Functional Ecology

British Ecological Society

Functional Ecology 2010, **24**, 149–158 doi: 10.1111/j.1365-2435.2009.01606.x

Carotenoid and melanin-based ornaments signal similar aspects of male quality in two populations of the common yellowthroat

Peter O. Dunn*,[1], Julia C. Garvin[1], Linda A. Whittingham[1], Corey R. Freeman-Gallant[2] and Dennis Hasselquist[3]

[1]*Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin, 53201, USA;* [2]*Department of Biology, Skidmore College, Saratoga Springs, New York 12866, USA; and* [3]*Department of Animal Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden*

Summary

1. Female preferences for particular male ornaments may shift between populations as a consequence of ecological differences that change the reliability and detectability of the ornament, but few studies have examined how ornaments function in different populations.

2. We examined the signalling function of male plumage ornaments in a warbler, the common yellowthroat (*Geothlypis trichas*), breeding in New York (NY) and Wisconsin (WI), USA. Males have two prominent ornaments: a black facial mask pigmented with melanin and a yellow bib pigmented by carotenoids. Previous studies in WI indicate that the size of the mask, and not the bib, is primarily related to female choice and male reproductive success. In NY, however, the pattern is reversed and attributes of the bib (size and colour), and not the mask, are the target of sexual selection.

3. We found that brightness of the yellow bib was the best signal of humoral immunity (immunoglobulin G) in NY and mask size was the best signal in WI, after controlling for breeding experience and capture date. Thus, similar aspects of male quality appeared to be signalled by different ornaments in different populations.

4. There was no difference between populations in the level of plasma carotenoids or the prevalence of malarial parasites, which may affect the costs and benefits of choosing males with particular ornaments in each location.

5. Even though females in different populations prefer different ornaments produced by different types of pigments, these ornaments appear to be signalling similar aspects of male quality. Our results caution against inferring the function of particular ornaments based simply on their type of pigment.

Key-words: carotenoids, habitat, immunity, intraspecific variation, multiple ornaments, melanin, sexually selected traits

Introduction

Males often attract mates using several different types of signals, including both morphological and behavioural traits. For example, male guppies (*Poecilia reticulata*) use both courtship displays and orange spots to attract mates (Endler & Houde 1995), and many birds use both song and plumage ornaments to attract their mates. The evolution of these multiple signals is complex, as different ornaments may be selected by female choice and male-male competition, and, in terms of female choice, some ornaments may be better indicators of male quality than others. For example, it has been suggested that ornaments pigmented with carotenoids (primarily red, yellow, orange) are more costly to produce than ornaments pigmented with melanin (primarily black and brown, Badyaev & Hill 2000; Hill & Brawner 1998), and, thus, are better indicators of male quality (condition or health). As a consequence, carotenoid-based ornaments may be more likely to be targets of female choice than melanin-based ornaments.

Carotenoid-based ornaments are thought to be costly signals of male quality because vertebrates cannot synthesize carotenoids and must acquire them in their diet.

---

*Correspondence author. E-mail: pdunn@uwm.edu

Furthermore, some types of carotenoids play an important role as antioxidants and in immune defence (Blount *et al.* 2003), so the carotenoids available for ornamentation may be limited by their allocation to the immune system (Lozano 1994; von Schantz *et al.* 1999). In contrast, melanins are readily synthesized by vertebrates from the amino acid tyrosine, which is not considered limiting (Fox 1976; von Schantz *et al.* 1999; Jawor & Breitwisch 2003). This difference in synthesis led to the hypothesis that melanin-based ornaments are less costly to produce and, thus, less likely to be used by females in mate choice.

However, this hypothesis has been controversial for several reasons. First, it focuses on the physiological costs of producing and depositing pigments and does not consider the social costs of maintaining ornaments of a given size or colour. For example, melanin-based ornaments are often used as signals of dominance in male-male interactions (Senar 1999; Ducrest, Keller & Roulin 2008). This intrasexual competition may enforce the honesty of melanin-based ornaments, despite a relatively low physiological cost of production (Tarof, Dunn & Whittingham 2005). Second, the hypothesis assumes that melanin-based ornaments are relatively less costly to produce and under tighter genetic control than carotenoid-based ornaments (Roulin & Dijkstra 2003; Mundy 2006), and, thus, melanin deposition is less affected by body condition and differences in the environment, such as diet (reviewed by Hill 2006a). On the other hand, several studies have shown that the expression of melanin-based feather colouration is associated with body condition (Veiga & Puerta 1996; Fitze & Richner 2002), immunocompetence (Roulin, Jungi & Dijkstra 2000; Gonzalez *et al.* 2001), parasite resistance (Roulin *et al.* 2001), stress hormones (Roulin *et al.* 2008) and minerals, particularly calcium (Niecke, Rothlaender & Roulin 2003; McGraw 2007). Furthermore, mate choice is clearly related to melanin-based ornaments in several bird species (Norris 1990; Roulin 1999; Tarof, Dunn & Whittingham 2005) and in some populations of guppies (Endler & Houde 1995; Schwartz & Hendry 2007). Thus, melanin-based ornaments may be reliable signals of male quality in a variety of species.

The information content of ornaments is also important for understanding geographic variation in female preferences for particular male ornaments. Theoretical models predict that female preferences may shift between populations as a consequence of small environmentally-induced differences in the costs of mate choice (Schluter & Price 1993; Johnstone 1996; van Doorn & Weissing 2006). Thus, females might differ in their relative preferences for carotenoid- and melanin-based ornaments in populations that differ in the costs of producing each type of ornament or the information that they signal about male quality. For example, variation in carotenoid-based ornamentation is often attributed to foraging ability and carotenoid availability in the habitat (Olson & Owens 1998; Grether, Hudon & Millie 1999). Thus, differences in carotenoid availability in a particular habitat could lead to shifts in the cost of producing ornaments and, hence, the honesty of the signal, which could shift female preferences. For example, in two populations of chuckwallas (*Sauromalus obesus*), females preferred males with brighter orange and yellow tails, which was associated with abundant food on their territories, but they showed no preference for males based on their colouration in a third population where there was relatively less food on each territory (Kwiatkowski & Sullivan 2002). Populations could also differ in the abundance and composition of parasites and pathogens, which could alter any trade-off between immunity and pigments used in ornamentation. Thus, studies of species that have both melanin- and carotenoid-based ornaments are valuable for understanding how environmental factors affect the way animals use ornaments to signal quality. However, few studies have examined ecological and geographic variation in ornament expression and what it signals about male quality.

