

Original Article

# Differential maturation of sexual traits: revealing sex while reducing male and female aggressiveness

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Sexually mature young males of many dichromatic species begin breeding while expressing female-like or incomplete adult phenotypes, which contradicts sexual selection theory. It is thought that by delaying the acquisition of adult appearance, young males may avoid aggression from other males, but reduce mating opportunities, resulting in trade-offs between these 2 life-history traits. Thus, an optimal young male phenotype should allow mating while reducing aggressiveness. Differential character maturation (i.e., the acquisition of adult appearance does not occur in all traits at the same time) has been described in bird species, but has largely been neglected in the study of delayed plumage maturation. Using the common kestrel *Falco tinnunculus*, we tested the prediction that maturation of different adult traits depends on the aggressiveness elicited by both male and female individuals and that young male phenotypes should be a combination of traits triggering low levels of aggressiveness while still revealing sex. We explored the pattern of delayed plumage maturation observed in 4 different adult male traits (head, rump, tail, and back plumages) in young breeding males captured over 8 years. We then analyzed the intensity of agonistic responses against these traits in breeding males and females by presenting young male decoys showing these mature characters. We found that those characters eliciting high aggressiveness in males (head and rump) were partly expressed in young males and only 1 (tail) of the 2 traits (tail and back) eliciting high aggressiveness in females was poorly expressed. Our study suggests that conspecific aggressiveness of both males and females can play a significant role in determining patterns of delayed plumage maturation. *Key words*: delayed plumage maturation, female mimicry, intrasexual competition, multiple messages, sexual selection, status signaling. [*Behav Ecol*]

## INTRODUCTION

Why sexually mature males of many sexually dichromatic species express immature or female-like phenotypes is an intriguing question in evolutionary ecology. If the adult appearance of males has fitness benefits by increasing their probability of breeding (Andersson 1994), why do sexually mature males in many taxa such as fishes, reptiles, birds, and mammals retain juvenile or female-like phenotypes? (Rohwer et al. 1980; Lyon and Montgomerie 1986; Shine et al. 2001; Rios-Cardenas et al. 2010) To resolve this apparent paradox, it has been proposed that immature or female-like phenotypes may help individuals avoid confrontations with other males by honestly signaling subordination, by sexual deception, or by decreasing their detectability, among other possibilities (reviewed by Senar 2006; Hawkins et al. 2012). Such a reduction in male–male conflicts increases survival or breeding opportunities, thus explaining how being less conspicuous can be adaptive (Conover et al. 2000; Greene et al. 2000; Berggren et al. 2004, but see Webster et al. 2008).

The retention of immature phenotypes by males has frequently been studied in birds and has mainly focused on plumage, namely delayed plumage maturation (DPM),

defined as the delayed acquisition of a definitive color and pattern of plumage until after the first potential breeding period, sensu Hawkins et al. (2012). However, studies analysing molt pattern in young birds have shown that the acquisition of adult plumage does not occur in all traits at the same time (e.g., Grant 1990). Furthermore, adult appearance is often restricted to some patches, whereas the rest of the feathers maintain a resemblance to juvenile plumage (Arroyo and King 1996; Senar et al. 1998; Vergara and Fargallo 2007). These observations suggest that adult appearance is rarely acquired in a homogeneous way throughout the plumage and instead, differential timing of maturation between traits is a common phenomenon, but the reasons behind such differences remain unexplored. Conspecific agonistic behavior is one of the selective pressures proposed to explain DPM and trait expression evolution. For example, a reduction in adult aggressiveness has been proposed as the causative explanation in several of the hypotheses explaining DPM such as the “Status Signaling,” “Conspecific Crypsis,” or “Female Mimicry” hypotheses (Senar 2006; Hawkins et al. 2012). However, if traits differ in the aggressive response they produce in conspecifics, similar differences in the degree of maturation between traits should be expected. The traits triggering higher conspecific aggressiveness are expected to be those showing higher delayed maturation (Karubian et al. 2009). Different traits can elicit differential conspecific aggressive responses if they are directed at different receivers (e.g., males vs. females, Andersson et al.

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2002), when differing in their relative signaling importance (Candolin 2003) or when varying in their conspicuousness (Chaine and Lyon 2008). For instance, those traits working as badges of status are expected to elicit more aggressive responses in the receivers than those without such social function (Senar 2006). Similarly, within traits signaling status, there may be differences in the elicited aggressiveness if traits differ in their relative importance (Mateos and Carranza 1997; Bókony et al. 2006; Chaine and Lyon 2008; Chaine et al. 2011). In all cases, if different traits elicit differential aggressiveness, a variation in their degree and timing of maturation is expected.

