Geographic variation in the function of ornaments in the common yellowthroat *Geothlypis trichas*

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We used controlled aviary experiments to study the role of male ornaments in male-male competition and female choice in the common yellowthroat *Geothlypis trichas*, a sexually dichromatic warbler. Previous aviary studies in Wisconsin, USA, indicated that males with larger black facial masks were dominant over males with smaller masks and preferred by females in mate choice experiments. In this study, we replicated those experiments in a population in New York, USA, where male mating success was related more consistently to the size of the yellow bib (throat, breast, and belly) than to the size of the mask. Similar to the study in Wisconsin, we found that males with larger masks were more likely to be dominant in New York, however, we found that males with larger bibs were preferred by females in New York, and there was no significant preference for males with larger masks. These results are consistent with the hypothesis that carotenoid-based ornaments are selected by female choice and melanin-based ornaments are selected by male-male competition. However, the pattern of female choice appears to vary between New York and Wisconsin. This geographic difference could be related to a variety of environmental factors (habitat, carotenoid and parasite abundance) that affect the costs and benefits of choosing males with particular ornaments in each location.

Several theoretical models of female choice predict that females should base their choice of mate on the single most efficient (i.e., detectable and honest) male ornament (Schluter and Price 1993, Johnstone 1996). However, males of many species possess several ornaments. One explanation for the evolution of multiple ornaments is that different ornaments are favored by different selective mechanisms, in particular, female choice and male-male competition. For example, in the red-collared widowbird *Euplectes ardens* female choice favors males with longer tails, and male-male competition for territories favors males with larger red collars on their chest (Pryke et al. 2001, Andersson et al. 2002). Thus, one of the first steps to understanding selection on ornamental traits is to determine whether the traits are favored by female choice or male-male competition, and, in the case of multiple ornaments, to determine if the same type of selection operates on each ornament.

Female choice may act on different ornaments than male-male competition, particularly when some ornaments are more revealing of male quality than others. For example, in species with both carotenoid (red, yellow, orange) and melanin (black, brown)-based ornaments, it appears that females often choose males based on the expression of carotenoid-based, rather than melanin-based, ornaments (Johnson et al. 1993, Brooks and Couldridge 1999, Badyaev and Hill 2000, Jawor and Breitwisch 2003). This pattern is predicted because ornaments produced from carotenoid pigments are generally thought to be better indicators of male quality (condition or health) than ornaments produced from melanin pigments (Hill and Brawner 1998, Badyaev and Hill 2000). This difference in the honesty of ornaments is thought to arise because vertebrates must acquire carotenoids directly from food and carotenoids are often limiting in the diet, whereas melanins can be synthesized by the individual from more commonly occurring compounds (Fox 1976, Olson and Owens 1998). As a consequence, melanin-based ornaments may be less revealing indicators of male quality and used less often in mate choice. Instead, they may be involved more often in male-male competition, where they function as signals of male dominance or fighting ability (Rohwer 1975, Rohwer 1982, Senar 1999). However, some recent studies suggest melanins may not be as inexpensive to produce as thought originally (Jawor and Breitwisch 2003, Griffith et al. 2006). Furthermore, if melanin-based ornaments are continually tested by competitors, then the cost of maintaining the ornament, rather than producing it, may ensure that it functions as an honest signal for mate choice (Tarof et al. 2005). Thus, it is possible that any type of pigmentation could be used in ornaments to signal status or mate quality. Our aim in this study was to investigate the roles of female choice and male-male competition in selection on both melanin-and carotenoid-based ornaments.
In previous studies in Wisconsin, USA, we examined the role of female choice and male-male competition on male ornamentation in the common yellowthroat *Geothlypis trichas*, a warbler with a yellow (carotenoid-based) bib (McGraw et al. 2003) and a black (melanin-based) facial mask. Females lack the mask and typically have a smaller and more subdued bib. Based on aviary experiments, we found that males with larger masks were favored in both male-male competition and female mate choice and, thus, the mask has dual functions (Tarof et al. 2005). Competition among males may help to enforce the reliability of mask size as an indicator of male quality, despite a potentially lower cost of production. We have also found that males with larger masks are more likely to gain social and extra-pair mates (Thusius et al. 2001), and fertile females are more likely to visit neighboring males with larger masks than their own social mate (Pedersen et al. 2006). To date, we have found little evidence that male-male competition or female choice favored males with larger or more colorful yellow bibs in Wisconsin.