In this study we examined two populations of the common yellowthroat (*Geothlypis trichas,* Linnaeus 1766) breeding in New York (NY) and Wisconsin (WI), USA. The common yellowthroat is a sexually dimorphic warbler (Fig. 1) in which males have a black facial mask pigmented with melanin and a yellow bib (throat, breast, and belly) pigmented solely by the carotenoid lutein (McGraw *et al.* 2003b). Lutein is widely used by birds to pigment their yellow feathers, but there is little evidence that it enhances immunity (Fitze *et al.* 2007). Both the black mask and yellow bib are produced once a year during the pre-basic moult, which occurs on the breeding grounds in August and September just before migration (Guzy & Ritchison 1999). Previous studies in WI suggest that the size of the mask, and not the bib, is primarily related to male reproductive success (Thusius *et al.* 2001a), female preferences in captivity (Tarof, Dunn & Whittingham 2005) and female extra-territorial forays (Pedersen, Dunn & Whittingham 2006). Mask size is also correlated positively with humoral immunity (Garvin *et al.* 2008). In contrast, accumulating evidence from NY indicates that male reproductive success (C. Freeman-Gallant unpublished data) and female preferences in captivity (Dunn *et al.* 2008) are related to the size or colour of the male bib, and less so to the size of the mask. This geographic difference in the targets of sexual selection suggests that the yellow bib serves different signalling

Fig. 1. Male common yellowthroat, illustrating the black facial mask and yellow bib. Photo by P. Dunn.

functions between populations, perhaps because its reliability as an indicator of male quality differs between the two populations. Based on our previous results, we predicted that measures of humoral immunity, particularly immunoglobulin G, would be more strongly related to characteristics of the yellow bib in NY than in WI, and, conversely, these measures would be more strongly related to the black mask in WI than in NY.

Materials and methods

STUDY SPECIES AND GENERAL METHODS

Common yellowthroats migrate in the spring to wetlands throughout most of North America and breed from May to August. Males defend small territories (Thusius *et al.* 2001a) and are typically monogamous (*c.* 3% of males are polygynous on our study areas). Males are easily recognized by their black facial mask and yellow bib; females lack the mask and typically have smaller and paler bibs.

We conducted field work at the University of Wisconsin-Milwaukee (UWM) Field Station in Saukville, WI (43°23′N, 88°01′W) and near Skidmore College in Saratoga Springs, NY (43°06′N, 73°48′W), USA. Measures of immunity and carotenoids were taken from the WI population during May to August 2003–2006 and from the NY population during May-June 2006. A larger sample was used to estimate body condition and return rate to the study area (2003–2007 in WI; 2005–2007 in NY). Both populations were surveyed almost daily throughout the season to determine arrival dates, territory occupancy and nesting success. Birds banded in earlier years on our study areas were considered experienced breeders, whereas birds banded for the first time were considered inexperienced breeders. We began intensive studies in 2002 in WI and 2005 in NY, so we could determine the breeding experience of birds used in this study starting 2003 in WI and 2006 in NY. In most cases, returning males settled on the same territory and always within 150 m of their previous territories. Breeding experience is likely to be correlated with traditional age classifications [second-year (SY) and after-second-year (ASY)] estimated from plumage differences, but these age estimates are reliable in less than 25% of males (Pyle 1997), so we did not use them for any analyses.

The WI study area consists of 5·4 ha of mixed red maple (*Acer rubrum*) and eastern larch (*Larix laricina*) swamp and willow/sedge marsh. In NY, birds were sampled at three main sites, two red maple swamps and a power-line corridor through deciduous woodland. Males were captured in mist nets early in the breeding season before egg-laying and banded with unique combinations of coloured plastic bands and an aluminium USFWS band. Small (≤ 40 μL) blood samples were collected via brachial venipuncture in capillary tubes from both males and females and centrifuged. Plasma was stored separately at −20 °C for later ELISA (enzyme-linked immunosorbent assay) analysis of immunoglobulin G levels and quantification of carotenoid concentration. We measured body mass, length of the wing, tail and tarsus of adults, and photographed males with still and video cameras to estimate the size of the yellow bib and black mask (Fig. 1). Sizes of bibs and masks were measured using IMAGE ANALYSIS software (details in Thusius *et al.* 2001a), and estimates were highly repeatable between different pictures of both the bib and mask (both R = 0·99), as well as between persons (R = 0·96 and 0·98 for bib and mask, respectively). From each male, we also collected four feathers from the centre of the bib to estimate bib brightness and saturation with a spectrometer (see Dunn *et al.* 2008). Four separate readings were performed for each bird and the results averaged. We used standard estimates of colour (Montgomerie 2006), including yellow brightness, which was the average reflectance between 550–625 nm (yellow), and yellow saturation, which was the sum of the reflectance values from 550 to 625 nm divided by total brightness (sum of reflectance from 320 to 700 nm). We also examined bib reflection in the ultraviolet (UV) part of the spectrum (320–400 nm), but there were no significant relationships with immunity (Table 1), so we do not discuss it further.

IMMUNOGLOBULINS

Constituent humoral immunity was estimated by assaying the concentration of immunoglobulin G (IgG) in each individual's plasma. IgG proteins form the main class of antibody molecules enabling humoral immunity, and are thought to indicate the health or nutritional state of free-living birds (Gustafsson *et al.* 1994; Goldsby *et al.* 2003; Morales *et al.* 2004). The concentration of IgG for each bird was measured using an indirect ELISA, which was adapted from Hasselquist *et al.* (1999) and is described in more detail by Garvin *et al.* (2008). Readings from duplicates were averaged and used as the IgG titre. In our analyses, we included plate number and absorbance values for positive and negative controls on each plate to account for variation between plates. Repeatability between duplicate samples of the same individual on the same plate was high (R = 0·96, ANOVA $F_{159,166}$ = 20·5, P < 0·001).

CAROTENOIDS

Total plasma carotenoid concentration was determined spectrophotometrically from samples in 2004 and 2006 (Tella *et al.* 2004). We diluted individual plasma samples 1:50 with 100% acetone for a total volume of 200 μL. After mixing vigorously to fully dissolve the carotenoids, the samples were centrifuged at 14 000 rpm for 10 min to precipitate the flocculent protein. We measured the resulting supernatant for absorbance of the carotenoid peak at 476 nm in a Beckmann Du-68 spectrophotometer. Following Tella *et al.* (2004), we calibrated carotenoid concentrations ($\mu g\ mL^{-1}$) using a standard curve of lutein (alpha-carotene-3,3′-diol, ChromaDex, Santa Ana, CA). Concentrations were $\log_{10}$ transformed for analysis.