Although the most likely factor promoting delayed maturation in young males is intrasexual aggressiveness (Conover et al. 2000; Karubian et al. 2008), female behavior can also modulate the acquisition of adult phenotype. Several benefits in terms of breeding success, such as an increase in access to females, have been thought to be associated with DPM (Greene et al. 2000). In addition, although largely neglected, female aggressiveness could also be a potential factor underlying the degree of adult resemblance in young males (Vergara and Fargallo 2007). Females are aggressive toward both sexes when competing for resources, such as territories or food, and toward the same sex when competing for mates (e.g., Sandell and Smith 1997; Smith and Sandell 1998; Mugeot et al. 2001). In many cases, immature males may closely resemble females, which in the absence of other phenotypic or behavioral traits may promote sexual deception (Hakkarainen et al. 1993). Indeed, the Female Mimicry Hypothesis posits that by resembling females, young males can deceive adult males into believing that they are females allowing them to establish a breeding territory in an area already occupied (Rohwer et al. 1980; Slagsvold and Saetre 1991; Hakkarainen et al. 1993). However, by resembling females, young males may increase the risk of being attacked by adult females (Vergara and Fargallo 2007). This effect has rarely been explored when studying the evolution of male DPM.

The common kestrel *Falco tinnunculus* (hereafter kestrel) is a dichromatic raptor species in which males still showing DPM can breed during their first year of life. The immature appearance of 1-year-old male kestrels decreases agonistic encounters with other males, likely increasing survival or access to females and thus favoring the evolution of DPM (Hakkarainen et al. 1993; Vergara and Fargallo 2007; Vergara et al. 2007). However, DPM in 1-year-old males is not uniformly distributed throughout the plumage. A proportion of 1-year-old males show adult appearance in some feather patches at the beginning of the breeding season while maintaining juvenile or almost adult-like resemblance in others (Village 1990; Vergara and Fargallo 2007, see below). Here, we tested in this species the hypothesis that differences in the aggressiveness elicited by different male traits explain differences in their maturation. First, we measured the variation in the degree of maturation (i.e., adult resemblance) of 4 secondary sexual traits: rump, head, back, and tail feathers in 1-year-old breeding males captured over 8 years. Second, we experimentally presented 1-year-old male decoys showing these mature characters in an alternate way and measured adult male and female aggressive responses to the decoy in order to evaluate the capacity of each trait to trigger adult aggressiveness. We predicted that plumage maturation in 1-year-old breeding males should be balanced between the benefits of mating and the costs of being attacked by both adult males and females.

## MATERIALS AND METHODS

### Study species

The common kestrel is a medium-sized raptor species that exhibits marked sexual dimorphism in body size (females 20%

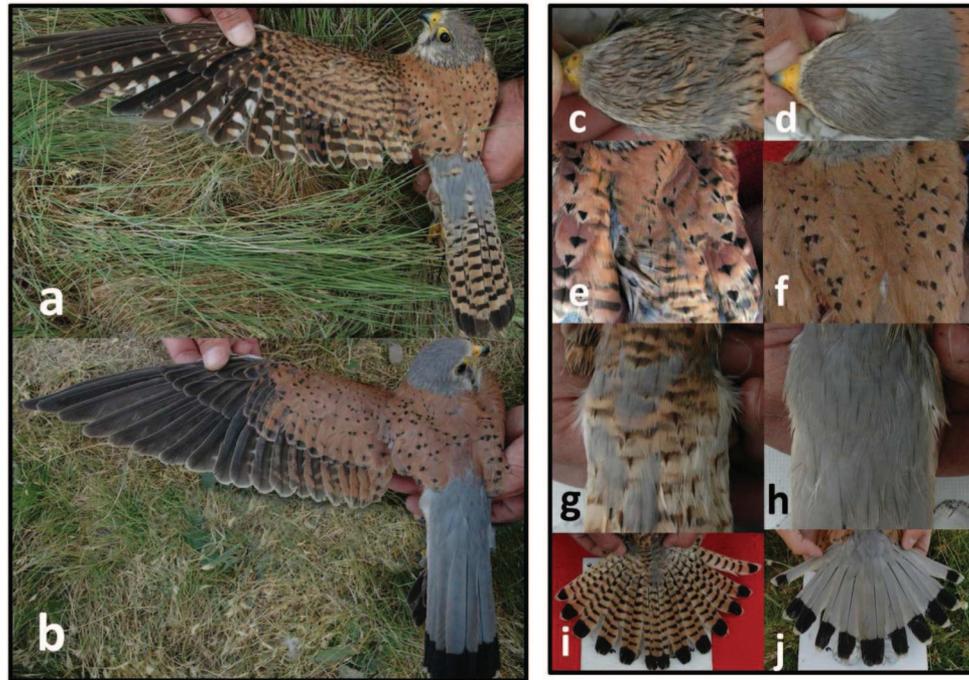
heavier than males) and plumage coloration (Village 1990; Palokangas et al. 1994). Adult males are reddish-brown, with black spots, rather than bars, on the back and the upper sides of the wings. Head, rump (considered as rump and upper-tail coverts), and tail vary from brown-gray to completely gray and are mainly unbarred (Figure 1). Females are brown on the head, back, and upper sides of the wings, with black bars, rather than spots. Female plumage coloration of the rump and tail varies from brown to completely gray, but is almost always black-barred (Vergara et al. 2009). Fledgling males are, in general, like adult females, with brown on the head and back and showing a varying brown-gray coloration in the rump and tail (Fargallo et al. 2007; Vergara and Fargallo 2008; Figure 1). The molt of young males differs greatly between traits over their first year of life showing clear adult resemblance in some traits (i.e., molted), but not in others at the beginning of the breeding season and even during their first winter (Village 1990; Vergara and Fargallo 2007).

