



## Condition and brightness of structural blue-green: motmot tail-racket brightness is related to speed of feather growth in males, but not in females

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Coloration plays an important role in sexual and social communication, and in many avian species both males and females maintain elaborate colours. Recent research has provided strong support for the hypothesis that elaborate female traits can be maintained by sexual or social selection; however, most research on female ornamentation has focused on pigment-based colours, and less is known about how structural colours are maintained. Both sexes of the turquoise-browed motmot (*Eumomota superciliosa*) have a blue-green racket-tipped tail, and it remains unknown if tail coloration serves as a sexual or social signal in one or both sexes. Here, we describe sexual dichromatism in the blue-green portion of the tail racket, and we test for a relationship between coloration and condition, as indicated by growth bars. Tail colour of both sexes has a similar spectral shape, and there is significant, although moderate, sexual dichromatism: males are brighter than females, and males have marginally greater blue-green saturation than females. The length of feather grown per day is positively related to overall feather brightness, but this relationship is only present in males. The relationship between male coloration and condition suggests that tail colour has the potential to convey information about individual quality during mate choice or contest competition. The lack of a similar relationship in females suggests that female tail colour does not convey the same condition-dependent information that we suggest may be reflected by male colour. Female tail colour may therefore reflect other aspects of condition, be involved in other (non-condition-dependent) forms of communication, or be expressed as a non-functional byproduct of genetic correlation between the sexes. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **106**, 673–681.

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In most taxa, males are ornamented and females are drab (Darwin, 1871, Amundsen, 2000a, b). However, some species exhibit mutual ornamentation, wherein both sexes maintain elaborate traits. In recent years, much research has focused on testing the adaptive value of ornamental traits when expressed in both sexes, and a number of hypotheses have been proposed to explain the evolution of these traits (for review, see Amundsen & Pärn, 2006). Many studies have supported the role of mutual sexual selection in maintaining male and female ornamentation, and these have demonstrated male preference for female traits in mammals (Domb & Pagel, 2001),

fish (Amundsen & Forsgren, 2001; South & Arnqvist, 2011), and birds (Jones & Hunter, 1993; Amundsen, Forsgren & Hansen, 1997; Hunt *et al.*, 1999; Torres & Velando, 2005). Furthermore, there is strong evidence that a positive relationship exists between female traits and phenotypic condition (Potti & Merino, 1996; Velando, Lessells & Márquez, 2001; Hanssen *et al.*, 2008) or genetic quality (Roulin *et al.*, 2000). Although the mutual sexual selection hypothesis has been widely supported and has thus gained wide acceptance (see Clutton-Brock, 2007; Kraaijeveld, Kraaijeveld-Smit & Komdeur, 2007), some studies have shown that males and females can use their ornaments in different signalling contexts, such that male traits are sexually selected, whereas female traits are maintained by different selective

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forces (i.e. for social signalling, Heinsohn, Legge & Endler, 2005; see also, LeBas, 2006; or pursuit-deterrent signalling, Murphy, 2006, 2007). In addition, some studies have failed to reveal any benefits associated with female ornamentation (Cuervo, de Lope & Møller, 1996; Muma & Weatherhead, 1989; Wolf *et al.*, 2004). Thus, it appears that under certain circumstances females can express elaborate traits for different adaptive reasons than those applicable to males, or can express male-like traits non-adaptively as a result of genetic correlation (Darwin, 1871; Lande, 1980). As such, it remains an open question as to whether females and males generally gain similar benefits from ornamentation, or whether females generally gain any benefits from expressing male-like traits.

Many studies on the signal value of ornamentation have focused on the role of coloration as a sexual or social signal (for a review, see Dale, 2006). The strong interest in bird coloration is driven, in part, by the fact that the diversity of feather colour is produced by various physiological mechanisms, thus allowing different colours to communicate different aspects of individual quality. Much research has focused on carotenoid-based colours, as the honesty-enforcing mechanisms underlying these condition-dependent signals are clear: carotenoids must be ingested, assimilated, and distributed (for a review, see Hill, 2006), and there is a trade-off between the use of carotenoids in ornamentation and their use in various physiological roles, which include serving as antioxidants and immunoenhancers (McGraw & Ardia, 2003). Although there has been much interest in mutually ornamented species with carotenoid-based traits (Jawor *et al.*, 2003; Griggio *et al.*, 2005; Nolan *et al.*, 2010; Martínez-Padilla *et al.*, 2011), fewer studies have investigated mutual ornamentation in species with structural-based plumage (Andersson, Örnborg & Andersson, 1998; Siefferman & Hill, 2005, Doutrelant *et al.*, 2008).

Although structural coloration is likely to entail some maintenance costs in terms of increased conspicuousness to predators (Fitzpatrick, 1998; but see Götmark, 1993), the costs associated with producing structural coloration are likely to be low (Prum, 2006). Structural coloration of (non-iridescent) feathers is created by the coherent scattering of light caused by alternating layers of ordered keratin and air pockets within a feather's spongy medullary layer (Prum *et al.*, 1999). The organization of these structures is governed by the self-assembling properties of macromolecules within the feather, and thus, feather microstructure is thought to be produced with few costs (Prum, 2006; Dufresne *et al.*, 2009). As such, we propose that in species in which only males are selected to maintain structurally coloured ornamenta-

tion, females may express male-like structural coloration non-adaptively. Because of the low production cost associated with structural coloration, we propose that selection against female structural coloration is unlikely to be sufficient to decouple the genetic correlation between the sexes. This is in contrast to what we would expect for carotenoid-based colours, where the high-costs of carotenoid ornamentation (Alonso-Alvarez *et al.*, 2004; Hórák *et al.*, 2006; Clotfelter, Ardia & McGraw, 2007) would select against female expression in the absence of a corresponding benefit.