Table 1. Pearson correlations between traits of male common yellowthroats from the NY (n = 22–38) and WI (n = 31–126) study sites. Significant correlations (P < 0·05) are indicated in bold with an asterisk. Partial correlations are shown for IgG after controlling for date of capture

	Black mask size	Yellow bib size	Yellow bib brightness	Yellow bib saturation	UV brightness
New York					
IgG	**0·37***	−0·05	**0·38***	0·20	0·27
Carotenoid conc.	−0·13	0·04	−0·01	0·03	< −0·01
Body mass	**0·35***	−0·11	−0·21	−0·04	0·15
Wisconsin					
IgG	**0·35***	0·17	−0·03	−0·22	−0·05
Carotenoid conc.	0·06	0·00	0·01	0·26	−0·20
Body mass	**0·23***	**0·46***	0·26	0·01	−0·12

MALARIAL INFECTION

Several studies of birds have examined immunoglobulin levels in relation to malarial parasites (particularly *Plasmodium*), and, as predicted, there is often a higher IgG level in infected individuals (Isobe & Suzuki 1987; Ots & Horak 1998; Morales *et al.* 2004). To be able to test for this possibility, we screened for the presence of hemosporidians by amplifying a 160 bp fragment of the parasites' mitochondria DNA following methods in Beadell & Fleischer (2005). We combined 1·0 μL of whole genomic DNA, 3·8 mM $MgCl_2$, 0·8 mM dNTPs, 0·8 mg mL^{-1} bovine serum albumin, 0·6 μM of each primer, and 0·5 U Taq in 10–30 μL reaction volumes. Cycling conditions followed Beadell & Fleischer (2005). Each adult was screened in two separate PCRs to minimize the occurrence of false negatives.

STATISTICAL ANALYSIS

We used multiple regression to test the prediction that characteristics of the bib (size, brightness and saturation) provide greater information about male immunity (IgG) to females in NY than in WI. We conducted separate multiple regressions for each ornamental trait (mask size and bib size, brightness and saturation) in relation to IgG and potentially confounding variables such as body mass and year. We analyzed mask and bib ornaments separately, because experimental evidence from aviary trials suggested that bib and mask ornaments were assessed separately by females (Tarof, Dunn & Whittingham 2005, Dunn *et al.* 2008). In each of the analyses we initially included the interactions between state (WI or NY) and IgG to test for different relationships in each location; if the interaction was not significant, then we present the reduced model with the effect of state included (Table 2). Following these initial analyses, we tested for the effects of breeding experience and malaria infection on the relationship between ornaments and IgG. Our previous studies indicate that experienced males generally had the largest ornaments, and they were more likely to attract social mates and sire extra-pair young than inexperienced males (Thusius *et al.* 2001a, C. Freeman-Gallant, unpublished data). We also examined some age-related changes in ornaments and immunity with 15 males sampled in each of 2 years in Wisconsin. In most analyses, however, we wanted to avoid pseudoreplication, so we only used the year with the most complete data for these 15 males (e.g. feathers for colour analysis were not always collected each year). In New York, males were sampled only in 1 year for these analyses.

To compare competing models with different predictors and sample sizes, we used partial F tests after stepwise elimination of variables with $P > 0·15$, while models with the same sample sizes were compared using Akaike's Information Criterion corrected for small samples (AICc), and the Akaike weight (w_i), which gives the relative likelihood of each model given the data (Burnham & Anderson 2002). All tests were two-tailed and performed using the statistical program JMP (SAS, 2003). Means are reported with their standard error unless stated otherwise.

Results

IS IMMUNITY RELATED TO ORNAMENT EXPRESSION?

Males with larger black masks had higher IgG levels and greater body mass, but there was no evidence that mask size was a better signal of IgG in one state than the other (Fig. 2, Table 2). Mask size increased in relation to IgG at similar rates in New York and Wisconsin (Fig. 2); thus, the state by IgG interaction was not significant ($P = 0·86$). In contrast, yellow brightness of the bib increased with IgG in New York, but not in Wisconsin (Fig. 2), and this difference produced a significant interaction between state and IgG (Table 2). Neither yellow bib size nor yellow saturation of the bib feathers showed significant differences between states in slopes or intercepts (Table 2, Fig. 2).

It is possible that malarial infection could influence IgG levels, and, in fact, birds with malaria infection had higher IgG levels than uninfected birds in NY ($t_{18} = 2·3$, $P = 0·035$), but not in WI ($t_{58} = 0·5$, $P = 0·63$). Malarial infections were common and there was no significant difference in the proportion of infected birds in WI (81%, 42/52) and NY (63%, 12/19; $\chi^2 = 2·3$ d.f. = 1, $P = 0·12$). IgG continued to show a positive relationship with mask size in both populations ($F_{1,60} = 5·4$, $P = 0·024$) after including malarial infection ($F_{1,60} = 0·5$, $P = 0·49$) and breeding experience ($F_{1,60} = 14·1$, $P < 0·001$) in the model in Table 2. The most parsimonious model for mask size (adjusted $R^2 = 0·26$, $n = 125$) included breeding experience ($F_{1,119} = 23·7$ $P < 0·001$), IgG ($b = 75·5 \pm 25·5$; $F_{1,119} = 7·1$, $P = 0·004$), year ($F_{1,119} = 2·7$, $P = 0·10$) and state ($F_{1,119} = 2·3$, $P = 0·13$).

We also examined the relationship between IgG and black mask size while controlling for age by comparing the IgG levels of the same Wisconsin males in two consecutive years

Table 2. Ornaments of male common yellowthroats in relation to IgG in NY and WI populations. The initial model included the five predictors on the left, including the interaction between state and IgG. This interaction was not included in the final model if it was non-significant. Variables included in the final model are indicated by their estimates and *P* values

	Black mask size		Yellow bib size		Yellow brightness		Yellow saturation	
Predictors	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
IgG	104·9	< 0·001	20·5	0·90	6·7	0·039	0·004	0·75
Body mass	18·1	0·012	58·7	0·17			< −0·001	0·88
State (NY/WI)	14·4	0·03	31·3	0·47	1·32	0·007	−0·004	0·23
Year	–	0·07	–	0·30			0·007	0·06
IgG × State					7·16	0·028		
n	151		100		69		69	
Adjusted R^2	0·16		0·09		0·09		< 0·01	

