



## Female plumage coloration signals status to conspecifics



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Intrasexual competition in female birds is a widespread phenomenon but remains scarcely explored. Females compete for limited resources and the expression of signals that indicate their social status will be favoured by natural selection, generating a dominance hierarchy among individuals. However, which signals might be involved in female–female competition is unclear. In this study, we tested the role of rump coloration as a badge of status within a context of intrasexual competition using common kestrels, *Falco tinnunculus*, in two populations over 3 years. We used natural decoys with two different ‘phenotypes’, since the expression of this melanin-pigmented trait within the brown–grey range has been suggested to be a reliable proxy of individual quality in female common kestrels. By showing natural decoys with grey and brown rumps to breeding females, we simulated territorial invasions of high- and low-quality females, respectively. Our results show that rump coloration generates a differential response during territorial invasions. Specifically, we found that grey-rumped decoys (high quality) elicited lower levels of aggressiveness. In addition, female agonistic response was negatively associated with clutch size. Based on our results, we suggest that female rump coloration works as a badge of status in breeding female kestrels. This trait may signal female competitive ability and can generate a dominance hierarchy among individuals in our population. We also suggest that aggressiveness can be costly to females in terms of reproductive outcome. Overall, we provide evidence that melanin-pigmented traits in females can play a key role in intrasexual competition.

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Intrasexual competition in females is a widespread phenomenon in the animal kingdom, although its implications in behavioural and evolutionary ecology remain little explored (Stockley & Campbell, 2013). Recent research suggests that females will compete for ecological resources, such as food or nesting sites, rather than for matings (LeBas, 2006; Rosvall, 2008; Tobias, Montgomerie, & Lyon, 2012), confirming the idea that female and male ornaments can be shaped by different selective forces (Rosvall, 2011a). In a competitive context, the expression of signals that regulate access to limited ecological resources will be favoured by selection (Amundsen, 2000). These signals, known as badges of status, allow contestants to evaluate the competitive abilities of other females without eliciting agonistic encounters, reducing the costs associated with aggressiveness (Rosvall, 2011b). However, how females signal individual status and what phenotypic traits are involved in the wild are still poorly understood.

The reliability of signals of social status has been explained by different hypotheses (Senar, 2003). First, signals of status are expected to be reliable proxies of individual status when they consistently have an associated behaviour, because receptors not only focus on the trait but also on the way individuals behave (sceptical receptor hypothesis; Järvi, Walsø, & Bakken, 1987; Rohwer, 1977; Rohwer & Rohwer, 1978). Second, it has been proposed that only high-quality individuals are able to afford the cost of expressing an enhanced signal of status. This cost may arise from increased intrasexual aggression (social control hypothesis; Rohwer, 1977; Rohwer & Rohwer, 1978), predation (differential predation hypothesis; Fugle & Rothstein, 1987; Fugle, Rothstein, Osenberg, & McGinley, 1984) or immunosuppression (Folstad & Karter, 1992). Finally, it has been suggested that dominant and subordinate individuals may follow alternative but evolutionarily stable strategies (mixed stable evolutionary strategy; Maynard Smith, 1982; Rohwer, 1982). This may be achieved, for example, if dominant and subordinate individuals allocate their resources differently, trading off resources to obtain high-quality territories and parental care (Studd & Robertson, 1985; but see Yezerinac & Weatherhead, 1997).

