

Moult speed constrains the expression of a carotenoid-based sexual ornament

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Abstract

We investigated the effect of moult speed on the expression of a sexually selected, carotenoid-based feather ornament in the rock sparrow (*Petronia petronia*). We experimentally accelerated the moult speed of a group of birds by exposing them to a rapidly decreasing photoperiod and compared the area and the spectral characteristics of their ornaments with those of control birds. Birds with accelerated moulting rate showed a smaller yellow patch with lower yellow reflectance compared to their slow-moulting counterparts. Considering that the time available for moulting is usually constrained between the end of the breeding season and migration or wintering, carotenoid feather ornaments, whose expression is mediated by moult speed, may convey long term information about an individual's condition, potentially encompassing the previous breeding season. Furthermore, the observed trade-off between moult speed and ornament expression may represent a previously unrecognized selective advantage for early breeding birds.

Introduction

Carotenoid pigmentation is one of the most frequent mechanisms for colouration of sexually selected ornaments, particularly in fish and birds (Goodwin, 1984; Olson & Owens, 1998), and has become a classical example of a condition-dependent display trait (e.g. Hill & Montgomerie, 1994; Horak *et al.*, 2000). Female preference for carotenoid ornaments seems to be widespread (e.g. Hill & McGraw, 2006), suggesting that the link between signal and condition may be maintained through some general mechanism. Two hypothesis have been put forward to explain how an honest association between carotenoid-based ornaments and condition can be maintained, starting from the observation that animals cannot synthesize carotenoids *de novo* but must obtain them through the diet (Goodwin, 1984; Brush, 1990). The 'carotenoid poor-environment' hypothesis suggests that, in environments in which the carotenoids

are limited, carotenoid-dependent sexual ornaments signal an individual's foraging ability, and hence, they can be used by females to assess male quality (Endler, 1980). The second, nonmutually exclusive hypothesis, focuses on the physiological function of carotenoids, which stimulate the immune system, prevent cancer, and protect against free radicals and oxidative damages (e.g. Diplock, 1991; Burri, 1997). Lozano (1994) suggested that, by choosing individual males with highly expressed carotenoid ornaments, females may not only choose males who are efficient in foraging and avoiding predators, but might also increase the likelihood that their mates, and consequently also their offspring, are healthy and better able to deal with future health problems. Females basing their mate choice on carotenoid-based ornaments would therefore obtain both indirect (e.g. Blount *et al.*, 2001; Evans *et al.*, 2004) and direct benefits, for example having a lower risk of getting pathogens from their mates (Blount *et al.*, 2003), or a greater likelihood that males will be able to provide adequate paternal care (e.g. Massaro *et al.*, 2003).

Many studies have been conducted on species in which carotenoid pigments are accumulated in body

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parts, such as beak, skin or wattles, from which carotenoids can be rapidly mobilized, if necessary (e.g. Faivre *et al.*, 2003). However, carotenoid signals in birds are often based on colour plumage, a fraction of carotenoids that is nonmovable and will reflect the carotenoid levels at the time of moulting. The expression of a carotenoid feather ornament is a joint outcome of four processes: (i) acquisition of carotenoids through diet (Hill & Montgomerie, 1994); (ii) structural modifications by biochemical transformation (Brush, 1990); (iii) deposition into feathers during plumage renewal (McGraw & Hill, 2001); (iv) seasonal variation through abrasion (Figuerola & Senar, 2005). Despite the fact that the moult is clearly a central process to the acquisition of a plumage, its role in the regulation of ornamental colouration has received little attention, possibly because moult is usually considered as a temporal buffer between more important biological events. Only few correlative studies considered the effect of feather growth rates on the expression of colour feather signals (Hill & Montgomerie, 1994; Senar *et al.*, 2003; Norris *et al.*, 2007), but, to the best of our knowledge, the effect of moult duration on signal expression has never been investigated experimentally. Indeed, timing, extent and rate of feather replacement can be highly regulated by birds, which adapt moult to season, geographical distribution and individual life-history (Helm & Gwinner, 2006). Delayed moult start has been found to negatively correlate with survival (Newton, 1966) and fat accumulation (Senar *et al.*, 1998), and positively with brood size (Bensch *et al.*, 1985; Siikamaki *et al.*, 1994), suggesting the existence of a trade-off between current reproduction and subsequent moult. A trade-off between moult speed and quality of carotenoid feather ornaments may mediate a selective advantage for early breeders and juveniles from early clutches (Svensson & Nilsson, 1997; Hemborg *et al.*, 2001). Indeed, in species in which the plumage is moulted at the end of the breeding season (Jenni & Winkler, 1994), early breeders and juveniles from early clutches have more time to moult before the arrival of the winter or the beginning of migration (Bojarinova *et al.*, 1999). Durations of adult complete moults and extensions of partial post-juvenile moults are clearly dependent on available time after reproduction (Jenni & Winkler, 1994). Birds usually cope with a delayed moult onset by increasing their moulting rate or by overlapping moult and migration (Norris *et al.*, 2004). However, increasing the moult rate is not costless, as it has been shown that shorter moult durations produce lower quality feathers (Dawson *et al.*, 2000; Serra, 2001). The effects of a delayed moult onset can therefore be mitigated by a higher moult speed, but at the expenses of plumage quality.