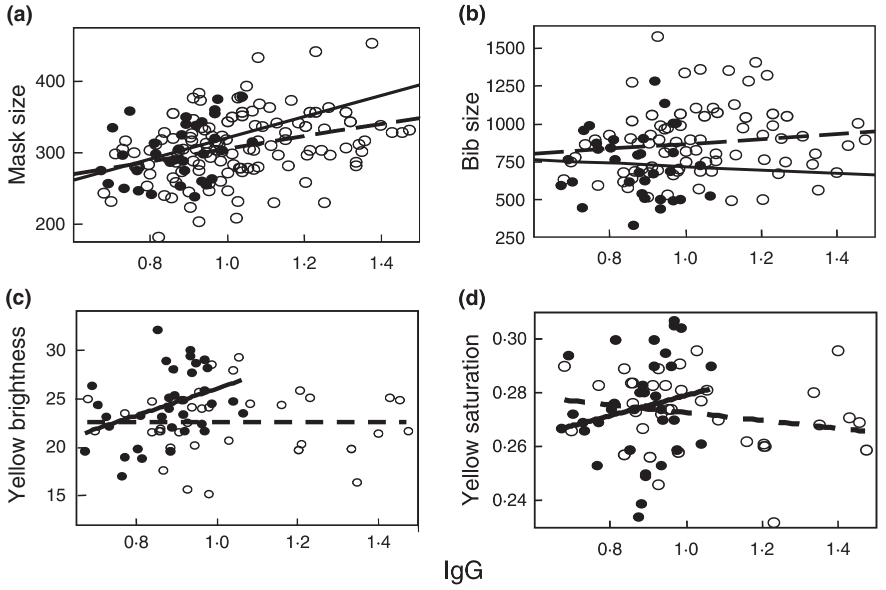

Fig. 2. Linear regressions between male ornaments and IgG in common yellowthroats in NY (filled circles, solid line) and WI (open circles, dashed line). (a) Mask size (mm^2) increased with IgG at similar rates in New York ($b = 147·0 \pm 66·4$, $F_{1,32} = 4·91$, $P = 0·03$) and Wisconsin ($b = 87·1 \pm 22·0$, $F_{1,121} = 15·65$, $P < 0·001$). (b) Bib size was not related to IgG in either NY ($b = -113·3 \pm 383·3$, $F_{1,31} = 0·09$, $P = 0·77$) or WI ($b = 168·3 \pm 140·1$, $F_{1,79} = 1·44$, $P = 0·23$). (c) Brighter yellow bibs were positively associated with IgG in NY ($b = 13·9 \pm 6·0$, $F_{1,32} = 5·37$, $P = 0·027$), but not in WI ($b = -0·46 \pm 2·53$, $F_{1,33} = 0·03$, $P = 0·86$). (d) Yellow saturation of the bib was not related to IgG in NY ($b = 0·04 \pm 0·03$, $F_{1,32} = 1·29$, $P = 0·26$) or WI ($b = -0·01 \pm 0·011$, $F_{1,33} = 1·70$, $P = 0·20$).

($n = 15$ males); similar data were not available from New York. Males with larger black masks had greater IgG levels ($F_{1,11} = 7·5$, $P = 0·019$) after controlling for age (year effect: $F_{2,11} = 5·2$, $P = 0·026$) in a model with male identity as a random effect ($R^2 = 0·52$). There was still a positive relationship between mask size and IgG ($F_{1,2} = 16·3$, $P = 0·056$) after adding malarial infection ($F_{1,2} = 6·2$, $P = 0·13$) to the model, although it was borderline in significance and it reduced the sample size from 15 to six males. Thus, we concluded that IgG was greater in males with larger masks, even after controlling for the age-related increases in IgG and mask size.

Yellow brightness of the bib was a better signal of IgG in NY, because the brightness of male bibs increased with IgG levels, whereas yellow brightness was not related to IgG in WI (Fig. 2). In NY, yellow brightness remained positively related to IgG ($F_{1,27} = 5·7$, $P = 0·025$) in a model that also included breeding experience ($F_{1,27} = 0·9$, $P = 0·36$) and its interaction with IgG ($F_{1,27} = 0·9$, $P = 0·33$). After controlling for malarial infection ($F_{1,16} < 0·1$, $P = 0·86$), there was no longer a significant relationship between IgG and bib brightness ($F_{1,16} = 2·4$, $P = 0·14$) in NY; however, our sample size decreased to 19 males, and the slope ($b = 13·0 \pm 8·4$) was similar to the significant bivariate results ($b = 11·8 \pm 5·0$) with almost twice the sample size ($n = 34$). This lack of change in slope suggests that IgG has a direct relationship with bib brightness, because the parameter value barely changed after controlling for malaria.

Malarial infection was not related to breeding experience in NY (likelihood $\chi^2{}_1 = 0·24$, $P = 0·63$) or WI (likelihood $\chi^2{}_1 = 0·16$, $P = 0·49$). There was also no difference in ornaments between infected and uninfected birds in NY (mask size: $t_{17} < 0·1$, $P = 0·99$; bib size: $t_{16} = 0·2$, $P = 0·86$; bib brightness: $t_{17} = 0·5$, $P = 0·64$; bib saturation: $t_{17} = 0·7$, $P = 0·49$) or WI (mask size: $t_{58} = 0·5$, $P = 0·61$; bib size: $t_{45} = 0·6$, $P = 0·54$; bib brightness: $t_9 = 0·1$, $P = 0·90$; bib saturation: $t_9 = 0·2$, $P = 0·85$).

The analyses above indicated that IgG was related to both mask size and brightness of the yellow bib in NY, whereas IgG was only related to mask size in WI (Table 1). Thus, in NY, we wanted to know if one ornament, mask size or yellow bib brightness, might be a better signal of IgG levels than the other ornament. In NY, we found the best predictors of IgG were yellow brightness of the bib ($F_{1,27} = 5·9$, $P = 0·022$), breeding experience ($F_{1,27} = 4·8$, $P = 0·039$) and capture date ($\mathrm{F}_{1,27} = 3·7$, $P = 0·065$). This model was superior (Akaike $w_\mathrm{i} = 0·97$) to the same model with black mask size included ($F_{1,25} = 1·5$, $P = 0·23$, $w_\mathrm{i} = 0·03$) and the initial model, which included all four ornaments ($w_\mathrm{i} < 0·01$). A similar analysis of the WI data indicated that black mask size ($F_{1,118} = 12·3$, $P < 0·001$) and capture date ($F_{1,118} = 7·1$, $P = 0·009$) were the best predictors of IgG levels. Bib traits and breeding experience were not significant when added to this model ($P > 0·19$). Thus, yellow bib brightness was the best signal of IgG levels in NY and black mask size was the best signal in WI, after controlling for breeding experience and capture date.

In previous aviary experiments, we found an effect of yellow bib size, and not bib brightness, on mate choice in NY (Dunn *et al.* 2008); however, with a larger sample of birds from both populations, including non-resident birds, there was a positive relationship between bib size and yellow brightness in both NY ($r = 0·30$, $n = 81$, $P = 0·006$) and WI ($r = 0·39$, $n = 36$, $P = 0·02$). There was no relationship between yellow bib saturation and bib size in either state ($P > 0{\cdot}26$).

