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Social phenotype extended to communities: Expanded multilevel social selection analysis reveals fitness consequences of interspecific interactions

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In social species, fitness consequences are associated with both individual and social phenotypes. Social selection analysis has quantified the contribution of conspecific social traits to individual fitness. There has been no attempt, however, to apply a social selection approach to quantify the fitness implications of heterospecific social phenotypes. Here, we propose a novel social selection based approach integrating the role of all social interactions at the community level. We extended multilevel selection analysis by including a term accounting for the group phenotype of heterospecifics. We analyzed nest activity as a model social trait common to two species, the lesser kestrel (*Falco naumanni*) and jackdaw (*Corvus monedula*), nesting in either single- or mixed-species colonies. By recording reproductive outcome as a measure of relative fitness, our results reveal an asymmetric system wherein only jackdaw breeding performance was affected by the activity phenotypes of both conspecific and heterospecific neighbors. Our model incorporating heterospecific social phenotypes is applicable to animal communities where interacting species share a common social trait, thus allowing an assessment of the selection pressure imposed by interspecific interactions in nature. Finally, we discuss the potential role of ecological limitations accounting for random or preferential assortments among interspecific social phenotypes, and the implications of such processes to community evolution.

KEY WORDS: Coevolution, coloniality, extended phenotype, lesser kestrel, jackdaw, social selection.

In social species, fitness consequences, quantified in a multilevel selection analysis, are associated with both individual and social phenotypes (Brodie 1992; Wolf et al. 1999; Bijma et al. 2007; Eldakar et al. 2010; McGlothlin et al. 2010). Specific social phenotypes are quantified from the expression of social traits, including behaviors, that have repercussions both in the context of cooperative and aggressive interactions among individuals (Goodnight et al. 1992; Aspi et al. 2003; Weinig et al. 2007; Eldakar et al. 2010; Goodnight 2013). Although social phenotypes of conspecifics contribute substantially to variance in individual fitness (Lyon and Montgomerie 2012; Roughgarden 2012), interactions in biological communities include those with heterospecifics. Thus, although selection analyses to date have quantified the influence of conspecific social phenotypes on variance in fitness, heterospecific social phenotypes also likely contribute to such variance, and thereby constitute a critical element affecting community structure and dynamics.

Research exploring the fitness consequences of social interactions among species has focused primarily on foraging and antipredator benefits among interacting members of multispecies assemblages (Bogliani et al. 1999; Hare and Murie 2007; Phelps et al. 2007; Goodale et al. 2010). There are cases where these advantages are not derived from a group size effect, but rather from specific morphological and behavioral traits of each species

composing the overall community. These species-specific traits allow each species to enjoy a series of benefits, from larger hunting territories to improved predator detection (Minta et al. 1992; Semeniuk and Dill 2006; Fallow and Magrath 2010) and thus may enhance fitness. For example, Minta et al. (1992) reported that coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) enjoyed a higher prey capture rate when they hunted together owing to the complementary nature of their species-specific morphology and hunting strategies (i.e., chasing prey above and below ground, respectively), or similar hunting advantages enjoyed by coral trout selectively recruiting morays (Vail et al. 2014).

Social selection occurs when fitness effects are mediated by social interactions, which, in turn, depend on the expression of group social traits (Wolf et al. 1998; Formica et al. 2012; Goodnight 2013). Thus, selection would not favor, for instance, small body size where this becomes a lethal trait in the context of agonistic interactions among a group of large-sized individuals (Formica et al. 2011). Because of their fitness consequences, phenotypes of neighboring conspecifics, together with phenotypic assortment, contribute to the total strength of selection when analyzed in a multivariate context (Aspi et al. 2003; Weinig et al. 2007; Eldakar et al. 2010; Goodnight 2013). Although many studies have examined the effects of heterospecific phenotypes on fitness (Bogliani et al. 1999; Pruitt and Ferrari 2011), there has been no attempt to establish a framework for a unified analysis that quantifies the fitness implications of both conspecific and heterospecific social traits.

