



Attractive males provide less parental care in two populations of the common yellowthroat

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Male ornaments may be signals of direct or indirect benefits to females that mate with those males. One important direct benefit to females is the level of male parental assistance they receive when provisioning young. Three main hypotheses attempt to explain the relationship between male ornament size and parental care. The good parent hypothesis predicts that males with larger ornaments will provide more care, while the differential allocation and trade-off hypotheses predict that they will provide less care. We examined the relationship between male ornamentation and parental care in two populations of common yellowthroats, *Geothlypis trichas*, in which the sexually selected male ornament differs. More ornamented males provided less parental care in both populations, contrary to the good parent hypothesis. However, females did not feed their nestlings more frequently when mated with more ornamented males, which is an additional prediction of the differential allocation hypothesis. Our results are most consistent with the trade-off hypothesis, which suggests that more ornamented males provide less care because they spend relatively more of their effort in pursuing extrapair mates or defending their territories from other males.

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Many species display conspicuous differences between the sexes in coloration. The evolution of this sexual dimorphism has been traditionally attributed to sexual selection, and mate choice in particular (Andersson 1994). Ornamental traits may provide cues about potential indirect benefits to a female, including 'good' genes that result in the increased viability or attractiveness of offspring (Linville et al. 1998). Ornaments could also indicate potential direct benefits, such as territory quality or the extent of male parental care. Because parental performance cannot usually be observed in advance of mate choice in short-lived species, the parental quality of a prospective mate must be appraised using indirect cues, such as ornaments (Nisbet 1973). Three main hypotheses have been

proposed to explain the relationship between male ornament size and parental care. Elaborate ornaments may indicate that males will provide a high level of parental care, as predicted by the good parent hypothesis (Hoelzer 1989). Alternatively, more ornamented males may provide less parental care as predicted by the differential allocation (Burley 1986) and trade-off (Williams 1966; Magrath & Komdeur 2003) hypotheses. The differential allocation hypothesis assumes that females paired with highly ornamented males provide more parental care to prevent the desertion of their relatively attractive mates, and, as a consequence, these males are free to avoid the costs of parental effort and invest in their own survival. In contrast, the trade-off hypothesis assumes that more ornamented males provide less parental care because they achieve relatively greater reproductive success from seeking mating opportunities, such as extrapair fertilizations or, in the case of polygynous species, additional mates.

The common yellowthroat, *Geothlypis trichas*, a socially monogamous and dimorphic warbler, offers an excellent opportunity to examine the relationship between male

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parental care and ornamental traits. Males have a conspicuous black facial mask and yellow bib (throat, breast and belly), which is absent (mask) or subdued (bib) in females. In Wisconsin, U.S.A., male mating success is related to the size of the male's black facial mask, which is produced by melanin pigments (Thusius *et al.* 2001), whereas in New York, mating success is related to the size of the yellow bib, which is produced by carotenoids (C. R. Freeman-Gallant, unpublished data). Most studies of male parental care and sexually selected male ornaments have focused on one ornamental trait (or multiple ones of the same type) in one population (Sundberg & Larsson 1994; Linville *et al.* 1998). In this study we examined the relationship between male ornamentation and parental care in two populations of common yellowthroats in which the sexually selected male plumage ornament differs.

This study had three main goals. First, we wanted to determine whether there was a relationship between male ornaments (mask and bib) and the amount of parental assistance provided by males. Theoretical and empirical studies suggest that male parental care could be correlated positively (Hill 1991; Keyser & Hill 2000; Massaro *et al.* 2003; Siefferman & Hill 2003) or negatively (Qvarnström 1997; Sanz 2001; Badyaev & Hill 2002) with male ornaments. Second, if there was a relationship, we wanted to determine which of the three hypotheses best explained the relationship. Finally, we wanted to determine whether the same or different ornaments were related to male parental care in New York and Wisconsin, where sexual selection appears to be operating on different male ornaments.

METHODS

Field work was conducted during May–July, in 2004 and 2005 in Wisconsin and New York, respectively. Research in Wisconsin was conducted in 5.4 ha of contiguous conifer bog and willow/sedge marsh at the University of Wisconsin-Milwaukee Field Station in Saukville, Wisconsin (43°23'N, 88°01'W). The study area is bordered by upland forest, fallow fields and an adjoining 810-ha bog. Research in New York was conducted primarily in conifer bogs and willow/sedge marshes near the campus of Skidmore College in Saratoga Springs, New York (43°08'N, 73°78'W). These habitats were along a power transmission corridor bordered by upland forest and, separately, a series of wet meadows in the Kayaderosseras watershed.

