated to a hide (burlap-covered frame or automobile). At the end of each 5-min observation interval, we stopped recording for another 5 min. During each observation session, we recorded 14 behavioral variables, including particular aspects of flight, vocalizations, nest-related behaviors, and interactions of the 2 species. We used a Principal Component Analysis (PCA) to preliminarily select those variables that best characterized lesser kestrel and jackdaw behavior at the colonies (Digby and Kempton 1987). The first components of the PCAs showed that most of the variation was explained by 3 variables with the highest weights (from -0.54 to -0.37 in PC1 and from 0.40 to -0.31 in PC2) and, therefore, we selected the following 3 behaviors for further analysis: 1) perched away—the number of times individuals perched on structures (e.g., trees or electrical poles or buildings) surrounding the structure housing the colony, as a measure of vigilance at a short distance from the colony; 2) perched on structure—the number of times individuals perched on the structure housing the colony, as a measure of vigilance at the colony; and 3) hole in—the number of times individuals entered a nest, as a measure of nest vigilance, in that inside their nest both lesser kestrels and jackdaws may detect and deter terrestrial predators, such as the black rat (*Rattus rattus*), that otherwise cause heavy nest losses (Mascara and Sarà 2006). We also recorded: 4) intraspecific aggression—the number of attacks and mobbing between individuals of the same species and 5) interspecific aggression—the number of attacks and mobbing between individuals of different species, as measures of intra- and interspecific interference, respectively. We also recorded another variable; the maximum number of individuals flying over the colony. The function of this behavior, however, might have depended on both intra- and interspecific competition or other types of social interactions (Cresswell et al. 2003;

Lima 2009). As we could not interpret whether the maximum number of individuals flying above the colony was a manifestation of vigilance or a product of competition based upon observations in the field, we did not consider this variable further in our analyses. During the 5 min intervals between colony observation periods, we recorded the presence or the absence (1/0) of any individual in, or in front of, single nests as a measure of nest attendance. Three different observers conducted observations at a distance of 10–20 m from the structure housing the colony. As colonies were close to main or secondary roads, both species were acclimatized to vehicular traffic, and thus when possible, we conducted observations from a car. Alternatively, we observed colony activities from a hide made of a folding wooden trestle (ca. 80 × 80 × 140 cm) covered by burlap that formed 4 walls and the ceiling of the structure. Burlap was attached to the trestle so that one side allowed access. On the opposite side, a 20 × 10 cm cutout allowed observations.

Model presentations

To compare responses of lesser kestrels and jackdaws to nest predator, competitor, and innocuous species, in single- and mixed-species nesting associations, we exposed each colony to 4 models (i.e., taxidermic mounts positioned in a perching posture), including a European magpie (*Pica pica*), a jackdaw, a lesser kestrel, and a woodpigeon (*Columba palumbus*). European magpies are common on the Gela Plain (Sarà M, unpublished data). They are generalist predators reported to depredate nests of a variety of species, including those of lesser kestrels and jackdaws (Cramp and Perrins 1993; Blanco and Tella 1997). Jackdaw models had a dual function: they represented nest competitors for other jackdaws and potential nest predators for lesser kestrels. Woodpigeons are innocuous species, feeding on plant material. They do not represent nest competitors for lesser kestrels or jackdaws as they nest in trees (Bogliani et al. 1999). Each model was attached to a wooden dowel (ca. 25 × 3 cm) that, during the presentation, was inserted in wall crevices or under tiles of the structure housing the colony. To ascertain whether aspects of the model presentation independent of the models themselves, including our presence, affected bird responses, we also exposed each colony to a dowel with no model attached (negative control). Each colony was, thus, exposed to 5 presentations, 4 with avian models and 1 with a control dowel. To avoid habituation to models or carryover aggression (Knight and Temple 1986), we conducted the 5 presentations at each colony on 2 consecutive days, 3 presentations on one day and the remaining 2 on the next one, or vice versa, with a 30 min pause between presentations within the same day. We positioned models on the colony structure with the use of a ladder and then retreated to the car or the hide. The distance between the model and the nearest jackdaw and/or kestrel nest was similar in single- and mixed-species colonies for each species and between species (Supplementary Material). We observed bird responses from 5 to 10 m from the colony. In 23 cases, however, it was not possible to set a hide at that distance, and thus, in those cases, we video recorded bird responses with a video camera (SONY Handycam DCR-DVD110E) set with a field of view equivalent to that we would have had from inside the hide. Trials lasted 10 min from when the first bird returned to within 5 m of the structure housing the colony. The presentation order of models was randomized via label draws. We employed 2 models for each species (1 and 2) whose presentation was randomized to ensure that the subject responses were in fact directed to the species and not to a specific model. During the 10 min presentation, we recorded the following variables: 6) hover—the number of times individuals