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Within a social context (Senar, 2006), melanin-based signals are particularly relevant in animal communication (Jawor & Breitwisch, 2003). Several examples have described how an enhanced expression of melanin-based badges leads to the discrimination of dominant from subordinate individuals (Jarvi & Bakken, 1984; Johnson & Fuller, 2014; Nakagawa, Ockendon, Gillespie, Hatchwell, & Burke, 2007; Rat, Dijk, Covas, & Doutrelant, 2014; Senar, Camerino, Copete, & Metcalfe, 1993; Tibbetts, 2006; Vergara & Fargallo, 2007) suggesting that these badges can act as social signals. Although these examples are biased towards males, there is growing evidence that females also show their social status since the expression of coloured traits mediates aggressiveness or dominance in females in various taxa (Crowhurst, Zanollo, Griggio, Robertson, & Kleindorfer, 2012; Midamegbe, Grégoire, Perret, & Doutrelant, 2011; Morales et al., 2014; Murphy, Hernández-Mucio, Osorio-Beristain, Montgomerie, & Omland, 2009; Murphy, Rosenthal, Montgomerie, & Tarvin, 2009; Pham, Queller, Tarvin, & Murphy, 2014; Swaddle & Witter, 1995). There is also a bias towards studying carotenoid-based traits: for example the size of the yellow patch in female rock sparrows, *Petronia petronia*, is a signal of their competitive ability (Griggio, Zanollo, & Hoi, 2010). However, the role of melanin-pigmented traits in female intrasexual competition is little explored (Crowhurst et al., 2012; Morales et al., 2014). In fact, only two studies have examined the role of a lack of melanization (i.e. white spots), finding that white flank spots and forehead patch can signal status in diamond firetails, *Stagonopleura guttata*, and pied flycatchers, *Ficedula hypoleuca*, respectively (Crowhurst et al., 2012; Morales et al., 2014). Thus, how variation in melanization of female traits signals individual status is still poorly understood.

A first step to understanding how signals of status have been maintained in evolutionary time is to explore the costs associated with female–female competition. In females, aggressiveness has been directly linked to cuckolding avoidance (Gowaty, 1981; Gowaty, Plissner, & Williams, 1989; Hobson & Sealy, 1990) or to regulating access to nesting sites (Rosvall, 2008). The related costs associated with this behaviour can be paid in terms of energy expenditure or physical damage (Cain & Ketterson, 2013). As a consequence, this might constrain direct investment in reproduction or other energetically demanding functions. Thus, if expressing a signal of high status allows females to avoid the costs of agonistic encounters, it might be expected that those females will have more resources to allocate to other energy-demanding functions, such as reproduction (Knaption & Falls, 1983; Kopachena & Falls, 1993; Rosvall, 2011b). Under this scenario, a positive selection of signals expressing social status in females is expected. However, our knowledge of the association between the expression of a social signal and levels of aggressiveness in females is extremely limited.

In this study, we simulated female territorial invasions by means of natural decoys to test female response within a context of intrasexual competition using common kestrels, *Falco tinnunculus*, as a study species. We presented decoys that differed solely in their expression of a melanin-pigmented trait: grey or brown rumps, representing high- and low-quality individuals, respectively (Vergara & Fargallo, 2007; Vergara, Fargallo, Martínez-Padilla, & Lemus, 2009). Previous studies in this species suggest that female plumage is under ecological rather than sexual pressure (López-Rull, Vergara, Martínez-Padilla, & Fargallo, 2016). Our main objective was to test the role of this plumage as a badge of status in a female–female competition context. We predicted that low-quality (brown-rumped) invaders will receive more attacks and that more aggressive females will pay a cost in terms of reproductive output.

## METHODS

### Study Area

The study took place in two populations. Population 1 is in a mountainous grassland area located in Campo Azálvaro, Segovia (1300 m above sea level, 40°40'N, 4°20'W) where 24–45 kestrel pairs breed each year in 62 nestboxes installed progressively between 1994 and 2005 (Fargallo, Blanco, Potti, & Viñuela, 2001; Fargallo et al., 2009). Population 2 is located in a cropland area in Villalar de los Comuneros, Valladolid (700 m above sea level, 41°32'N, 5°08'W) where 26–64 pairs breed each year in 100 nestboxes installed in 2009 (Paz et al., 2013). Decoy presentations (see below) were performed in populations 1 and 2 during the breeding seasons of 2012–2014 and 2013, respectively.

