

## Male traits expressed in females: direct or indirect sexual selection?

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**Summary.** Colored epaulets in female red-winged blackbirds (*Agelaius phoeniceus*) could be due either to direct sexual selection favoring the maintenance of this trait in females due to intrasexual competition for breeding opportunities, or to sexual selection favoring bright epaulets in males indirectly causing expression of the trait in females by genetic correlation. Older females tend to be brighter than younger females. Also, brighter females tend to breed earlier in the season than dull females. These patterns are consistent with both of the hypotheses. In a series of experiments in which males and females were presented with taxidermic mounts of dull and bright females, the plumage of these mounts had no influence on the response of either males or females. Also, the response of females was independent of their own plumage. The results of all of the experiments consistently supported the interpretation that male plumage characteristics expressed in female red-winged blackbirds have no functional value and are a consequence of genetic correlation with males. Since recent studies have also indicated that female aggression has no functional value, we speculate that this too could be due to genetic correlation with a trait favored in males.

### Introduction

Darwin (1871) proposed the theory of sexual selection to account for the evolution of characters apparently detrimental to their bearers' survival. He reasoned that the bright and elaborate plumage and large size of male birds must give them a reproductive advantage to balance the survival cost these features impose. That advantage stems from

females finding brighter males more attractive or because large size or bright plumage assist males in defeating their rivals when competing for access to females or the resources females require. Although important issues remain to be resolved regarding the mechanism of sexual selection, there is at least consensus that sexual selection is responsible for sexually dimorphic features expressed in males (Partridge and Harvey 1986). By contrast, the expression in females of homologous, sexually-selected male traits has received very little attention, and certainly no consensus regarding their evolutionary origin. Here we present the first study aimed at testing the two principal hypotheses proposed to explain the expression of "male" traits in female birds.

Although some morphological features are unique to either males or females, the sexes share much of their anatomy and a trait is therefore designated as "male" or "female" based only on differences in expression of the trait between the sexes. For example, in red-winged blackbirds (*Agelaius phoeniceus*), the focus of this study, both sexes have upper secondary wing coverts (the epaulets). In adult males, which are otherwise uniformly black, these feathers are a brilliant red and are the basis for the species' name. In the cryptic, brown females, the epaulets are much duller than in males, but in some individuals these feathers have some red or orange. Thus, females with red or orange epaulets are exhibiting a 'male' trait.

The expression of male traits in females can evolve for one of two reasons. Either there is some direct advantage conferred on females expressing the trait, or expression is due to genetic correlation with a trait selected for in males. Consider genetic correlation first. When sexual selection favors changes in some trait in males, the homologous trait in females will change in concert because fe-

males also carry the genes for that trait (Lande 1980). Thus, genetic correlation between males and females will slow the rate of evolution of sexual dimorphism (Fisher 1958; Lande 1980; Lande and Arnold 1985). Even if the trait is disadvantageous to females (e.g. perhaps red epaulets make nesting females more conspicuous to predators), hundreds of thousands of generations might be required to achieve complete sexual dimorphism where there is full expression of the trait in males and complete suppression of the trait in females (Lande 1980). By the genetic correlation hypothesis, therefore, epaulets have no functional value in female red-winged blackbirds, and are merely the indirect consequence of sexual selection on males.

The other possibility is that epaulets in females have some functional value, analogous to their function in males. In male red-winged blackbirds, the epaulets play an important role in territorial and dominance interactions (Peek 1972; Smith 1972; Eckert and Weatherhead 1987a, Roskaf and Rohwer 1987) and may be used by females to assess aspects of male quality when choosing mates (Eckert and Weatherhead 1987b). While there is some question of whether females are truly territorial (Hurly and Robertson 1984, 1985; Searcy 1986, 1988), they are clearly aggressive toward one another. Females approach and attack other females (Nero 1956a, b), and female models (Weatherhead and Robertson 1977b; La Prade and Graves 1982; Yasukawa and Searcy 1982) and respond to playbacks (Beletsky 1983a, b) on their mate's territory. When acting aggressively, females employ displays such as bill tilts and song spreads that are homologous with those used by males (Nero 1956a; Orians and Christman 1968). In the case of the song spread display, the wings are spread to maximize display of the epaulets. Therefore, if aggression ensures a female access to a particular male and his resources, maintenance of a "male" trait in females could be a consequence of sexual selection acting directly on females. In this case, genetic correlation could be the mechanism whereby females had acquired the trait initially, but regardless of its origin, maintenance of the trait would be due to a balance between natural selection favoring cryptic appearance and sexual selection for intrasexual competitive ability.