Both sexes of the turquoise-browed motmot (*Eumomota superciliosa*) have a similarly long blue-green racket-tipped tail. Previous work on the species indicates that male tail length, but not female tail length, is associated with sexually selected benefits: males with longer tail wires (barbless region of the central tail feathers above the terminal feather rackets) have greater pairing success; pair with females that lay larger clutches; and have greater fledgling success (Murphy, 2007). Female tail length, however, is not related to measures of pairing or reproductive success, and there is no evidence for assortative mating for tail length (Murphy, 2008). Instead, the shorter female tail (the tail is 10% shorter in females, Murphy, 2007) is thought to represent the naturally selected optimum (for efficacy) for the wag-display used to deter pursuit (Murphy, 2006).

As a first step to investigate the potential signalling role of tail-racket coloration, we quantified the sexual dichromatism of the blue-green region of the tail rackets. We additionally investigated whether tail-racket colour has the potential to reflect phenotypic condition by testing for a relationship between growth-bar distance and coloration. Growth-bar distance represents the length of feather grown over a 24-h period, and indicates the energetic investment in feather growth during the molt (Grubb, 1989). Growth-bar distance can thus serve as an estimate of energy reserves and phenotypic condition during the molt (Grubb, 1991; Jenkins *et al.*, 2001). A positive relationship between feather growth rate and colour would be consistent with a hypothesis that coloration may function as a sexual or social signal in this species.

## MATERIAL AND METHODS

### STUDY SPECIES AND COLLECTION OF FEATHERS

*Eumomota superciliosa* is socially monogamous, and males and females invest heavily in parental care (Scott & Martin, 1983). The species breeds colonially in the Yucatan Peninsula. Colonies are often located in natural sinkholes, but they also readily breed in limestone quarries and other man-made structures (Scott & Martin, 1983). Both sexes have elongate tails

that comprise approximately 60% of the overall length of the bird, and the central two tail feathers terminate in large racket-shaped tips (Murphy, 2007). The species molts once per year in the non-breeding season (T.G. Murphy, pers. observ.).

We collected central tail feathers from 55 female and 69 male colonially breeding *E. superciliosa* near the Ria Lagartos Biosphere Reserve in northern Yucatan, Mexico (21°33'N, 88°05'W). Feathers were collected between April and May (during the pre-laying part of the breeding season) in 2000, 2001, and 2002. Each year, motmots were captured with mist nets placed around breeding colonies located within limestone quarries. As part of another study on the communication function of the tail, we collected ricketed central tail feathers by plucking or cutting central tail feathers. Additionally, we collected feathers that were dropped (fright molt) during capture. All feathers came from colour-banded individuals, and in cases where feather samples were collected from the same individual in multiple years, we used the feathers collected from the most recent year. Only adult birds were used in this study because the tail feathers of yearlings are highly worn and abraded (T.G. Murphy, pers. observ.). All birds were sexed by laparotomy because access to molecular sexing facilities was limited; we observed no adverse effects from using this procedure (procedure performed with anaesthetic, as specified under Cornell University's Institutional Animal Care and Use Committee IACUC protocol 99-23, and 99-23-02).

#### MEASUREMENT OF COLORATION

Reflectance measurements were taken on the blue-green portion of the tail rackets. One of us (T.T.P.) measured the colour with an Ocean Optics USB2000+ spectrometer and PX-2 pulsed xenon lamp (Ocean Optics Inc., Dunedin, FL, USA). Measurements were taken blind to the sex of the bird. Individual feathers were placed on black felt (a non-reflective substrate), and care was taken to allow the feather to lie naturally so that the distance between the barbs was consistent between feathers. This was necessary because the barbules are black, and when barbs are spread apart the overall feather appears less reflective (i.e. more black). The probe was mounted in a holder that excluded ambient light and fixed the probe tip approximately 7 mm from the feather surface. The use of the probe holder ensured that we consistently measured a surface area of approximately 5 mm in diameter. The probe was held at 90° to the feather, and visual inspection of spectral curves indicated that specular reflectance (which can occur at incident angles) did not distort our measures (i.e. no curves yielded abnormal brightness; maximum

reflectance values were consistently below 30%). The probe was placed on haphazardly chosen locations on the blue-green portion of the racket for a total of five spectral readings per feather. The probe was moved at least 2 mm between each measurement. We quantified reflectance ( $R$ ) as the proportion of light reflected off the feather, compared with a Spectralon white standard (Labsphere Inc., North Sutton, NH, USA), at 1-nm intervals across the avian visual range (320–700 nm). The white standard was kept in a housing that ensured that the probe tip did not touch the surface of the standard, thereby preventing the transfer of oil and dirt from the feather to the standard. The spectrometer was calibrated to the standard between the measurements of each feather.