### Study Species

The common kestrel is a medium-sized raptor with a marked sexual dimorphism in body size (females are 20% heavier) and plumage coloration (Palokangas et al., 1994; Village, 1990). Females are brown on the head, back and upper sides of the wings, with black bars rather than spots (Lopez-Idiáquez, Vergara, Fargallo, & Martínez-Padilla, 2016). The amount of grey coloration on the rump of females is variable, from completely brown (0% grey) to fully grey (100% grey; Vergara et al., 2009). In our study, the average percentage of grey coloration in rumps of breeding females is 67.37% in population 1 ( $N = 81$ ) and 70.65% in population 2 ( $N = 23$ ).

### Breeding Performance and Female Information

We monitored nests every 2 days to detect laying date (day that the first egg was laid; Martínez-Padilla et al., 2004), and to record clutch size (population 1 mean = 4.84, range 2–7,  $N = 83$ ; population 2 mean = 4.65, range 3–7,  $N = 26$ ) and number of fledglings (population 1 mean = 3.36, range 0–6,  $N = 83$ ; population 2 mean = 3.03, range 0–6,  $N = 26$ ). Females were captured during incubation by netting. At the time of capture, body mass (to the nearest g), wing and tarsus length (to the nearest mm) of all females were recorded. The proportion of the greyness of the rump was also determined as previously described (Vergara et al., 2009): 0%, only brown coloration; 100%, only grey coloration. We also determined whether females were yearlings (1 year old) or adults ( $\geq 2$  years old) by using ring codes or plumage features (Vergara & Fargallo, 2007).

### Experimental Manipulation: Decoys and Rump Greyness

We exposed a natural decoy of an adult female to test whether there were differences in the aggressive response of breeding females to grey- or brown-rumped decoys during the prelaying period. Decoys were stuffed dead kestrels obtained from recovery centres (see below) and were presented in two different treatments: grey or brown rumps. Rumps constitute unique structures obtained as a whole piece from dead kestrels, and could easily be fixed and removed from the decoys with a pin. A total of eight different decoys and 15 different rumps were used. To avoid a decoy-dependent effect on any of the variables used to assess aggressive response of females (see below), we randomly used different decoys and rumps.

Decoys were displayed on a 1 m tall stick at a distance of 10 m from the nestbox (following Vergara, De Neve, & Fargallo, 2007; Vergara & Fargallo, 2007; Vergara, Martínez-Padilla, & Fargallo, 2012). The studied nests were chosen when a female was

detected in its surroundings as a cue for later breeding (see Vergara et al., 2007). Decoys were always presented with the rump pointing towards the entrance of the nestbox. We removed the decoy if females did not return after 1 h of observation. When females returned, we measured their aggressive behaviour for 10 min. Observations were carried out between 0730 and 1730 hours using binoculars (10 × 52) and a telescope (20–30 × 60) from a car located further than 200 m away in order to avoid interference with female behaviour. If the car was not a plausible option, we recorded female behaviour from the ground, at a similar distance to observations made from the car. When possible, we repeated observations of the same female (mean number of observations per female in a single year:  $1.52 \pm 0.09$ ; range 1–3) but always over a minimum interval of 3 days between two consecutive observations. As soon as females laid their first egg, we stopped the observations at those nests.

#### Assessment of Aggressiveness

We assessed aggressive behaviour in three different ways. We first recorded whether or not there was an aggressive response once the female returned to the nest. Second, we quantified the aggressive intensity when females returned to the nest. We categorized this behaviour into five levels: '0' for no response, the individual was present but did not attack; '1' for attacks with no contact with the decoy, just alarm calls, flights, looping or hovering over the decoy; '2' for attacks with only one physical contact with the decoy; '3' for attacks with more than one contact with the decoy; '4' for situations in which females perched on the decoy and pecked it. Third, and finally, we recorded the number of attacks. These approaches have been successfully used in different studies with the same species in population 1 (Vergara et al., 2007, 2012; Vergara & Fargallo, 2007).