We propose a novel approach to integrate and assess the role of social interactions at the community level by including interactions between heterospecifics. To this end, we applied and extended multilevel selection analysis paralleling the social selection approach (Wolf et al. 1999; Bijma et al. 2007; McGlothlin et al. 2010; Formica et al. 2011) to explore the effects of heterospecific social phenotypes on individual fitness. Although we sought to determine potential fitness consequences of heterospecific traits rather than addressing the implications of those for evolutionary response, we applied social selection analysis as this provides the most appropriate tool to integrate social with focal (i.e., nonsocial) phenotypes.

Simple parameters such as partial regression coefficients provide linear selection gradients (β) that measure the effect of a trait on the individual's fitness while multiple regressions on quadratic trait values provide nonlinear selection gradients (γ) that describe decreasing or increasing trait variance (Lande and Arnold 1983; Brodie et al. 1995; Kingsolver et al. 2001). As detailed below, in addition to the focal and conspecific social components included in social selection analysis to date (Wolf et al. 1999), we incorporated a third term into the original formulation of the total effect of selection (s) to capture the heterospecific social component, thus providing a more comprehensive estimation of organismal fitness when all social interactions within the entire community are taken into account.

We applied this approach to test whether social phenotypes of heterospecifics affect individual fitness in a community in Sicily (Italy) where two social species, the lesser kestrel (*Falco naumanni*) and the jackdaw (*Corvus monedula*), interact as co-breeding species within structures harboring colonies (Sarà 2010; Sarà et al. 2012; Di Maggio et al. 2013). This system represents an ideal model as both single- or mixed-species nesting colonies occur within the overall study area (Roëll 1978; Negro and Hiraldo 1993; Calabuig et al. 2010; Campobello et al. 2012). We previously found that, when together, these species decreased overall vigilance efforts at their colony (Campobello et al. 2012), thus indicating potential fitness benefits.

We tested a behavioral trait that is common to all avian species; nest attendance, which incorporates both vigilance and activity at the nest, and thus is presumably under selection pressure owing to its direct fitness implications (Caro 2005; Lind and Cresswell 2005). Nest attendance serves different functions. Breeding individuals incubate eggs and feed chicks; hence, insufficient attendance would result in hatching failure or chick starvation (Nord and Nilsson 2011; Beamonte-Barrientos et al. 2010; Kim et al 2010; Martin et al. 2011). Presence of adults inside their nest or in close proximity to the nest also deters nest predators (i.e., both terrestrial and avian predators such as rats *Rattus rattus* and magpies *Pica pica*, respectively) and allows rapid defense in the event of a predator attack (Cresswell et al. 2003). Nest predators are an important cause of nest failure as they may fully or partially remove clutches and broods (Sodhi et al. 2004). Breeding individuals do not hesitate to engage in nest defense via mobbing or physical attacks when they detect predators approaching their nest (Russell and Wright 2009). Where overexpressed, however, activity at the nest may instead exert the "Geiger-counter effect" (Martin 1988) attracting predators, and thus diminishing breeder fitness.

Within populations, variance of nest attendance among breeders has been related to ecological, morphological, and behavioral proxies. Different attendance phenotypes may therefore result from interactions between availability of food resources in the vicinity of nesting sites and locomotor and foraging skills (Martin 1993; Beamonte-Barrientos et al. 2010). In any case, different nest activity levels expressed as different attendance phenotypes would characterize high- or low-quality foragers or parents with differential fitness values (Cresswell et al. 2003).

Although seldom defined as such, the very presence of individuals can also be considered a social trait. The presence of conspecifics influences a variety of processes, from selection of habitat, nesting, and foraging territories to antipredator responses (Danchin et al. 1998; Doligez et al. 2002; Coolen et al. 2005; Campobello and Hare 2007; Campobello and Sealy 2011a, 2011b).

Under local enhancement (Thorpe 1956), conspecifics attract other individuals in that their presence alone reveals suitable patches. Still, the presence of conspecifics, mediated by a group size effect, allows each individual to reduce vigilance efforts and increase other activities such as foraging (Beauchamp 2010; Hare et al. 2014). The presence of heterospecifics has also been identified as a proxy of reproductive advantages. According to the predator-protection hypothesis, for example, timid species select breeding sites close to pugnacious ones so as to capitalize upon the deterrent effect of the latter species against nest predators (Norrdahl et al. 1995; Quinn and Ueta 2008).

