Dual functions of a melanin-based ornament in the common yellowthroat

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Melanin-based ornaments often function as signals in male–male competition, whereas carotenoid-based ornaments appear to be important in female mate choice. This difference in function is thought to occur because carotenoid pigments are more costly to produce than melanins and are thus more reliable indicators of male quality. We examined the role of melanin- and carotenoid-based ornaments in male–male competition and female choice in the common yellowthroat *Geothlypis trichas*, a sexually dichromatic passerine. Males display a black facial mask produced by melanin pigmentation and a bright yellow bib (throat, breast and belly) produced by carotenoid pigmentation. In controlled aviary experiments, mask size was the best predictor of both male–male competition and female mate choice, and, therefore, mask size may be regarded as an ornament of dual function. These dual functions may help to maintain the reliability of mask size as an indicator of male quality, despite the potentially low cost of production. The size of the bib was unrelated to male–male competition or female choice, but there was a tendency for females to prefer males with more colourful bibs. We propose that the black mask is important in competition for territories with other males and for attracting females. Our results highlight the need for more studies of the mechanisms of sexual selection in species with ornaments composed of different pigment types.

Keywords: aviary; female choice; *Geothlypis trichas*; male–male competition; plumage colour; sexual selection

1. INTRODUCTION

In many animals, males possess secondary sexual traits (ornaments) that are used to attract mates. Most explanations for the evolution of male plumage ornaments focus on sexual selection operating through two mechanisms: female choice and male–male competition (reviewed by Andersson 1994). Females may prefer males with more extravagant ornaments if these ornaments are honest advertisements of potential benefits to females (Zahavi 1975; Hamilton & Zuk 1982). For ornaments to be honest, they must be costly to produce or maintain (Zahavi 1975; Kodric-Brown & Brown 1984). In colourful ornaments, honesty may be indicated by the type of pigment (Owens & Hartley 1998; Badyaev & Hill 2000). For example, carotenoid-based ornaments (e.g. red, yellow, orange) are generally thought to be better indicators of male quality (condition or health) than melanin-based (e.g. black, brown) ornaments (Hill & Bawner 1998; Badyaev & Hill 2000). This difference in the honesty of ornaments is thought to arise because carotenoids are more costly to use as signals than melanins and, hence, more indicative of male quality (Badyaev & Hill 2000). Vertebrates acquire carotenoids from food, and carotenoids can be limited in the diet, or costly to absorb and metabolize prior to incorporation into feathers (Fox 1976; Olson & Owens 1998). On the other hand, melanin can be synthesized from amino acids which are generally not considered limiting (Fox 1976; Jawor & Breitwisch 2003). Consequently, it is thought that melanin-based ornaments are less likely to be used by

females in mate choice and more likely to be involved in male–male competition and function as signals of male dominance or fighting ability (reviewed by Senar 1999; Jawor & Breitwisch 2003). However, recent studies suggest that melanins may not be as inexpensive to produce as originally thought, and, as a consequence, melanin-based ornaments may function as honest signals (Jawor & Breitwisch 2003). Our aim in this study was to investigate the roles of female choice and male–male competition in selection on a melanin-based ornament.

We examined the role of female choice and male–male competition on male ornaments in the common yellowthroat, *Geothlypis trichas*, a bird with yellow and black plumage ornaments composed of carotenoid and melanin pigments, respectively. Common yellowthroats (10 g) are socially monogamous, sexually dichromatic passerines. Males display three prominent ornaments: a conspicuous melanin-based black facial mask, a carotenoid-based (primarily lutein; McGraw *et al.* 2003) yellow bib (throat, breast and belly) and a whitish border above the mask. These ornaments are absent (mask and border) or subdued (bib) in females. Previously, we found that males with larger masks arrived earlier on the breeding grounds and were more likely to attract a social mate (29% of males were unmated) and gain extrapair fertilizations (Thusius *et al.* 2001). Therefore, while it appears that male mask size is influenced by sexual selection, the mechanisms (female choice or male–male competition) influencing its expression are not known, and the role of the bib and border in female choice and male–male competition have not been studied previously.

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We performed aviary experiments to determine if female choice and male–male competition were related to ornament expression (both natural and manipulated) in male common yellowthroats. We examined female choice and male–male competition separately and then in combination to determine if these mechanisms favoured the same or different ornaments. To date, relatively few studies have investigated the role of plumage ornaments in relation to both male–male competition and female choice (Johnson 1988; Sorenson & Derrickson 1994), although there is evidence that both mechanisms may operate on the same ornament (Borgia 1979; Kodric-Brown & Brown 1984; Berglund *et al.* 1996).

