

Inter-annual variation and information content of melanin-based coloration in female Eurasian kestrels

PABLO VERGARA^{1*}, JUAN A. FARGALLO¹, JESÚS MARTÍNEZ-PADILLA² and JESÚS A. LEMUS¹

¹*Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales-CSIC, José Gutiérrez Abascal 2, 28006, Madrid, Spain*

²*Aberdeen Centre for Environmental Sustainability (ACES), University of Aberdeen & The Macaulay Institute, School of Biological Sciences, Tillydrone Avenue, Aberdeen AB24 2TZ, UK*

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Competition for resources (e.g. mates or food) is the main evolutionary explanation for conspicuous ornaments in males, although this idea is not generalized in females. Whether or not the expression of melanin coloration is dependent on environmental conditions remains controversial. We studied three different melanin-based female traits in the Eurasian kestrel *Falco tinnunculus*, a sexually dichromatic species, for a period of 10 years: grey coloration in rump and tail and the width of the black subterminal tail band. We analysed these traits for within-individual variation among years, as well as their possible link with indices of quality, such as age, body size, and breeding performance. The results obtained demonstrate that female melanin-based coloration increased from yearlings to adults. In addition, the expression of female rump coloration covaried positively with the environmental conditions in the previous year (i.e. measured as clutch size at population level). Finally, we found a positive correlation between grey rump coloration and clutch size. These results suggest that the expression of rump coloration, a melanin-based trait, is environmentally constrained, and we propose that this character could function as an indicator of individual quality in female Eurasian kestrels. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 97, 781–790.

ADDITIONAL KEYWORDS: age – breeding success – eumelanin – phenotypic plasticity – pheomelanin – sexual selection – signalling theory.

INTRODUCTION

Male–male competition for mates or other resources, such as food, is the main evolutionary explanation for the development of conspicuous ornaments in males or sexual dichromatism (Darwin, 1871; Andersson, 1994). Although less well understood, ecological differences can also promote sexual divergences in the development of traits (Andersson, 1994; Amundsen & Pärn, 2006). Ornaments in both sexes may have evolved to signal individual quality; thus, a higher expression of the signal could provide a more efficient procurement of resources by influencing male mating decisions (Cornwallis & Birkhead, 2007a) or avoiding

agonistic encounters (Griggio *et al.*, 2005). This mechanism would work if producing and maintaining signals are costly activities (Zahavi, 1975). This idea has been traditionally studied in males and framed in a sexual selection (Hill, 2006) or social context (Senar, 2006).

However, the origin and significance of producing and maintaining costly ornaments in adult females remains widely unknown (Amundsen, 2000; Amundsen & Pärn, 2006). Several studies have suggested that conspicuousness of female ornaments could be the result of a genetic correlation between sexes (Lande, 1980; Muma & Weatherhead, 1989; Hill, 1993; Potti, 1993; Cuervo, de Lope & Møller, 1996; Tella *et al.*, 1997). This hypothesis has been experimentally confirmed in the Barn Owl *Tyto alba* (Roulin

*Corresponding author. E-mail: vergara@mncn.csic.es

et al., 2001a). Other studies have proposed that female coloration may be involved in sex or species recognition (Mayr, 1963; Burley, 1981) and it has also been suggested to proximately reflect sex hormone levels (Kimball & Ligon, 1999). Finally, competition for resources, such as mates or food, has been proposed, mainly in the past decade, to be the most important force promoting the development of conspicuous ornaments in females (Amundsen & Pärn, 2006).