In this study we examined the role of focal and social attendance phenotypes (both conspecific and heterospecific) in terms of their fitness consequences on each species, in both single- and mixed-species colonies of lesser kestrels and jackdaws. We also verified whether specific combinations of attendance phenotypes resulted in fitness advantages among all possible interspecific assortments.

Methods

STUDY SITE AND SPECIES

We conducted research in the "Biviere e Macconi di Gela" Special Protection Area (Italy; 37°01'N, 14°20'E; hereafter Gela Plain), a roughly 450 km^2 area 200 m a.s.l., characterized primarily by cereal and artichoke cultivation and Mediterranean garrigue vegetation (Sarà 2010; Triolo et al. 2011; Sarà et al. 2014). Across the Gela Plain, numerous rural buildings, each of them defined as a colony, offered suitable nesting cavities under roof tiles and inside wall crevices for both lesser kestrels and jackdaws (Campobello et al. 2012; Sarà et al. 2012). Both species are secondary-cavity nesters forming either single- or mixed-species nesting colonies. When nesting together, both species decreased vigilance frequency, but only kestrels decreased defense efforts, thus revealing an asymmetrical reciprocal influence on colony activity (Campobello et al. 2012). Across the Gela Plain, colony buildings average approximately 7 km apart from each other (range: 0.6–19 km, Di Maggio et al. 2013). Both study species are strictly monogamous and have biparental care, with both males and females present at the nest, incubating eggs and feeding chicks (Henderson et al. 2000; Di Maggio et al. 2015).

DATA COLLECTION

From April through June 2009, we conducted observations of lesser kestrel and jackdaw activity at single nests in colonies with two different types of species association: single-species colonies, where either lesser kestrels or jackdaws nested (LK-single and JD-single, respectively, hereafter), and mixed-species colonies where both species nested (mixed, hereafter). We observed a total of 16 colonies, five of which were LK-single, another five JD-single, and the remaining six were mixed colonies. Within colonies, we recorded data from 1 to 31 active nests of lesser kestrels and 1–10 nests of jackdaws. The presence of individuals at the colony was quantified as the activity of the breeders in proximity of their nest. Accordingly, during each 20-min session of focal observations (the minimum time necessary to obtain nest activity rates representative of hourly rates based on preliminary observations; D. Campobello, J.F. Hare, M. Sarà unpubl. data), we recorded the number of times any individual entered the nest or remained perched in front of the nest entrance (i.e., within approximately 0.5 m). The time allocated to observations of single nests occurred within a longer observation session during which unique blocks of time were devoted to scan and all-occurrence sampling as part of a broader investigation of the implications of interspecific breeding associations (Campobello et al. 2012). Each observation session started 10 min after we had retreated to a hide (burlap-covered frame or automobile, Campobello et al. 2012). We observed each active nest of both species two to seven times in different nest stages. An active nest was defined as the cavity where at least one egg was laid.

Each nest was inspected three to four times over the nesting cycle to record reproductive parameters, including the number of eggs and nestlings. As part of a long-term study, nestlings and adults found in the nests were marked with numbered aluminum and colored bands. In a posteriori data treatment, we attributed a specific stage (i.e., prelaying, laying, incubation, and brooding) to each nest for each inspection and observation day. We based nest stage identification on nest check data and/or a backdating process standardized on seven days for laying, 29 days for incubation, and 31 days for brooding for lesser kestrels, and on six days for laying, 15 days for incubation, and 32 days for brooding for jackdaws (Cramp and Simmons 1980; Sarà et al. 2012). Times of nest failure were set at the midpoint between the last two checks (Di Maggio et al. 2013). Accordingly, any observation conducted after the nest failure date was not included in the dataset analyzed here.