We investigated the potential trade-off between moult speed and the expression of a carotenoid sexually selected signals in rock sparrows (*Petronia petronia*). In

this species, both males and females have a carotenoid yellow throat patch, although in females the patch is, on average, smaller than in males (Pilastro *et al.*, 2003). The size of this yellow patch shows a large phenotypic variation, and it has been shown that: (i) patch size does not correlate with age (Pilastro *et al.*, 2003); (ii) early breeders of both sexes have a larger patch than late breeders (Pilastro *et al.*, 2003); (iii) patch size is sexually selected in both sexes (Griggio *et al.*, 2005, 2007); (iv) patch is a badge of status in males (Griggio *et al.*, 2007). We increased the speed of the post-breeding moult of a group of rock sparrows by rapidly decreasing the photoperiod and compared the size (area) and the spectral characteristics of the yellow patch with that of a group of individuals whose photoperiod decreased at a slower rate. We also measured the effect of moult speed on the size of the distal white spots on the rectrices (tail feathers). Males display their tail to females during courtship (Cramp & Perrins, 1994) and females prefer males with large white spots on the tail (M. Griggio, unpublished results), suggesting that they are sexually selected.

Material and methods

Housing condition

We used twenty-five rock sparrows (15 males and 10 females, all yearlings). They were caught in mist-nets near L'Aquila (42°23'N; 13°18'E), central Italy, between 6 and 8 August 2003. Birds were then moved to Ozzano Emilia BO (44°28'N; 11°30'E), housed in individual indoor cages (58 × 33 × 31 cm) and fed *ad libitum* with a commercial mixture of canary seeds and canary egg food; fresh apples were given twice a week. A multi vitamin complex was provided in tap water for 10 days every 3–4 months. Birds were preventively treated against cestoda (praziquantel), coccidia (sulphadimethoxine) and fungine (amfotericina B) infections twice a year. During the moult experiment, no cestoda or coccidia infections were identified by faecal analyses and no birds showed signs of ectoparasites.

Birds completed their first moult by November 2003 and did not breed in spring 2004. Birds were kept on natural light conditions until 25 June 2004, when two individuals were observed to commence moult. On this date, they were divided in two groups, housed in two neighbouring indoor rooms. Each group was exposed to two decreasing photoperiods. The 'slow-moulting' group (Treatment A: eight males and five females) was exposed to a 2 min day⁻¹ decrease, the 'fast-moulting' group (Treatment B: seven males and five females) to a 8 min day⁻¹ decrease. Each room was illuminated by eight white fluorescent tubes (36 W each). An incandescent lamp (400 W) with a starting rheostat was switched on for 30 min twice a day to simulate dawn and dusk from/to total darkness.

Morphometrics

We took standard measurements of flattened wing chord length and tail length to the nearest 1 mm, bill length from skull and tarsus length to the nearest 0.1 mm. Body mass was recorded to the nearest 0.1 g. These measurements were taken at three different stages: during the capture session (August 2003), at the end of the first autumnal complete moult (December 2003) and before the start of the experiment (June 2004).

Moult recording

From 25 June 2004 to the end of the moult (20 October in the fast-moulting group, 23 December in slow-moulting group), each bird was weighed and moult was checked every seven days (checking dates). Primary moult was recorded according to Ashmole (1962): old feathers were scored 0, new feathers 5 and growing ones from 1 to 4 depending on their stage of growth. We assumed as primary moult starting date the checking date before the first primary scoring ≥ 1 was found. Primaries were numbered from the innermost (P1) to the outermost long primary (P9). The vestigial tenth primary was excluded from analyses. Seven plumage areas were identified for body moult (cap, ear coverts, mantle, rump, flanks, breast and throat) and moult was scored for each plumage area as follows: 0 = all old feathers, 1 = moult start (1–30% growing or new feathers), 2 = about half feathers in moult (31–60%), 3 = approaching the end of moult (61–99%), 4 = moult finished (all feathers renewed).