#### Ethical Note

The decoys and rumps used in this study were obtained from dead kestrels provided by Grupo de Rehabilitación de la Fauna Autóctona su Hábitat (GREFA) and CRAS Madrid-Viñuelas with permission of the Consejería de Medio Ambiente y Ordenación del Territorio of the Comunidad Autónoma de Madrid (10/253520.9/13). Kestrels were not killed to carry out this study and wild kestrels were not harmed by the agonistic encounters against the decoys or by the manipulation. Licences to study kestrels were provided by the regional government of Castilla y León (Expte: EP/CYL/105/2012; SENEP/SG/256/2013; EP/CyL/58/2014).

#### Statistical Analyses

All analyses were carried out in R statistical software using lme4 and lmerTest packages (Bates, Maechler, & Bolker, 2013; Kuznetsova, Brockhoff, & Christensen, 2013). Female aggressiveness was coded for the three indices considered as follows for each observation: aggressive response (0: did not attack; 1: attacked); aggressive intensity (the five levels described above); number of attacks.

In a first set of models, we performed generalized linear mixed models (GLMM) to explore any potential influence of the decoys themselves on aggression levels. We included the three indices of aggressiveness used as dependent variables and the decoys as explanatory variables. Distributions of errors were Poisson and binomial when the dependent variables were attack intensity and number of attacks and aggressive response, respectively, in all models. Second, we ran GLMM to study the influence of the treatment (grey or brown rump) on female aggressiveness. The

three indices of aggressiveness were considered dependent variables in separate models. In these, treatment was included as a fixed factor and observation day (date the observation was made according to the Julian calendar), weight, rump coloration and age (young/adult) of the female as covariates. As previous studies have shown that male presence can affect females' willingness to initiate agonistic encounters (Jonart, Hill, & Badyaev, 2007) we also included male presence as a covariate in our models. Rump coloration, weight and observation day were standardized to a mean of 0. Third, we analysed the relationship between aggressiveness and reproductive output. We performed GLMMs considering the three proxies of aggression levels considered as dependent variables, and laying date, clutch size and number of fledglings as explanatory variables. Treatment and observation day were also included in the models to control for their effect on the dependent variables. The reproductive variables and observation day were also standardized to a mean of 0 before including them in the models. Coloration of female rumps and observation day were included as covariates.

All models included the study area and year as covariates and individual identity and nest as random factors. Model selection followed a backward-stepwise procedure in which all variables were initially included. Nonsignificant variables ( $P > 0.05$ ) were removed sequentially. To explore whether the order of presentation of the two colours had any effect of habituation, we ran separate models for the three dependent variables of aggressive behaviour described above. In these models, order of presentation, treatment and their interaction were the explanatory variables, in addition to observation day as covariate. Nest and individual identity were considered as random factors. Distributions of errors for each model were those described above for each of the dependent variables.

## RESULTS

#### Decoy Influence

We did not find any significant influence of a particular decoy on the results for any of the variables of aggressiveness (aggressive response:  $P > 0.211$ ; aggressive intensity:  $P > 0.132$ ; number of attacks:  $P > 0.076$ ) or any effect of habituation of females to colours (all  $P > 0.952$ ).

#### Decoy Rump Coloration

We did not find any statistically significant effect of either our treatment or any of the variables on aggressive response (Table 1). For aggressive intensity, we found a significant negative relationship with observation day (Table 1). Specifically, aggressive intensity decreased as the breeding season progressed. Finally, our results suggest an effect of our treatment on number of attacks (Table 1, Fig. 1). Decoys with brown rumps were attacked significantly more than grey ones (Table 1). None of the aggressiveness variables were found to be significantly explained by body mass, age (1 year old versus adult), rump coloration, study area or the presence of the male (Table 1).