However, in a population in northern New York, USA, we have found that males with larger bibs are consistently more likely to gain a social mate than males with smaller bibs (C. Freeman-Gallant unpubl. data). Although mask size was related positively to bib size, it was related to pairing success in just one of three years, and, thus, mask size appears to be a less consistent target of selection in New York than in Wisconsin. These results suggest that selection varies in intensity or targets (mask or bib) in different populations. This case is particularly interesting because the ornaments of common yellowthroats appear to be similar in both populations (they belong to the same subspecies), yet female choice appears to be acting more consistently on a carotenoid-based ornament in one population and a melanin-based ornament in the other. Note that other studies have found differences in sexual selection between populations, but in most cases, male ornamentation also differs between populations (e.g., Endler and Houde 1995). In this paper, we examine how male ornaments function in female choice and male-male competition in New York using the same aviary experiments we conducted previously in Wisconsin (Tarof et al. 2005). In particular, we wanted to determine if females in New York prefer males with larger bibs, rather than masks, and how the mask and bib are used in male-male competition. Our goal, then, was to identify more precisely the targets and mechanisms of selection on ornaments in each population, so we can begin to develop hypotheses for why selection differs between populations.

**Methods**

**Aviary experiments**

We conducted experiments in a large outdoor aviary (5.4 × 8 m) near Skidmore College in Saratoga Springs, New York, USA. The aviary and procedures were identical to our previous experiments in Wisconsin (see Tarof et al. 2005), except for a change in the order of experiments and a shorter time for the male-male competition experiment (see below). Trials were conducted during 14–27 May 2005 and 10–20 May 2006.

Birds were caught in nearby wetlands, weighed and transported to the aviary within 20 min where they were allowed to acclimate for at least 1 h. Birds were also allowed at least 15 min to acclimate after moving to a new compartment between experiments (see below). Observations were made from a blind 5 m from 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 (before laying) and we captured birds from at least two territories apart (most extra-territorial forays are to immediate neighbors, Pedersen et al. 2006).

Most trials consisted of both a female preference (n = 18 trials) and male-male competition (n = 17 trials) experiment (n = 22 trials total). In the female preference experiment, which was conducted first, a single female was placed in a large compartment (2.7 × 8 m) and allowed to choose between two males placed in adjoining but separate compartments (each 2.7 × 2.7 m). The female could observe the males through a wire mesh wall and the males could see the female, but the males were hidden from each other by plywood walls. Males rarely sang, so it is unlikely this behavior influenced our results. Males were assigned randomly to two of three compartments adjoining the female’s compartment, so there was always one male compartment that remained empty as a control. This experiment allowed us to determine female preference for males 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. Note that most of the female’s compartment (93%) 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. These experiments were all conducted before laying to ensure that females were sexually receptive. After the 1 h female preference trial, the female was returned to her territory and released, and the two males were then allowed to interact in a second experiment that examined the role of male ornaments in male-male competition.

In the male-male competition experiment, we placed pairs of males in the large aviary compartment (2.7 × 8 m) and recorded agonistic interactions for 1 h (we performed this experiment over 2 h in Wisconsin). 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 behaviors, we calculated a dominance index (interactions/h) for each male. Food and water were supplied ad lib in each compartment in an area away from the preference zone. Overall, adults gained weight during captivity (males: 0.46 ± 0.06 g, n = 43, t = 7.4, P < 0.001; females: 0.30 ± 0.13 g, n = 18, t = 2.36, P = 0.049) and were returned to their territories within 5 h of their initial capture. All birds appeared healthy at the end of the experiments.
Ornament measurements