flew without changing position in the air at about 5 m above the model; 7) approach—the number of times the individuals came closer than 2 m to the model with a U-shaped swooping flight, first closing their distance to the model and then flying away from it; 8) attack—the number of times individuals made physical contact with the model; 9) “kee-chee” call—the number of “kee-chee-chee” calls of lesser kestrels (Cramp 1980); 10) “kaar” call—the number of kaar calls uttered by jackdaws (Röell 1978; Cramp and Perrins 1993).

Colony size

As part of a larger investigation (Sarà 2010), from 24 April to 3 July 2009, we conducted at least 3 nest checks at each colony. For each species, we were able to determine the number of active nests, where at least 1 egg was laid. In turn, this allowed us to determine the number of active breeders at each colony for each species. We divided colonies into 2 size categories, small and large, according to the number of active breeders present at each colony. As jackdaw colonies were generally smaller than those of lesser kestrels, we adopted 2 different size range criteria to identify small and large colonies. For lesser kestrels, colonies that contained 2–32 breeders were considered small, whereas those with 34–62 breeders were considered large. For jackdaws, colonies with 2–8 breeders were considered small, whereas those with 10–20 breeders were considered large.

Statistical analyses

Colony vigilance and nest attendance

We first checked whether confounding factors affected lesser kestrel and jackdaw behavior at the colony with a repeated-measures Multivariate Analysis of Variance (MANOVA), where colony (16 levels, 1 per colony site), time (3 levels; AM, noon, and PM), observer (3 levels, 1 per observer), and observation interval (4 levels: first–fourth per session) were treated as fixed independent factors and behavioral categories a–e were the dependent variables. To test whether each species modified its behavior depending on the type of association and/or colony size, we used repeated-measures MANOVAs and ANOVAs (Underwood 1997), where we investigated the interaction effects among the species (2 levels: lesser kestrel and jackdaw), type of association (2 levels: single and mixed species), and colony size (2 levels: small and large) on behavioral categories a–e as dependent variables. To test whether nest attendance at nests changed between single and mixed colonies, we used contingency tables contrasting the presence versus the absence at nests in single- versus mixed-species colonies for each species. Thus, contingency tables analyzed the percentage of the presence/the absence per active nest on the total number of observations with Yates-corrected chi-square tests (Zar 1999).

Response to predators and competitors

We first checked whether confounding factors affected lesser kestrel and jackdaw responses to the 5 model types with a repeated-measures MANOVA. We treated the observation mode (3 levels: video, car, and hide), the specific model within each of the 5 types (2 levels: 1 and 2), and the order in which each model was presented (5 levels: first–fifth) as independent variables, whereas variables f–j were treated as the dependent variables. To test whether lesser kestrels and jackdaws responded differently in single- versus mixed-species colonies to the 5 models, we performed repeated-measures MANOVA and ANOVAs with species (2 levels: lesser kestrel and jackdaw), association (2 levels: single and mixed), and model species (5 levels: magpie, jackdaw, lesser kestrel, woodpigeon, and control) as fixed independent factors and