### Adult resemblance: molt pattern and coloration

We conducted the study in the Campo Azávaro region (central Spain), an extensive homogenous grassland where trees or high bushes are scarce and most kestrels breed in nest boxes (Fargallo et al. 2009). In the study population, 13% (range 7–27%) of breeding males are 1-year old (Vergara and Fargallo 2007). During the breeding seasons of 2004–2011, we captured thirty-two 1-year-old breeding males during the chick-rearing period by using nest-box traps. We measured the degree of adult resemblance in 4 different feather patches: head, rump, back, and tail (Figure 1). The degree of adult resemblance in rump, tail, and back was considered as the percentage of molted feathers in each trait by direct observation in the field (see Vergara and Fargallo 2007). Coloration in the rump, back, and tail strongly differs between adults and unmolted 1-year-old males, thus making this measure an adequate index of the degree of resemblance of 1-year-old males to adult males (i.e.,  $\geq 2$ -year old). In the case of head plumage, although some individuals produce brown feathers during the molt, gray head coloration of the first molt in 1-year-old males is correlated with percentage of molt ( $r_s = 0.41$ ,  $P = 0.020$ ,  $N = 32$ ). Thus, we considered the proportion of gray coloration (0% = completely brown and 100% = completely gray) by direct observation in the field as an index of adult resemblance.

### Experimental design

During the prelaying period (March–May) of 2007, we presented natural 1-year-old male decoys to assess aggressiveness of breeding kestrels to different male traits. We presented 1 decoy per trial on a 1-m-tall stick at a distance of 10 m from the nests, always in the same location at each nest (Vergara and Fargallo 2007). The decoy (unmolted 1-year-old male) was presented under 4 different treatments: (1) “Rump treatment,” 1-year-old male with adult male rump plumage, (2) “Back treatment,” 1-year-old male with adult male back plumage, (3) “Head treatment,” 1-year-old male with adult male head plumage, and (4) “Tail treatment,” 1-year-old male with adult male tail plumage. To avoid bias in the date of presentation and confounding effects due to habituation to decoys, we randomly selected the treatment to be presented at each observation, but avoided repeated treatments. We used 5 different 1-year-old unmolted male decoys among which 2 adult rumps, 2 adult backs, 2 adult heads, and 2 adult tails were randomly interchanged. Adult rumps, backs, heads, and tails were entirely extracted from dead adult males and fixed onto the decoys with pins or glue. Decoys were always



**Figure 1**  
Plumage differences between 1-year-old (a, c, e, g, i) and adult (b, d, f, h, j) male breeding kestrels in the full plumage (a, b), head (c, d), back (e, f), rump (g, h), and tail (i, j).

situated with their rumps directed toward the targeted nest and were presented when we observed at least 1 individual of the pair close to the nest. If breeders did not return 1 h after the presentation of the decoy, we removed it. When kestrels returned to the nest or within 50 m of the decoys, we recorded their agonistic behavior over a 10-min period. There were no visual obstacles between nests and decoys. To measure the intensity of this behavior we categorized it into 5 levels as has been done in previous work (Vergara et al. 2007): “0” = no response (the individual was present, but it did not attack), “1” = attacks without contact (until kestrel flies less than 2 m from the decoy), “2” = only 1 attack with contact, “3” = more than 1 attack with contact, and “4” = perching on and pecking of the decoy. Decoys were repaired and placed in the same posture for each observation. When both partners were present, we estimated the aggressive behavior for both sexes separately. We used binoculars (8×30) and a telescope (20–30×60) to perform observations. The minimum time interval between 2 consecutive observations of the same nest was 3 days. We considered the fertile stage to begin 8 days before laying and the prefertile stage greater than 8 days before laying (range = 9–46 days before laying, see Vergara et al. 2007 for more details about this categorization). Observations were carried out between 7:00 AM and 1:00 PM by a single observer in a car situated greater than 200 m from the nests to avoid disturbance. We monitored nests every 2 days to detect laying date (day of the first egg laid in the nest). Once females laid the first egg, we stopped decoy experiments.