After the aviary experiment, we remeasured body mass (to nearest 0.1 g) and measured tarsus and wing length (to nearest 0.1 mm). We also used a video camera to record pictures of the ornaments of males held in standardized positions (left, right profiles and on back with beak held down) in front of a grid of 1 cm grey and white squares. Later, we captured still images from the videotape and imported them into image analysis software (ImageJ 1.32j; http://rsb.info.nih.gov/ij). After scaling the image with the 1 cm grid, we measured two still images of each side of the head (4 images) and two images of the bib by tracing the outline of each ornament. We defined mask size (mm²) as the sum of size estimates from the left and right sides of the head (averaged for the two images on each side). All size estimates were performed by two authors and averaged for a final estimate of ornament size. Repeatability between persons, calculated using the intraclass correlation coefficient (Zar 1999), was high for mask ($r_{ ICC} = 0.94$, $P < 0.001$), and bib size ($r = 0.94$, $P < 0.001$). Prior to release from the aviary, we plucked approximately five central breast feathers to estimate the hue, saturation, and brightness of the bib using a spectrometer (USB2000, Ocean Optics, Dunedin, Florida). Reflectance spectra from the yellow bib of common yellowthroats showed one peak in the ultraviolet (UV, 320 to 400 nm), a dip from 400 to 500 nm and then a high plateau of reflectance above 520 nm. We estimated mean brightness (mean of reflectance values) in both the UV and yellow (550 to 625 nm) ranges. Hue was estimated as the wavelength of maximal reflectance in the 320 to 700 nm range, and saturation was estimated as the sum of the reflectance values from 550 to 625 nm (yellow) divided by total brightness (sum of reflectance from 320 to 700 nm, see Montgomerie 2005 for review).

Results

In the female preference experiment, females spent more time near the male with the larger than the smaller yellow bib (paired $t_{17} = 3.44$, $P = 0.003$; Fig. 1). Females did not spend more time near the male with the larger mask (paired $t_{17} = 0.61$, $P = 0.55$; Fig. 1), nor with males whose bibs had greater hue (paired $t_{17} = .53$, $P = 0.61$), saturation (paired $t_{17} = 1.79$, $P = 0.09$), or brightness in either the ultraviolet (paired $t_{17} = 1.17$, $P = 0.26$) or yellow range (paired $t_{17} = 0.37$, $P = 0.71$). The preferred male had a larger bib in 16 of 18 trials (binomial test, $P < 0.001$), while the preferred male had a larger mask in 12 of 18 trials (binomial test, $P = 0.071$). Similar patterns of mate preference were observed when we compared the ornaments of preferred and non-preferred males (Table 1). On average, bibs of the two males in each trial differed by $175 \pm 31.1$ mm², or 28% of mean bib size ($627$ mm²), and masks differed by $35 \pm 5.3$ mm², or 12% of mean mask size ($292$ mm²). Bib and...

Fig. 1. Female preference time (min) for males with larger and smaller bibs in dichotomous choice trials in New York (a, paired $t_{17} = 3.44$, $P = 0.003$) and Wisconsin (b, paired $t_{9} = 0.45$, $P = 0.66$), and larger and smaller masks in New York (c, paired $t_{17} = 0.61$, $P = 0.55$) and Wisconsin (d, paired $t_{9} = 4.0$, $P = 0.003$). Bars indicate one SE. Wisconsin data are from Tarof et al. (2005).
mask size were not correlated in this sample ($r = 0.17, n = 36, P = 0.31$), although they were correlated in a larger sample from both this New York population (C. Freeman-Gallant unpubl. data) and the Wisconsin population (P. Dunn unpubl. data). Overall, male bib and mask size were not correlated with body mass, wing or tarsus length or bib hue, saturation or brightness (all $P > 0.10$).

Females typically made clear choices of a particular male as they spent an average of $81 \pm 3.6\%$ of their preference time near the preferred male ($n = 18$ trials; range $51–100\%$). Although the preference area was just $7\%$ of the total area of the compartment available to females, all females except one spent at least $20\%$ of their time in a preference area (preference time averaged $24 \pm 2.8$ min, range: $6–54$ min). Our results were qualitatively similar after deleting the trial in which the female spent only $10\%$ of her time in the preference area. Females showed no bias in preference for a particular male compartment (left, right or center; likelihood chi-square = $3.33, df = 2, P = 0.19$).