Using mean reflectance curves, we calculated the five following colour metrics: mean brightness (mean  $R$  from 320 to 700 nm); UV hue (wavelength at  $R_{\max}$  between 320 and 400 nm); blue-green hue (wavelength at  $R_{\max}$  between 400 and 700 nm); UV saturation [(sum of  $R$  from 320 to 400 nm)/mean brightness]; and blue-green saturation [(sum of  $R$  from 475 to 575 nm)/mean brightness] using the program CLR 1.05 (Montgomerie, 2008; for further details see Montgomerie 2006: table 3.2). The two measures of hue (UV and blue-green hue) were highly correlated ( $r = 0.85$ ,  $P < 0.0001$ ; probably because of the phenomenon of double scattering, see Noh *et al.*, 2010), so we excluded UV hue from our analyses (correlations among other colour metrics were low:  $r < 0.50$ ). The repeatability (the intraclass correlation coefficient, following Lessells & Boag, 1987) of colour metrics was calculated on a subset of 30 feathers by measuring the same feather on different days. The repeatability was high for all colour metrics: mean brightness ( $F_{29,30} = 19.6$ ,  $P < 0.0001$ ,  $r = 0.90$ ); saturation (only calculated for UV saturation) ( $F_{29,30} = 40.3$ ,  $P < 0.0001$ ,  $r = 0.95$ ); and blue-green hue ( $F_{29,30} = 105.6$ ,  $P = 0.0001$ ,  $r = 0.98$ ).

#### MEASUREMENT OF GROWTH BARS

To assess the level of blue-green feather growth over a 24-h period, we measured growth bars following the methods of Grubb (1989, 1991). A single growth bar consists of two smaller bands (one light and one dark) oriented perpendicular to the feather shaft. The width of these two bands represents the length of feather produced over a 24 h period (Grubb, 1989). To measure the distance between growth bars, we affixed each feather racket to a piece of paper, which was then laid on a piece of foam. Using a small-gauge needle, we punched a hole in the paper at the junction of the dark portion of each growth bar with the adjoining lighter portion. This was repeated for between five and seven growth bars on each racket.

We measured the distance between the holes in the paper with digital calipers and calculated the mean growth-bar distance for each feather. When we collected both central tail feathers from an individual (41 females and 46 males), we computed a mean value for feather growth rate.

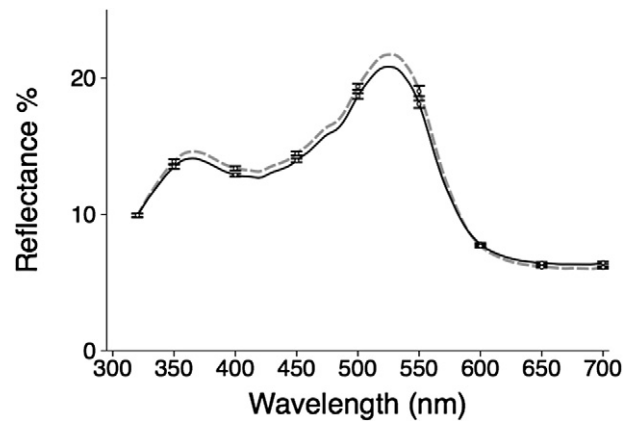
#### STATISTICAL ANALYSIS

To test whether the blue portion of the tail racket is sexually dichromatic, we separately tested each colour variable (as the dependent variable) using four separate general linear models (GLMs), with sex as the independent variable. Additionally, we used GLMs to test whether each colour variable (as the dependent variable) was predicted by mean growth-bar distance. Analyses were run with data for the sexes combined, and models included the interaction term 'sex\*mean growth-bar distance' to assess whether there was a sexual difference in the relationship between colour and feather growth rate. The year was included as a random effect in each model to account for annual variability in conditions that could affect feather growth or colour development across the population (e.g. climate or food abundance). Predictors were kept in the model when  $P < 0.10$ . The normality of residuals (from regression of mean growth-bar distance against each measures of coloration) were confirmed by visual inspection and with a Shapiro–Wilk  $W$ -test ( $P > 0.6$  in all tests). Statistics were performed with JMP 9.03 (SAS Institute Inc., Cary, NC, USA).

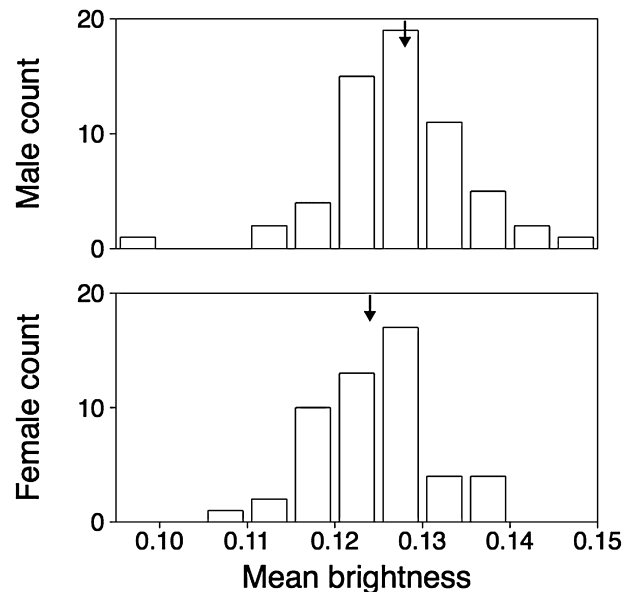
### RESULTS

#### SEXUAL DICHROMATISM

The overall shape of the colour spectra from the tail racket was similar for the sexes (Fig. 1), and male rackets were significantly brighter and more saturated in the blue-green than female rackets (brightness,  $F = 3.56_{3,120}$ , model  $P = 0.02$ ,  $R^2 = 0.09$ , year  $P = 0.07$ , sex  $P = 0.01$ ; blue-green saturation,  $F = 7.79_{3,120}$ , model  $P < 0.001$ ,  $R^2 = 0.16$ , year  $P = 0.007$ , sex  $P = 0.005$ ). However, the degree of sexual dichromatism was moderate to slight: on average, males are 8% brighter than females (means  $\pm$  SEs: males,  $0.13 \pm 0.01$ ; females,  $0.12 \pm 0.01$ ), and only 2% more saturated than females (means  $\pm$  SEs: males,  $0.47 \pm 0.01$ ; females,  $0.46 \pm 0.01$ ). The distribution of brightness was not similar for the sexes: males were normally distributed around the mean, with a large proportion of males having brightness above the mean, whereas among females, the distribution was skewed, with fewer individual females having very bright feathers (Fig. 2). No significant sexual dichromatism was found in the other