#### Ethical note

Kestrels used for decoys (i.e., taxidermic mounts) were provided by Grupo de Recuperación de Fauna Autóctona (GREFA, Madrid) and Centro de Recuperación de Especies Protegidas de Buitrago de Lozoya (Madrid), under the license 10/211297 (Consejería Medio Ambiente y Ordenación del Territorio, Comunidad de Madrid). No individual was sacrificed to carry out the present study as

all kestrels used for decoys had died previously (e.g., due to collision with traffic or power lines). Fieldwork and animal manipulation were carried out following ethical procedures as described in Guidelines for the Use of Animals in Research (The Association for the Study of Animal Behaviour). The permission to carry out the fieldwork, including animal captures, was given by the Consejería de Medio Ambiente de la Junta de Castilla y León (project: CGL2004-04479/BOS).

#### Statistical analyses

Differences in the degree of DPM between the 4 study characters were analyzed with nonparametric procedures, as molt percentages and head coloration did not show normal distributions. To analyze the results of the decoy presentation experiment we used Generalized Linear Mixed Models (Proc GLIMMIX procedure) in SAS 9.2. Agonistic breeder behavior (log link function, Poisson distribution) was the response variable and treatment (4 levels: rump, back, head, or tail) and sex (males vs. females) were included as fixed factors. Post hoc comparisons were used to analyze differences between treatments. Breeding stage (fertile vs. prefertile) and partner presence (present vs. not present) were also included as fixed factors in models to control for potential differences in aggressiveness (Vergara et al. 2007). We did not repeat the same treatment in each individual although more than 1 observation per individual was carried out in some cases. Thus, to avoid pseudoreplication in the models and because both males and females from the same nest were challenged with the decoy, we included the nest in the model as a random factor. No differences in aggressive behavior were found between individual decoys or plumages (rumps, heads, backs, and tails) used for observations (GLIMMIX all  $P > 0.11$ ), for which reason we did not differentiate between decoys or plumages in the models. No differences between treatments were found in laying date and date of decoy presentation (GLIMMIX all  $P > 0.42$ ).

## RESULTS

### Differences in DPM between traits

One-year-old males showed different states of maturation in head, back, rump, and tail plumages within and between individuals, with the difference being significant in all within-individual paired comparisons among head, rump, back, and tail (Table 1, Figure 2). The back showed the most advanced maturation followed by rump and head, with the tail showing the lowest degree of adult resemblance (Figure 2). DPM of rump and back was positively correlated (Spearman correlation,  $r_s = 0.46$ ,  $df = 30$ ,  $P = 0.007$ ). Back and tail ( $r_s = -0.50$ ,  $df = 30$ ,  $P = 0.003$ ) and rump and tail ( $r_s = -0.35$ ,  $df = 30$ ,  $P = 0.043$ ), however, were negatively correlated. No significant correlations were observed between DPM of head and rump ( $r_s = 0.11$ ,  $df = 30$ ,  $P = 0.544$ ), head and back ( $r_s = 0.13$ ,  $df = 30$ ,  $P = 0.470$ ), or head and tail ( $r_s = -0.11$ ,  $df = 30$ ,  $P = 0.544$ ).

### Experimental treatment

In total, we made 51 male observations from 29 nests and 60 female observations from 31 nests. In 41 observations both members of the pair were present at the same time. We carried out 1.7 (range 1–3) and 1.9 (range 1–3) observations per male and female, respectively, and 3.6 observations per nest (range 1–6). The intensity of attacks did not differ between males and females (GLIMMIX,  $F_{1,73} = 0.01$ ,  $P = 0.912$ ) or between treatments considering both sexes together (GLIMMIX,  $F_{3,73} = 1.25$ ,  $P = 0.296$ ). However, the model showed a significant treatment  $\times$  sex interaction (GLIMMIX,  $F_{3,73} = 6.08$ ,  $P = 0.009$ , Figure 3). The intensity of attacks performed by males differed among treatments, although not significantly (GLIMMIX,  $F_{3,19} = 1.89$ ,  $P = 0.166$ ). Post hoc comparisons showed that breeding males attacked young male decoys showing adult rumps, heads, and tails more aggressively than decoys with adult backs, although only the comparison between rump and back was significant (Table S1, Supplementary material). The comparison between head and rump was close to the significant level, but the other comparisons were not significant (Table S1, Supplementary material, Figure 3). Females also showed differences between treatments in the intensity of attacks against decoys (GLIMMIX,  $F_{3,26} = 5.03$ ,  $P = 0.007$ , Figure 3). Breeding females attacked decoys with adult backs and tails more aggressively compared with decoys with adult rumps or heads, with all the comparisons being significant (Table S1, Supplementary material, see Figure 3). No differences were observed between rump and head and between tail