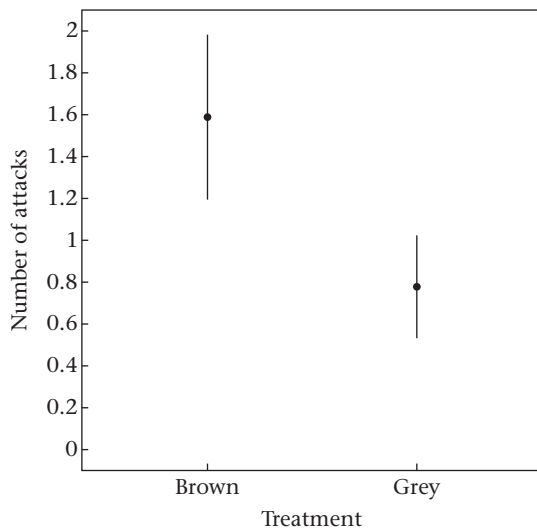
#### Reproductive Variables

Clutch size was negatively related to both number of attacks (GLMM:  $-0.628 \pm 0.295$ ,  $F = 6.048$ ,  $P = 0.020$ ; Fig. 2a) and aggressive intensity (GLMM:  $-0.573 \pm 0.250$ ,  $F = 5.763$ ,  $P = 0.021$ ; Fig. 2b). In relation to aggressive response, we found a marginally significant effect, where females that attacked had smaller clutch sizes ( $P = 0.065$ ). We did not find any significant relationship

**Table 1**  
Effect of treatment on three variables of aggressiveness in breeding females of common kestrels

Parameter	Aggressive response (N=70)					Aggressive intensity (N=70)					Number of attacks (N=70)				
	Estimate	SE	F	P	ES	Estimate	SE	F	P	ES	Estimate	SE	F	P	ES
Treatment	-1.304	0.853	F1=3.681	0.126	7	-0.466	0.313	F1=5.691	0.099	7	<b>-0.620</b>	<b>0.284</b>	<b>F1=10.831</b>	<b>0.029</b>	
% Grey in attacker's rump	0.442	0.711	F1=0.004	0.534	1	0.231	0.259	F1=0.122	0.374	1	0.192	0.285	F1=0.036	0.500	2
Weight	0.774	0.588	F1=0.956	0.188	3	-0.569	0.585	F1=1.236	0.330	2	0.296	0.247	F1=0.688	0.231	4
Study area	1.252	1.469	F1=0.516	0.394	4	1.019	0.779	F1=0.368	0.191	4	0.524	0.569	F1=0.928	0.357	6
Age	-1.054	1.347	F1=0.433	0.433	5	-0.362	0.579	F1=0.037	0.532	3	-0.597	0.698	F1=0.102	0.390	1
Observation day	-1.241	0.727	F1=8.002	0.087		<b>-0.640</b>	<b>0.252</b>	<b>F1=8.516</b>	<b>0.011</b>		<b>-0.546</b>	<b>0.247</b>	<b>F1=5.163</b>	<b>0.027</b>	
Year			F2=1.002	0.380	2			F2=0.658	0.228	5			F2=1.409	0.288	5
Male presence	-1.694	1.223	F1=2.682	0.166	6	-0.600	0.368	F1=2.622	0.102	6	-0.308	0.402	F1=0.569	0.443	3

Results of the generalized linear mixed models of aggressiveness variables (aggressive response, aggressive intensity and number of attacks) in female common kestrels. ES denotes the exclusion sequence of the nonsignificant terms of the model, age represents whether individuals were yearlings or adults. Variables included in the final models are in bold; values for excluded variables refer to the step before their exclusion. Greyness of the rump is percentage of grey in the rump of females (see [Methods](#) for further details).



**Figure 1.** Number of attacks of adult female common kestrels on brown- and grey-rumped decoys. Means are given with SEs.