**Figure 1.** Mean spectral reflectance of blue-green tail feathers of male (dashed line) and female (solid line) *Eumomota superciliosa*. Standard error bars shown at 50-nm intervals.



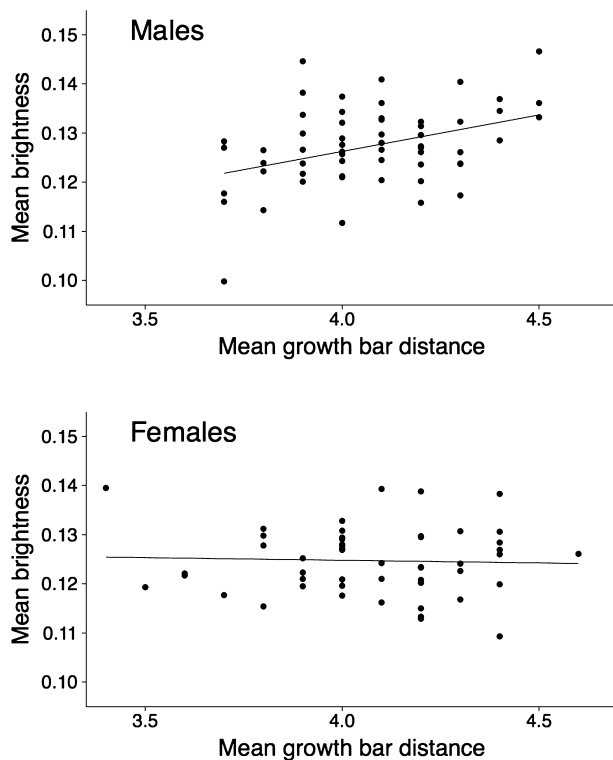
**Figure 2.** Histogram of mean brightness of blue-green tail feathers of male (top) and female (bottom) *Eumomota superciliosa*. Arrows indicate the mean brightness for each sex.

colour metrics: there was no evidence of sexual difference in blue-green hue ( $F = 1.7_{3,120}$ , model  $P = 0.18$ ), but there was a trend for males to have a higher UV saturation ( $F = 10.9_{3,120}$ , model  $P < 0.0001$ ,  $R^2 = 0.21$ , year  $P < 0.0001$ , sex  $P = 0.06$ ).

#### GROWTH BARS AND COLOUR

Based on growth-bar distance, there was no sexual difference in the length of feather growth per day ( $F = 0.12_{1,109}$ ,  $P = 0.73$ ). Feathers grew, on average

(mean  $\pm$  SD),  $4.1 \pm 0.2$  mm per day, ranging from 3.4 to 4.6 mm, which means that some individuals grew up to 35% more tail feather per day. The mean growth-bar distance was significantly correlated with mean brightness, and there was a significant interaction between sex and growth-bar distance ( $F = 4.87_{4,106}$ , model  $P = 0.001$ ,  $R^2 = 0.16$ , year  $P = 0.049$ , sex  $P = 0.02$ , growth-bar distance  $P = 0.03$ , growth-bar distance\*sex  $P = 0.013$ ), thus indicating that the sexes differ in their relationship between growth-bar distance and coloration. When the sexes were run separately, mean brightness was significantly correlated with growth-bar distance in males, but not in females (males,  $F = 5.33_{2,57}$ , model  $P = 0.0076$ ,  $R^2 = 0.16$ , year  $P = 0.63$ , growth-bar distance  $P = 0.003$ ; females,  $F = 4.14_{2,48}$ , model  $P = 0.35$ , year  $P = 0.005$ , growth-bar distance  $P = 0.79$ , Fig. 3). The analysis on males was repeated after removing an outlier that had both low brightness and short growth bars, and results were not qualitatively different ( $F = 3.49_{2,56}$ , model  $P = 0.037$ ,  $R^2 = 0.11$ , year  $P = 0.98$ , growth-bar distance  $P = 0.01$ ). There were no significant relationships between growth-bar distance and other measures



**Figure 3.** Relationship between growth-bar distance and mean brightness of the racket-shaped tail feather of *Eumomota superciliosa*. Males are shown above females. One male outlier was removed (lower left) for analysis (see text).

of tail colour: blue-green hue ( $F = 2.01_{4,106}$ , model  $P = 0.10$ , year  $P = 0.054$ , sex  $P = 0.31$ , growth-bar distance  $P = 0.80$ , growth-bar distance\*sex  $P = 0.08$ ); UV saturation ( $F = 7.56_{4,106}$ , model  $P < 0.0001$ ; year  $P < 0.0001$ ; sex  $P = 0.17$ ; growth-bar distance  $P = 0.85$ ; growth-bar distance\*sex  $P = 0.80$ ); and blue-green saturation ( $F = 6.48_{4,106}$ , model  $P < 0.0001$ , year  $P = 0.003$ , sex  $P = 0.003$ , growth-bar distance  $P = 0.15$ , growth-bar distance\*sex  $P = 0.79$ ).