2. METHODS

(a) Plumage ornaments

We conducted experiments in an outdoor aviary from May to June 2002 to 2004 at the University of Wisconsin–Milwaukee Field Station in Saukville, Wisconsin, USA. A description of common yellowthroat breeding biology and general field methods can be found in Thusius *et al.* (2001). We captured birds using mist nets and measured their body mass (to nearest 0.1 g), tarsus length (to nearest 0.1 mm) and male plumage ornaments, including the size of the mask, bib and border and the colour of the bib. Prior to release in the aviary, we used a Sony video camera to record the ornaments of males in front of a grid of 1 cm grey and white squares. Males were held in standardized positions (left, right profiles and on back with beak held down) and recorded from 40 cm in a darkened box with a 3 W halogen video light. We captured two still images of each side of the mask and border (four images) and two images of the bib. Ornament size was estimated by tracing the outline of each ornament using image analysis software (see Thusius *et al.* 2001 for more details). We defined mask size and border size (mm²) as the sum of the mean areas, respectively, for each side of the head. All size estimates were performed by two authors and averaged for a final estimate of ornament size. Repeatability between persons, calculated using intraclass correlation coefficients (Zar 1999), was high for mask ($r=0.99$), bib ($r=0.98$) and border size ($r=0.98$).

We estimated the hue, saturation and brightness of the bib using Adobe Photoshop Elements v.2.0 (Adobe Systems 2002). Images were standardized for colour and brightness using a grey square included in each image and calibrated the grey point tool so that the red, green and blue channels were set to 72, 86 and 110, respectively, on a scale of 0–255 (cf. Massaro *et al.* 2003). The eyedropper tool (set to average 5×5 pixels) was then placed over three points, each in the centre of the chin, neck and breast. Hue (0, red; 60, yellow; 120, green), saturation (%), and brightness (%) at each of these nine points were recorded and averaged. We entered these three variables into a principal components analysis (PCA) to yield a single bib colour score (PC I) that was used in analyses. The first principal component explained 50% of bib colour variation and loaded positively for hue (0.51) and brightness (0.58) and negatively for saturation (−0.63).

(b) Aviary experiments

Adult birds were captured and placed in a large outdoor aviary (figure 1) for up to 24 h. Birds acclimated in separate compartments for at least 1 h before the first trials began and were allowed at least 15 min to acclimate after moving

Figure 1. Floor plan of the aviary ($8 \times 8 \times 2.7$ m) showing the male–male competition compartment (east side), three central male compartments and the compartment (west side) in which the female was held during the preference (II) and mate choice (III) experiments. The female compartment consisted of a 30 cm-wide ‘choice’ area (shaded) and a neutral area (unshaded). Dotted lines represent 0.5 cm mesh hardware cloth walls. Thin solid lines indicate plywood walls. Doors are shown by thick solid lines. Food and water dishes were located centrally in each compartment.

to a new compartment between experiments. Observations were made from blinds 5 m east and west of the aviary. We captured three new birds (two males, one female) for each trial to avoid pseudoreplication. It was unlikely that birds in the experiment had much prior experience with each other as the trials were conducted early in the season (usually before laying) and capture distances between birds (range 125–1232 m) were at least 2.8 times larger than the average territory diameter (mean = 45 m).

Trials consisted of three experiments: (I) male–male competition; (II) female preference; and (III) mate choice (simultaneous male–male competition and female preference). Experiments were conducted in sequence with unmanipulated males. We also conducted the same experiments with males that had the size of their masks manipulated (see §2c). These experiments allowed us to examine mask size independent of other male characteristics, such as age, that could also influence behaviour (older males tend to have larger masks; Thusius *et al.* 2001). In the case of manipulated males, we began with experiments II and III, and conducted experiment I separately with males that had not interacted previously. Thus, in our trials with unmanipulated males, there could have been carryover effects from the male–male competition experiment (I) into the female preference and mate choice experiments (II and III), but this was not possible in trials in which mask size was manipulated. Adults typically gained weight during captivity (males: 0.3 ± 0.1 g, $n=88$; females: 0.03 ± 0.2 g, $n=19$), and appeared to breed on their territories after release.