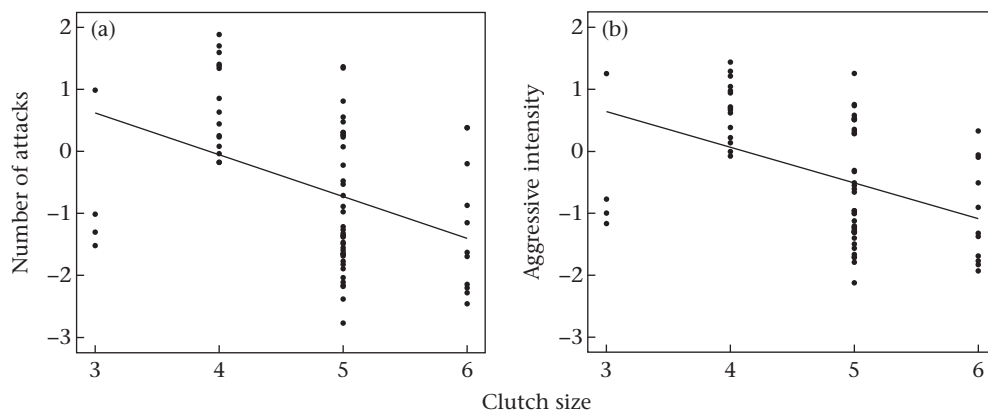
between any of the aggressive values and laying date ( $P > 0.135$ ) or number of fledglings ( $P > 0.355$ ).

## DISCUSSION

Our results suggest that rump coloration mediates the intensity of aggression of prelaying female common kestrels. Specifically, we

found in a multiannual and spatially replicated experiment that females were more aggressive towards decoys with brown rumps. Further, we argue that aggressive behaviour can be a costly activity for females, since we found that female aggressiveness was negatively associated with clutch size.

The between-treatment difference found for the number of attacks indicates that female plumage coloration works within the signalling system of kestrels. This result agrees with previous studies in showing that female ornamentation can work as a status signal in a female competition context ([Crowhurst et al., 2012](#); [Griggio et al., 2010](#); [Morales et al., 2014](#)). These studies explored carotenoid ([Griggio et al., 2010](#)) and depigmented ([Crowhurst et al., 2012](#); [Morales et al., 2014](#)) traits, making our study the first to investigate the role of melanin-based coloration in a female–female competition context. In addition, our results support the recent view that intrasexual competition for limited resources plays an essential role in the evolution of female phenotypes ([Tobias et al., 2012](#)). This is also supported by the fact that more feminized phenotypes, including plumage coloration, increase postfledging survival during winter ([López-Rull et al., 2016](#)). Our study indicates that females with greyer rumps can be perceived as more competitive individuals. Thus, plumage coloration can be considered a signal of social status that allows conspecifics to evaluate the probability of success in agonistic confrontations, as proposed by the status signalling theory ([Rohwer, 1975](#)). Therefore, grey rump coloration, which is costly to produce ([Fargallo, Laaksonen, Korpimäki, & Wakamatsu, 2007](#)) and reflects high individual quality ([Fargallo et al., 2007](#); [Vergara & Fargallo, 2008](#); [Vergara et al., 2009](#)), may provide benefits within this hierarchical system of dominance in adult females. It is interesting, however,



**Figure 2.** Relationships between clutch size and female aggressiveness. On the y-axis we show the predicted values of the models performed in each case. (a) Number of attacks; (b) aggressive intensity (see [Methods](#) for further details).



that, according to our results, rump coloration affects not female willingness to attack but the number of attacks. This result may suggest that females always respond to a territorial invasion and that it is the intensity of the response, measured as number of attacks, that changes depending on the intruder's rump coloration. We do not have a clear explanation for this result, but it might be caused by a small sample size, although the two proxies of intensity of aggressiveness (considering only females that responded, i.e. aggressive intensity, or all females, i.e. number of attacks) have the same estimates, suggesting the same pattern. Possibly, a given threshold of stimulus is needed to trigger a more intensive response by females towards brown decoys.