Ornament size

The size of the yellow throat patch (yellow area) was measured by placing a strip of transparent acetate over the throat of birds, holding it on its back on a plane surface with the bill perpendicular to it, and drawing the contour of the yellow area. A detailed description of the throat patch measurements can be found in Pilastro *et al.* (2003) or Griggio *et al.* (2005).

The area of the white tail patches was measured with the same method, drawing the contour of the white area on a strip of transparent acetate placed on the flattened rectrices. Only the right side of the tail was considered (six feathers). Drawings were scanned using a Hp scanjet 2002 at 600 d.p.i. and areas calculated with UTHSCSA Image Tool software (<http://ddsdx.uthscsa.edu/dig/download.html>). A total area of white patches was then calculated by summing the areas of the six rectrices (total white area).

Spectrometry

At the end of the moult, we measured spectral reflectance (at ± 2 nm resolution) of the yellow throat patches

with an Ocean Optics S2000 Spectrometer (range 338–1024 nm; Ocean Optics, Dunedin, FL, USA). A fibre-optic measuring probe (Ocean Optics) was used to transfer the light from a halogen lamp (Ocean Optics LS-1) to the feathers and to pass the light reflected back to the spectrometer. The probe was held at 90° angle to the feather surface and ambient light was excluded with a black tube that held the probe tip at 3 mm distance from the surface. Five consecutive measurements were taken from the centre of the patch, lifting and replacing the probe each time, and averaged for each bird. Reflectance spectra were recorded with OOIBase32 software (Rev 2.21; Ocean Optics, Dunedin, FL, USA) in relation to a WS-2 white standard and to dark which were measured before each measurement session.

Reflectance spectra were restricted to wavelengths between 400 and 700 nm to calculate colour indices. We measured hue, which can be understood as the principal colour of the feather, chroma, representing the spectral purity of a colour, total reflectance (brightness) and yellow reflectance (reflectance between 550 and 625 nm), following the formulae proposed by Saks *et al.* (2003).

Statistical analyses

Univariate ANOVAS were carried out to model the effect of sex and treatment (factors) on biometric and morphological variables pre- and post-experiment. All variables were tested for homogeneity of variance and normality of distribution. Only the duration of the moult of the yellow patch feathers showed a significant violation of the assumption of the homogeneity of the variance, also after log transformation. Using ranks instead of the original variable, however, allowed to attain the homogeneity of the variance and gave substantially the same results as the original variable (data not shown). In the pre-treatment tests, the interaction between factors was not considered. Statistical analyses were carried out using SPSS ver. 13 (SPSS Inc. Chicago, IL, USA).

Results

Before the experiment, there were no significant differences between the two treatment groups in wing length (treatment: $F_{1,21} = 0.472$, $P = 0.50$, sex: $F_{1,21} = 26.92$, $P < 0.001$, interaction: $F_{1,23} = 1.81$, $P = 0.19$), body mass (treatment: $F_{1,21} = 0.25$, $P = 0.63$, sex: $F_{1,21} = 0.24$, $P = 0.63$, interaction: $F_{1,23} = 1.04$, $P = 0.32$), and yellow area (treatment: $F_{1,21} = 0.27$, $P = 0.61$, sex: $F_{1,21} = 1.43$, $P = 0.25$, interaction: $F_{1,23} = 1.09$, $P = 0.31$). Sexes differed only in wing length, males having on average 4.1 mm (4.3%) longer wings than females. Wing length, included as a covariate into the following models, was not significantly associated with any of the dependent variables considered below (data not shown).