STATISTICAL ANALYSES

To quantify fitness consequences of nest attentiveness by both individuals and groups, we first defined focal or nonsocial phenotypes as nest activity of focal individuals and quantified it as the number of times individuals entered the nest or perched in front of it. As in Formica et al. (2011), we assumed that each observation constituted a potential interaction. Accordingly, conspecific social phenotype was determined as the mean of activity recorded among conspecifics nesting in the same colony, excluding the value recorded for the focal pair (Wolf et al. 1999; Formica et al. 2011). Thus, for each breeding pair, we quantified the mean of conspecific activity during each of our

observation sessions. With the same approach, heterospecific social phenotype was determined as the mean of activity values recorded among heterospecifics nesting in the same colony. Thus, for each breeding pair, we quantified the mean of heterospecific activity during each of our observation sessions. In single-species colonies, there was no activity from heterospecifics. In other words, conspecific (Wolf et al. 1999; Formica et al. 2011) and heterospecific phenotypes are defined as "social" because they are phenotype means of groups recorded in the community unit in our study system, the breeding colony. The "social" is opposed to the "nonsocial" phenotypes as they refer to the activity of single-breeding individuals rather than groups.

We compared number of fledglings, focal, conspecific, and heterospecific activity, within each species, with analysis of variance (one-way ANOVA, Underwood 1997) where the association type (single- vs. mixed-species) was treated as a fixed factor. As indicated above, single-species colonies were, by definition, those with no heterospecifics activity.

To quantify the fitness consequences of nest activity intensity, we conducted a multiple linear regression of the relative fitness on focal and social activity, where the relative fitness (w) of each pair was quantified as the number of their offspring (Table SA1) divided by the mean number of offspring produced by breeding pairs across the entire population (Brodie et al. 1995; Eldakar et al. 2010; Formica et al. 2011). Focal and social activity values were standardized in relation to population values so that their mean equaled zero and variance equaled one (Møller et al. 2009). Partial regression coefficients on single terms (β, Lande and Arnold 1983; Brodie et al. 1995; Wolf et al. 1999) represented the measure of the trait effect on the individual's fitness, whereas those on quadratic terms (γ, Wolf and Brodie 1998, Winn 2004, Stinchcombe et al. 2008) described the forces acting on phenotypic variance. When applied to social selection, $\gamma < 0$ represents reducing, whereas $\gamma > 0$ represents increasing phenotypic variance, thereby implying stabilizing versus disruptive selection, respectively (Moore 1990; Brodie et al. 1995; Kingsolver et al. 2001). When complex interactions between phenotype distributions occur, γ values are, however, difficult to interpret and therefore graphical tools are required to correctly describe the fitness function (Schluter 1988; Brodie et al. 1995). The fitness surface was therefore depicted with spline graphs using standardized focal, conspecific, and heterospecific social activity and w values. All analyses, except where noted otherwise, were conducted with STATISTICA 10.0 (StatSoft Inc. 2001).

The overall fitness effect (s) on activity phenotype was estimated with the following equation:

$$s = P\beta_N + \beta_{consp} + \beta_{heterosp}, \tag{1}$$

where P is the total variance of the trait recorded in focal individuals, β_N is the partial regression coefficient of the relative fitness of the trait recorded in focal individuals (i.e., nonsocial selection gradient *sensu* Wolf et al. 1999; Formica et al. 2011) and β_{consp} and $\beta_{heterosp}$ are the partial regression coefficients of the relative fitness on the phenotype means recorded in groups of conspecifics (β_s, where s stands for social *sensu* Wolf et al. 1999; McGlothlin et al. 2010; Formica et al. 2011) and heterospecifics, respectively. With a more extensive dataset, quantification of selection pressure could have included coefficients of correlational selection, and thus the occurrence of any selection pressure derived from the interaction between focal and social phenotypes on focal traits (Brodie 1992).

We realize that our dataset collected in a single year is limited in terms of drawing inferences from an evolutionary response perspective. Such inferences, as previously mentioned, are beyond the scope of our study, which instead aims to provide a framework for a unified analysis capable of integrating all community components into a common selective pressure.

Results

LESSER KESTRELS

Lesser kestrels experienced significantly lower nest success in mixed-species than in single-species colonies, fledging a lower number of chicks when nesting in association with jackdaws (ANOVA, $F_{1,71} = 6.34$, $P = 0.014$, Table SA1). Fitness values were not, however, associated with the level of nest activity recorded either among individuals or groups (Table 1). Both selection gradients, β and γ, were nonsignificant ($t_{315} =$ [range] -0.97–0.03, $P > 0.05$) revealing that the frequency of nest activity by individuals and groups, composed of both conspecifics and heterospecifics, did not affect kestrel relative fitness or its variance (Table 1). Accordingly, the overall effect of nest activity on fitness (s) was low (Table 1).