Based on our results, we suggest that aggressive behaviour of females is an armament within an intrasexual competition context and probably under social selection. We base this statement on two main results. First, we found that aggressiveness of conspecifics was modulated by a badge of status, since greyer female decoys received fewer attacks from breeding females. Thus, showing an enhanced signal of status (higher proportion of greyness in the rump) is expected to prevent aggressive confrontations with other females. Second, our results suggest that aggressiveness can be considered a costly activity since it was negatively correlated with clutch size. This cost can be explained from different perspectives. According to the handicap principle (Zahavi, 1975), only high-quality individuals are able to afford the cost of being more aggressive. Specifically and according to our results, highly aggressive females are expected to be negatively selected because their aggressiveness would detract resources for reproduction (Cain & Ketterson, 2013; Fitzpatrick, Berglund, & Rosenqvist, 1995; Rosvall, 2011b) and only an intermediate expression of this trait would gain fitness benefits (Chenoweth, Doughty, & Kokko, 2006). Our results agree with this idea since more aggressive females produced smaller clutches, although our small sample size does not allow us to test the association between levels of aggression and clutch size at intermediate levels of aggression. Alternatively, the negative association between aggressiveness and clutch size can arise from an opposite perspective. One might expect that due to high reproductive costs (Stearns, 1992), females laying smaller clutches can be more aggressive simply because they have more energy to invest. This is unlikely in kestrels because female body condition before and during laying is tightly associated with male quality since only males provide food to breeding females (Village, 1990). Thus, the costs of being aggressive might be associated with mate quality. Under this idea, it is highly unlikely that females mated with low-quality males, laying smaller clutches, increase their aggressiveness, a costly activity for a low reproductive investment, at least in terms of clutch size. From a mechanistic point of view, testosterone levels may explain the association between clutch size and aggressive behaviour, as previous studies have shown that testosterone modulates aggressiveness (Bókony, Garamszegi, Hirschenhauser, & Liker, 2008; Jawor & Breitwisch, 2003) and is negatively associated with reproductive output (Rutkowska, Cichoń, Puerta, & Gil, 2005; Veiga & Polo, 2008). In either case, from an evolutionary perspective, highly aggressive females are expected to be negatively selected. Surprisingly, previous studies in the same area (population 1) and with the same species found different results: clutch size was positively correlated with aggressiveness (Vergara et al., 2007). However, the methodological approach is not comparable to our study. Vergara et al. (2007) used three decoys, including two males, so the aggressive response they reported cannot be linked specifically to a female–female encounter, as is the case in the present study.

We found that aggressiveness decreased during the breeding season. This result may be explained by the early arrival of better quality females to the breeding grounds. This can increase female

competition for both obtaining and keeping a mate at the beginning of the breeding season (Village, 1990; Wiklund & Village, 1992). As the breeding season progresses, the number of single females and the potential risks of being cuckolded decrease, as does aggressiveness. This idea has been described for red-winged blackbirds, *Agelaius phoeniceus*: females develop a more aggressive response towards other females showing interest in mating with the territory-owning male (Yasukawa & Searcy, 1982). Another nonexclusive explanation may be that the quality of territories and mates and, thus, the reproductive value of late-breeding females decrease as the breeding season progresses, and the cost of an aggressive behaviour might not compensate for maintaining low-quality territories or mates.

Overall, our results show that female rump coloration works as a badge of status in breeding female common kestrels. Greyer individuals of better quality (Fargallo et al., 2007; Vergara et al., 2009) were less intensely attacked than browner individuals. This indicates that kestrels are sensitive to variations in the expression of this colour trait (grey–brown rump coloration) and that rump coloration may signal status, at least in an intrasexual context. In addition, our study supports the idea that premating aggressiveness may impose costs observable in subsequent reproduction.

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