DIFFERENCES BETWEEN STATES IN ORNAMENTS AND IMMUNITY

Brightness of the yellow bib was greater and more variable among males in NY than in WI (Table 3). Yellow saturation of the bib was also greater among males in NY than in WI, but it was more variable in WI than NY. On the other hand, mask size tended ($P = 0{\cdot}062$) to be more variable in WI than in NY (Table 3), as might be expected if females choose males based on more variable traits that signal male quality. There was no difference between states in IgG (after controlling for date) or carotenoid concentration (Table 3). We also examined potentially confounding relationships between components of immunity and condition by performing correlations between IgG, carotenoids and body mass. The only significant relationship was a positive correlation between body mass and carotenoid concentration ($r = 0{\cdot}26$, $n = 56$, $P = 0{\cdot}049$).

RETURN RATE IN RELATION TO MALE ORNAMENTS AND QUALITY

Different male traits were related to annual return rate (apparent survival) in each population. In NY, males with larger bibs were more likely to return to the study area (the year following their first known year of breeding; Table 4). This pattern was also associated with pairing success, as males with small bibs were less likely to attract a social mate and none of these failed breeders returned to the NY study area (C. Freeman-Gallant unpublished data). No other ornaments were related to return rate. In contrast, no ornaments were related to return rate in WI; however, body mass was greater among males that returned to the study area (Table 4); in this case, body mass was related positively to both breeding experience ($F_{1,68} = 11{\cdot}7$, $P = 0{\cdot}001$) and whether the male returned the next year ($F_{1,68} = 6{\cdot}4$, $P = 0{\cdot}014$). Body mass was not related to return rate in NY (Table 4), despite similar sample sizes and a higher return rate in NY (40%, 33/82) than in WI (28%, 25/88). Thus, return rate was only associated with bib size in NY and with body mass in WI.

Table 3. Traits of male common yellowthroats from the NY and WI study sites. The *P* value for Bartlett's test indicates the probability that the two populations have similar variances. A *t*-test controlling for unequal variances was used when the variances were significantly different. CV is the coefficient of variation. Significant test results ($P < 0.05$) are indicated in bold

	NY				WI						
	Mean	SD	CV (%)	*N*	Mean	SD	CV (%)	*N*	Bartlett's *P*	*t/F*	*P*
Black mask size	313·6	37·9	12·1	82	308·0	45·9	14·9	127	0·062	0·92	0·35
Yellow bib size	682·9	181·2	26·5	82	863·9	214·7	24·9	82	0·13	5·84	**< 0·001**
Yellow bib brightness	28·6	4·20	14·7	82	22·8	3·13	13·7	36	**0·05**	7·47	**< 0·001**
Yellow bib saturation	0·36	0·002	0·6	82	0·27	0·014	5·2	36	**< 0·001**	18·9	**< 0·001**
IgG (LSM)	0·975	0·0316	3·2	35	0·997	0·0148	1·5	122	–	0·355	0·56
Carotenoid conc.	1·27	0·39	30·7	24	1·15	0·39	33·9	31	0·99	1·06	0·29
Body mass	10·3	0·53	5·1	82	10·5	0·54	5·1	127	0·88	3·03	**0·002**

Table 4. Return rate (apparent survival) of male common yellowthroats in relation to male traits. Analyses only use return rate and traits from the first year a male was seen on the study area (excludes a second year of data from 14 males). Significant test results are indicated in bold

	Did not return			Returned				
	Mean	SE	*n*	Mean	SE	*n*	*t/F*	*P*
New York								
Black mask size	310·5	5·41	49	318·1	6·5	34	0·90	0·370
Yellow bib size	651·6	25·8	48	727·0	30·6	34	1·89	0·063
Yellow bib brightness	28·3	0·599	49	29·2	0·731	33	1·05	0·297
Yellow bib saturation	0·36	0·004	49	0·35	0·004	33	1·22	0·224
IgG	0·890	0·023	15	0·923	0·032	8	0·68	0·42
Carotenoid conc.	1·36	0·09	10	1·32	0·168	3	0·19	0·85
Body mass	10·5	0·064	81	10·5	0·094	33	0·176	0·86
Wisconsin								
Black mask size	304·5	6·68	54	317·8	10·7	21	1·06	0·29
Yellow bib size	837·2	38·4	34	913·65	50·09	20	1·2	0·23
Yellow bib brightness	23·6	0·95	11	22·1	2·25	2	0·62	0·54
Yellow bib saturation	0·275	0·004	11	0·290	0·008	2	1·58	0·14
IgG	1·0	0·022	53	1·0	0·0358	20	*F* = 0·038	0·845
Carotenoid conc.	1·0	0·115	9	1·7	–	1	2·1	0·068
Body mass	10·4	0·063	54	10·8	0·102	21	3·76	**0·0003**

Discussion

Most studies of sexual selection have focused on one ornamental trait in one population, and, as a consequence, examples of selection acting on different traits in different populations remain rare. In two populations of common yellowthroats we found that different ornamental traits (yellow bib brightness and black mask size) signalled similar aspects of male quality. As predicted, we found that one component of the most important sexually selected ornament in New York, the brightness of the carotenoid-based bib, was associated with higher IgG levels (Table 2). Although size of the melanin-based mask was also correlated with IgG levels in NY (Table 1), the relationship became non-significant after controlling for bib brightness, breeding experience, and capture date. In Wisconsin, mask size was sexually selected, and it was also correlated positively with IgG, as well as body mass (Table 2), which was associated with apparent survival (Table 4). Thus, despite the predicted differences in the cost of producing carotenoid- and melanin-based ornaments, we found that the black mask and yellow bib were both sexually-selected and related to similar aspects of male quality, but in different populations. Differences between populations in natural and sexual selection are expected to produce differences in the costs and benefits of mate choice, leading to divergence in female preferences. Our results indicate that although preferences for particular ornaments may change, they may still reveal similar aspects of male quality.

GEOGRAPHIC DIFFERENCES IN SEXUAL SELECTION

Previously we discovered different patterns of sexual selection on male ornaments in our two populations. In NY, selection on male reproductive success acts primarily on size and colouration of the yellow bib (C. Freeman-Gallant, unpublished data), and females in aviary experiments appear to prefer males with larger bibs in NY, but not in WI (Dunn *et al.* 2008). In contrast, sexual selection acts primarily on size of the black mask in WI (Thusius *et al.* 2001b; Pedersen, Dunn & Whittingham 2006), and females in aviary experiments prefer males with larger masks in WI but not in NY (Tarof, Dunn, & Whittingham 2005; Dunn *et al.* 2008). We also found that yellow brightness of the bib was greater and more variable in NY than in WI, whereas black mask size tended to be more variable in WI than in NY (see also Dunn *et al.* 2008). These differences between populations are consistent with female choice of the most variable ornament between populations. Thus, in NY, choosing a male with a brighter yellow bib and, in WI, choosing a male with larger black mask would result in a mate with higher levels of IgG, and in WI greater body mass and survival. In NY, males that returned the following year also tended to have larger bibs, suggesting that the ornament might also indicate survival ability. However, this might have occurred simply because males with smaller bibs were less likely to pair, and the following year they may have dispersed outside the study area (rather than dying). In any case, males with smaller yellow bibs were probably lower quality, although the specific reason still needs to be determined.