(i) Experiment I

To examine the role of ornaments in male–male competition, we performed experiments with pairs of males (dyads). We housed dyads in one large compartment in the aviary, and recorded agonistic interactions for 3 h (for 2 h

on the afternoon the two males were caught and for 1 h the following morning). These interactions included the number of fights (physical contact), chases and perch supplants (flying/hopping to another male's position without a chase) initiated by each male. A male that initiated a fight, chase or supplant always won the interaction. From the sum of these behaviours, we calculated a dominance index (interactions per hour) for each male. The first principal component from a PCA of fights, chases and supplants explained 47% of the variation in agonistic behaviour and was correlated highly with the dominance index ($r^2=0.84$, $p<0.0001$). For simplicity, we used the dominance index in subsequent analyses. We also quantified the rate of male singing, chipping and feeding.

(ii) Experiment II

Following experiment I, the two males were placed in separate compartments (chosen randomly) in the centre of the aviary (figure 1). One central compartment remained empty as a control. Next, we introduced one female, who had not observed the males previously, into a large compartment next to both males where she could see the males through wire mesh, but the males were hidden from each other by plywood walls (figure 1). This experiment allowed us to determine female preference for males with different ornamental traits in the absence of male–male competition. Female preference was estimated as the total time during a 1 h observation session that the female spent in a 30 cm wide strip in front of the compartment of either male (figure 1). Note that most of the female's compartment was a neutral area where we did not consider the female to be showing any preference. The 'preferred' male was the male with whom the female spent the most time. Females typically made clear choices of males as they spent an average of $86 \pm 2.6\%$ of their preference time near the preferred male ($n=22$ trials; range 55–100%). The female preference and mate choice experiments (II and III) were all conducted before laying to ensure that females were sexually receptive.

(iii) Experiment III

After experiment II, the doors between the three central compartments and the large female compartment were opened allowing the three birds access to each other. This design allowed simultaneous observation of male–male competition and female choice. After a 15 min acclimation period, we began a 1 h observation session in which we recorded the same behavioural variables described in experiments I and II. In this experiment, a female was considered to prefer a male if she entered the male's central compartment (and the male remained inside), entered the preference area in front of a male's compartment (and the male remained inside) or was within 30 cm of a male when both birds were in the large compartment. We also recorded the elapsed time before the female and a male approached each other (latency to respond), and the bird that initiated the approach. The 'chosen' male was the male with whom the female spent the most time.

(c) Mask manipulations

In separate aviary trials using different birds, we manipulated the mask size of males because this was the only ornament associated with male–male competition and female preference in trials with unmanipulated males (see §3). One randomly chosen male in each dyad had his mask enlarged,

while the other male had his mask reduced. To increase mask size, we applied black ink from a felt-tip marker to the ventral edge of the black mask (where the mask meets the yellow throat), and then applied a line of yellow acrylic paint next to this enlarged region. To reduce mask size, we applied a line of yellow paint to the ventral edge of the mask. Note that both enlarged and reduced males had paint applied in a thin layer on their throats to control for potential feather matting that might have affected behavioural interactions. However, our observations indicated no difference in behaviour between unmanipulated and manipulated birds (see §3). Analysis of the ink and paint with a spectrometer revealed a close match with the natural mask and throat colours (S. A. Tarof *et al.*, unpublished work). Except for the mask size adjustment, manipulated and unmanipulated birds were handled identically.

We enlarged masks within the natural size range (269–501 mm² in this sample) to approximately 447 mm² (the median of the upper third of mask size, 357–501 mm²) and reduced it to approximately 286 mm² (the median of the lower third of mask size, 269–314 mm²). Masks were enlarged by $22 \pm 3.0\%$ of their original size to an average of 404 ± 20.4 mm² and reduced by $21 \pm 2.5\%$ of their original size to an average of 288 ± 11.8 mm². After manipulation, the mask of enlarged males averaged $42 \pm 6.2\%$ larger than that of reduced males. The magnitude of our mask manipulations was generally random with respect to the natural (pre-manipulation) mask size; there was no significant relationship between the percentage of change in mask size (before and after manipulation) and the natural mask size ($r=-0.32$, $n=36$, $p=0.06$). The negative trend was driven primarily by two males with naturally large masks (482–501 mm²) that received large decreases in mask size, which makes the experiment more conservative.

We used multiple logistic regression in JMP (SAS Institute 1995) to analyse male dominance (1 for dominant, 0 for subordinate) in relation to mask, bib and border size, bib colour and tarsus length (an index of body size). For analysis of female preferences, we used paired *t*-tests with Bonferroni corrections to our significance level (Rice 1989) to adjust for multiple tests. In these analyses, we could not use logistic regression because of low sample sizes. Means are presented with standard errors ($\pm$ s.e.m.).