## DISCUSSION

We tested whether structural coloration of the racketed tail of *E. superciliosa* has the potential to reflect the phenotypic condition of one or both sexes. We show that male tail rackets are moderately brighter than female rackets, and that males, but not females, that grow their tail feathers at a faster rate during the annual molt have more colourful (brighter) feathers. Our results suggest that brightness of the tail racket has the potential to indicate phenotypic condition in males. As such, it is possible that receivers are selected to assess coloration during mate choice or contest competition; however, this conjecture is preliminary, as experimental evidence (e.g. showing receiver response) is required to fully assess the hypothesis that male tail coloration functions as a condition-dependent signal.

The difference in brightness among males of different condition may have arisen because males with greater energy reserves during molt are able to reduce the time needed to fully grow their feathers while also increasing signal value by producing brighter feathers. In contrast, males with large energy demands or small energy reserves may only be able to grow feathers with suboptimal reflectance. Our findings are consistent with other correlational studies that have found a positive relationship between structural coloration and feather growth rate (blue grosbeaks, *Guiraca caerulea*, Keyser & Hill, 1999; blue-black grassquits, *Volatinia jacarina*, Doucet, 2002). Our results also agree with the findings of Griggio *et al.* (2009) that blue tits (*Cyanistes caeruleus*) that were induced to molt at a faster rate (with molt speed controlled through photoperiod manipulation) grew feathers with reduced brightness in the ultraviolet range. The reduced feather brightness presumably occurred because these birds were forced to produce more feather per day than was energetically optimal. Taken together, these results build on a growing body of work that links structural coloration to phenotypic condition. For example, structural colours have been found to relate to parasites in *C. caeruleus* (Harper 1999) and satin bowerbirds, *Ptilonorhynchus violaceus* (Doucet & Montgomerie, 2003; Doucet *et al.*, 2006); survival in

*C. caeruleus* (Sheldon *et al.*, 1999); residual mass in the blue-tailed bee-eater, *Merops philippinus* (Siefferman *et al.*, 2007); size in blue grosbeaks, *Guiraca caerulea* (Keyser & Hill, 1999, 2000); and age in the western bluebird, *Sialia mexicana* (Budden & Dickinson, 2009). Furthermore, experimental manipulations indicate that structural coloration is reduced when birds experience nutritional stress during molt (brown-headed cowbird, *Molothrus ater*, McGraw *et al.*, 2002; eastern bluebird, *Sialia sialis*, Siefferman & Hill, 2005, but see Peters *et al.*, 2011), when they are infected with coccidial parasites (turkey, *Meleagris gallopavo*, Hill, Doucet & Buchholz, 2005), or when there are developmental abnormalities during feather development (black grouse, *Tetrao tetrix*, Siitari *et al.*, 2007).

Even though these studies suggest that structural coloration is condition dependent, there is much disagreement as to whether there exists a mechanism that links phenotypic condition to the nanoscale organization of keratin, air pockets, and pigments that produce structural colours (Prum, 2006; Peters *et al.*, 2011). Structural colours arise through a developmental process regulated by the intrinsic chemical properties of macromolecules. These properties lead to self-assembly of the macromolecules into specific spatial assemblages (Prum, 2006), and because of this self-assembly, it is thought that phenotypic condition will not affect their organization (but see Griggio *et al.*, 2009 for a relationship between hue and experimental stress). However, the self-assembly mechanisms underlying macromolecule spacing are linked only to between-individual variation in hue, whereas variation in saturation and brightness are affected by other mechanisms (Shawkey *et al.*, 2003; Prum, 2006). Some mechanisms that influence structural brightness include the abundance of heavily melanized barbules (Andersson, 1999) and, possibly, the number of melanin granules within the spongy medullary layer of feather barbs (see Shawkey *et al.*, 2003). In addition, increased thickness of the keratin cortex in barb cross-sections can reduce light reflectance because the cortex absorbs light (Finger, Burkhardt & Dyck, 1992, Andersson, 1999; Shawkey *et al.*, 2005). As such, birds may trade-off between brightness and the structural integrity provided by the cortex (Shawkey *et al.*, 2005). In motmots, it may be that males that are able to invest more energy into the rate of feather growth are also able to create feathers that reflect more light. That is, higher quality males may produce more precisely aligned scattering structures, with reduced cortex thickness, resulting in a blue-green with higher brightness (see Andersson, 1999; Shawkey *et al.*, 2003, 2005).

Our findings that female colour has a similar spectral shape to males, but unlike males, females express