GEOGRAPHIC VARIATION IN SIGNALLING

We hypothesized that female choice varied between NY and WI because different ornaments were more revealing of male quality in one population than the other. This could occur, for example, if there were geographic differences in the availability of carotenoids used to pigment the yellow bib, or differences in how carotenoids trade-off with immunity (Saino *et al.* 1999). For example, in great (*Parus major*) and blue (*Cyanistes caeruleus*) tits, yellow feathers on the belly are paler in a range of habitats thought to be poor quality because they have fewer caterpillars, a source of carotenoids (reviewed by Ferns & Hinsley 2008). However, we found no geographic difference in the level of circulating carotenoids in the plasma (Table 3), suggesting that carotenoid availability did not differ between our populations. Although, some recent studies have found support for a trade-off between carotenoids and immunity (Faivre *et al.* 2003; McGraw & Ardia 2003a), we found no evidence of an association between carotenoids and IgG or body mass (Fitze *et al.* 2007; Constantini & Møller 2008). Lutein is the only carotenoid present in the feathers of common yellowthroats and its role in immune function is unclear (Fitze *et al.* 2007), so a lack of relationship may not be surprising.

There is less evidence in birds that melanin-based ornaments vary geographically in their information content. Although the expression of melanin-based ornaments is often suggested to be under strong genetic control, the evidence is mixed (Griffith, Parker & Olson 2006). Environmental conditions (Fargallo *et al.* 2007), corticosterone levels (Roulin *et al.* 2008) and minerals in the diet (McGraw 2007) can affect the expression of melanin-based plumage, and these could produce geographic differences between populations. In common yellowthroats, the size of the melanin-based mask was related positively to IgG and body mass in both states, which suggests that it might be influenced by environmental conditions, but we did not find a geographic difference in its signalling function.

The signalling function of ornaments may also vary geographically if parasites affect the information content of ornaments in different ways in each population. In the case of common yellowthroats, however, we found no relationship between malarial infection and ornament expression in either population. Malarial infection was related to higher IgG levels in NY, but not in WI. Natural antibodies, of which IgG is the most common immunoglobulin in circulation, can act as a player in innate immunity and hence contribute to the first line of defence against a wide range of pathogens (Lemke, Coutinho & Lange 2004). Most studies of birds have examined immunoglobulin levels in relation to malarial parasites, and, as predicted, there is often a higher IgG level in infected individuals (Isobe & Suzuki 1987; Ots & Horak 1998; Morales *et al.* 2004). To our knowledge, only one other study has examined immunoglobulins in relation to ornamental traits in birds; in house sparrows (*Passer domesticus*) there was no relationship between immunoglobulins and badge size, a melanin-based ornament (Gonzalez, Sorci & De Lope 1999).

It is possible that the higher IgG levels of males with brighter bibs in NY might be an effect of malarial infection, rather than a sign of greater humoral immunity. However, in NY, the slope of the relationship between bib brightness and IgG changed very little after controlling for malarial infection, which suggests that the relationship was not an artefact of infection. Thus, it seems more likely to us that males with brighter yellow bibs have better immune function and may produce more antibodies (IgG), regardless of infection, just as males with larger black masks in WI produced more IgG after controlling for infection. Although, the prevalence of malarial parasites was not related to ornament expression in either population, there are geographic differences in the frequency of various haemosporidian parasites (i.e. *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*) in common yellowthroat populations in the northeastern and northcentral US, which corresponds to our NY and WI study areas, respectively (Pagenkopp *et al.* 2008). This requires more study, but it raises the intriguing possibility that geographic variation in the coevolution of malaria parasites and their hosts (Thompson 1999; Dybdahl & Storfer 2003) might lead to switches in the particular ornament that is most revealing of male quality.

Lastly, it is possible that geographic differences occur as a consequence of co-evolutionary races between male advertisement and female preferences for male ornaments (van Doorn & Weissing 2006). Over evolutionary time, female choice may select for different (and more elaborate) male ornaments as the information content of a particular male ornament changes. Thus, at various times and geographic locations, female choice may be focused on the most revealing male ornament, but the particular ornament preferred by females may vary between populations for arbitrary reasons. We have not found any evidence of consistent temporal changes in the strength of selection on male ornaments, but our studies have been relatively short (< 9 year span).

An increasing number of studies have examined how ornaments are produced and function in different populations (Hill 1994; Endler & Houde 1995; Kwiatkowski & Sullivan 2002; Schwartz & Hendry 2007), and in some cases researchers are finding complicated patterns of selection that vary geographically. For example, in some classic systems such as guppies, female preferences for orange colour on males have long been known to vary with predation risk (Endler 1980). But there is also more recent evidence that the effects of predation differ depending on the types of predators and the physical environment, which affects the conspicuousness of various male ornaments to both predators and potential mates (Millar *et al.* 2006; Schwartz & Hendry 2007). Given this variation, it should probably not be surprising that we found different ornaments are sexually selected in different populations and they indicate similar (survival and IgG) aspects of male quality. To date, however, examples of geographic variation in male ornaments and mating success are relatively rare in birds (e.g. Neuman, Safran & Lovette 2007; Takahashi *et al.* 2008) and there have been few functional studies of the differences in ornaments (Hill 2006b).

In summary, we found that carotenoid-based bib attributes, which are known to be sexually-selected traits in NY, signalled humoral immunity (IgG), and possibly survival. In contrast, only size of the melanin-based mask was correlated positively with humoral immunity in WI, and both mask and bib size were correlated with body mass, which was related to apparent survival. These patterns are generally consistent with previous studies that indicate the yellow bib is the target of sexual selection in NY and the black mask is the target of sexual selection in WI. Thus, similar aspects of male quality appeared to be signalled by different ornaments in different populations. These results are predicted when environmental factors (habitat, carotenoid and parasite abundance) affect the costs and benefits of choosing males with particular ornaments in each location. Additional studies in other locations may help to reveal the causes of these geographic differences.

Acknowledgements

We thank B. Abroe, J. Betz, J. DeCoste, A. DeWitt, I. Levin, J. Maurer, D. Mitchell, M. Pedersen, S. Sollecito, D. Steinberger, C. Taff and T. Tsunekage for assistance in the field or laboratory, and the editor and reviewers for helpful comments. Financial support was provided by a collaborative grant from the National Science Foundation to POD and LAW (IBN-0416536) and CFG (IBN-0412746), and grants from the Swedish Research Councils (VR, Formas), Carl Trygger Foundation and Crafoord Foundation to DH. This research was approved by the UWM (02-03-82 and 03-04-11) and Skidmore College (#69) Animal Care and Use Committees.