3. RESULTS

(a) Unmanipulated males

(i) Experiment I: male–male competition

Males with larger masks were dominant in 15 out of 20 trials (binomial test, $p=0.015$). Mask size differed between dominant and subordinate males by 51.5 ± 10.0 mm², which was 16% of mean mask size ($n=40$ males). Dominant males won 11.7 ± 1.8 interactions per hour and subordinates won 2.4 ± 0.9 interactions per hour (paired $t_{19}=6.7$, $p<0.0001$). Only mask size was a significant predictor of dominance (dominant, 1; subordinate, 0) in a multiple logistic regression that included all measured ornaments (see table 1) and tarsus length as an index of body size (likelihood $\chi^2=5.9$, d.f.=1, $p=0.015$). Mask size was not correlated with border size, body mass, body condition, tarsus or tail length (all $p>0.10$), but tended to correlate positively with bib size ($r=0.10$, $n=40$, $p=0.053$) and also with wing chord length ($r=0.51$, $p=0.001$). Bib size was only

Figure 2. Female preference time (min per h) for males in experiments II and III with unmanipulated (*a* and *c*, respectively) and experimentally enlarged and reduced (*b* and *d*, respectively) masks. Bars indicate 1 s.e.m.

Table 1. Ornament and tarsus size of dominant and subordinate male common yellowthroats in the male–male competition experiment (I; unmanipulated birds; $n=20$ trials).

	dominant		subordinate		multiple logistic regression	
	mean	s.e.m.	mean	s.e.m.	χ^2	p
mask size	334.5	11.42	297.6	9.46	5.90	0.015
bib size	653.7	33.94	673.0	38.3	1.54	0.21
border size	128.3	7.94	107.6	10.1	0.66	0.41
bib colour (PCI)	0.01	0.229	−0.01	0.31	0.20	0.65
tarsus length	20.6	0.14	20.6	0.13	0.16	0.69

related positively to wing chord length ($r=0.40, p=0.01$). Border size was not correlated with other morphological variables (all $p>0.10$).

(ii) Experiment II: female preference

Females preferred the male with the larger mask in all 10 trials with unmanipulated males (binomial test, $p=0.01$). Females spent more time near the male with the larger mask than with males with the smaller mask (paired $t_9=4.0, p=0.003$; figure 2*a*). Mask size of the preferred males was larger than that of non-preferred males after a Bonferroni correction for five tests ($p=0.004$; table 2). In contrast, bib and border size and tarsus length did not differ significantly between preferred and non-preferred males (table 2). There was a tendency for females to prefer males with more colourful bibs (PCI), but the difference was not significant after adjusting for multiple tests

(table 2). In addition, males did not differ in the rate of singing, chipping, feeding or soliciting copulation (all $p>0.14$), which suggests that there were no differences in behaviour (including carryover effects from experiment I) that might have influenced female preferences.

(iii) Experiment III: mate choice

After experiment II, the doors between aviary compartments were opened and the female and both males were able to interact. Thus, experiment III was not independent of experiment II, but it allowed us to determine if female mate preferences remained the same when males could interact with each other and the female. Indeed, females were consistent; as in experiment II, they preferred the male with the larger mask in all 10 trials. Females spent more time near the male with the larger than the smaller mask (paired $t_9=5.8, p<0.001$; figure 2*c*). As in

Table 2. Ornament and tarsus size of preferred and non-preferred males in the female preference experiment (II; unmanipulated birds; $n=10$ trials). (Results were the same for the mate choice experiment (III) because females preferred the same males in both experiments).

	preferred male		non-preferred male		paired t	p
	mean	s.e.m.	mean	s.e.m.		
mask size	361.1	16.37	302.9	10.27	3.8	0.004 ^a
bib size	691.0	32.35	690.6	69.78	0.01	0.99
border size	125.3	12.85	116.7	16.05	0.37	0.72
bib colour (PCI)	0.46	0.36	-0.54	0.22	2.6	0.029 ^b
tarsus length	20.8	0.16	20.8	0.24	0.7	0.95

^a Significant after Bonferroni correction for five tests ($\alpha=0.01$).

^b Non-significant after Bonferroni correction.

experiment II, the mask sizes of preferred males was larger than those of non-preferred males because females preferred the same males in both experiments (see table 2).