Recently, it has been shown that female signalling is positively associated with age and/or experience (Potti, 1993; Cuervo *et al.*, 1996; Tella *et al.*, 1997; Komdeur *et al.*, 2005; Bortolotti *et al.*, 2006; Hegyi *et al.*, 2008b), survival prospects (Hörak *et al.*, 2001; Roulin & Altwegg, 2007), body size (Amundsen, Forsgren & Hansen, 1997), body condition (Velando, Lessels & Marquez, 2001; Bortolotti *et al.*, 2006), breeding performance and/or immunocompetence (Hanssen, Folstad & Erikstad, 2006; Polo & Veiga, 2006; Potti & Merino, 1996; Morales *et al.*, 2007; Doutrelant *et al.*, 2008), predator avoidance (Avilés, Solís & Valencia, 2008), within-clutch variation in yolk androgens (Gil, Lacroix & Potti, 2006), egg size (Szigeti *et al.*, 2007), offspring quality (Roulin *et al.*, 2000, 2001b, 2003; Siefferman & Hill, 2005), or nestling feeding rate (Jawor *et al.*, 2004), all supporting the idea that female ornamentation may indicate individual quality. In addition, observational and experimental studies have reported assortative mating with respect to individual ornamentation (Roulin, 1999; Griggio *et al.*, 2005; Bortolotti *et al.*, 2006; Hegyi *et al.*, 2007b, but see also Bortolotti *et al.*, 2008) and that more ornamented females are more frequently courted (Torres & Velando, 2005), are selected as primary females in polygynous mating systems (Hegyi *et al.*, 2007a), and obtain more and higher quality sperm from high-quality males during the mating process (Cornwallis & Birkhead, 2007a, 2007b) than less conspicuous females. Furthermore, Hegyi *et al.* (2008a) have also shown that female agonistic behaviour against territorial intruders covaried positively with the expression of the intruder female trait, suggesting a role of female ornamentation in territorial competition. The current evidence suggests that selection has acted on male and female traits quite independently, implying no conflict between the genetic correlation and functional explanations of female ornamentation (Kraaijeveld, Kraaijeveld-Smit & Komdeur, 2007). However, it is necessary to carry out more studies regarding the meaning of female traits to fully understand how selection pressures and ecological constraints influence female ornamentation (Amundsen & Pärn, 2006).

Melanins are one of the most important groups of pigments involved in male and female coloration in

animals (Ito & Wakamatsu, 2003), including birds (McGraw, 2006). These pigments are synthesized by individuals in a metabolic process called melanogenesis, which is dependent on the essential amino acid tyrosine (Murphy, 1994) and are responsible for reddish-brown, brown, black, or grey coloration of bird feathers. The effect of ecological constraints (i.e. food) on melanin-dependent traits is unclear (Griffith, Parker & Olson, 2006; McGraw, 2008). Several studies have shown that environmental factors have no effect on melanin-based plumages (Roulin, Richner & Ducrest, 1998; Roulin & Dijkstra, 2003; Bize *et al.*, 2006), suggesting that their expression is under strong genetic control and is not condition-dependent (Majerus, 1998; Roulin, 2004, 2007). However, taking into account that numerous studies have found that melanin-based traits in birds are correlated with individual quality (Jawor & Breitwisch, 2003), the idea that melanin-based traits may develop independently of the individual condition at a given time is in apparent disagreement with the idea about the honesty of signalling. This phenomenon remains an unresolved question (Roulin, 2004), although Ducrest, Keller & Roulin (2008) have proposed recently that pleiotropic effects of the *Pomc* gene, which regulates melanin-synthesis, might explain why melanin-based coloration is linked to individual quality. On the other hand, an effect of environmental factors (Veiga & Puerta, 1996; Griffith, Owens & Burke, 1999; Fitze & Richner, 2002; Poston *et al.*, 2005; Fargallo *et al.*, 2007a; McGraw, 2007) on melanin-dependent ornamentation has also been described (Hill, 2006), providing another explanation for the link between individual quality and melanin-based traits. Nevertheless, a recent review of these topics (Griffith *et al.*, 2006) demonstrated that we do not currently have enough data to make any general conclusions regarding the condition-dependence or the level of genetic determination of melanin-based traits; but see also McGraw (2008).

In the present study, we first studied the within-individual variation among years in adult female melanin-based coloration in the Eurasian kestrel *Falco tinnunculus* for a period of 10 years. We studied one trait present in both males and females (the black subterminal tail band), and also two traits expressed by females and nestlings but not by adult males (grey extension in black-barred tail and rump, see Material and methods). In the Eurasian kestrel, grey tail feathers are considered to be ornaments, whose expression in adults is associated with fitness components (Palokangas *et al.*, 1994). Furthermore, grey rump coloration in nestling males has been found to reflect environmental growth conditions (Fargallo *et al.*, 2007a, b) and individual competitive capacity to

obtain food resources (Vergara & Fargallo, 2008). In addition, in the American kestrel *Falco sparverius*, the subterminal tail band is a character apparently used in female mate choice (Wiehn *et al.*, 1997). First, we explored the condition-dependence of the three studied female melanin-based traits. If melanogenesis is in part dependent on environmental conditions, we predict that the expression of the studied traits will be associated with environmental conditions of the previous year, being higher after good years (i.e. high food availability). Second, we explored whether melanin-based traits in female kestrels are correlated with individual features potentially reflecting quality. We studied whether these melanin-based female traits can indicate quality in terms of age, body size, and breeding performance. If melanin-dependent traits indicate quality of the female, the expression of the characters should be positively correlated with these variables.