Graphical representation suggests a trend where lesser kestrel fitness peaked in highly active individuals ($\triangledown$ in Fig. 1A) when nesting in single-species colonies. In mixed-species colonies, the same highly active phenotypes were the least favored, especially when associated with highly active heterospecific groups. In mixed-species colonies, the most favored individuals ($\blacktriangledown$ in Fig. 1A) were those with low to moderate nest activity. Despite potential fitness advantages of being less active when in presence of jackdaws, similar activity phenotypes were recorded in single- and mixed-species colonies, either as focal individuals (ANOVA, $F_{1,317} = 0.038$, $P = 0.845$) or as a group ($F_{1,317} = 0.136$, $P = 0.712$, Fig. 2A).

Table 1. Partial regression coefficients indicate the effect size of nest activity phenotypes on lesser kestrel and jackdaw fitness (β) and its variance (γ).

	Lesser kestrel ($N = 319$)				Jackdaw ($N = 117$)			
	β	SE	γ	SE	β	SE	γ	SE
Focal phenotype	−0.056	0.057	−0.009	0.057	0.109	0.091	0.104	0.093
Conspecific social phenotype	−0.008	0.058	−0.059	0.057	**0.240**	**0.091**	0.073	0.093
Heterospecific social phenotype	−0.032	0.056	0.002	0.057	**−0.212**	**0.089**	−0.144	0.092
s	−0.096				0.137			

Bold values indicate significant effect size values for each phenotype category (i.e., social conspecifics and heterospecifics). The overall effect sizes of community activity on fitness are shown by *s* values as in equation (1) described in the text.
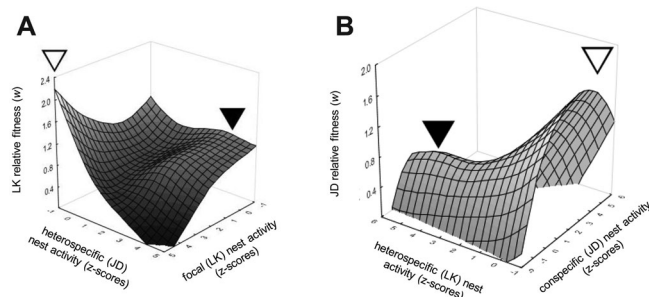

Figure 1. Thin plate splines representing fitness surfaces of (A) lesser kestrels (LK, *N* = 319) and (B) jackdaws (JD, *N* = 117) and where relative fitness (*w*) is a function of the interactions between focal and social phenotypes as measures of standardized values of nest activity. In (A) *w* is shown as function between LK focal and heterospecific (JD) social phenotypes whereas in (B) *w* is a function between conspecific (JD) and heterospecific (LK) social phenotypes. Symbols indicate the fitness peaks in single (▽) and mixed (▼) species colonies, respectively.

JACKDAWS

Jackdaws nesting in colonies with and without heterospecifics had similar nest success as they fledged the same number of chicks (ANOVA, $F_{1,23} = 0.001$, $P = 1.00$, Table SA1). Fitness values were, however, significantly associated with conspecific and heterospecific social activity. Specifically, linear selection gradients, β, showed that relative fitness significantly increased with conspecific (Table 1, $t_{113} = 2.63$, $P = 0.0097$) and decreased with heterospecific ($t_{113} = -2.39$, $P = 0.0185$) group activity, whereas nonsignificant (t_{113} = [range] −1.55–1.12, $P > 0.05$) nonlinear selection gradients, γ, indicated that nest activity, either by individuals or groups including conspecifics or heterospecifics, did not affect jackdaw fitness variance. The overall effect on fitness (*s*) was higher than that recorded for kestrels, although it was lowered as the result of opposite effects of conspecific versus heterospecific nest activity (Table 1).