and back treatments (Table S1, Supplementary material). Post hoc comparisons also showed that attacks of females to back and tail treatments were significantly more aggressive than those attacks by males on the same traits (Table S1, Supplementary material). On the other hand, males attacked the head treatment significantly more aggressively than females (Table S1, Supplementary material). Also males tended, but not significantly so, to attack the rump treatment more aggressively than females (Table S1, Supplementary material). Breeding period (GLIMMIX,  $F_{1,71} = 0.00$ ,  $P = 0.995$ ) or partner presence (GLIMMIX,  $F_{1,72} = 0.74$ ,  $P = 0.392$ ) did not significantly affect the intensity of attacks in breeding kestrels. The intensity of attacks was not related within pairs (GLIMMIX,  $F_{1,19} = 0.20$ ,  $P = 0.66$ ).

## DISCUSSION

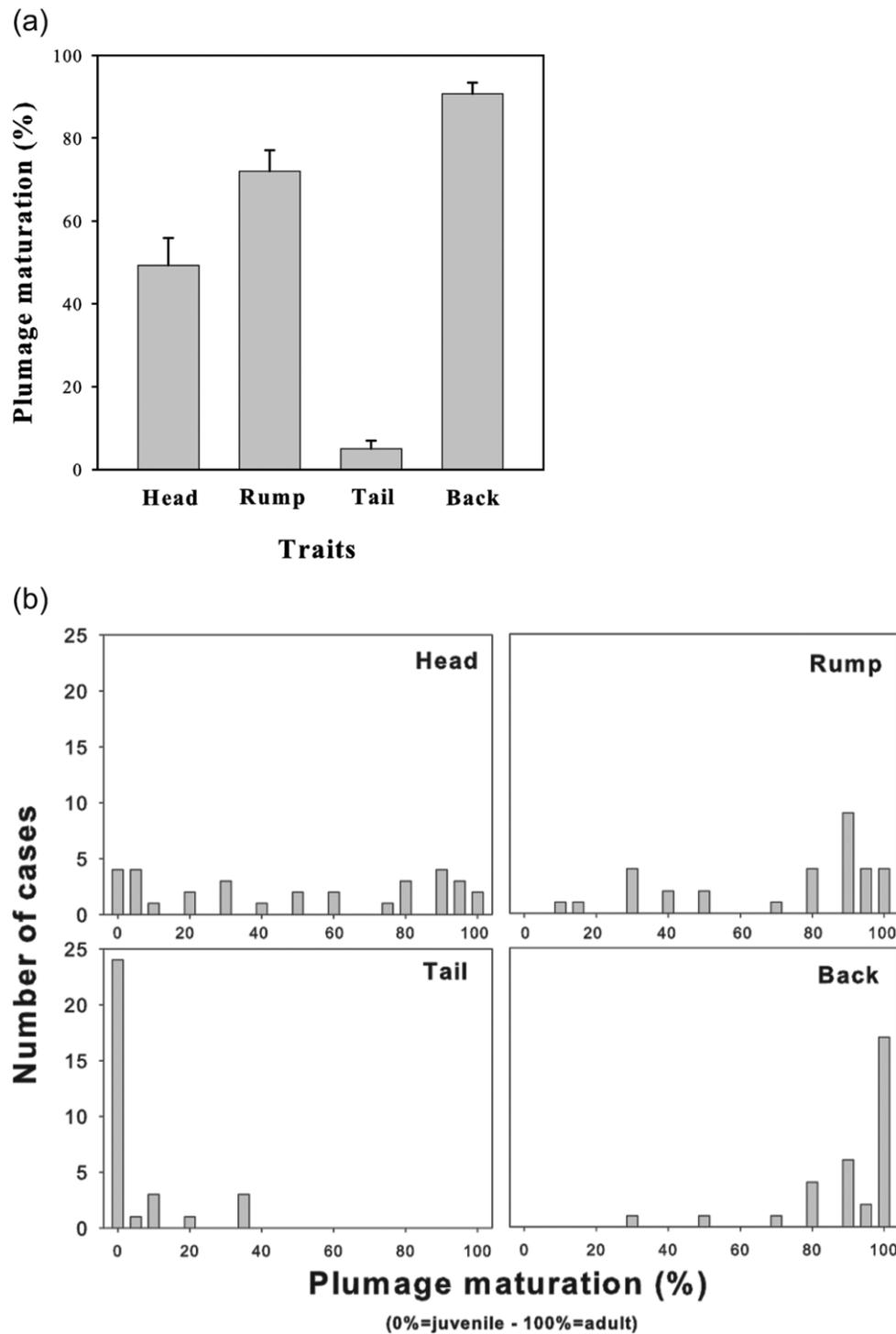
There is a general consensus that juvenile phenotypes diminish the aggressiveness of adults toward young individuals in several taxa such as fishes (Fricke 1980; Mahon 1994), reptiles (Martin and Forsman 1999), and particularly in birds (Senar 2006). However, this juvenile appearance is often restricted to a limited number of traits, mostly to those involved in social and sexual signaling functions. By separately exposing adult mature characters in young male decoys it is possible to investigate the relative effect that each character has on the aggressive behavior of adults. Our study showed that the overall intensity of aggressive responses toward the decoys was similar between males and females and that the 4 study characters are subject to a similar degree of conspecific aggressiveness. However, elicited aggressiveness was dependent on the specific adult trait exhibited in combination with the sex of the attacker. Specifically, our study indicates that adult head and rump triggered the highest intensity of male aggressive behavior followed by tail, with adult back plumage eliciting the lowest aggressive response from breeding males. However, differences were only significant between head and back and marginally significant between rump and back. In the case of females, back and tail provoked the highest intensity of aggressive responses and they were less aggressive against decoys with molted heads and rumps.