MATERIAL AND METHODS

STUDY SPECIES

The Eurasian kestrel (hereafter kestrel) exhibits marked sexual dimorphism in body size (females are 20% heavier than males) and plumage coloration (Village, 1990; Palokangas *et al.*, 1994). Females are brown on the head, back, and upper sides of the wings with black bars. Both males and females show a wide black subterminal band on their tails. They also exhibit great variation in plumage coloration on the rump and tail, from brown to completely grey, but always black barred. Adult males are reddish-brown, with black spots on the back and on the upper sides of the wings. The head, rump, upper tail-coverts, and tail are grey and always unbarred. The rump and upper tail-coverts (hereafter rump) in male adults are plain grey, whereas rumps in adult females, 1-year-old females, and fledglings (males and females) show brown, grey, or both colorations, but are always barred. The eumelanin/pheomelanin pigment ratio is 7.1, 2.9, and 0.1 for grey, black, and brown kestrel coloration, respectively (Fargallo *et al.*, 2007a). The moult of body feathers in juveniles (from August to April) is highly variable: although some birds change all their body feathers before they are 1 year old, others replace very few (Vergara & Fargallo, 2007). In our population, 15.2% of breeding males (5-year data, $N = 138$ breeding attempts) and 28.2% (13-year data, $N = 368$ breeding attempts) of breeding females are 1 year old.

STUDY AREA AND GENERAL PROCEDURES

The study was conducted during the breeding seasons of 1997–1998, and 2001 to 2008, in the Campo

Azálvaro region (central Spain), where most kestrels breed in nest boxes (Fargallo *et al.*, 2001). Nests were monitored to detect laying date (day of the first egg laid in the nest) and to record clutch size (range 3–7). Breeding females were captured during incubation and chick-rearing periods and body measurements (tarsus, wing and tail lengths, and body mass) were recorded. Binary age, 1-year-old or adults (range 2–9), was determined by ring codes of individuals marked as nestlings or yearlings (identified by plumage). All chicks and all breeding females were ringed from 1995 and 1996, respectively, onward.

FEMALE TRAITS

We estimated the percentage of grey with respect to brown covering the whole rump and tail (0% = completely black-barred brown and 100% = completely black-barred grey) of female individuals by direct observation in the field. Rump coloration (from 2002 to 2008) and tail coloration (from 2003 to 2008) were estimated by J.A.F. We estimated the repeatability of measurements in 21 individuals (Lessells & Boag, 1987). J.A.F. measured rump and tail coloration and the width of the black subterminal tail band (see below) in 21 dead individuals. J.A.F. measured these individuals again, 24 h later, although in a different order (i.e. randomly ordered in the second case) from the first measurement. Measurements of rump and tail coloration were highly repeatable (rump: $r = 0.90$, $F_{20,21} = 17.41$, $P < 0.001$; tail: $r = 0.94$, $F_{20,21} = 38.16$, $P < 0.001$, $N = 21$). To verify whether the data collected by direct observations were a reliable estimation of real kestrel grey coloration, from 2004 to 2006, we measured grey rump and tail coloration in 82 females by digitally photographing the rump (camera: Nikon D70, objective: 18–70 mm, AF-S Nikkor DX). We then imported the images into ImageJ, version 1.33 (US National Institutes of Health, USA; <http://rsb.info.nih.gov/ij/>) to determine the grey area (i.e. number of pixels) with respect to the whole rump and tail (0% = completely black-barred brown and 100% = completely grey). Measurements from the images were also repeatable (for procedures, see Fargallo *et al.*, 2007a, b). The proportion of grey coloration measured by direct observation in the field was closely correlated with that measured from the photographs for rump ($r_s = 0.84$, $P < 0.001$) and tail ($r_s = 0.90$, $P < 0.001$). In addition, in 1997 and 1998, and from 2001 to 2008, we measured the width of the black subterminal tail band (hereafter tail band) in the six tail feathers on the left side. Tail-band width was estimated as the mean value of these six feather measurements. This variable was highly repeatable ($r = 0.98$, $F_{20,21} = 131.35$, $P < 0.001$, $N = 21$). Rump moult status (i.e. percent-