Graphical representation of fitness surface revealed interactions of social nest activity between conspecifics and heterospecific phenotypes. In single-species colonies, fitness increased with
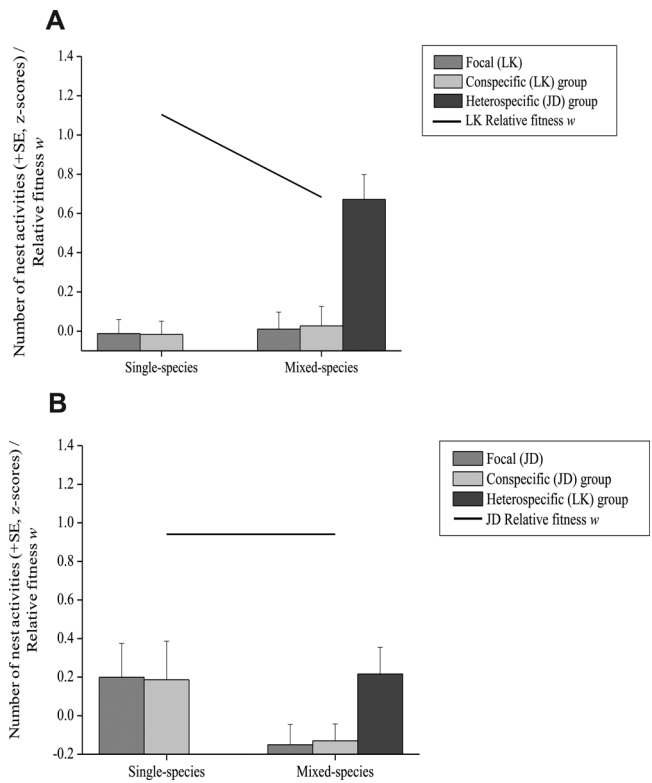

Figure 2. Relative fitness (*w*) and nest activity from the (A) lesser kestrel (LK, *N* = 319) and (B) jackdaw (JD, *N* = 117) perspective in single- and mixed-species colonies. Nest activity is represented as mean (±SE) of standardized values (*z*-scores) of focal and both conspecific and heterospecific social phenotypes.

conspecific nest activity (▽ in Fig. 1B). In mixed-species colonies, jackdaw relative fitness dropped, as the activity phenotype of heterospecifics was more intense. When associated with kestrels, the combination that allowed jackdaws to maximize their fitness was within a conspecific group with a moderate activity phenotype (▼ in Fig. 1B). In accordance with this result, jackdaw phenotypes were less active when together with lesser kestrels than without them, although this activity difference failed to achieve significance (ANOVA, $F_{1,117} = 3.34$, $P = 0.069$, Fig. 2B).

Discussion

Our results reveal that phenotypes of heterospecific neighbors serve as a relevant social component affecting individual fitness only for one of the species comprising our study communities. This asymmetry in the role played by the behavioral expression of group traits was associated with fitness consequences impinging upon the jackdaw as one of the components of the multispecies assemblage. By implementing a multilevel social selection analysis incorporating the social heterospecific component, we revealed complex interactions of phenotypes between conspecific and heterospecific neighbors suggesting suboptimal fitness outcomes for kestrels and significant phenotype assortments affording enhanced fitness among jackdaws.

Lesser kestrel fitness appeared uninfluenced by nest activity, either by individuals, conspecifics, or heterospecifics. We detected, however, a significant reduction in the reproductive output of lesser kestrels when they shared colony structures with jackdaws. Although visual examination of their fitness surface suggested an optimal assortment with reduced activity in the presence of heterospecifics, activity phenotypes were homogeneously assorted in single- and mixed-species colonies, without and with jackdaws, respectively.

Unlike kestrels, jackdaws experienced the most dramatic fitness consequences of variation in social phenotypes. Activity phenotypes of conspecifics and heterospecifics exerted positive and negative effects, respectively, on jackdaw relative fitness. Inspection of the fitness surface revealed that interactions between these opposing forces resulted in highly active jackdaws experiencing the greatest success in single-species colonies, and moderately active jackdaws being most successful in mixed-species colonies. Contrary to our findings for lesser kestrels, the assortment that maximized fitness for jackdaws occurred in mixed-species colonies where jackdaw groups were characterized by less-active phenotypes than those in single-species colonies.