Table 1

ANOVA results showing the effects of association, colony size, and their interaction on the behavioral variables recorded among lesser kestrels nesting without (small: $N = 64$, large: $N = 60$) and with (small: $N = 119$, large: $N = 60$) jackdaws, and among jackdaws nesting without (small: $N = 68$, large: $N = 64$) and with (small: $N = 96$, large: $N = 84$) lesser kestrels

	Perched away		Perched on structure		Hole in	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Species	4.59	0.033	50.72	< 0.001	0.08	0.772
Association type	1.72	0.190	19.11	< 0.001	33.71	< 0.001
Colony size	46.24	< 0.001	28.08	< 0.001	41.39	< 0.001
Species × colony size	1.08	0.300	0.90	0.343	5.94	0.015
Species × association type	3.12	0.078	30.65	< 0.001	1.25	0.264
Species × colony size × association	5.07	0.025	14.77	< 0.001	3.48	0.062
	Interspecific aggression		Intraspecific aggression			
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>		
Species	8.23	0.004	1.34	0.248		
Association type	6.06	0.014	4.48	0.035		
Colony size	1.17	0.280	3.53	0.061		
Species × colony size	3.10	0.079	0.71	0.401		
Species × association type	2.07	0.150	0.01	0.908		
Species × colony size × association	0.87	0.352	1.76	0.185		

Significant differences ($P < 0.05$) are indicated by bold font.

variables f–j as the dependent variables. We conducted this test after excluding the effect of the distance between the model and the nearest kestrel and/or jackdaw nest on mobbing intensity. A Multivariate Analysis of Covariance with Species and Association type as factors and distance of models to nearest nest as a covariate revealed that this last continuous factor did not have an effect on the mobbing responses of lesser kestrels and jackdaws ($F_{5,101} = 1.11$, $P = 0.360$).

For all ANOVAs, we square-root transformed those variables when Cochran's *C*-tests revealed significant departure from homogeneity of variance among treatment groups. We conducted a total of 5 ANOVAs/MANOVAs. In 3 of those, all

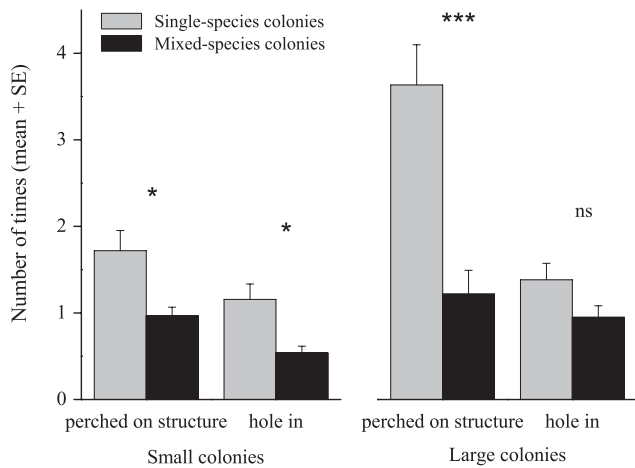
variables met the homogeneity of variance assumption, whereas in the other 2, some variables (1 out of 5 and 4 out of 6, respectively) were not homogeneous after transformation. ANOVA tests are not, however, susceptible to either Type I or Type II error with large sample sizes even when the homoscedasticity assumption is violated (Underwood 1997; Zar 1999), and thus, to keep methods of analysis uniform throughout, we employed ANOVA even for the 5 variables where variances were heterogeneous among treatment groups. For all ANOVAs, we tested differences between each pair of treatments using post hoc Student–Newman–Keuls (SNK) tests (Underwood 1997).