Most females approached the male with the larger mask soon after the doors were opened. On average, females moved towards the male with a larger mask within 4.6 (± 2.2) min (range 0–17 min), and seven of 10 females entered the compartment of the male with the larger mask within 2 min. The male with the smaller mask either moved into the empty female's preference compartment (six males) or stayed in his own central compartment (four males). In experiment III, males with larger masks remained dominant, but males rarely interacted with each other, and thus rates of male–male aggression were over 10 times lower (0.5 ± 1.3 interactions per hour) than in experiment I (7.0 ± 1.0 interactions per hour; t -test: $t_{62}=4.1$, $n=64$, $p=0.0001$).

(b) Males with manipulated masks

(i) Experiment I: male–male competition

In the mask manipulation experiments, the male–male competition trials were conducted after the female preference and mate choice trials, and these males had no prior experience together. Overall, males with experimentally enlarged masks had a greater dominance index than males with reduced masks in 13 out of 18 trials (binomial test, $p=0.033$). However, between dyads of males, the dominance index of males with enlarged (14.0 ± 9.3 interactions per hour), and reduced (6.9 ± 3.4 interactions per hour) masks did not differ (paired $t_{17}=0.67$, $p=0.51$). Upon closer inspection, we found that the total number of agonistic interactions was greater when males with reduced masks won the trial (49.6 ± 5.2 interactions) than when males with enlarged masks won the trial (20.5 ± 6.9 interactions; $t_{16}=4.4$, $p<0.001$). This suggests that males with enlarged masks were more likely to lose if they had interacted, and had thus been challenged, more often by the male with the reduced mask. In contrast, there was no such trend in the experiment with unmanipulated males (i.e. males with larger masks were not more likely to win or lose after more interactions; $t_{18}=1.4$, $p=0.17$). If males establish dominance based on cues that are correlated with the original (pre-manipulation) mask size, then we would expect dominance to be associated with original mask size. However, the pre-manipulation mask size of dominant

(337 ± 8.1 mm²) and subordinate (360 ± 14.4 mm²) males did not differ (paired $t_{17}=1.5$, $p=0.15$).

(ii) Experiment II: female preference

Females preferred the male with the enlarged mask in 11 out of 12 trials (binomial test, $p=0.003$), and they spent more time near the male with the enlarged (23.1 ± 4.5 min) than the reduced (7.5 ± 3.1 min) mask (paired $t_{11}=2.5$, $p=0.028$; figure 2b). The original (pre-manipulation) mask size of enlarged (293 ± 8.1 mm²) and reduced (301 ± 14.4 mm²) males did not differ (paired $t_{11}=0.52$, $p=0.62$).

(iii) Experiment III: mate choice

Females spent more time near the male with the enlarged than the reduced mask in nine out of 12 trials (binomial test, $p=0.054$). In the three other trials, females spent their time foraging away from both males and thus did not show a preference. Excluding these three trials, females spent more time near the male with the enlarged than the reduced mask (paired $t_8=3.8$, $p=0.005$; figure 2d). In two trials, females copulated with males that had enlarged masks.

4. DISCUSSION

Our aviary experiments revealed that the melanin-based facial mask of common yellowthroats was associated with both male–male competition and female mate choice. The size and colour of the bib and size of the border were not related significantly to either type of behaviour. Observations from the wild indicate that males with larger masks are more likely to establish a territory early in the season, gain a social mate and acquire extrapair fertilizations (Thusius *et al.* 2001). These results are unusual because melanin-based ornaments have rarely been associated with female choice in birds (see Jawor & Breitwisch 2003). Most theoretical and empirical studies have viewed the evolution of male ornaments from the standpoint of female choice, and have not considered its interaction with male–male competition (Berglund *et al.* 1996). Our study indicates that the same ornament (mask size) is involved in both male–male competition and female choice. Although there is evidence that ornaments often have such dual roles, this is frequently overlooked in studies of sexual selection (reviewed by Berglund *et al.* 1996). The dual function of male ornaments has important implications because male–male competition provides a potential means of maintaining the honesty of ornaments for

females choosing mates, even when the ornament is relatively inexpensive to produce (Kodric-Brown & Brown 1984).