There was no evidence that females preferred the male that was dominant in the subsequent male-male competition trial. Note that the female preference trials were always conducted before the male-male competition trials, so females could not see any male interactions; however, it is conceivable that females could base their mate choice on subtle cues that were also associated with male dominance. Nonetheless, there was no significant preference for the dominant male (binomial test, $P = 0.23$; preferred in 6 of 11 experiments in which we conducted both female preference and male-male competition trials; two experiments were excluded because the males did not interact).

After the female preference trials, the female was removed and males were released into the large compartment of the aviary for one hour where they could interact. In these male-male competition trials, males with larger masks were dominant in 13 of 15 trials (binomial test, $P = 0.003$). As noted above, we excluded two trials where the males did not interact and dominance could not be determined. Mask size differed between dominant and subordinate males by an average $26.6 \pm 4.7$ mm$^2$ ($n = 15$ pairs), which was $9\%$ of mean mask size (297 mm$^2$). Males with larger masks also had a higher dominance score ($5.6 \pm 0.9$ interactions/h) than males with smaller masks ($1.5 \pm 1.1$ interactions/h; paired $t_{14} = 2.4, P = 0.029$). Mask size increases with age (Thusius et al. 2001), so the difference in dominance might also be related to male age. However, in a previous experiment we manipulated the size of the mask and found similar effects of mask size on dominance (Tarof et al. 2005), which suggests that mask size influences male-male competition independent of male age. In contrast, males with larger bibs won eight of 15 trials (binomial test, $P = 0.20$) and they did not have a higher dominance score ($3.5 \pm 1.0$ interactions/h) than males with smaller bibs ($3.6 \pm 1.2$ interactions/h; paired $t_{14} = 0.07, P = 0.95$). All interactions, except for one, were won by the bird that was later considered dominant. In the one exception, the subordinate supplanted the dominant once (in 11 other interactions the dominant chased or supplanted this subordinate).

Our results suggest that females prefer males with larger yellow bibs in New York (this study) and larger black masks in Wisconsin (Tarof et al. 2005). Next, we examined whether there were geographic differences in the size and variability of these ornaments that might explain differences in female preferences. Among aviary birds, masks were both smaller and less variable in New York than in Wisconsin (CV of 9.8 and 15.8, respectively, Table 2). However, there was no difference between populations in the mean size or variability of the bib (CV of 24.1 in both populations, Table 2). Thus, female choice appeared to be associated with the relatively more variable trait in New York (bib size was more variable than mask size), but this does not explain why females in Wisconsin appeared to base their preferences on mask size, which was less variable than bib size.

### Table 1. Traits of preferred and non-preferred males in the female preference experiment ($n = 18$ trials).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Preferred male</th>
<th>Non-preferred male</th>
<th>Paired t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Mask size (mm$^2$)</td>
<td>297.0</td>
<td>6.0</td>
<td>288.6</td>
<td>7.8</td>
</tr>
<tr>
<td>Bib size (mm$^2$)</td>
<td>686.3</td>
<td>38.7</td>
<td>567.8</td>
<td>32.3</td>
</tr>
<tr>
<td>Hue (nm)</td>
<td>675.5</td>
<td>6.3</td>
<td>670.5</td>
<td>5.3</td>
</tr>
<tr>
<td>UV brightness</td>
<td>13.4</td>
<td>0.9</td>
<td>12.9</td>
<td>1.0</td>
</tr>
<tr>
<td>Yellow brightness</td>
<td>21.6</td>
<td>1.3</td>
<td>22.9</td>
<td>1.5</td>
</tr>
<tr>
<td>Saturation</td>
<td>0.286</td>
<td>0.005</td>
<td>0.293</td>
<td>0.004</td>
</tr>
</tbody>
</table>

Table 2. Traits of male common yellowthroats used in aviary experiments in NY and WI. 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.