Table 2

P values of SNK post hoc tests of ANOVAs on the vigilance variables of lesser kestrels nesting without (small: $N = 64$, large: $N = 60$) and with (small: $N = 119$, large: $N = 60$) jackdaws, and jackdaws nesting without (small: $N = 68$, large: $N = 64$) and with (small: $N = 96$, large: $N = 84$) lesser kestrels

Lesser Kestrel					Jackdaw				
Perched on structure MS = 0.56					Perched away MS = 0.52				
	Single		Mixed			Single		Mixed	
	Small	Large	Small	Large		Small	Large	Small	Large
Single					Single				
Small	—	< 0.001	0.019	—	Small	—	0.866	0.002	—
Large			—	< 0.001	Large			—	0.570
Mixed					Mixed				
Small				0.939	Small				< 0.001
Large				—	Large				—
Hole in MS = 0.48					Hole in MS = 0.48				
	Single		Mixed			Single		Mixed	
	Small	Large	Small	Large		Small	Large	Small	Large
Single					Single				
Small	—	0.441	0.012	—	Small	—	0.165	< 0.001	—
Large			—	0.350	Large			—	0.519
Mixed					Mixed				
Small				0.012	Small				< 0.001
Large				—	Large				—

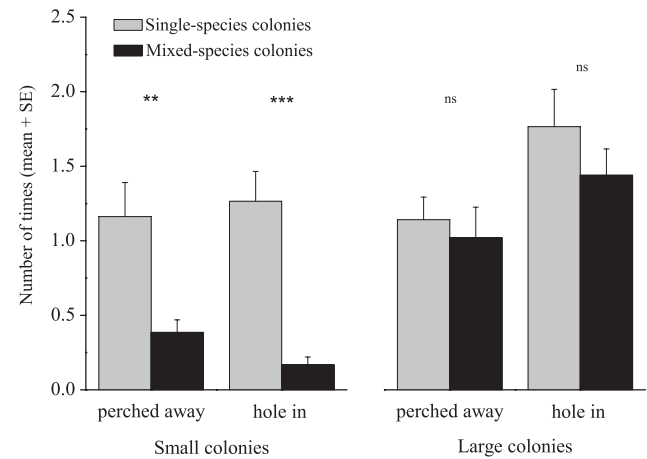
Significant differences ($P < 0.05$) are indicated by bold font. Nonbiologically relevant comparisons are indicated with —.

**Figure 1**

Changes in lesser kestrel vigilance-related behaviors in small and large colonies without (single-species colonies: small: $N = 64$, large: $N = 60$) and with (mixed-species colonies: small: $N = 119$, large: $N = 60$) jackdaws.

RESULTS

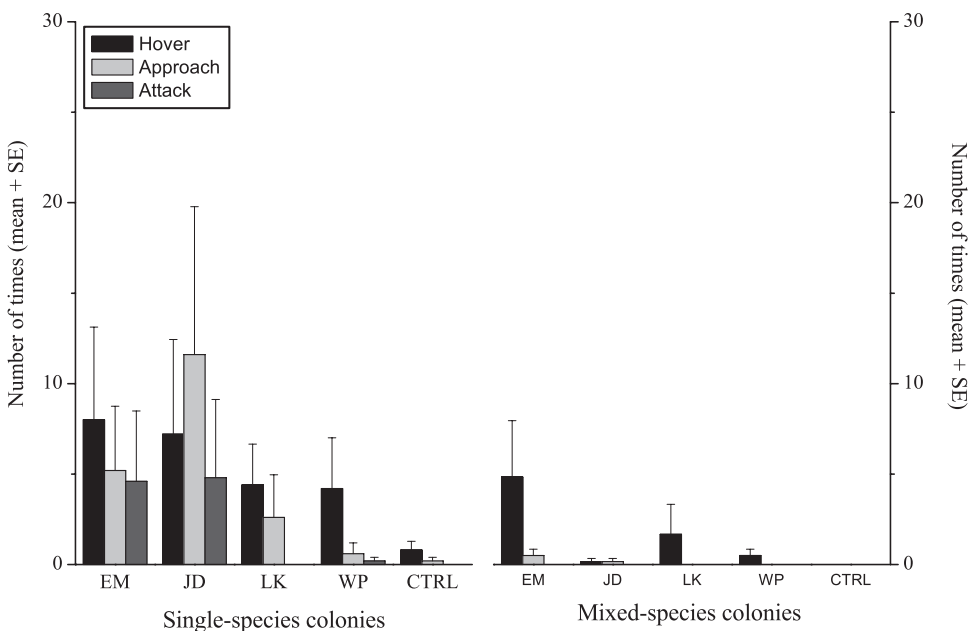
The overall vigilance of lesser kestrels and jackdaws was affected by colony size (MANOVA, $N = 615$, $F_{5,603} = 2.60$, $P = 0.024$) and association type ($F_{5,603} = 7.70$, $P < 0.001$), as well as the interaction between those factors ($F_{5,603} = 4.26$, $P < 0.0001$). For each species, univariate analyses (Table 1) revealed that each vigilance variable was affected by either colony size (hole in) or type of association (perched on structure), or the interaction between those factors (perched away and perched on structure). Within each species, however, intra- and interspecific aggression were unaffected by these factors or the interaction between them (Table 1, species \times colony size and species \times association type). In particular for lesser kestrels, post hoc SNK tests showed that vigilance at the colony (perched on structure) and vigilance at the nest (hole in) tended to increase with colony size. The presence of nesting jackdaws, however, reversed this tendency as these manifestations of vigilance were reduced in mixed-