age of moulted feathers) is not correlated with rump coloration either in 1-year-old ($P = 0.15$) or adult females ($P = 0.34$). In addition, all individuals have moulted tail feathers at the beginning of the breeding season. Thus, it is unlikely that moult status may confound the three studied female traits. Controlling by binary age [general linear mixed model (GLMM): $F_{1,71} = 53.86$, $P < 0.001$], grey rump and tail coloration were positively intercorrelated (GLMM: $F_{1,71} = 39.45$, $P < 0.001$, estimate = 0.41, $N = 216$). The interaction between tail coloration and binary age was not significant ($P = 0.46$). Controlling for binary age (GLMM: $F_{1,67} = 73.39$, $P < 0.001$), rump and tail coloration and their interactions with binary age were not correlated with tail band (all $P > 0.22$).

STATISTICAL ANALYSIS

GLMM in SAS statistical software (SAS 1989–1996 Institute Inc.) were conducted to analyse inter-annual coloration variation and the relationships between female traits and indices of quality. When variables did not show a normal distribution, residuals from these models were checked for normality. All of them showed a normal distribution (Kolmogorov–Smirnov test: all $P > 0.05$), for which the use of GLMMs was adequate. Degrees of freedom were calculated by the Satterthwaite approximation. First, we examined differences between yearlings and adult birds using the three studied traits as dependent variables, binary age as fixed factor, and individual and year as random factors (i.e. to avoid pseudo-replication; Hurlbert, 1984). Clutch size in the previous year at population level was also included as covariate to test whether previous environmental conditions influence the expression of the three studied traits. Relevant two-term interactions were also included in models. Second, we assessed the effect of age as well as environmental conditions in the previous year as within-individual change in the studied characters. We considered trait change as the difference in the expression of the three studied characters between two consecutive years (i.e. second year measurement minus first year measurement). Trait change was included as dependent variable, first year binary age as fixed factor, first year age-standardized trait and first year clutch size at population level as covariates, and female identity and year as random factors. Binary age-standardized female traits were calculated by subtracting the mean of each binary age trait (yearling or adults) from each individual trait value. Relevant two-term interactions were also tested. To confirm that within-individual variation in the studied traits was not a result of mea-

surement errors, we analysed whether the error in our measurements was lower than the within-individual variation among years. In all cases, the error in our measurements (as previously noted) was lower than the within-individual variation among years (measured in 17 adult individuals during two years randomly selected; analysis of variance: rump coloration, $F_{1,32} = 15.55$, $P > 0.001$; tail coloration, $F_{1,32} = 22.58$, $P > 0.001$, tail band, $F_{1,32} = 5.39$, $P = 0.026$). Finally, we examined whether body measurements, laying date, and clutch size (included as response variables) were correlated with binary age-standardized female traits (covariates). Binary age (fixed factor) and their interaction with age-standardized female traits were also included in models. Individual identity and year were included as random factors.

RESULTS

AGE, WITHIN-INDIVIDUAL VARIATION, AND PREDICTORS FROM THE PREVIOUS YEAR

Rump coloration was significantly explained by binary age (GLMM: $F_{1,84} = 170.63$, $P < 0.001$, $N = 241$) and clutch size at the population level in the previous year (GLMM: $F_{1,84} = 4.78$, $P = 0.031$, estimate = 40.29, SE = 18.4). Rump grey coloration was less expressed in 1-year-old females ($29.4 \pm 4.1\%$) than in adults ($70.5 \pm 3.8\%$) and, after poor quality years, females showed less grey in the rump. The rest of the variables and interactions were not significant (all $P > 0.1$). As a result of the low number of years measured, the clutch size of the previous years at the population level showed a bimodality distribution in this case. Another analysis using a binary categorization of this variable based on mean showed similar results (GLMM: clutch size in the previous year at population level, $F_{1,84} = 11.92$, $P < 0.001$; binary age $F_{1,84} = 170.92$, $P > 0.001$; Fig. 1). Tail grey coloration and tail band were similarly less expressed in 1-year-old females as in adults (GLMM: tail coloration, $F_{1,72} = 119.0$, $P < 0.001$, $N = 216$; 1-year-old = $2.6 \pm 2.6\%$, adults = $35.9 \pm 2.3\%$; tail band, $F_{1,101} = 203.81$, $P < 0.001$, 1-year-old = 17.2 ± 0.3 mm, adults = 21.0 ± 0.2 mm) but were not correlated to the rest of the studied variables (all $P > 0.1$). Only three out of 61 (4.9%) 1-year-old females showed grey in the tail, whereas 55 out of 67 (82.1%) showed some grey in the rump.