<table>
<thead>
<tr>
<th>Trait</th>
<th>New York (Mean SD CV n)</th>
<th>Wisconsin (Mean SD CV n)</th>
<th>Bartlett’s P</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mask size</td>
<td>296 (29.1 9.8 44)</td>
<td>316 (49.9 15.8 40)</td>
<td>0.0007</td>
<td>2.22</td>
<td>0.02</td>
</tr>
<tr>
<td>Bib size</td>
<td>628 (151.4 24.1 46)</td>
<td>663 (160.1 24.1 40)</td>
<td>0.72</td>
<td>1.0</td>
<td>0.30</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>19.9 (0.61 3.1 44)</td>
<td>20.6 (0.61 3.0 40)</td>
<td>0.96</td>
<td>5.6</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

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Discussion

In both populations, the black mask functioned in male-male competition and males with larger masks were more likely to be dominant over other males. However, in contrast to our previous aviary experiments in Wisconsin, we found that females in New York preferred males with larger yellow bibs, rather than larger black masks. Thus, the results from New York are consistent with the prediction that carotenoid-based ornaments are more likely to be associated with female choice and melanin-based ornaments are more likely to be associated with male-male competition. A similar pattern of female mate preference for carotenoid-based ornaments (particularly bill color), but not melanin-based ornaments, has been observed in American goldfinches Carduelis tristis, (Johnson et al. 1993), and mallards Anas platyrhynchos (Omland 1996). However, there are some notable exceptions to this pattern, including carotenoid-based plumage ornaments that are used in male-male competition (Pryke et al. 2001) and melanin-based ornaments that are used in female choice (Safran et al. 2005). Below we review similar cases of geographic variation in female choice, and we examine possible hypotheses for changes in female choice between populations.

Geographic differences in female preferences for male ornaments have been demonstrated in guppies Poecilia reticulata, (Endler and Houde 1995), house finches Carpodacus mexicanus, (Hill 1994) and chuckwallas Saromalus obesus, (Kwiatkowski and Sullivan 2002). In all three taxa, there is also evidence that female preferences for the carotenoid-based ornaments are related to the availability of food (Kwiatkowski and Sullivan 2002), or, specifically, carotenoids in the environment (Grether 2000, Hill et al. 2002). For example, in two of three chuckwalla populations, brightness of the carotenoid-based colors of males was associated with the abundance of plants eaten by males on their territories, and females preferred males with brighter colors in two populations (Kwiatkowski and Sullivan 2002). In contrast, there was no significant preference for male coloration in the third population, where males had fewer resources on their territory (food and crevices) and population density was lower than in the other two populations. Thus, female choice appeared to be stronger (for carotenoid-based ornaments) in the populations with greater male density, which has also been reported in guppies (Jirotkul 1999). To the best of our knowledge, geographic variation in female preferences of birds has been studied under controlled conditions in the aviary (i.e., eliminating habitat differences and male interference) only in house finches. In this species, females show a similar directional preference for males with a larger red bib, even in subspecies (C. m. griscorni) in which males have smaller bibs (Hill 1994). There is also evidence suggesting geographic variation in mating preferences in house sparrows Passer domesticus, and flycatchers Ficedula hypoleuca and F. albicollis. In Denmark, male house sparrows with larger black bibs are preferred and more likely to gain a mate, but on an island off the coast of England, males with smaller bibs have greater mating success (reviewed by Griffith et al. 1999). In Ficedula flycatchers the white forehead patch is sexually selected in Sweden and Spain, but it is smaller and not sexually selected in Norway, where overall plumage color seems to be more important in mating success (Dale et al. 1999). One possible explanation for this pattern is that the ornament has lost much of its variation among males over evolutionary time, and, thus, it has lost its value as a signal of male quality for females. Thus, past selection may be responsible for the evolution of male ornaments, but that selection may now be weak or non-existent. This historical selection hypothesis (similar to the “unreliable signal hypothesis” of Möller and Pomiankowski 1993) has been proposed for the lack of correlation between sexual or natural selection and the expression of ornaments in red-winged blackbirds Agelaius phoeniceus, (Westneat 2006), and red junglefowl Gallus gallus, (Ligon and Zwartjes 1995).