**Figure 2**

Changes in jackdaw vigilance-related behaviors in small and large colonies without (single-species colonies: small: $N = 68$, large: $N = 64$) and with (mixed-species colonies: small: $N = 96$, large: $N = 84$) lesser kestrels.

species colonies relative to the single-species colonies (Table 2 and Figure 1). This decrease of both perching on the structure and entering the nest were maintained in mixed-species colonies (ANOVA, perched on structure: $F_{1,607} = 30.65$, SNK test: $MS = 0.58$, $P < 0.001$; hole in: $F_{1,607} = 1.25$, SNK test: $MS = 0.48$, $P < 0.001$) when they were compared regardless of their size (Figure 1). Lesser kestrels did not change their overall presence in close proximity to the nest between single- and mixed-species colonies (Yates-corrected $\chi^2 = 0.00$, $P = 1.00$). Of a total of 819 observations in single-species colonies and 504 in mixed-species colonies, lesser kestrels were present at each nest 3.37 and 3.70 times per observation session, respectively.

As for lesser kestrels, jackdaws in larger colonies tended to increase vigilance, both at a distance from the colony (perched away) and at the nest. The presence of lesser kestrels, however, affected the vigilance in small colonies only with a decrease of both vigilance variables (Table 2 and Figure 2). In mixed-species colonies, both the decrease in the number of times

**Figure 3**

Responses of lesser kestrels nesting without (single-species colonies, $N = 25$) and with (mixed-species colonies, $N = 30$) jackdaws to magpie (EM), jackdaw (JD), lesser kestrel (LK), woodpigeon (WP), and control models (CTRL).