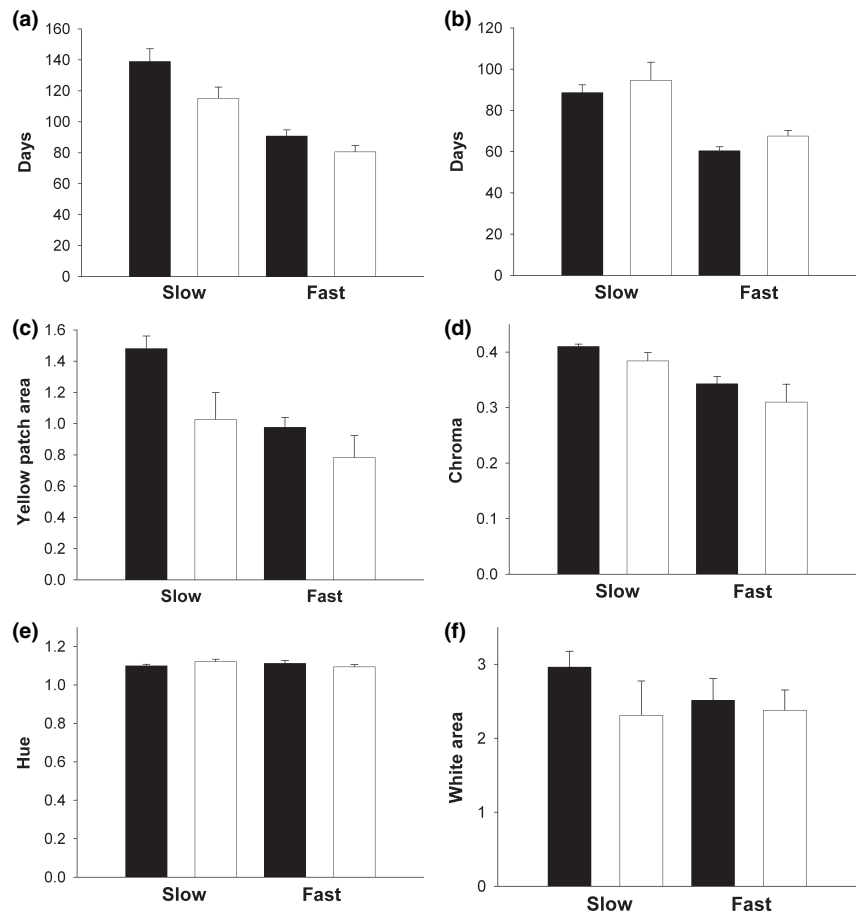


Fig. 1 Moult duration (days) of the primary feathers (a) and of the yellow feathers on the throat patch (b), and area (cm², c), chroma (d), and hue (e) of the yellow breast patch, and total area (cm²) of white spots on the rectrices (f) in the slow- (black bars = males, $n = 7$, empty bars = females, $n = 5$) and fast-mouling group (black bars = males, $n = 8$, empty bars = females, $n = 5$). Bars are mean \pm SE.

Birds exposed to a faster shortening of day-length had a shorter mean duration of primary moult (treatment: $F_{1,21} = 37.37$, $P < 0.001$, sex: $F_{1,21} = 6.33$, $P = 0.02$, interaction: $F_{1,23} = 1.00$, $P = 0.39$), and yellow patch feather moult (treatment: $F_{1,21} = 36.21$, $P < 0.001$, sex: $F_{1,21} = 2.05$, $P = 0.17$, interaction: $F_{1,23} = 0.02$, $P = 0.90$). Males had a longer primary moult, requiring 19 days more than females to complete the moult (Fig. 1a–b).

The yellow area was significantly larger in slow-mouling birds, with males having larger patches than females (treatment: $F_{1,21} = 11.36$, $P < 0.01$, sex: $F_{1,21} = 6.55$, $P = 0.02$, interaction: $F_{1,23} = 1.07$, $P = 0.31$). Yellow reflectance (treatment: $F_{1,21} = 18.45$, $P < 0.001$, sex: $F_{1,21} = 3.35$, $P = 0.08$, interaction: $F_{1,23} = 0.043$, $P = 0.84$) and chroma (treatment: $F_{1,21} = 17.99$, $P < 0.001$, sex: $F_{1,21} = 2.88$, $P = 0.11$, interaction: $F_{1,23} = 0.05$, $P = 0.82$) were significantly higher in the slow-mouling group, whereas no effect was detected on hue (treatment: $F_{1,21} = 0.37$, $P = 0.55$, sex: $F_{1,21} = 0.06$, $P = 0.82$, interaction: $F_{1,23} = 2.74$, $P = 0.11$) and brightness (treatment: $F_{1,21} = 0.61$, $P = 0.45$, sex: $F_{1,21} = 0.001$, $P = 0.99$, interaction: $F_{1,23} = 0.03$, $P = 0.87$) (Fig. 1c–d and Fig. 2).