Our findings thus have two major implications. First, social phenotypes of heterospecifics may be integral to the accurate assessment of fitness within communities and, second, interspecific assortments between social phenotypes have distinct fitness consequences for interacting species. In the following sections, we examine both of these implications in detail.

SOCIAL PHENOTYPES OF HETEROSPECIFICS

In classical multilevel social selection, selection gradients β and γ indicate linear and not nonlinear (i.e., stabilizing and disruptive) selection forces. Identifying specific selective pressures was beyond the scope of our study, but as mentioned earlier, adopting terms of, and referring to multilevel selection studies may

provide insight into community dynamics influencing social traits and comparable measures to assess the importance of effect sizes associated with those in our system.

Our results revealed the most significant effects as β gradients, indicating linear, yet opposite, selective forces on conspecific and heterospecific phenotypes, for only one of the species composing the mixed-species assemblages. Although few studies have examined the role of behavioral traits on phenotypic selection, our β values fell within the median and mean range of |β| for most investigations of morphological, life-history and phenological traits (Kingsolver et al. 2001). Our linear selection gradients also fell within the 25th percentile of studies with β values significantly different from zero (Kingsolver et al. 2001).

We previously reported that both jackdaws and lesser kestrels decreased overall vigilance at the colony when nesting in the same structures (Campobello et al. 2012), whereas here we report that only jackdaws decreased nest attendance. Different trends in different traits (i.e., colony vigilance and nest activity) are consistent with the presence of opposing selective forces. It is not unusual to record different and even contrasting forces operating on the same trait (Weinig et al. 2007; Eldakar et al. 2010). For example, linear and nonlinear forces acting on the body size of dragonflies were explained as favoring two different fitness-relevant components; territoriality and fertilization success (Moore 1990).

None of the nonlinear selection gradients (γ) differed significantly from zero. The highest value was reported, once again, in the jackdaw system for heterospecific social phenotypes. Its negative sign suggested reduced variance, and hence stabilizing selection toward heterospecific activity means. Visual representation revealed a fitness surface compatible with this interpretation (Brodie et al. 1995). Stabilizing and disruptive selection related to phenotypic variance are, however, uncommon in nature, and when reported as significant contributors to fitness estimates, are more often than not weaker than linear selection values (Kingsolver et al. 2001; Stinchcombe et al. 2008; Haller and Hendry 2014).

INTERSPECIFIC ASSORTMENT BETWEEN SOCIAL PHENOTYPES

As mentioned above, kestrels and jackdaws assorted their social phenotypes with suboptimal and positive fitness consequences, respectively. Was this phenotypic assortment the result of: (1) a behavioral effect where individuals reinforce a common behavioral pattern? or (2) preferential assortment with specific phenotypes?

Phenotype reinforcement is inconsistent with either kestrels, that showed no flexibility in the expression of their social phenotype, or jackdaws, that showed a less active, and thus opposite,

phenotype in the presence of heterospecifics. Although reinforcement of behavioral patterns is commonly reported among conspecifics (Wolf et al. 1999) as instances of phenotypic flexibility (Berrigan and Scheiner 2004), our results are not in accord with its occurrence in an interspecific context.

Preferential assortment with specific social phenotypes is another mechanism that can explain the observed interspecific phenotype combinations in jackdaws. Selective association with specific phenotypes is reported to reverse the negative effect of social selection for body size in forked fungus beetles (*Bolitotherus cornutus*; Formica et al. 2011), to allow nonaggressive male water striders (*Aquarius remigis*) to locate more favorable contexts in which to mate (Eldakar et al. 2010), and to enhance alternative reproductive strategies in white-throated sparrows (*Zonotrichia albicollis*, Formica et al. 2004). We are unable to provide evidence that selective assortment was practiced by one or both species, but our results suggest that this mechanism is most plausible among jackdaws. Whenever advantages or disadvantages are recorded following social interactions, we can refer to cases of reciprocity or agonistic relationships, respectively (Clutton-Brock et al. 1998; Radford et al. 2011). Among jackdaws, we found an assortative phenotypic combination that prevented a fitness decrease, whereas among kestrels, no specific assortment was associated with disadvantages in terms of fitness outcomes. This cannot be the result of any selective assortment on the part of lesser kestrels.