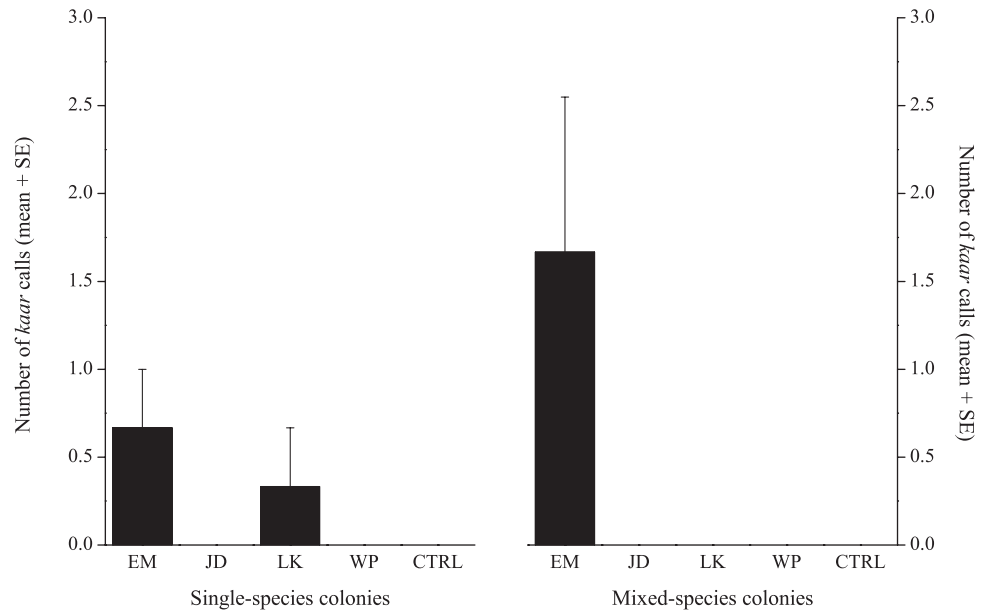


Figure 4

Number of kaar calls of jackdaws nesting without (single-species colonies, $N = 15$) and with (mixed-species colonies, $N = 15$) lesser kestrels to magpie (EM), jackdaw (JD), lesser kestrel (LK), woodpigeon (WP), and control models (CTRL) in small colonies.

individuals perched away ($F_{1,607} = 3.12$, SNK test: $MS = 0.52$, $P = 0.011$) or entered the nest ($F_{1,607} = 1.25$, SNK test: $MS = 0.48$, $P < 0.001$) were maintained when colonies were compared regardless of their size (Figure 2). Jackdaws decreased nest attendance significantly when nesting in mixed colonies with lesser kestrels (Yates-corrected $\chi^2 = 14.87$, $P = 0.001$). Of a total of 192 observations in single-species colonies and 372 observations in mixed-species colonies, jackdaws were in proximity to nests 12.11 and 5.19 times per observation session, respectively.

Within each species, the overall response to potential predator, competitor, and innocuous species was affected by the association type (MANOVA $F_{5,86} = 4.03$, $P = 0.002$). In particular, lesser kestrels nesting with jackdaws responded to all model presentations with a decreased number of hovers (ANOVA: $F_{1,90} = 5.09$, $P = 0.026$; SNK test: $MS = 1.05$, $P < 0.001$) and approaches (ANOVA: $F_{1,90} = 16.15$, $P < 0.001$; SNK test: $MS = 0.71$, $P < 0.001$) relative to conspecifics nesting in single-species colonies (Figure 3). Lesser kestrels in mixed-versus single-species colonies responded to models with a similar number of attacks ($F_{1,90} = 3.34$, $P = 0.071$; SNK test: $MS = 7.52$, $P = 0.054$), although lesser kestrels nesting in single-species colonies directed most responses to jackdaw and magpie models. The jackdaw models elicited the highest number of approaches among all models tested (SNK test: $MS = 0.71$, P range < 0.001 – 0.003) and a higher number of attacks than the woodpigeon model ($MS = 7.52$, $P = 0.002$). Still, in single-species colonies, magpies elicited a higher number of approaches ($P = 0.049$) and attacks ($P = 0.010$) than the woodpigeon models (Figure 3).

Jackdaws in mixed-species colonies responded similarly to those in single-species colonies to each individual model type (SNK test: MS range = 0.71 – 7.52 , P range = 0.095 – 1.000). They never attacked any model and performed a similar number of hovers (single- versus mixed-species colonies, respectively: mean \pm standard error: 0.56 ± 0.23 versus 0.17 ± 0.11 ; SNK test: $MS = 1.05$, $P = 0.426$), approaches (0.04 ± 0.04 versus 0.57 ± 0.34 ; $MS = 0.71$, $P = 0.494$), and kaar calls (0.72 ± 0.34 versus 0.30 ± 0.14 ; $MS = 0.84$, $P = 0.095$). Because we detected a significant effect of mixed association on vigilance in small colonies only, we then restricted our analyses accordingly. In small colonies, jackdaws responded differently to the different model species (ANOVA, $F_{4,20} = 5.17$, $P = 0.005$)

with magpies eliciting the highest number of kaar calls, both in single- and mixed-species colonies (SNK test, $MS = 0.30$, P range = 0.011 – 0.005 , Figure 4). Magpies also elicited a higher number of kaar calls in mixed- than in single-species associations ($P = 0.037$, Figure 4). An equivalent test restricted to large colonies revealed no significant effect of the association type and/or model presented on all variables considered (ANOVA, $F_{4,15}$ range = 0.59 – 1.15 , $P > 0.05$).