Sex deception is a widespread phenomenon in nature (Rohwer et al. 1980; Rios-Cardenas et al. 2010), and indeed, is one of the hypotheses proposed to explain DPM in birds (Senar 2006), including the study species (Hakkarainen et al. 1993). It has been shown that kestrels are not able to recognize the sex of unmolted 1-year-old males (Hakkarainen et al. 1993; Vergara and Fargallo 2007). As in other bird species (e.g., Mougeot et al. 2001; Sternalski et al. 2012), conspecific agonistic behavior in kestrels is higher in intrasexual than in intersexual contests (Wiklund and Village 1992; Vergara and Fargallo 2007; Vergara et al. 2007). It is thus feasible to deduce that the higher levels of aggressiveness of females to tail and back treatments are due to the fact that females identify the decoy as a female individual, thus increasing the level of intraspecific competition. Grayness in the rump and tail of adult female kestrels is 70% and 36% on average, respectively (Vergara et al. 2009). Although these 2 traits as well as the backs of females are generally black-barred, there is great variation from strongly to weakly marked black bands (personal observation). Thus, it is possible that in the absence of behavioral displays, the only character unequivocally identifying the male sex is the gray coloration of the head. If we consider within-treatment sexual differences in aggressive behavior as an index of sex recognition (Vergara and Fargallo 2007), our results suggest that the decoys showing adult male-like plumage on the

Table 1

Results of the Wilcoxon matched pairs tests analyzing the differential degree of adult resemblance between the 4 study traits in 1-year-old breeding males

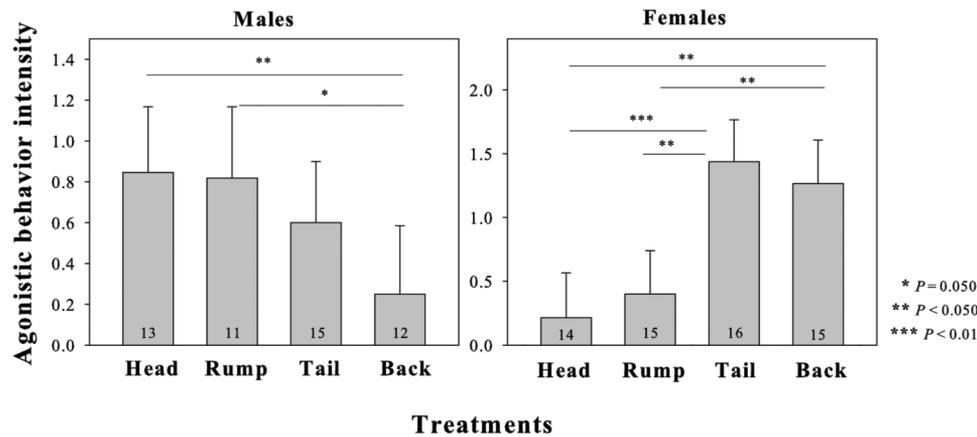
Traits	N	Z	P
Head versus back	32	4.16	<0.001
Head versus rump	32	2.72	<0.001
Head versus tail	32	4.27	<0.001
Back versus head	32	4.16	<0.001
Back versus rump	32	3.73	<0.001
Back versus tail	32	4.91	<0.001
Rump versus head	32	2.72	<0.001
Rump versus back	32	3.73	<0.001
Rump versus tail	32	4.84	<0.001
Tail versus head	32	4.27	<0.001
Tail versus back	32	4.91	<0.001
Tail versus rump	32	4.84	<0.001