Melanin-based ornaments could maintain their honesty as signals of male quality if they are badges of status (Rohwer 1975) that are continually tested by competitors (reviewed by Senar 1999). In other words, they could be costly to maintain rather than to produce. Male common yellowthroats appear to use their black facial mask in agonistic encounters with other males throughout the breeding season (Lewis 1972; S. A. Tarof *et al.*, unpublished work). Males with larger masks may face higher frequencies of male aggression over territories, food or mates. In our mask manipulation experiment, males with enlarged masks (i.e. a dishonest signal on average) were more likely to lose if there were more agonistic interactions, supporting the prediction that cheaters will eventually lose. Game theory models predict that male–male competition can maintain the honesty of ornaments even when they are relatively inexpensive to produce (Maynard Smith & Harper 1988). Thus, inexpensive melanin-based ornaments can be reliable signals for mate choice if they are constantly tested in male–male competition. This provides a relatively straightforward and widespread mechanism for the maintenance of ornaments used in mate choice (Berglund *et al.* 1996). Most research has focused on carotenoid-based ornaments, and thus it remains unclear how widespread is the use of melanin-based ornaments in mate choice.

In contrast to the melanin-based mask, we found no strong relationships between the colour or size of the carotenoid-based bib and either female choice or male–male competition. These findings are surprising given the number of studies that have found that females prefer males based largely on the colour or size of carotenoid-based ornaments in birds and fish (Endler & Houde 1995; Brooks & Coultridge 1999; Badyaev & Hill 2000; Jawor *et al.* 2003). It is possible that a relationship exists between bib colour and mate choice in common yellowthroats, as we found that females tended to prefer unmanipulated males with greater PCI scores for bib colour (primarily greater hue (more yellow) and brightness; table 2; this was not significant after correcting for multiple tests). PCI was not correlated with mask size ($r=0.12$, $n=20$, $p=0.63$), so if bib colour is in fact a cue for mate choice, then it would appear to have an independent effect, suggesting that females might use multiple ornaments to choose mates. Thus, further study of the function of bib colour is needed.

Few studies of captive birds have examined simultaneously the roles of male ornaments in both female choice and male–male competition. In several aviary studies male–male competition and female choice have appeared to favour different traits (e.g. Johnson 1988; Sorenson & Derrickson 1994). In contrast, the same ornament (mask size) appeared to be involved in female choice and male–male competition in common yellowthroats, despite the presence of two other prominent ornaments. Berglund *et al.* (1996) reviewed studies of male ornaments and found that they often appear to serve as signals in both female choice and male–male competition. However, in many cases, the evidence is somewhat ambiguous, as ornaments assigned a role in female choice were simply correlated with male mating success in

the wild, which could also be influenced by male–male competition. Thus, more controlled studies in captivity that examine female choice and male–male competition separately are needed to obtain a clearer understanding of how selection maintains male ornaments.

Lastly, we address some potential criticisms of this study. As in any study of captive animals, it could be argued that the results are not related directly to the behaviours of interest in the wild. For example, the male–male competition observed in the aviary may actually be related to competition over food, rather than competition for territories and mates. Several lines of evidence suggest that this is not the case. Our previous field studies of the same population indicate that males with larger masks establish a territory and pair with a mate earlier in the spring (Thusius *et al.* 2001). Furthermore, in one of the first experimental studies of male ornaments in birds, Lewis (1972) covered the entire mask of male common yellowthroats with greenish-yellow paint so they resembled females. Subsequently, these males had more aggressive interactions with neighbouring males. Our aviary results are consistent with these field studies suggesting that mask size plays a role in male–male competition for territories and mates. Similarly, it could be argued that the female behaviour we observed was not actually indicative of mate preferences or choice, but rather of female's preference to be near dominant males that may, for example, provide greater protection from harassment or predators. However, females did not observe male dominance interactions prior to the preference experiment (II), and, in some cases, females copulated with their preferred male in experiment III. Furthermore, mask size is related to extrapair fertilization success in the wild (Thusius *et al.* 2001). Finally, it is possible that the results of experiment II with unmanipulated males were affected by the outcome of male–male interactions in experiment I. However, our mask manipulation experiments, in which males had no prior interaction, eliminated any possible carry-over effects, and revealed that female preferences were based on mask size rather than another ornament or characteristic such as age.

In conclusion, our results suggest that the mask of common yellowthroats is important in both male–male competition and female choice, and thus the mask may be regarded as an ornament of dual function. Two main implications of our study are: (i) that male ornaments can have dual functions, which may help to maintain their honesty, despite a low cost of production; and (ii) that melanin-based ornaments may be the target of female mate choice, even in species that also have carotenoid-based ornaments. The generality of these results needs to be addressed in other species with controlled aviary experiments.

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