References

Badyaev, A.V. & Hill, G.E. (2000) Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biological Journal of the Linnean Society*, **69**, 153–172.

Beadell, J. & Fleischer, R. (2005) A Restriction enzyme-based assay to distinguish between avian hemosporidians. *Journal of Parasitology*, **91**, 683–685.

Blount, J.D., Metcalfe, N.B., Arnold, K.E., Surai, P.F., Devevey, G.L. & Monaghan, P. (2003) Neonatal nutrition, adult antioxidant defences and sexual attractiveness in the zebra finch. *Proceedings of the Royal Society of London Series B*, **270**, 1691–1696.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.

Constantini, D. & Møller, A.P. (2008) Carotenoids are minor antioxidants for birds. *Functional Ecology*, **22**, 367–370.

van Doorn, G.S. & Weissing, F.J. (2006) Sexual conflict and the evolution of female preferences for indicators of male quality. *American Naturalist*, **168**, 742–757.

Ducrest, A.-L., Keller, L. & Roulin, A. (2008) Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution*, **23**, 502–510.

Dunn, P.O., Whittingham, L.A., Freeman-Gallant, C.R. & DeCoste, J. (2008) Geographic variation in the function of ornaments in the common yellowthroat. *Journal of Avian Biology*, **39**, 66–72.

Dybdahl, M.F. & Storfer, A. (2003) Parasite local adaptation: red queen versus suicide king. *Trends in Ecology & Evolution*, **18**, 523–530.

Endler, J.A. (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, **34**, 76–91.

Endler, J.A. & Houde, A.E. (1995) Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution*, **49**, 456–468.

Faivre, B., Gregoire, A., Preault, M., Cezilly, F. & Sorci, G. (2003) Immune activation rapidly mirrored in a secondary sexual trait. *Science*, **300**, 103.

Fargallo, J.A., Laaksonen, T., Korpimäki, E. & Wakamatsu, K. (2007) A melanin-based trait reflects environmental growth conditions of nestling male Eurasian kestrels. *Evolutionary Ecology*, **21**, 157–171.

Ferns, P.N. & Hinsley, S.A. (2008) Carotenoid plumage hue and chroma signal different aspects of individual and habitat quality in tits. *Ibis*, **150**, 152–159.

Fitze, P.S. & Richner, H. (2002) Differential effects of a parasite on ornamental structures based on melanins and carotenoids. *Behavioral Ecology*, **13**, 401–407.

Fitze, P.S., Tschirren, B., Gasparini, J. & Richner, H. (2007) Carotenoid-based plumage colors and immune function: Is there a trade-off for rare carotenoids? *American Naturalist*, **169**, S137–S144.

Fox, D.L. (1976) *Animal Biochromes and Structural Colours*. University of California Press, Berkeley, CA.

Garvin, J.C., Dunn, P.O., Whittingham, L.A., Steeber, D.A. & Hasselquist, D. (2008) Do male ornaments signal immunity in the common yellowthroat? *Behavioral Ecology*, **19**, 54–60.

Goldsby, R.A., Kindt, T.J., Osborne, B.A. & Kuby, J. (2003) *Immunology*. W.H. Freeman, New York.

Gonzalez, G., Sorci, G. & De Lope, F. (1999) Immunocompetence and condition-dependent sexual advertisement in male house sparrows (*Passer domesticus*). *Journal of Animal Ecology*, **68**, 1225.

Gonzalez, G., Sorci, G., Smith, L.C. & deLope, F. (2001) Testosterone and sexual signalling in male house sparrows (Passer domesticus). *Behavioral Ecology and Sociobiology*, **50**, 557–562.

Grether, G.F., Hudon, J. & Millie, D.F. (1999) Carotenoid limitation of sexual coloration along an environmental gradient in guppies. *Proceedings of the Royal Society of London B*, **266**, 1317–1322.

Griffith, S.C., Parker, T.H. & Olson, V.A. (2006) Melanin- versus carotenoid-based sexual signals: is the difference really so black and red? *Animal Behaviour*, **71**, 749–763.

Gustafsson, L., Nordling, D., Andersson, M.S., Sheldon, B.C. & Qvarnström, A. (1994) Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philosophical Transactions of the Royal Society of London B*, **346**, 323–331.

Guzy, M.J. & Ritchison, G. (1999) Common Yellowthroat. *The Birds of North America* (eds A. Poole & F. Gill), Vol. 448, pp. 1–23. The Birds of North America, Philadelphia, PA.

Hasselquist, D., Marsh, J.A., Sherman, P.W. & Wingfield, J.C. (1999) Is avian humoral immunocompetence suppressed by testosterone? *Behavioral Ecology and Sociobiology*, **45**, 167–175.

Hill, G.E. (1994) Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. *Behavioral Ecology*, **5**, 64–73.

Hill, G.E. (2006a). Environmental regulation of ornamental coloration. *Avian Coloration* (eds G.E. Hill & K.J. McGraw), Vol. 1, pp. 507–560. Harvard University Press, Cambridge, MA.

Hill, G.E. (2006b) Female mate choice for ornamental coloration. *Avian Coloration* (eds G.E. Hill & K.J. McGraw), pp. 137–200. Harvard University Press, Cambridge, MA.

Hill, G.E. & Brawner, W.R. (1998) Melanin-based plumage coloration in the house finch is unaffected by coccidial infection. *Proceedings of the Royal Society of London B*, **265**, 1105–1109.

Isobe, T. & Suzuki, K. (1987) Immunoglobulin M and G immune response to *Leucocytozoon caulleryi* in chickens. *Japanese Journal of Veterinary Science*, **49**, 333–339.

Jawor, J.M. & Breitwisch, R. (2003) Melanin ornaments, honesty, and sexual selection. *The Auk*, **120**, 249–265.

Johnstone, R.A. (1996) Multiple displays in animal communication: 'Backup signals' and 'multiple messages'. *Philosophical Transactions of the Royal Society of London B*, **351**, 329–338.

Kwiatkowski, M. & Sullivan, B. (2002) Geographic variation in sexual selection among populations of an iguanid lizard, *Sauromalus obesus* (= *ater*). *Evolution*, **56**, 2039–2051.

Lemke, H., Coutinho, A. & Lange, H. (2004) Lamarkian inheritance by somatically acquired maternal IgG phenotypes. *Trends in Immunology*, **25**, 180–186.

Lozano, G.A. (1994) Carotenoids, parasites, and sexual selection. *Oikos*, **70**, 309–311.

McGraw, K. (2007a) Dietary mineral content influences the expression of melanin-based ornamental coloration. *Behavioral Ecology*, **18**, 1137–1142.