The three studied traits were not significantly repeatable within individuals between 1 and 2 years of age (all $P > 0.33$). However, the repeatability within adults (considering the first two consecutive adult measurements per individual) was large for the three studied characters (rump coloration, $F_{1,18} = 7.99$,

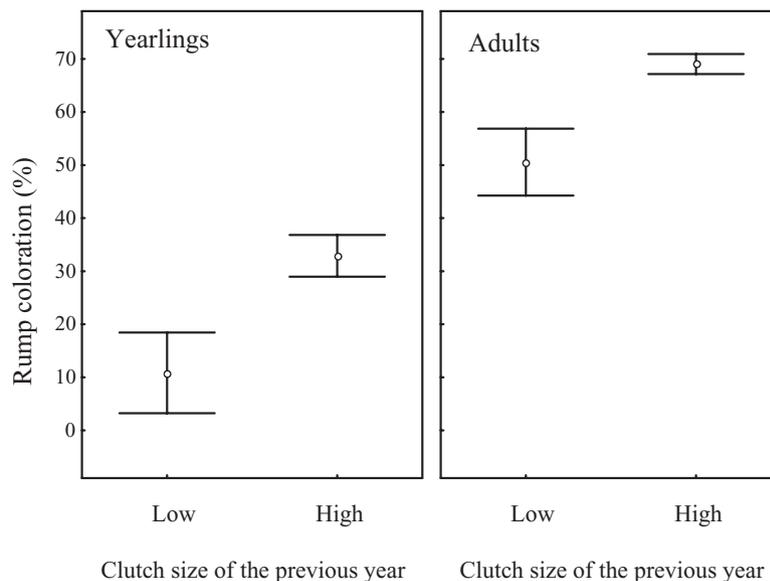


Figure 1. Correlation between rump coloration and clutch size in the previous year at population level in yearlings and adults. Data are the mean \pm SE.

$P < 0.001$, $r = 0.80$, $N = 19$; tail coloration, $F_{1,17} = 16.78$, $P < 0.001$, $r = 0.88$, $N = 18$; tail band, $F_{1,18} = 10.85$, $P < 0.001$, $r = 0.83$, $N = 19$). In addition, change in rump coloration was negatively explained by original binary age-standardized rump coloration (GLMM: $F_{1,32} = 74.21$, $P < 0.001$, estimate = -0.69 , SE = 0.08 , $N = 88$) and binary age (GLMM: $F_{1,32} = 51.16$, $P < 0.001$, 1-year-old = $44.57 \pm 4.5\%$; adults $13.0 \pm 2.6\%$). The rest of the studied variables and interactions were not significant (all $P > 0.21$). Individuals increased rump grey coloration after 1 year with low expression of this trait and yearlings showed higher values with respect to such changes (Fig. 2A). Changes in tail coloration was significantly explained by binary age (GLMM: $F_{1,27} = 31.39$, $P < 0.001$, 1-year-old = $30.2 \pm 4.8\%$; adults $2.6 \pm 2.6\%$, $N = 75$) and marginally and negatively by original binary age-standardized tail coloration (GLMM: $F_{1,27} = 3.09$, $P = 0.089$, estimate = -0.11 , SE = 0.06 ; Fig. 2B). The rest of the variables and interactions were not significant (all $P > 0.15$). Both yearlings and adults increased tail coloration after 1 year with low expression of this trait, but this increase was higher among yearlings, although not significantly so (Fig. 2B). Finally, change in tail band was significantly and negatively explained by first year binary age-standardized tail band (GLMM: $F_{1,32} = 21.35$, $P < 0.001$, estimate = -0.31 , SE = 0.06 , $N = 99$; Fig. 2C) and binary age of the first year (GLMM: $F_{1,32} = 68.09$, $P < 0.001$, 1-year-old = 3.32 ± 0.4 mm; adults 0.2 ± 0.2 mm). The rest of the variables and interactions were not significant (all $P > 0.18$).