In both the New York and Wisconsin populations, males return to the breeding grounds in early May; females arrive 3–10 days later. Females build the nest and incubate the eggs (2–5 per clutch), while both sexes feed the young (Guzy & Ritchison 1999). Birds can have two broods, but most (96% in Wisconsin and 91% in New York) had only one successful brood during the 2 years of this study. Nestling age was determined from known hatch dates ($N = 44$ nests) or estimated from body size and feather development of known-age nestlings ($N = 2$ nests). Nestling mass was measured on two consecutive days between days 3 and 5 of the nestling

period in order to estimate average growth rate. Fledging typically occurred on day 8 or 9.

To assess the relationship between ornamental traits and provisioning rate, we measured the feeding rate (feeds/h) of 46 breeding pairs of common yellowthroats ($N = 24$ and $N = 22$ nests in Wisconsin and New York, respectively). Field work was conducted in Wisconsin in 2004 and New York in 2005, so each individual was observed only in one year. Provisioning behaviour was recorded using 8-mm video cameras (Sony handycams) on tripods positioned 2–3 m from the nest. Video cameras were camouflaged using paint and vegetation to minimize disturbance. Feeding behaviour at each nest was recorded during 0600–1600 hours on days 3, 5 and 7 of the nestling period (hatching = day 0). As a consequence of poor weather and predation, we were not able to record parental care on all 3 days at all nests. Following an initial 60-min acclimation period, estimates of feeding rates were made from the number of food loads brought to the nest by each parent during a 1–3-h recording period (mean 2.7 h). Only the first brood of each pair that reached day 3 of the nestling period was used in our analyses, and all nests of polygynous males were excluded ($N = 3$). Additionally, to determine whether males with larger ornaments fed larger prey items to their nestlings, we counted the number of visits to the nest in which the prey item was smaller or larger than the beak of the male for a subset ($N = 10$) of males from each population. This subset contained the five least and most ornamented (mask size in Wisconsin, bib size in New York) males within each population that were observed on day 7 of the nesting period (when prey items are easiest to see in the video). Estimates of prey size at each nest were based on five consecutive provisioning trips.

We used mixed models with restricted maximum likelihood in JMP 5.0.1 (SAS Institute 2003) to examine the relationship between the rate at which parents fed their nestlings and male ornamental traits. All of our analyses of feeding rates included a unique code for each nest, and nestling age and number of young in the nest as random effects. The nest code controlled for the nonindependence of repeated observations of the same pair. Male feeding rate was not related to time of day in Wisconsin ($r^2 = 0.037$, $N = 64$, $P = 0.12$) or New York ($r^2 = 0.005$, $N = 46$, $P = 0.63$) and, thus, we did not include time of day as a variable in our analyses.

Adults were captured using mist nets and fitted with unique combinations of coloured plastic leg bands and a numbered aluminium band. We measured the ornaments of males (mask and bib) and females (bib) following methods in Thusius *et al.* (2001) and Tarof *et al.* (2005). Briefly, the head and breast of birds were recorded on videotape in front of a grid of 1-cm squares. We captured two still images of each side of the mask (4 images total) and two images of the bib. Size was estimated by tracing the outline of each ornament using image analysis software and taking the averages of multiple images (see Thusius *et al.* 2001). All size measurements in both populations were performed by D.P.M. and two additional individuals. Repeatability between images, calculated using the intraclass correlation coefficients (Zar 1999), was high for both mask ($r = 0.97$)

and bib ($r = 0.99$) size, as in our previous studies of the Wisconsin population (Thusius et al. 2001; Tarof et al. 2005). For consistency, we only used size measurements made by D.P.M. Colour characteristics (hue, brightness and saturation) of bibs were determined using Adobe Photoshop Elements 2.0 (Adobe Systems 2002) after adjusting contrast, brightness and hue with standards in each photograph (see Tarof et al. 2005). Hue, brightness and saturation were entered into a principal component analysis (PCA) to yield a single bib colour score (PC 1) that was used in the analyses. In Wisconsin, the first principal component explained 54% of the variation and loaded positively for hue (0.51) and brightness (0.58) and negatively for saturation (-0.63 ; Tarof et al. 2005). In New York, the first principal component explained 50% of the variation and also loaded positively for hue (0.71) and brightness (0.70) and negatively for saturation (-0.03).