The historical selection hypothesis could explain the evolution of multiple ornaments, if female preferences switch from one trait to another as selective environments change. In common yellowthroats, we found that one ornament in each population (bib in Wisconsin and mask in New York) was apparently not preferred by females. The historical selection hypothesis predicts that these ornaments should be less variable in the population where they are not the focus of female mate choice. As predicted, bib size was more variable than mask size in New York (CV of 24.1 and 9.8, respectively), but the same pattern existed in Wisconsin (Table 2), where we might have expected bib size to be less variable. Comparing between populations, however, mask size was more variable and larger in Wisconsin than in New York, while bibs were similar in size and equally variable at both sites (Table 2). Thus, it is possible that over the range of this species female preferences change depending on how variable ornaments are relative to each other. In this case, mask size was more variable relative to bib size in Wisconsin (ratio of mask to bib CV = 0.66) than in New York (0.41). The absolute strength of female preferences did not appear to differ geographically, as there was no difference between New York and Wisconsin in the time females spent next to the preferred male (19.3 ± 2.7 and 20.4 ± 4.8 min, respectively; t = 0.21, P = 0.83), nor the total time they spent next to either male (23.6 ± 2.8 and 21.9 ± 4.8 min, respectively; t = 0.34, P = 0.74; Wisconsin data from Tarof et al. 2005).

Although we have treated the mask and bib as separate ornaments, the birds may actually perceive them as a single, composite ornament. In this case, it is possible that females prefer males with the largest overall ornament in both New York and Wisconsin. Indeed, females in New York spent more time next to the male with the larger (17.7 ± 3.1 min) than the smaller (5.9 ± 1.2 min) combined ornament (paired t17 = 3.19, P = 0.005). However, this relationship was driven by bib size, as mask size alone was not related to female preference time (P = 0.55, Fig. 1) and the size of the two ornaments was not correlated in this particular sample, although they are correlated in larger samples from both study areas (unpubl. data). Thus, the evidence so far seems to suggest that females in New York were choosing males based primarily on bib size.

If the mask and bib function as two independent ornaments, then it is puzzling why females prefer males
with larger bibs in New York and larger masks in Wisconsin. One possible explanation is that differences in habitat or the intensity of selection on each ornament influence their efficiency in each population (i.e., detectability and honesty, Schluter and Price 1993). However, the aviary experiments control for differences in habitat (both aviaries were in open fields), so it seems more likely that there are geographic differences in the ornaments or female preferences. Geographic differences in the abundance of carotenoids or parasites that affect carotenoid uptake (Hill et al. 2002), could affect the cost of bib production and, consequently, the honesty of the bib as an indicator of male quality in our two populations.

In conclusion, our results from this New York population indicate that the black mask of male common yellowthroats is involved in male-male competition, as it is in Wisconsin, but the yellow bib is the target of female choice only in New York. This pattern in which carotenoid-based ornaments are selected by female choice and melanin-based ornaments are selected by male-male competition is consistent with the hypothesis that carotenoid-based ornaments are more costly to produce and more revealing of male quality than melanin-based ornaments (Hill and Brawner 1998, Badayaev and Hill 2000). However, this does not appear to be a consistent pattern across the range of the species, as females in Wisconsin preferred males with a larger black mask in our aviary experiments (Tarof et al. 2005), and mask size, but not bib size, was related to extra-territorial forays by females (Pedersen et al. 2006) and both social and extra-pair mating success (Thusius et al. 2001, Garvin et al. 2006). This geographic difference in selection could be related to a variety of environmental factors (habitat, carotenoid and parasite abundance) that affect the costs and benefits of choosing males with particular ornaments in each location. Ongoing studies are examining the color of the bib (using spectrometry), parasite loads and level of plasma carotenoids in each population.

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