**Figure 2** Differences in the average (a) and number of cases (b) of plumage maturation (0% = immature and 100% = adult) between traits in 1-year-old males ( $N = 32$ ). Plumage maturation in back, rump, and tail was measured as the percentage of feathers molted to adult plumage. Bars and whiskers in (a) are mean and standard error of mean (SEM), respectively.

tail and back were mainly considered females and those decoys expressing adult male appearance in the head and rump were considered males because significant (or nearly significant in the case of the head treatment) between-sex differences were observed in these characters. The role of intrasexual aggressiveness in females is poorly understood, but it has been suggested as an important selection force shaping the evolution of their behavioral and phenotypic

traits (Midamegbe et al. 2011). In particular, recent studies have shown that female aggressiveness can drive the evolution of female coloration because it may indicate individual quality of the bearer (Midamegbe et al. 2011). Gray coloration in the rump and tail of female kestrels is indicative of age and quality (Village 1990; Vergara et al. 2009). Nestling females very rarely show gray in their tails (4.9% of individuals, see Vergara et al. 2009), and these feathers are very rarely molted



**Figure 3** Male (left) and female (right) agonistic behavior intensity against 1-year-old male decoys under different treatments. Bars and whiskers are mean and SEM, respectively. Sample sizes per treatment are given on bars. Lines indicate significant pairwise comparisons between treatments.

before the autumn of their second year of life (Village 1990). Therefore, breeding females could perceive decoys in the rump and tail treatments as high-quality females. If so, their territorial intrusion could be interpreted by females as a potential risk of mate or nest site loss.

Adults and young individuals often differ in their expression of secondary sexual traits, with those displayed by adults usually of higher "quality" (e.g., brighter, bigger, etc.) (e.g., Török et al. 2003). However, such age differences are often only apparent in some traits, but not in others (Vergara and Fargallo 2007; Nakawaga and Burke 2008; Karubian et al. 2009). An optimal phenotype for young males at the time of reproduction would be one allowing them to obtain a mate while reducing adult male and female aggression. In support of this idea, Karubian et al. (2009) showed that in the red-backed fairywren *Maturus melanocephalus* (a species showing DPM), young males invest in individual traits differentially, with the investment being lower in those traits working as a badge of status than in those working in other signaling contexts (Karubian et al. 2009). The differential cost, in terms of aggressive interactions with dominant males, associated with the expression of each trait is the most likely explanation for such differences in trait expression (Karubian et al. 2009). Similarly, the differentially heightened importance of intra- or intersexual competition processes has been suggested to explain the absence of age differences in badge size but not in mask size in the house sparrow *Passer domesticus* (Nakawaga and Burke 2008). Our results indicate that molting only tail or back plumage is a risky strategy for 1-year-old male kestrels because by resembling females they increase the risk of being attacked by females and decrease the probability of mating. This can explain why these phenotypes are not found in 1-year-old male kestrels during the breeding season. On the other hand, by completely molting the head feathers (and probably also the rump feathers) 1-year-old males face a higher risk of being attacked by adult males. Back plumage coloration of males has been found to be positively correlated with body condition of females (Vergara and Fargallo 2011); that is, females of better condition prefer to mate with males with better back coloration, even when they are young (Palokangas et al. 1994). Females may require more than 1 trait to correctly evaluate mate quality, sex, or age (Candolin 2003). Previous findings in the kestrel support this use of multiple cues in female mate choice (Palokangas et al. 1994; Zampiga et al. 2008a, 2008b; Vergara and Fargallo 2011). First, or juvenal plumage is pale and weak, clearly showing the effects of abrasion 9–10 months after fledging during the

breeding season in the case of kestrels (Village 1990; personal observation). Therefore, by showing renewed plumage of better quality at that time 1-year-old males may increase mating options without provoking adult aggressive encounters if combined with gray feathers (adult male plumage) on the head and rump. This phenotype was observed on average in our population. Back plumage was the character showing the highest average maturation per individual (91%), followed by rump (72%), head (49%), and finally tail (5.0%). These differences become more obvious when comparing the frequency of individuals showing complete adult appearance in the character (i.e., 100% of feathers molted). In these cases, 17 of 32 individuals showed complete adult resemblance on the back, but this frequency was lower for the other traits: only 2, 4, and none of the 32 captured 1-year-old males showed 100% adult appearance on the head, rump, and tail, respectively.