BODY MEASUREMENTS AND BREEDING PERFORMANCE

Body mass at incubation and body mass during the rearing period were different between yearling and adults, adults being heavier in both cases (GLMM: body mass at incubation, $F_{1,101} = 14.74$, $P < 0.001$, $N = 320$, 1-year-old = $240.8 \text{ g} \pm 2.4$, adults = $248.9 \text{ g} \pm 2.1$; body mass during the rearing period, $F_{1,38} = 8.95$, $P = 0.005$, $N = 141$, 1-year-old = 212.2 ± 3.6 g, adults = 220.9 ± 3.1 g), but were not significantly explained by the three studied age-standardized traits or their interactions with binary age (all $P > 0.1$). We did not find differences in tarsus length between adults or yearlings (GLMM, $P = 0.94$) and this was not significantly explained by the three studied age-standardized traits and interactions (all $P > 0.1$). Tail length was positively correlated with age-standardized tail band (GLMM: $F_{1,99} = 12.89$, $P < 0.001$, estimate = 0.48 , SE = 0.13 , $N = 307$) and also was different between yearlings (165.6 ± 0.6 mm) and adults (170.9 ± 0.6 mm; GLMM: $F_{1,99} = 73.58$, $P < 0.001$). Rump and tail coloration and the studied interactions did not explain variance in tail length. Similarly, wing length was significantly longer in adults (254.7 ± 0.6 mm) than in yearlings (252.1 ± 0.7 mm; GLMM: $F_{1,96} = 24.60$, $P < 0.001$), and was positively correlated with age-standardized tail band (GLMM: $F_{1,96} = 6.40$, $P = 0.013$, estimate = 0.37 , SE = 0.14 , $N = 304$). The other two female age-standardized traits and their interactions with age did not explain any variation in wing length (all $P > 0.1$). Laying date was significantly explained by

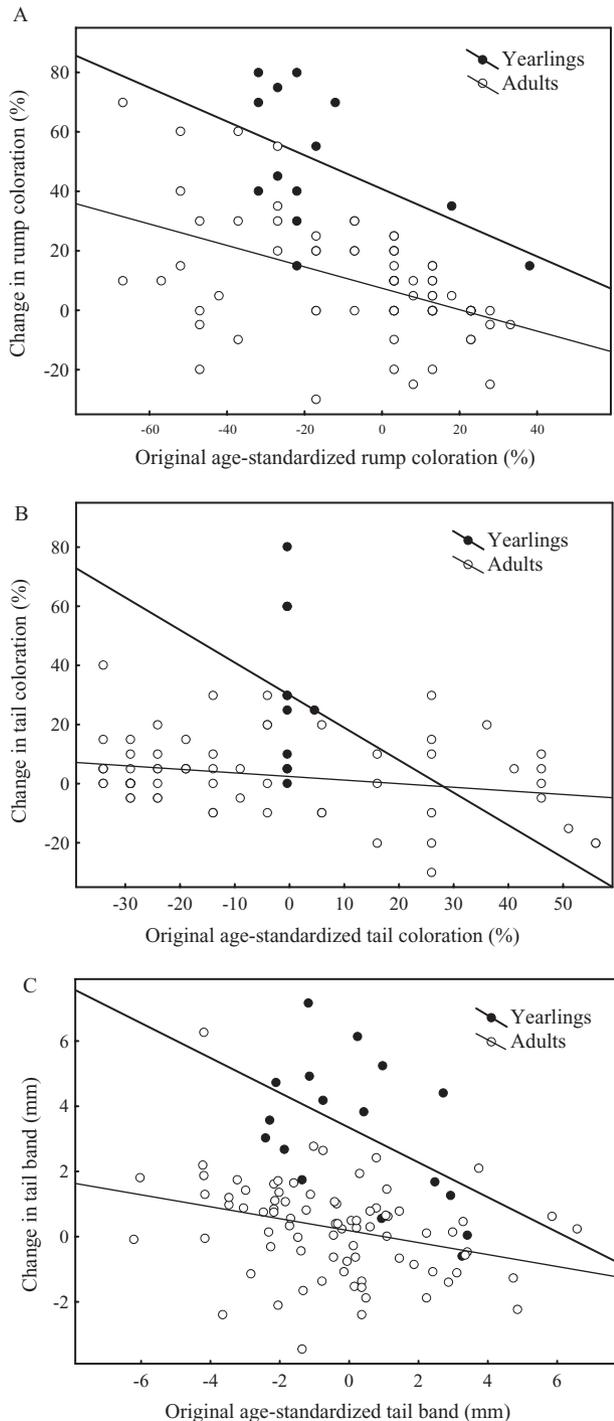


Figure 2. Correlation between change in three studied traits (A, rump coloration; B, tail coloration; C, tail band) during two consecutive years and the original age-standardized trait. Yearlings and adults are represented by different symbols.