Ecological limitations, however, can provide a third explanation for negative assortment of kestrel with jackdaw phenotypes. Despite negative fitness consequences, the association of kestrels with jackdaws is consistent with random assortment in conjunction with ecological limitations. Lesser kestrels have more rigid resource requirements than the more flexible jackdaws. Lesser kestrel nesting sites require specific features (Sarà et al. 2012) whereas jackdaws have a broad range of nesting sites where they are found breeding successfully (Henderson and Hart 1993). As in other populations (Catry et al. 2013), at our study site, buildings housing colonies are progressively deteriorating, reducing nest site availability and precluding the potential benefit accrued by increasing the number of individuals breeding synchronously within the same colony (Di Maggio et al. 2013). Finally, young individuals are despotically displaced by conspecific adults in small colonies, often to suboptimal nesting sites (Serrano and Tella 2007), and breeding philopatry appears to be disrupted by anthropogenic causes (Di Maggio et al. 2015). Given myriad ecological constraints, further investigations exploring nest site limitation and temporal overlap in nesting (Bellia et al. 2011) between these two species (Serrano and Tella 2007, 2012) may provide new insight into the factors promoting suboptimal interspecific assortment.

Conclusions

We developed a novel approach to integrate the quantification of social selection pressures at the community level. Long-term studies with longitudinal datasets would find in our model a robust method to quantify selection pressure and selective forces, incorporating ecological and evolutionary forces into a unified interspecific perspective. In most communities, species express one or more traits that can be considered social traits, whose phenotypes differentially affect conspecific and heterospecific fitness. Although our analysis employed nest activity, our methods could as readily have been applied to aggressiveness between spiders (Pruitt and Ferrari 2011), alarm call rates between birds (Radford et al. 2011), foraging success between mammals (Minta et al. 1992), or predator detection among fish (Semeniuk and Dill 2006, Vail 2014), to name only a few systems amenable to heterospecific selection analysis. Wherever there are interacting species, including animal–plant interactions, it would be possible to quantify each of their phenotypes as a component exerting a potential selection pressure on other members of the community.

Our findings reveal that interspecific social traits may be incorporated meaningfully as a component of an overall multilevel selection analysis and that conspecific and heterospecific social phenotypes interact, resulting in complex combinations of fitness consequences. In our study, we revealed an asymmetric interaction between two species nesting in the same colony, whereby only one of those species (jackdaws) was affected by the social phenotype of both conspecifics and heterospecifics. To explain the observed interspecific assortment between social phenotypes, our findings fail to support a reinforcement process for common behavioral traits, whereas they are consistent with the occurrence of random and preferential assortments for kestrels and jackdaws, respectively, particularly in the face of ecological constraints on suitable kestrel nesting habitat. We are not, however, able to ascertain whether the suggested preferential assortment of jackdaw phenotypes is the result of phenotypic plasticity dependent upon ecological conditions (Pruitt and Ferrari 2011; Ghalambor et al. 2013). Multiple phenotypes are suggested to evolve in a variable environment where organisms have access to the elements necessary to assess environmental variation (Roff 1996).

The present study also offers a novel approach to address the pressing question of biodiversity loss within communities (Diaz et al. 2006). Biodiversity loss represents one possible axis of community evolution, which can be promoted or retarded by reciprocal selective pressures that define the coevolutionary relationship among interacting species. If social phenotypes can be quantified in the extended community using the methods we have advanced, new perspective could also be gained into the factors promoting and maintaining metacommunity structure, and more

specifically, the demographic processes that link the communities within (Goodnight 2011).

Thus, although the present analysis falls short of offering a comprehensive explanation of the fitness consequences associated with interspecific associations between jackdaws and lesser kestrels, our integrated selection analysis served to illuminate directions worthy of further investigation. Further studies of ecological limitations, such as nest site availability, are warranted to provide additional insight into how interspecific interactions shape social dynamics in our system. The application of our method to other biological communities, and to metacommunities, however, is likely to yield more broadly applicable evolutionary and ecological insights.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table SA1. Number of offspring (mean $\pm$ SE) produced in nests of lesser kestrels and jackdaws when in structures without (single-species colonies) or with (mixed-species colonies) the other species nesting.