tail coloration independent of their investment in feather growth, suggest that female tail colour does not function identically to male tail colour. This conclusion is necessarily tentative, as we measured only one aspect of condition and so have limited power in interpreting negative results; however, if this interpretation is correct, it is of interest to ask why female motmots maintain such elaborate coloration. One possibility is that female tail colour may reflect the condition of some other phenotypic aspect that we did not measure; as such, female colour may function as a sexual/social condition-dependent signal, as we speculate it does in males. Alternatively, female colour may be involved in non-condition-dependent forms of communication, such as species or individual recognition and pursuit deterrence (see Murphy, 2006), or female coloration could function as a conventional signal or a runaway sexually selected signal. Another possible explanation for the expression of female tail colour is that it is non-adaptive. Because of the low production cost associated with the hue of structural colours, it is possible that females express the blue-green hue but gain no benefit from its expression. In support of this idea, hue did not vary, on average, between males and females, whereas mean brightness, and to a lesser extent, blue-green saturation, were significantly different between the sexes. As brightness is likely to entail some production costs (Shawkey *et al.*, 2003), or other costs, such as increased visibility to predators (see Doucet, 2002), females may be selected to express a less bright version of the same hue that is expressed in males. In other words, our finding of a relationship between condition and brightness in males may indicate that males are selected to express their ornament in a costly fashion (i.e. expressing with high brightness), whereas females are selected to express a low-cost version of the colour (i.e. the same hue, but with low brightness). In support of the idea that female tail colour may be expressed as a non-functional byproduct of selection on males, the skewed distribution of tail colour among females indicates that few females had tails that were extremely bright, suggesting that there is no directional selection for females to express very bright feathers.

Another possible explanation for the differences in tail-feather brightness reported here, is that carotenoid pigments play a role in creating the observed blue-green hue of the tail feather. Carotenoid pigments absorb light of short wavelengths, and as a result reduce brightness and shift the hue towards green (Dyck, 1971, Prum, 2006). In *E. superciliosa*, we have found that carotenoids play a role in colouring tail feathers (Murphy, unpubl. data, based on thermochemical carotenoid extraction, following McGraw *et al.*, 2005), so it is possible that birds with duller

feathers (i.e. females and males that grow feathers slowly) may have deposited more carotenoids in their feathers than birds with brighter feathers. However, we find this explanation highly unlikely because carotenoids are known to strongly affect hue, and we observed no differences in hue between the sexes, or between males that produced feathers at different rates. Thus, although carotenoids do play a role in colouring the motmot tail feather, differences in carotenoids are unlikely to account for our observed patterns of sexual dichromatism and the relationship between molt speed and brightness.

Based on the results presented here, it appears that the expression of bright tail feathers in male motmots may be favoured by selection because they reflect the quality of the male. It is also possible that females express tail coloration non-adaptively. It is important to note that these conclusions are necessarily speculative, as our ability to make inferences are limited by the correlational nature of our data, and because our study is based on a single measure of condition. It is interesting, however, to consider how our version of the genetic correlation hypothesis might apply to other species with female ornamentation. Specifically, our hypothesis makes distinct predictions about the evolution of sexual dichromatism depending on whether males express structural- or carotenoid-based coloration. We predict that females of species with structural coloration will express similar, but less costly, versions of male-like structural colours. In contrast, we predict that species that colour their plumes with carotenoids, which requires limited nutrients to be ingested, assimilated, and allocated (Hill, 1990, 1991; McGraw, Nolan & Crino, 2006), will more often exhibit female ornamentation that is highly dissimilar to male ornamentation, or that there will be a complete lack of carotenoid-based ornamentation in females. For future research on female coloration, we suggest that, in addition to functional hypotheses, attention should be given to the possibility that females express structural-based colours without an associated signalling benefit.

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#### REFERENCES

- Alonso-Alvarez C, Bertrand S, Devevey G, Gaillard M, Prost J, Faivre B, Sorci G. 2004. An experimental test of the dose-dependent effect of carotenoids and immune activation on sexual signals and antioxidant activity. *The American Naturalist* **164**: 651–659.
- Amundsen T. 2000a. Why are female birds ornamented. *Trends in Ecology and Evolution* **15**: 149–155.
- Amundsen T. 2000b. Female ornaments: genetically correlated or sexually selected. In: Amundsen T, Espmark Y, Rosenqvist G, eds. *Animal signals: signaling and signal design in animal communication*. Norway: Tapir Academic Press, 133–154.
- Amundsen T, Forsgren E. 2001. Male mate choice selects for female coloration in a fish. *Proceedings of the National Academy of Sciences of the United States of America* **98**: 13155–13160.
- Amundsen T, Forsgren E, Hansen LTT. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **264**: 1579–1586.
- Amundsen T, Pärn H. 2006. Female coloration in birds: a review of functional and non-functional hypotheses. In: Hill GE, McGraw KJ, eds. *Bird coloration volume 2: function and evolution*. Cambridge (MA): Harvard University Press, 280–345.
- Andersson S. 1999. Morphology of UV reflectance in a whistling-thrush: implications for the study of structural colour signalling in birds. *Journal of Avian Biology* **30**: 193–204.
- Andersson S, Örnberg J, Andersson M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**: 445–450.
- Budden AE, Dickinson JL. 2009. Signals of quality and age: the information content of multiple plumage ornaments in male western bluebirds *Sialia mexicana*. *Journal of Avian Biology* **40**: 18–27.
- Clotfelter E, Ardia DR, McGraw KJ. 2007. Red fish, blue fish: trade-offs between pigmentation and immunity in *Betta splendens*. *Behavioral Ecology* **18**: 1139–1145.
- Clutton-Brock T. 2007. Sexual selection in males and females. *Science* **318**: 1882–1885.
- Cuervo JJ, de Lope F, Møller A. 1996. The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behavioral Ecology* **7**: 132–136.
- Dale J. 2006. Intraspecific variation in colouration. In: Hill GE, McGraw KJ, eds. *Bird coloration volume 2: function and evolution*. Cambridge (MA): Harvard University Press, 36–86.