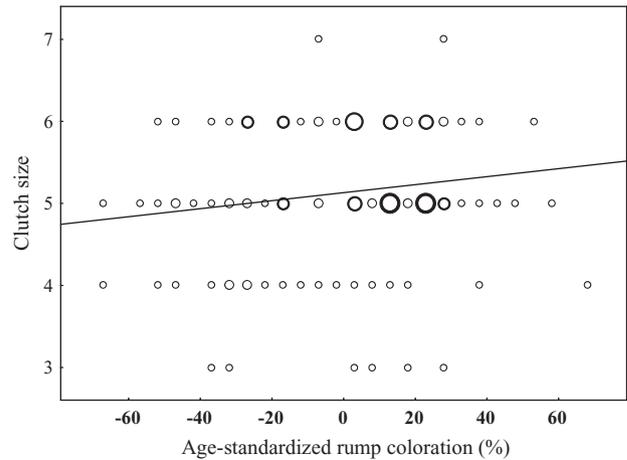


Figure 3. Correlation between clutch size and binary age-standardized rump coloration. The number of cases is represented by different sized symbols (smallest to largest, < 3, 3–6, 7–9, 10–12, 13–15, and > 15).

binary age (GLMM: $F_{1,114} = 18.81$, $P < 0.001$, $N = 336$), adults laying earlier (1-year-old = 37.9 ± 1.9 , adults = 32.7 ± 1.7 ; where 1 = 1 March), but not by the three studied female age-standardized traits or interactions (all $P > 0.1$). Finally, controlling for laying date (GLMM: $F_{1,81} = 51.01$, $P < 0.001$, estimate = -0.03 , $SE < 0.01$) and binary age (GLMM: $F_{1,81} = 27.11$, $P < 0.001$, 1-year-old = 4.8 ± 0.1 , adults = 5.3 ± 0.1), binary age-standardized grey rump coloration explained the variation in clutch size (GLMM: $F_{1,81} = 4.29$, $P = 0.041$, estimate = 0.01 , $SE < 0.01$, $N = 233$; Fig. 3). Females showing greyer rumps laid more eggs. The rest of the female characters and interactions were not significantly correlated with clutch size (all $P > 0.1$).

DISCUSSION

Whether or not the expression of melanic coloration is condition-dependent remains controversial (Griffith *et al.*, 2006). However, recent experimental studies in birds suggest that nutritional compounds, health status, and the level of intracellular antioxidants and hormones, such as testosterone and corticosterone, can mediate the expression of melanic coloration (Veiga & Puerta, 1996; Fitze & Richner, 2002; Poston *et al.*, 2005; Fargallo *et al.*, 2007a, b; McGraw, 2007; Galvan & Alonso-Alvarez, 2008; Roulin *et al.*, 2008; see also a recent review by McGraw, 2008). The present study showed that melanin-based coloration in females may indicate their individual quality (in terms of age and clutch size). Individual quality, however, can be a reflection of either genetic or environmental capacity to obtain resources. A starting point in disentangling both determinants is the

analysis of within-individual variation under different environmental circumstances.

INTER-ANNUAL VARIATION

The present study shows that the within-individual expression of rump coloration varied among years, and that this variation was correlated with environmental conditions in the previous year and was not a result of female age. This result suggests that melanin-based coloration in this species can be environmentally constrained (Fargallo *et al.*, 2007a, b) and that some extent of phenotypic plasticity exists in this trait. The observed correlation between rump grey coloration and clutch size in the previous year at a population level may indicate that, under favourable conditions (e.g. high food availability), females develop a higher expression of this melanin-based trait (for similar approaches, see Hegyi *et al.*, 2007c, 2008b). In the case of grey tail coloration and black tail band, we did not find a similar correlation. One possibility could be that rump coloration is more sensitive to environmental constraints than tail traits. The fact that there is no significant correlation between tail traits and environmental conditions of the previous year (i.e. measured as clutch size at the population level), or between change in the expression of the studied traits and environmental predictors, remains unresolved. However, the negative relationship between the original trait and the subsequent change in the character, also within adults, is in agreement with previous studies (Hegyi *et al.*, 2008b), and supports the idea that the development of the studied traits is dependent on the conditions of the previous year.