Behavior of lesser kestrels and jackdaws were unaffected by the interaction among colony site, observer, observation time, and interval (MANOVA, $N = 615$, $F_{90,1494} = 1.07$, $P = 0.31$). Responses of lesser kestrels and jackdaws to models were not affected by the interaction among hide type, model number, and presentation order (MANOVA, $N = 110$, $F_{30,314} = 0.53$, $P = 0.98$).

DISCUSSION

When nesting with jackdaws, lesser kestrels decreased both their vigilance and response to potential predators. Parallel to that, in mixed-species colonies, jackdaws decreased their vigilance and nest attendance especially in small colonies, but, unlike lesser kestrels, jackdaws in those small colonies increased the frequency of alarm calls when confronted with a potential predator.

Interspecific information has been suggested to be of greater value than that conveyed intraspecifically, in that it provides species-specific cues and signals that are otherwise unavailable in monospecific groups (Seppänen et al. 2007). Specifically, the value of interspecific information appears to be a product of the trade-off between the similarity of the ecological niche and the competition between the species composing the assemblage (Seppänen et al. 2007). The closer the ecological niches of the associated species, the more relevant the information is likely to be, but with that, comes more intense competition between the species (Goodale et al. 2010). In the mixed-species association we studied, neither colony size or association type nor the interaction between those variables, resulted in an increased intra- or interspecific aggression for either species. This result is consistent with nesting site availability being sufficient to preclude nest site competition within and between species (Serrano and Tella 2007) and with an ongoing expansion of the lesser kestrel population recorded since the 1980s (Sarà 2010). The

absence of aggression within jackdaws may also be explained by the abundance of nest sites in our study area relative to that in previous studies, in which nest-boxes provided the only nest sites available for jackdaws (Henderson and Hart 1993; Liebers and Peter 1998).

The absence of direct competition for nest sites and the different foraging preferences (Donazar et al. 1993; Soler et al. 1993) place lesser kestrels and jackdaws in distinct ecological niches. They do, however, share the same set of nest predators (Forero et al. 1996; Blanco and Tella 1997), a sufficient condition for selection to favor the exchange of interspecific information regarding predator detection and defense (Quinn and Ueta 2008). Given their greater propensity to fly (Cramp 1980), lesser kestrels may have provided jackdaws with information on predator presence from a different perspective as revealed by mixed-species flocks of associated species foraging on different layers of a forest (Goodale and Kotagama 2008). Interspecific alarm calls have proven to convey information about predator type and presence (Rainey et al. 2004; Templeton and Greene 2007; Fallow and Magrath 2010) and jackdaws, as a corvid species with a rich call repertoire (Cramp and Perrins 1993), may have provided lesser kestrels with refined information regarding potential predators. In other words, decreased vigilance of both lesser kestrels and jackdaws in mixed- versus single-species colonies may be attributable to a mutual exchange of information resulting from the heightened aerial vigilance provided by lesser kestrels, and the enhanced alarm signaling afforded by jackdaws.