RESULTS

In both Wisconsin and New York, males with larger ornaments fed their young at a lower rate, but the ornament associated with male parental care differed between populations. In Wisconsin, males with larger masks had a lower feeding rate ($F_{1,38} = 5.68$, $P = 0.02$) in a mixed model that included nest code, nestling age and the number of nestlings as random effects (Table 1, Fig. 1). In contrast, males in New York with larger bibs had a lower feeding rate ($F_{1,21} = 5.72$, $P = 0.03$; Table 1, Fig. 1). In separate mixed models, male bib size was not related to male feeding rate in Wisconsin, nor was male mask size related to male feeding rate in New York (Table 1). Male bib colour was not related to male feeding rate in either population (Table 1). These results were based on 180.9 h of recordings during 64 observation sessions at 24 nests in Wisconsin and 120.6 h of recordings during 46 observation sessions at 22 nests in New York.

In Wisconsin, a female's feeding rate was not related to her social mate's mask size ($F_{1,38} = 0.72$, $P = 0.40$; Fig. 1), but was correlated negatively with her social mate's feeding rate ($F_{1,38} = 4.68$, $P = 0.04$), suggesting that females responded to lower male feeding rates, but not directly to male ornamentation. In New York, female feeding rate was also not related to the bib size of the female's social mate ($F_{1,21} = 0.03$, $P = 0.96$; Fig. 1), and there was no relationship between male and female feeding rates ($F_{1,21} = 0.29$, $P = 0.10$; mixed models with nest code,

nestling age and the number of nestlings as random effects). Finally, there was no relationship between total feeding rate of both parents and male mask size in Wisconsin ($F_{1,38} = 0.68$, $P = 0.42$), or male bib size in New York ($F_{1,21} = 0.48$, $P = 0.50$).

We examined the growth rate of nestlings (averaged for each brood) to determine whether the lower feeding rate of more ornamented males influenced the growth of their young. However, the growth rate of nestlings in Wisconsin was not related to male mask ($F_{1,16} = 0.38$, $P = 0.55$) or bib ($F_{1,16} = 0.64$, $P = 0.44$) size in a mixed model with nestling age and number of young as random effects. In a similar mixed model, nestling growth rate in New York was not related to male mask ($F_{1,9} = 0.26$, $P = 0.62$) or bib ($F_{1,9} = 0.08$, $P = 0.78$) size. Next, we examined the size of prey that males fed to nestlings to determine whether males with larger ornaments (and lower feeding rates) compensated by bringing larger prey items to their nestlings. However, the proportion of feeding trips with prey larger than the bill (arcsine transformed) was not related to male mask size in Wisconsin ($r^2 = 0.056$, $N = 10$, $P = 0.51$) or bib size in New York ($r^2 = 0.001$, $N = 10$, $P = 0.92$).

Feeding rates did not differ between the sexes ($F_{1,169} = 2.99$, $P = 0.09$), but they were lower in New York (2.3 ± 0.24 feeds/h) than in Wisconsin (3.3 ± 0.19 feeds/h; $F_{1,169} = 4.08$, $P = 0.045$) in a mixed model (Table 2). There was no interaction between sex and population in the analysis ($F_{1,169} = 0.83$, $P = 0.36$).

DISCUSSION

Males with larger ornaments provided less parental care in common yellowthroats, but the ornament differed between our two study populations. Male parental care was related negatively to mask size in Wisconsin and to bib size in New York. Since mask size in Wisconsin (Thusius et al. 2001) and bib size in New York (C. R. Freeman-Gallant, unpublished data) are both related positively to male mating success, it is clear that females are not choosing male common yellowthroats with larger ornaments because they provide more assistance feeding young than less ornamented mates. Instead, the negative relationship between male ornamentation and paternal care may be due to females providing more parental care when mated to more ornamented mates (differential allocation hypothesis), or the result of a trade-off between male parental care and other activities, such as mating effort or

Table 1. Mixed models of male feeding rate (feeds/h) in relation to male ornamental traits in common yellowthroats in Wisconsin and New York

Male ornamental trait	Wisconsin			New York		
	Estimate	$F_{1,38}$	P	Estimate	$F_{1,21}$	P
Mask size (mm ²)	-0.018	5.68	0.02	<-0.001	0.003	0.95
Bib size (mm ²)	<0.001	0.04	0.84	-0.003	5.72	0.03
Bib colour (PC 1)	-0.082	0.06	0.81	0.167	0.94	0.34

Separate models were performed for each ornament and location. Each model included territory, nestling age and the number of nestlings as random effects. Bib colour (PC 1) is the first principal component score (see Methods). Significant P values are in bold.