Nevertheless, there are few studies analysing within-individual variation in the expression of characters, but the results obtained have shown that environmentally determined traits varied within years in the same individual. This is the case of the carotenoid-based plumage trait in the male great tit *Parus major* (Senar & Quesada, 2006) as well as in the depigmented patch sizes in the female pied flycatcher *Ficedula hypoleuca* (Morales *et al.*, 2007) and in the collared flycatcher *Ficedula albicollis* [both in males (Griffith & Sheldon, 2001; Török, Hegyi & Garamszegi, 2003) and females (Hegyi *et al.*, 2008b)]. On the other hand, low within-individual variation has been observed in the expression of a highly genetically-influenced melanin-based plumage trait in great tit males (Senar & Quesada, 2006). The results obtained in the present study are in agreement with these previous studies and suggest that rump coloration in female kestrels is partially environmentally determined. However, the high level of repeatability shown for the three studied traits within adults also

indicates an important genetic regulation and/or early environmental influence on the expression of these characters.

TRAIT CHANGE AND AGE

We showed a higher expression of the studied traits in adults than in yearlings. This fact may be explained, on the one hand, by a change in the expression of characters with an increase in age or, on the other hand, by an association of the expression of the character with survival prospects (Gil, Cobb & Slater, 2001). In other words, individuals with greyer rumps and tails and larger tail bands may be more likely to survive than individuals with browner rumps and narrower tail bands. Analyses within individuals and between yearlings and adults showed that this difference between yearlings and adults is the result of a significant trait increase during the transition from yearling to adult plumage, rather than differences in survival prospects depending on the expression of the traits.

CLUTCH SIZE AND RUMP COLORATION

We have shown that a female trait, rump greyness, predicts breeding performance (measured as clutch size) in kestrels, similar to that occurring in other bird species (Roulin *et al.*, 2001a; Bókony & Liker, 2005; Hanssen *et al.*, 2006; Polo & Veiga, 2006; Morales *et al.*, 2007; Doutrelant *et al.*, 2008). Thus, greyness in females may indicate their intraspecific competitive capacity to obtain resources (e.g. food) before laying. In addition, the results obtained in the present study may be explained if rump coloration is a sexually selected trait. In kestrels, males are the main food provider to females and chicks during reproduction (Village, 1990; Fargallo *et al.*, 2002) and clutch sizes are good indicators of male quality in terms of food provisioning (Korpimäki & Wiehn, 1998; Fargallo *et al.*, 2002). It is expected that high-quality males select greyer females that consequently lay more eggs than browner ones. In any case, greyer females appear to have a higher capacity to obtain resources, including food and mates.

EUMELANOGENESIS VERSUS PHEOMELANOGENESIS

Grey colour in kestrels is produced at the expense of brown colour in feathers (Fargallo *et al.*, 2007a). Melanin coloration in the rump and tail of nestling male and adult female kestrels constitutes an interesting system that provides a visual or phenotypic indication of the predominant melanogenesis pathway (i.e. eumelanogenesis or pheomelanogenesis) occurring during feather production. Wolff (2003)

noted that pheomelanogenesis is the default biochemical pathway in the production of melanin pigments, which might imply that the production of eumelanin is more costly than pheomelanin. Accordingly, Jawor & Breitwisch (2003) proposed that, if pheomelanogenesis and eumelanogenesis are differentially costly, the expression of a melanin character could serve as an honest indicator of condition. In kestrels, the production of grey implies higher values in the ratio of eumelanin to pheomelanin than the production of black and brown coloration (Fargallo *et al.*, 2007a) and it is also linked with indices of individual quality (present study; Vergara & Fargallo, 2008). These facts are in agreement with the hypothesis proposed by Jawor & Breitwisch (2003), although future studies analysing the different costs of both melanin pigments may help to corroborate such idea.

In conclusion, in the present study, we have shown that the expression of a melanin-based trait, rump coloration, was correlated with environmental conditions in the previous year (i.e. measured as clutch size at the population level). This result suggests that this trait is in part environmentally determined. In addition, we have shown that the three studied female traits increased from 1-year-old birds to adults and we found a correlation between female grey rump coloration and clutch size. This means that melanin-based coloration in female kestrels could function as an indicator of quality (i.e. in terms of age and clutch size), and thus may be favoured in sexual and social selection (Senar, 2006). The results obtained in the present study suggest that competition for resources is involved in the acquisition of conspicuous coloration in females, similar to that occurring in males (Amundsen, 2000; Amundsen & Pärn, 2006), although future experimental studies should manipulate these characters to test these ideas.

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