In mixed-species colonies, changes in defense responses were not, however, symmetrical for the 2 species. Lesser kestrels, in accordance with their reduced vigilance, decreased their defensive efforts. When confronted with a predator, jackdaws maintained the same intensity of mobbing responses (approaches or hovers) recorded in single-species colonies but increased the number of alarm calls produced. Thus, only lesser kestrels appear to benefit from the interspecific association via reduced effort expended upon defense behavior. By contrast, the interspecific association appeared to elicit increased defensive effort on the part of jackdaws. The response of jackdaws is made more intriguing by the apparent colony size effect. Whereas mixed-species association with jackdaws affected lesser kestrel defense independently of colony size, the mixed-species association with lesser kestrels significantly altered jackdaw behavior only in small colonies. Thus jackdaws increased their alarm calls when nesting with both lesser kestrels and a low number of conspecifics. Increased alarm-signaling rates have been reported to be effective in the recruitment of neighbors of colonial Montagu's harriers (*Circus pygargus*) confronted with predator models (Arroyo et al. 2001). In the harriers, alarm call rate was inversely correlated with the number of individuals present, though alarm call rate was directly correlated with the number of recruits attacking the model, thereby decreasing individual antipredator effort (Arroyo et al. 2001). If this mechanism applies to jackdaws, their increased alarm calling in mixed-species colonies could be explained as a tool to recruit neighbors that are not present in single-species colonies. Why jackdaws do not increase the rate of alarm calling in large colonies, however, is unclear, though perhaps there is some threshold of colony size beyond which the recruitment of additional individuals diminishes profitability as defined by the trade-off between predator deterrence and interindividual interference.

The asymmetric behavioral change in the 2 study species indicates asymmetries in information exchange (Stensland et al. 2003). Commensal (Norrdahl et al. 1995; Beier and Tungbani 2006), mutualistic (Wiklund 1979), or parasitic (Sullivan 1984; Groom 1992) relationships have been reported on the bases of the production and use of information by associated

species (Quinn and Kokorev 2002; Sergio et al. 2004). Studies of mixed-species groups have, however, focused on the fitness benefits accrued by the protected species only (Burger 1984; Norrdahl et al. 1995; Richardson and Bolen 1999; Vaänänen 2000; Nguyen et al. 2006; Smith et al. 2007), tacitly assuming that it is the aggressiveness of one species toward the mutual predators that explains such interspecific attractions (Ueta 1994; Larsen and Grundetjern 1997; Bogliani et al. 1999; Quinn et al. 2003). No attempts, however, have been made to test directly for reciprocal behavioral influences as the mechanism underlying enhanced fitness for associating allospecifics (Stensland et al. 2003; Goodale et al. 2010). Unlike the vast majority of predator protection studies, our results reveal potential mutualistic advantages in terms of decreased vigilance for both species and decreased defense efforts for lesser kestrels but not jackdaws. Thus, the presumptive protector species (i.e., the lesser kestrel) is the one that appears to have benefited the most from the multispecies aggregation.

Cooperation among unrelated individuals is often inferred to result from benefits derived via reciprocal altruism (Trivers 1971; Clutton-Brock 2009; Connor 2010). The stable expression of reciprocity over time, however, requires that any initial investment on the part of the actor, that benefits a recipient or recipients at the actor's cost, be repaid to the actor in the future (Trivers 1971; Raihani and Bshary 2011). An evolutionarily stable system of reciprocity thus imposes an underlying cost in terms of the evolution and maintenance of a cognitive mechanism allowing a system of score keeping, thereby negating the prospect of an actor taking the sucker's payoff (Trivers 1971; Connor 2010). Although reciprocal altruism has been proposed as a potential mechanism promoting cooperative avian mobbing (Krams et al. 2008), a more likely explanation is that mobbing, particularly where it involves members of different species, is a result of by-product mutualism (Russell and Wright 2009), interspecific mutualism in general, or perhaps even manipulation (Brown 1983; Clutton-Brock 2009). On the Gela Plain, jackdaws increased their alarm calling effort only when lesser kestrels were present, and presumably received the offsetting benefit of enhanced predator detection and/or deterrence afforded by the greater number of lesser kestrels flying above mixed-species colonies. Our present data offer no insight, however, into which of the competing mechanisms account for the reciprocal interspecific changes in behavior documented among lesser kestrels and jackdaws participating in mixed-species nesting associations. Addressing that question represents a compelling direction for future research (Clutton-Brock 2009; Raihani and Bshary 2011), though such research must also incorporate measures of seasonal reproductive success, thereby documenting the fitness implications to individuals residing in single- versus mixed-species colonies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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