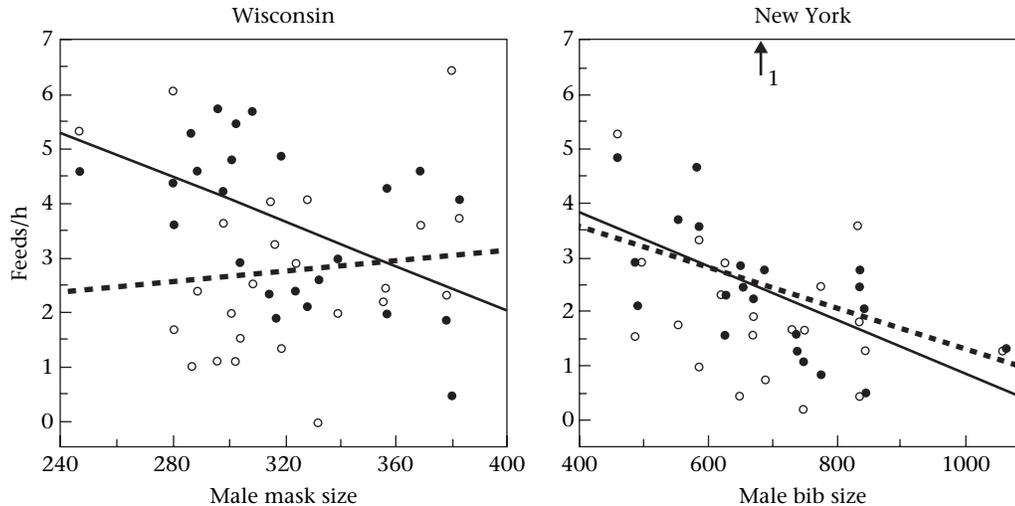


Figure 1. Provisioning rates (mean feeding visits/h) of male (●) and female (○) parents to nestling common yellowthroats in relation to male ornament size (mm^2). Note that each data point is the average of the raw provisioning rates at one nest ($N = 24$ nests in Wisconsin; $N = 22$ nests in New York). Lines (male: solid; female: dashed) are from a linear regression using these averaged data, but the relationship was tested with a mixed model (see Table 2 and Results). We made the feeding rate axis similar for both populations for ease of comparison. As a consequence, one data point was outside the figure (a female in New York fed nestlings 15 times per h; indicated by the arrow and '1').

competition with other males (trade-off hypothesis). It is unlikely that males with larger ornaments reduce their level of parental care because they have lower paternity in their nest. In Wisconsin, there was no relationship between within-pair paternity and mask size (Thusius et al. 2001), nor was there a relationship between the provisioning rate of males and their within-pair paternity (Peterson et al. 2001).

Burley's (1986) differential allocation hypothesis proposes that females choose more ornamented males to acquire indirect benefits (e.g. good genes for their offspring). Females paired with more attractive and elaborately ornamented males are assumed to provide more parental care to prevent the desertion of their relatively attractive mates. As a result, their male partners can gain a survival advantage by providing a lower level of parental care (Sanz 2001). The differential allocation hypothesis makes two predictions: (1) a negative correlation between the expression of male secondary sexual traits and their level of parental care, and (2) a positive correlation between female parental care and male ornamentation. We found support for the first prediction in common yellowthroats, consistent with some studies of birds (Burley 1988; de Lope & Møller 1994; Qvarnström 1997; Sanz 2001; Badyaev & Hill 2002)

but not others (Lozano & Lemon 1996; Rhode et al. 1999; Prévault et al. 2005). Some of these same studies also found support for the second prediction of the differential allocation hypothesis (Burley 1988; de Lope & Møller 1994; Qvarnström 1997; Badyaev & Hill 2002). However, female common yellowthroats did not feed young more frequently when paired with more ornamented males in either Wisconsin or New York (Fig. 1). Similar patterns have been reported in pied flycatchers, *Ficedula hypoleuca* (Sanz 2001) and yellow warblers, *Dendroica petechia* (Studd & Robertson 1985). In both of these species, the elaboration of the male's secondary sexual ornament (forehead patch and breast streaking, respectively) was related negatively to male parental care, but females did not alter their provisioning effort in relation to the attractiveness of their partner. These studies suggested that more ornamented males were reducing their level of parental care to increase their investment in other activities, such as pursuing extrapair copulations (Sanz 2001) or territorial defence (Studd & Robertson 1985). Thus, the differential allocation hypothesis does not provide an adequate explanation for the patterns of parental care we found in yellowthroats and it is unclear whether it provides a general explanation for the relationship between male ornaments and parental care in birds.