McGraw, K.J. & Ardia, D.R. (2003a) Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. *The American Naturalist*, **162**, 704–712.

McGraw, K.J., Beebee, M.D., Hill, G.E. & Parker, R.S. (2003b) Lutein-based plumage coloration in songbirds is a consequence of selective pigment incorporation into feathers. *Comparative Biochemistry and Physiology B*, **135**, 689–696.

Millar, N.P., Reznick, D.N., Kinnison, M.T. & Hendry, A.P. (2006) Disentangling the selective factors that act on male colour in wild guppies. *Oikos*, **113**, 1–12.

Montgomerie, R. (2006). Analyzing colors. *Bird Coloration* (eds G.E. Hill & K.J. McGraw), Vol. 1, pp. 90–147. Harvard Univ. Press, Cambridge, Massachusetts.

Morales, J., Moreno, J., Merino, S., Tomás, G., Martínez, J. & Garamszegi, L.Z. (2004) Associations between immune parameters, parasitism, and stress in breeding pied flycatcher (*Ficedula hypoleuca*) females. *Canadian Journal of Zoology*, **82**, 1484–1492.

Mundy, N.I. (2006). The genetic basis of color variation. *Avian Coloration* (eds G.E. Hill & K.J. McGraw), Vol. 1, pp. 469–506. Harvard University Press, Cambridge, MA.

Neuman, C.R., Safran, R.J. & Lovette, I.J. (2007) Male tail streamer length does not predict apparent or genetic reproductive success in North American barn swallows *Hirundo rustica erythrogaster*. *Journal of Avian Biology*, **38**, 28–36.

Niecke, M., Rothlaender, S. & Roulin, A. (2003) Why do melanin ornaments signal individual quality? Insights from metal element analysis of barn owl feathers. *Oecologia*, **137**, 153–158.

Norris, K.J. (1990) Female choice and the evolution of the conspicuous plumage coloration of monogamous male great tits. *Behavioral Ecology and Sociobiology*, **26**, 129–138.

Olson, V.A. & Owens, I.P.F. (1998) Costly sexual signals: are carotenoids rare, risky or required? *Trends in Ecology and Evolution*, **13**, 510–514.

Ots, I. & Horak, P. (1998) Health impact of blood parasites in breeding great tits. *Oecologia*, **116**, 441–448.

Pagenkopp, K., Klicka, J., Durrant, K., Garvin, J. & Fleischer, R. (2008) Geographic variation in malarial parasite lineages in the common yellowthroat (*Geothlypis trichas*). *Conservation Genetics*, **9**, 1577–1588.

Pedersen, M., Dunn, P.O. & Whittingham, L.A. (2006) Extra-territorial forays are related to a male ornamental trait in the common yellowthroat. *Animal Behaviour*, **72**, 479–486.

Pyle, P. (1997) *Identification Guide to North American Birds, Part I*. Slate Creek Press, Bolinas, CA.

Roulin, A. (1999) Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. *Behavioral Ecology*, **10**, 688–695.

Roulin, A. & Dijkstra, C. (2003) Genetic and environmental components of variation in eumelanin and phaeomelanin sex-traits in the barn owl. *Heredity*, **90**, 359–364.

Roulin, A., Jungi, T.W. & Dijkstra, C. (2000) Female barn owls (*Tyto alba*) advertise good genes. *Proceedings of the Royal Society of London Series B*, **267**, 937–941.

Roulin, A., Dijkstra, C., Riols, C. & Ducrest, A.-L. (2001) Female- and male-specific signals of quality in the barn owl. *Journal of Evolutionary Biology*, **14**, 255–266.

Roulin, A., Almasi, B., Rossi-Pedruzzi, A., Ducrest, A.-L., Wakamatsu, K., Miksik, I., Blount, J.D., Jenni-Eiermann, S. & Jenni, L. (2008) Corticosterone mediates the condition-dependent component of melanin-based coloration. *Animal Behaviour*, **75**, 1351–1358.

Saino, N., Stradi, R., Ninni, P., Pini, E. & Møller, A.P. (1999) Carotenoid plasma concentration, immune profile, and plumage ornamentation of male barn swallows (*Hirundo rustica*). *American Naturalist*, **154**, 441–448.

SAS (2003) *JMP 5.0.1 User's Guide*. SAS Institute, Cary, NC.

von Schantz, T., Bensch, S., Grahn, M., Hasselquist, D. & Wittzell, H. (1999) Good genes, oxidative stress and condition-dependent sexual signals. *Proceedings of the Royal Society of London B*, **266**, 1–12.

Schluter, D. & Price, T. (1993) Honesty, perception and population divergence in sexually selected traits. *Proceedings of the Royal Society of London, B*, **253**, 118–122.

Schwartz, A.K. & Hendry, A.P. (2007) A test for the parallel co-evolution of male colour and female preference in Trinidadian guppies (*Poecilia reticulata*). *Evolutionary Ecology Research*, **9**, 71–90.

Senar, J.C. (1999) Plumage coloration as a signal of social status. *International Ornithological Congress* (eds N.J. Adams & R. Slotow), Vol. 22, pp. 1669–1686. BirdLife South Africa, Durban, South Africa.

Takahashi, M., Arita, H., Hiraiwa-Hasegawa, M. & Hasegawa, T. (2008) Peahens do not prefer peacocks with more elaborate trains. *Animal Behaviour*, **75**, 1209–1219.

Tarof, S., Dunn, P.O. & Whittingham, L.A. (2005) Dual functions of a melanin-based ornament in the common yellowthroat. *Proceedings of the Royal Society of London, B*, **272**, 1121–1127.

Tella, J.L., Figuerola, J., Negro, J.J., Blanco, G., Rodríguez-Estrella, R., Forero, M.G., Blázquez, M.C., Green, A.J. & Hiraldo, F. (2004) Ecological, morphological and phylogenetic correlates of interspecific variation in plasma carotenoid concentration in birds. *Journal of Evolutionary Biology*, **17**, 156–164.

Thompson, J.N. (1999) Specific hypotheses on the geographic mosaic of coevolution. *The American Naturalist*, **153**, S1–S14.

Thusius, K.J., Dunn, P.O., Peterson, K.A. & Whittingham, L.A. (2001a) Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. *Behavioral Ecology*, **12**, 633–639.

Thusius, K.J., Peterson, K.A., Dunn, P.O. & Whittingham, L.A. (2001b) Male mask size is correlated with mating success in the common yellowthroat. *Animal Behaviour*, **62**, 435–446.

Veiga, J.P. & Puerta, M. (1996) Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proceedings of the Royal Society B: Biological Sciences*, **263**, 229–234.

Received 25 February 2009; accepted 1 June 2009
Handling Editor: Juan Soler