- Darwin C. 1871.** *The descent of man and selection in relation to sex*. London: John Murray.
- Domb LG, Pagel M. 2001.** Sexual swellings advertise female quality in wild baboons. *Nature* **410**: 204–206.
- Doucet SM. 2002.** Structural plumage colouration, male body size, and condition in the blue-black grassquit. *Condor* **104**: 30–38.
- Doucet SM, Montgomerie R. 2003.** Structural plumage colour and parasites in satin bowerbirds *Ptilonorhynchus violaceus*: implications for sexual selection. *Journal of Avian Biology* **34**: 237–242.
- Doucet SM, Shawkey MD, Hill GE, Montgomerie R. 2006.** Iridescent plumage in satin bowerbirds: structure, mechanisms and nanostructural predictors of individual variation in colour. *Journal of Evolutionary Biology* **209**: 380–390.
- Doutrelant C, Grégoire A, Grnac N, Gomez D, Lambrechts MM, Perret P. 2008.** Female coloration indicates female reproductive capacity in blue tits. *Journal of Evolutionary Biology* **21**: 226–233.
- Dufresne ER, Noh H, Saranathan V, Mochrie SGJ, Cao H, Prum RO. 2009.** Self-assembly of amorphous biophotonic nanostructures by phase separation. *Soft Matter* **5**: 1792–1795.
- Dyck J. 1971.** Structure and spectral reflectance of green and blue feathers of the Rose-faced Lovebird (*Agapornis roseicollis*). *Biologiske Skrifter* **18**: 1–67.
- Finger E, Burkhardt D, Dyck J. 1992.** Avian plumage colours: origin of UV reflection in a black parrot. *Die Naturwissenschaften* Origin of UV reflection in a black parrot, **79**: 187–188.
- Fitzpatrick S. 1998.** Colour schemes for birds: structural coloration and signals of quality in feathers. *Annales Zoologici Fennici* **35**: 67–77.
- Götmark F. 1993.** Conspicuous coloration in male birds is favoured by predation in some species and disfavoured in others. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **253**: 143–146.
- Griggio M, Serra L, Licheri D, Campomori C, Pilastro A. 2009.** Molt speed affects structural feather ornaments in the blue tit. *Journal of Evolutionary Biology* **22**: 782–792.
- Griggio M, Valera F, Casas A, Pilastro A. 2005.** Males prefer ornamented females: a field experiment of male choice in the rock sparrow. *Animal Behaviour* **69**: 1243–1250.
- Grubb TC. 1989.** Ptilochronology: feather growth bars as indicators of nutritional status. *The Auk* **106**: 314–320.
- Grubb TC. 1991.** A deficient diet narrows growth bars on induced feathers. *The Auk* **108**: 725–727.
- Hanssen SA, Hasselquist D, Folstad I, Erikstad KE. 2008.** A label of health: a previous immune challenge is reflected in the expression of a female plumage trait. *Biology Letters* **4**: 379–381.
- Harper D. 1999.** Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. *Animal Behaviour* **58**: 553–562.
- Heinsohn R, Legge S, Endler JA. 2005.** Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science* **309**: 617–619.
- Hill GE. 1990.** Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behaviour* **40**: 563–572.
- Hill GE. 1991.** Plumage colouration is a sexually selected indicator of male quality. *Nature* **350**: 337–339.
- Hill GE. 2006.** Environmental regulation of ornamental color. In: Hill GE, McGraw KJ, eds. *Bird coloration volume 1: mechanisms and measurements*. Cambridge (MA): Harvard University Press, 507.
- Hill GE, Doucet SM, Buchholz R. 2005.** The effect of coccidial infection on iridescent plumage colouration in wild turkeys. *Animal Behaviour* **69**: 387–394.
- Hórák P, Zilmer M, Saks L, Ots I, Karu U, Zilmer K. 2006.** Antioxidant protection, carotenoids and the costs of immune challenge in greenfinches. *Journal of Experimental Biology* **209**: 4329–4338.
- Hunt S, Cuthill IC, Bennett ATD, Griffiths R. 1999.** Preferences for ultraviolet partners in the blue tit. *Animal Behaviour* **58**: 809–815.
- Jawor JM, Linville SU, Beall SM, Breitwisch R. 2003.** Assortative mating by multiple ornaments in northern cardinals (*Cardinalis cardinalis*). *Behavioral Ecology* **14**: 515–520.
- Jenkins KD, Hawley DM, Farabaugh CS, Cristol DA. 2001.** Ptilochronology reveals differences in condition of captive white-throated sparrows. *Condor* **103**: 579–586.
- Jones IL, Hunter FM. 1993.** Mutual sexual selection in a monogamous seabird. *Nature* **362**: 238–239.
- Keyser AJ, Hill GE. 1999.** Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **266**: 771–777.
- Keyser AJ, Hill GE. 2000.** Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology* **11**: 202–209.
- Kraaijeveld K, Kraaijeveld-Smit FJL, Komdeur J. 2007.** The evolution of mutual ornamentation. *Animal Behaviour* **74**: 657–677.
- Lande R. 1980.** Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**: 292–305.
- LeBas NR. 2006.** Female finery is not for males. *Trends in Ecology and Evolution* **21**: 170–173.
- Lessells CM, Boag PT. 1987.** Unrepeatable repeatabilities – a common mistake. *The Auk* **104**: 116–121.
- Martínez-Padilla J, Vergara P, Pérez-Rodríguez L, Mougeot F, Casas F, Ludwig SC, Haines JA, Zeineddine M, Redpath SM. 2011.** Condition- and parasite-dependent expression of a male-like trait in a female bird. *Biology Letters* **7**: 364–367.
- McGraw KJ, Ardia DR. 2003.** Carotenoids, immunocompetence, and the information content of sexual colours: an experimental test. *The American Naturalist* **162**: 704–712.
- McGraw KJ, Hudon J, Hill GE, Parker RS. 2005.** A simple and inexpensive chemical test for behavioral ecologists to determine the presence of carotenoid pigments in animal tissues. *Behavioral Ecology and Sociobiology* **57**: 391–397.