Since time and energy are limited, males may face a trade-off between parental care and other activities such as seeking additional mating opportunities or territorial defence. For example, male European starlings, *Sturnus vulgaris*, reduce the amount of time they spend incubating when the opportunity to attract additional mates increases, reflecting a direct trade-off between male parental care and mating effort (Smith 1995). A trade-off between male parental care and extrapair copulations might also lead to a negative correlation between male parental care and ornamentation in socially

Table 2. Means, standard deviations (SD) and coefficients of variation (CV) for feeding rate (feeds/h) of male and female common yellowthroats

Sex	Wisconsin ($N=24$ pairs)			New York ($N=22$ pairs)		
	Mean	SD	CV	Mean	SD	CV
Males	3.69	0.26	7.05	2.43	0.29	11.93
Females	3.02	0.26	8.61	2.23	0.29	13.00

monogamous species (Williams 1966; Magrath & Komdeur 2003). An important assumption of this model is that extrapair copulations are possible (i.e. females are fertile) during the period of male parental care. In both of our study populations opportunities for male parental care and extrapair fertilizations overlap extensively because nesting is asynchronous as a result of predation (followed by renesting) and second broods. In addition to the predicted negative relationship between male ornamentation and paternal care, the trade-off model predicts that more attractive males will decrease their parental care in order to expend more effort in the pursuit of extrapair copulations (Magrath & Komdeur 2003). In a radiotracking study of common yellowthroats in Wisconsin, we found that males with larger masks were more likely to leave their territory and visit the territories of fertile females than were males with smaller masks (Pedersen et al. 2006). This finding provides support for the prediction that more ornamented males will expend more effort in the pursuit of extrapair copulations. However, we still do not know whether there is an actual conflict between the time and effort spent pursuing extrapair copulations and providing parental care. Overall, our results are consistent with the predictions of the trade-off model and suggest that more ornamented males may be reducing their parental effort in order to increase their mating effort.

The observed negative correlation between male parental care and ornamentation in the common yellowthroat could also be explained by a trade-off between parental effort and male–male competition. Highly ornamented males may be subject to more frequent bouts of male–male competition as a result of territorial disputes and, thus, trade-off parental effort with territory defence (Qvarnström & Forsgren 1998). This alternative version of the trade-off mechanism has been proposed to explain reduced male parental care in studies of the collared flycatcher, *Ficedula albicollis* (Qvarnström 1997), pied flycatcher (Sanz 2001) and three-spined stickleback, *Gasterosteus aculeatus* (Sargent 1985). Although male common yellowthroats with larger masks are more dominant in an aviary setting (Tarof et al. 2005), it is unknown whether highly ornamented males spend more effort in competitive activities, such as territory defence, in the wild.

Regardless of the manner in which a behavioural trade-off is made, lower rates of food delivery can have severe consequences for offspring fitness and survival. If provisioning rate is an accurate predictor of prey mass delivered to young, as it is in other species of birds (Nolan et al. 2001; McCarty 2002), then we would expect young in nests of more ornamented males to be in poorer condition, especially in the New York population. However, we found that nestling growth rate was not related to male ornament size in either population, suggesting that prey loads delivered at nests of more ornamented males may be larger or more nutritious. Our results do not support this idea because the size of prey delivered to nestlings was not related to the size of male ornaments in either population. Nevertheless, our estimate of prey size was imprecise and, thus, further study is needed of how male and female provisioning interact to influence nestling growth and survival.

Within each of our study populations, the same male ornament was positively related to male mating success and negatively related to male parental care; however, it is not clear why the specific ornament differed between populations. One possible explanation is that different ornaments have different functions in each population because differences in habitat or the intensity of selection on each ornament influence their efficiency (i.e. detectability and honesty; Schluter & Price 1993). For example, the facial mask of male common yellowthroats is a badge of status related to male dominance and territory defence, as well as female mate choice, at least in Wisconsin (Tarof et al. 2005). Breeding territories of common yellowthroats are denser and each male has more conspecific neighbours in Wisconsin than in New York (P.O. Dunn, unpublished data). It is possible that the lower territory density in New York leads to fewer male–male interactions and weaker selection on mask size, which could ultimately reduce its efficiency as an indicator of male quality. There might also be geographical differences in carotenoid abundance or parasites that affect carotenoid uptake (Hill 2002), which 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, we found that male parental care was related negatively to the size of two different sexually selected male ornaments in two populations of common yellowthroats. We suggest that more ornamented males may be reducing their parental effort in order to increase their effort devoted to extrapair mating or male–male competition. Further research is needed to determine whether this lower level of male parental assistance imposes a cost on females, as the growth rate of nestlings was not lower at nests of more ornamented males. Overall, our results are most consistent with the trade-off hypothesis, rather than the good parent or differential allocation hypothesis.

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