The total white area was positively correlated to the yellow area ($R^2 = 0.465$, $F_{1,23} = 19.99$, $P < 0.001$). No differences were found when comparing the total white

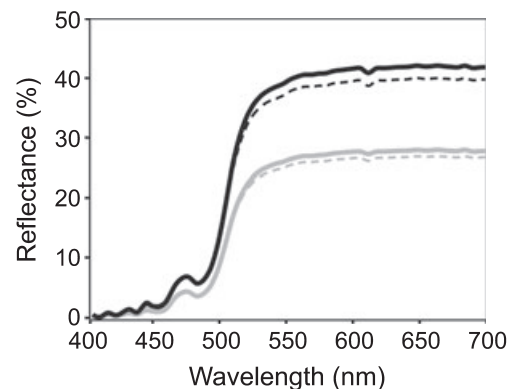


Fig. 2 Reflectance spectra of the yellow patch of slow-mouling males ($n = 8$, solid black line) and females ($n = 5$, dashed black line), fast-mouling males ($n = 7$, solid grey line) and females ($n = 5$, dashed grey line). Illumination and reflection were taken at 90° to the sample's surface.

area of the two treatments (treatment: $F_{1,23} = 0.38$, $P = 0.54$, sex: $F_{1,23} = 1.62$, $P = 0.28$, interaction: $F_{1,23} = 0.71$, $P = 0.41$). However, this result was largely influenced by a single outlier, a female of the slow-moulting group that had a very small white area (54.0 mm^2 ; mean white area = $267.6 \text{ mm}^2 \pm 63.6 \text{ SD}$). Removing this outlier from the analysis resulted in a nearly significant effect of moult speed on white area (treatment: $F_{1,22} = 3.75$, $P = 0.067$, sex: $F_{1,22} = 0.30$, $P = 0.59$, log transformation).

Discussion

Day-length change resulted in an increased moult speed in the individuals exposed to a more rapidly decreasing photoperiod, in agreement with previous experiments (e.g. Dawson *et al.*, 2000). Moult speed had a significant effect on the quality of the carotenoid sexually selected signal, determining a similar reduction of the yellow area and the yellow reflectance of the throat patch in both males and females, despite possible differences in plasma carotenoids among the sexes (Hill *et al.*, 1994). In particular, fast-moulting rock sparrows showed a decrease in total area, yellow reflectance and chroma of the throat patch, whereas hue and total brightness did not vary between treatments. This suggests that moult speed did not affect the perceived colour of feathers (i.e. in the wavelengths which contribute most to the total radiance, Hill & McGraw, 2006), but the saturation of the yellow colour. Considering that both treatments received the same diet, they shared similar levels and composition of carotenoid in the plasma. Carotenoids are passively incorporated into the growing feathers through lipid diffusion into feather follicles (Hill & McGraw, 2006 and references therein) and a slower feather growth rate may allow the deposition of a larger quantity of carotenoids into feather structure.

In the rock sparrow it has been shown that the size of the yellow patch is sexually selected (Griggio *et al.*, 2005, 2007). The effect of yellow chroma in inter- and intra-sexual interactions, however, has never been studied. In species in which the effect of ornament size and spectral properties have been studied simultaneously, it has been shown that both aspects of carotenoid feather signal quality are important in sexual selection. However, the relative importance of the two aspects can differ among species. For instance, in the red-collared widowbird (*Euplectes ardens*), collar redness seems to be more important than collar size to indicate male dominance status in male contest competition (Pryke *et al.*, 2002), whereas in the red-shouldered widowbird (*Euplectes axillaris*), territorial competition is more influenced by signal size (Pryke & Andersson, 2003). Interestingly, our results suggest that moult speed affects the two components of the carotenoid signal quality (yellow area and yellow reflectance) in the rock sparrow. Thus, moult speed may be an important determinant of the overall

quality of carotenoid feather signals, irrespective of the signal component which is more tightly linked to different fitness aspects (Badyaev *et al.*, 2001).

This study represents, to our knowledge, the first experimental evidence that the expression of carotenoid feather signals is constrained by moult duration. We demonstrated that moult speed significantly affected signal quality even in birds that were in good health and had unlimited access to dietary carotenoids. This effect might be relevant in natural conditions, where food and carotenoids are often unequally distributed resources and birds are exposed to diseases during moult. Correlative studies published so far did not find evidence of a trade-off between moult speed and quality of carotenoid signals. For example, male House Finches (*Carpodacus erythrinus*) with brighter plumage grew tail feathers at a faster rate than males with less colourful plumage (Hill & Montgomerie, 1994). Similarly, Senar *et al.* (2003) found that carotenoids but not melanins were positively correlated to growth-bar width in Great Tits (*Parus major*). Moult strategy has been found to influence a carotenoid signal in the American Redstart (*Setophaga ruticilla*) (Norris *et al.*, 2004), in which late reproducing males are forced to moult during their southward migration. This overlap between moult and migration results in poorer quality sexual signals, probably due to physiological stress during moult reducing carotenoid deposition in feathers (Hill, 2000). Although late-breeding males may be forced to moult at a faster rate (Norris *et al.*, 2004), a more recent study, based on the analysis of growth bars, failed to find any association between moult speed and chroma (Norris *et al.*, 2007). However, low-quality individuals may have both lower carotenoid availability (Olson & Owens, 1998) and lower moult speed (Hill & Montgomerie, 1994), resulting in a non significant or even a positive correlation between carotenoid signal and moult speed.