- McGraw KJ, Mackillop EA, Dale J, Hauber ME. 2002.** Different colours reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Evolutionary Biology* **205**: 3747–3755.
- McGraw KJ, Nolan PM, Crino OL. 2006.** Carotenoid accumulation strategies for becoming a colourful House Finch: analyses of plasma and liver pigments in wild moulting birds. *Functional Ecology* **20**: 678–688.
- Montgomerie R. 2006.** Analyzing colours. In: Hill GE, McGraw KJ, eds. *Bird coloration volume 2: function and evolution*. Cambridge (MA): Harvard University Press, 90–147.
- Montgomerie R. 2008.** CLR, version 1.05. Kingston (Canada): Queen's University. Available at: <http://post.queensu.ca/~mont/color/>
- Muma KE, Weatherhead PJ. 1989.** Male traits expressed in females: direct or indirect sexual selection. *Behavioral Ecology and Sociobiology* **25**: 23–31.
- Murphy TG. 2006.** Predator-elicited visual signal: why the turquoise-browed motmot wag-displays its racketed tail. *Behavioral Ecology* **17**: 547–553.
- Murphy TG. 2007.** Racketed tail of the male and female turquoise-browed motmot: male but not female tail length correlates with pairing success, performance, and reproductive success. *Behavioral Ecology and Sociobiology* **61**: 911–918.
- Murphy TG. 2008.** Lack of assortative mating for tail, body size, or condition in the elaborate monomorphic turquoise-browed motmot (*Eumomota superciliosa*). *The Auk* **125**: 11–19.
- Noh H, Liew S, Saranathan V, Prum R, Mochrie G, Dufresne E, Cao H. 2010.** Double scattering of light from biophotonic nanostructures with short-range order. *Optics Express* **18**: 11942–11948.
- Nolan PM, Dobson FS, Nicolaus M, Karels TJ, McGraw KJ, Jouventin P. 2010.** Mutual mate choice for colourful traits in king penguins. *Ethology* **116**: 635–644.
- Peters A, Kurvers RHJM, Roberts ML, Delhey K. 2011.** No evidence for general condition-dependence of structural plumage colour in blue tits: an experiment. *Journal of Evolutionary Biology* **24**: 976–987.
- Potti J, Merino S. 1996.** Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **263**: 1199–1204.
- Prum RO. 2006.** Anatomy, physics and evolution of avian structural colours. In: Hill GE, McGraw KJ, eds. *Bird coloration volume 1. Mechanisms and measurements*. Cambridge (MA): Harvard University Press, 295–353.
- Prum RO, Torres R, Williamson S, Dyck J. 1999.** Two-dimensional Fourier analysis of the spongy medullary keratin of structurally coloured feather barb. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **266**: 13–22.
- Roulin A, Jungi TW, Pfister H, Dijkstra C. 2000.** Female barn owls (*Tyto alba*) advertise good genes. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267**: 937–941.
- Scott PE, Martin RF. 1983.** Reproduction of the turquoise-browed motmot *Eumomota superciliosa* at archaeological ruins in Yucatan Mexico. *Biotropica* **15**: 8–14.
- Shawkey MD, Estes A, Siefferman L, Hill GE. 2005.** The anatomical basis of sexual dichromatism in non-iridescent ultraviolet-blue structural coloration of feathers. *Biological Journal of the Linnean Society* **84**: 259–271.
- Shawkey MD, Estes AM, Siefferman LM, Hill GE. 2003.** Nanostructure predicts intraspecific variation in ultraviolet-blue plumage colour. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**: 1455–1460.
- Sheldon BC, Andersson S, Griffith SC, Örnborg J, Sendecka J. 1999.** Ultraviolet colour variation influences blue tit sex ratios. *Nature* **402**: 874–877.
- Siefferman L, Hill GE. 2005.** Evidence for sexual selection on structural plumage colouration in female eastern bluebirds (*Sialia sialis*). *Evolution* **59**: 1819–1828.
- Siefferman L, Wang YJ, Wang YP, Yuan HW. 2007.** Sexual dichromatism, dimorphism, and condition-dependent colouration in Blue-tailed Bee-eaters. *Condor* **109**: 577–584.
- Siitari H, Alatalo R, Halme P, Buchanan K, Kilpimaa J. 2007.** Color signals in the black grouse (*Tetrao tetrix*): signal properties and their condition dependency. *American Naturalist* **169**: Suppl 1, S81–S92.
- South SH, Arnqvist G. 2011.** Male, but not female, preference for an ornament expressed in both sexes of the polygynous mosquito *Sabethes cyaneus*. *Animal Behaviour* **81**: 645–651.
- Torres R, Velando A. 2005.** Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxii*. *Animal Behaviour* **69**: 59–65.
- Velando A, Lessells CM, Márquez JC. 2001.** The function of female and male ornaments in the Inca tern: evidence for links between ornament expression and both adult condition and reproductive performance. *Journal of Avian Biology* **32**: 311–318.
- Wolf WL, Casto JM, Nolan V, Ketterson ED. 2004.** Female ornamentation and male mate choice in dark-eyed juncos. *Animal Behaviour* **67**: 93–102.