Interestingly, a similar trait-specific molt pattern and differential adult resemblance between characters have been described in 1-year-old males of the closely related species, the lesser kestrel *Falco naumanni*. Similar to the study species, 1-year-old lesser kestrel males during their first breeding season retain their juvenile appearance in the tail, as the molt of this trait is uncommon during the first year of life (Ortego 2010). Further studies in other species and taxa can clarify whether the pattern of differential maturation between traits observed in a wide variety of species can also be explained in this way.

Differences in the state of maturation among different characters could also be determined in part by the different capacity of the birds to conceal these traits. It is well known that some sexual ornaments are displayed during intra- or intersexual encounters in many fish (e.g., skin coloration see Leclercq et al. 2010) and bird species (e.g., combs in Tetraonids: Holder and Montgomerie 1993; Rintamäki et al. 2000). By hiding signaling traits, males may avoid unnecessary fights (Rintamäki et al. 2000; Chaine and Lyon 2008). This behavior could explain why the state of maturation is significantly higher in rump than in head plumage, 2 characters triggering similar aggressive response in adult males. One-year-old males can hide their rumps by covering them with wings in the presence of adult males, thus avoiding their aggressive response. Similar context-dependent rump concealment has been proposed in other birds (Chaine and Lyon 2008). As decoys are static, all traits were similarly detected by breeders, and thus, elicited similar aggressiveness. However, such aggressive behaviors may differ in wild

individuals because of the concealment of the rump, but not of the other traits. If so, a lower degree of delayed maturation (i.e., higher adult resemblance) would be expected in the rump as compared with those traits that cannot be concealed (e.g., tail). Interestingly, among the traits that elicited highly aggressive responses from males (i.e., head and rump), rump was the trait that significantly showed the most advanced maturation.

Another idea suggested to explain DPM is that young males are unable to achieve mature plumages because of the energetic cost of feather molt (molt constraint hypothesis, Rohwer 1986; Moreno and Soler 2011). Such energetic constraints would similarly explain delays in the acquisition of full adult appearance in other morphological and behavioral traits (e.g., Cucco and Malacarne 2000). However, the degree of plumage maturation observed in the young male kestrels in our population did not support this prediction because a large trait more costly to produce in terms of feather production (back) was found to show a higher degree of maturation than 2 smaller traits (head and rump).

### The cost of gray traits

Although DPM in young male kestrels in our population corresponds on average to the phenotype predicted by the results of sexual and social contexts, there is great variation among individuals, especially in the state of maturation of head and rump plumages. Previous findings suggested that male and female kestrels with grayer rumps or tails are those of better quality (Fargallo et al. 2007; Vergara and Fargallo 2008, 2011; Vergara et al. 2009, 2010; Parejo et al. 2011). Our study agrees with these previous findings but also supports the idea that gray showiness imposes social costs in kestrels (Fargallo et al. 2007). We demonstrated that by displaying gray colorations, young males increased the risk of eliciting higher levels of aggression from adult males and females. Thus, only high-quality individuals or those in prime condition that can afford such costs are able to express gray traits. This may also explain the phenotype in both male and female yearling kestrels. Young males and females show less grayness in their tails and rumps than adult males, but also less than that in adult females. Mean tail grayness (i.e., the percentage of gray covering the entire surface of the trait) in young males and females is 15% and 3%, respectively, whereas in adult females it is 36% (Fargallo JA, Martínez-Padilla J, Vergara P, unpublished data; Vergara et al. 2009). These phenotypic age and sex differences can be understood if grayness signals status in a hierarchical dominance system (Senar 2006). Expressing some gray coloration benefits the fledglings by indicating quality within the same age-class (Vergara and Fargallo 2008), but expressing too much gray coloration could compromise those benefits by increasing adult aggressive responses. This idea should be specifically tested in the future. Interestingly, gray coloration is also age-dependent in other kestrel species such as the lesser and the American kestrel *Falco sparverius* (Cramp and Simmons 1980; Smallwood 1989; Ortego 2010). Furthermore, the extent of gray coloration in the wing (i.e., patch size) is an indicator of male quality in lesser kestrels (Aparicio and Cordero 2001), thus supporting the likely role of gray coloration in mediating sexual and social conflicts.

In conclusion, the present study suggests that conspecific aggressiveness is a likely framework to explain differences in the degree of maturation among different traits signaling sex and quality. Our results also suggest that not only adult male but also adult female aggressive behavior can modulate young male phenotype in a sexually dichromatic species by influencing differences in timing of maturation in different traits.

### SUPPLEMENTARY MATERIAL

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

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