The effect of photoperiod change on moult speed was substantially similar between the sexes, although a slightly longer primary moult duration was observed in males of both treatments. Considering that the two sexes are similar in body mass and therefore may also have similar production of daily feather mass, this difference may be due to males having longer wings, assuming similar shedding rates (Dawson, 2003). Alternatively, males may have a slower growth rate of primary feathers than females and hence produce higher quality primary feather, because slower growth rates lead to higher quality feathers (Dawson *et al.*, 2000; Serra, 2001). Males might be more willing to invest in moult than in parental care (Bensch *et al.*, 1985; Siikamaki *et al.*, 1994).

In contrast to the carotenoid signal, the effect of moult duration on the area of the white spots of tail feathers was, at best, marginally significant (after removing an outlier), although their reflectance was not measured and we cannot exclude an effect of treatment on their spectral characteristics. This may be surprising,

considering that indirect evidence suggests that the white spots are sexually selected (males spread the tail, offering a good view of the white spots to females during courtship displays, Cramp & Perrins, 1994) and are likely to be involved in mate acquisition (M. Griggio, unpublished results). The smaller effect of moult duration observed on white spots (which are not obtained by pigment deposition during moult), as compared with that observed on yellow area and chroma of the throat patch, may indicate that these ornaments are less sensitive to condition than carotenoid feathers (McGraw & Hill, 2000; Jacot & Kempnaers, 2007; but see Griffith *et al.*, 2006). Further investigation, however, will be necessary to draw any conclusion about the relative effect of moult duration on melanin, carotenoids and UV signals.

In temperate regions moult is usually temporally constrained between the end of reproduction and migration or wintering (Holmgren & Hedenström, 1995). Thus, the quality of carotenoid feather ornaments, mediated by moult duration, may signal not only condition during (or immediately preceding) the moult, but an individual's performance during the whole previous breeding season (or the time of birth for first year birds), as high quality birds usually begin the reproduction early in the season and may have more time to complete their moult after breeding. Thus, the moult-constrained expression of carotenoid signals may represent an additional, long term cost of late breeding (e.g. O'Donald, 1972; Norris *et al.*, 2004), which results in poorer quality signals in the following breeding season in both parents and offspring (McGraw *et al.*, 2005). The difference in moult duration between the two experimental rock sparrow treatments was about 27 days for the yellow patch and 43 days for the primaries; a variation of the same magnitude as observed in natural conditions (e.g. Barnard, 1995; Hemborg, 1999). It is therefore likely that variation in moult speed contributes to the phenotypic variation in the expression of colour feather signals (see Hill, 2006 for a recent review). In addition to other nonmutually exclusive mechanisms, like intra-sexual competition (Griggio *et al.*, 2007), the observed link between moult duration and the quantity of carotenoids deposited into the feathers may explain how the honesty of small, apparently arbitrary signal (the area of the yellow patch is just 1.5 cm² on average) is maintained in the rock sparrow (Pilastro *et al.*, 2003) and other species with similar ornaments.

According to the predictions of the 'carotenoid poor-environment' hypothesis (Endler, 1980) and the 'immunomodulation hypothesis' (Lozano, 1994), carotenoid feather signals have been shown to be influenced by both dietary carotenoids and immune challenges (see Hill, 2006 for a review). It would be interesting to know what is the relative importance of moult speed, carotenoid availability and health condition in determining the expression of carotenoid feather signals, also considering that moult speed is a metabolically demanding process

and is likely to affect a bird's nutritional and health condition. Thus, fast moulting may indirectly amplify the effects of an immune challenge or dietary carotenoid scarcity on ornament expression. An experimental study manipulating moult speed and dietary carotenoids or providing birds with an immune challenge may be useful to investigate how these specific environmental factors affect the expression of carotenoid feather signals.

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