Several patterns of behavior would be consistent with both hypotheses. If bright plumage in females is a consequence of female-female competition (i.e. direct sexual selection), then bright females, being more competitive, should migrate earlier in the spring and start breeding sooner. If bright plumage is due to genetic correlation with

males, then females should reflect the male pattern of older, brighter males migrating sooner and occupying territories earlier than younger, duller males. These predictions are useful to examine, because while not allowing us to distinguish between the two hypotheses, they weaken both if they fail.

There are a number of predictions regarding the causes and consequences of plumage variation among female red-winged blackbirds that do differ between the two hypotheses. Although we do not address the causes of plumage variation here, a complete test of the two hypotheses will require determining the inheritance of plumage brightness in females. The two hypotheses predict very different consequences for bright plumage in females. If colored epaulets are maintained through female-female competition, then bright females should be more aggressive than dull females, females should respond differently to territorial intrusions by bright and dull females, and males should respond differently to bright and dull females (it is not clear whether they should prefer bright females, perhaps because they are of superior quality, or dull females, perhaps because they would be less effective at inhibiting settlement by other females on the male's territory). If plumage brightness reflects female quality, males may also provide more parental care to the offspring of bright females. In all cases the genetic correlation hypothesis predicts no effect of female plumage.

We test all of these predictions in this study. To assess the response of territorial males and females to the plumage of female intruders, we use model presentations to simulate intrusions. While this approach does not allow for the intruder to interact with resident birds, it does allow observations to be standardized in a way not possible if one relied on observations of real intruders. The use of model birds has been used successfully to study the function of epaulets in male red-winged blackbirds (Roskaf and Rohwer 1987). We focus primarily on variations in epaulet color. However, because the plumage on the throat immediately below the bill (hereafter the chin) also exhibits substantial color variation, we also assess possible effects of this variation.

## Methods

### General methods

Research was conducted along paved highways within 30 km of the Queen's University Biological Station north of Kingston, Ontario in the spring and summer of 1986 and 1987. On a daily basis beginning 1 April, we monitored female settlement on the territories centered around cattails (*Typha latifolia*)

growing in the ditches. All observations were made using binoculars from a truck parked along the road. Females were not individually marked until after they were established on territories so we did not influence settlement patterns. Early in the spring females were sometimes observed on particular territories and sometimes not. We considered a female to have settled on a territory once we saw a female on three consecutive visits to that territory (Teather et al. 1988). When females had settled we caught them either by decoy trapping (Smith 1972; Picman 1979) or by mist net. All birds were banded with a unique combination of three colored aluminum bands and a numbered U.S. Fish and Wildlife Service band. Most females remained on the territories on which we banded them, confirming our assumption regarding settlement. We measured body mass of each female to the nearest 0.5 g, wing length to the nearest mm, and quantified plumage brightness (see below).

To increase our sample of females for which we had plumage information, we caught females by mist-netting in a spring roost (Weatherhead and Greenwood 1981) 25 km south of the biological station. After quantifying their plumage, we used these females in aviary studies of plumage variation and dominance (Muma and Weatherhead, in preparation).

We also obtained data on the initiation of breeding by females from local marsh-nesting populations which were the subject of a separate investigation by PJW. Marshes were searched every second day through the breeding season in 1986 and 1987 and all nests were marked and mapped. Females associated with nests were mist-netted, banded and their plumage brightness quantified.

Finally, to determine the extent to which males in the roadside population fed nestlings, we observed nests on the day the nestlings were five days old. By this time, most males who are going to feed nestlings have begun to do so (Patterson 1979; Muldal et al. 1986). Nest watches lasted one hour and were conducted between 0800 and 1500 h from a truck parked approximately 20 m from the nest. All nests belonged to primary females.

#### Quantification of female plumage brightness

We classified epaulet and chin color according to color swatches from the *Naturalists' Color Guide* (Smithe 1975). Swatches representing the range in color variation of epaulets and chins were then ranked subjectively according to brightness. We then compared Munsell (1961) color scores of value and chroma to our scoring scheme. Value measures the lightness of a color with dark colors given scores of 1, 2, and 3 while light colors are scored between 8 and 9.5. Chroma refers to the intensity or purity of a color. Low scores on this scale indicates intense, saturated color. Swatches that we ranked as bright generally had low value scores and high scores on the chroma scale (i.e. dark and saturated). We chose nine categories for epaulet colors ranging from vivid orange to pale yellow and eight categories of chin colors ranging from strong yellowish pink to light gray (Table 1). In the field epaulets and chins were held next to the color swatches for comparison and were assigned the scores of the color they most closely resembled.

#### Model presentations to females

Decoy traps take advantage of a female's aggressive response to a perceived intruder, simulated by a taxidermic mount of a female in the trap and a tape recording of aggressive female vocalization. The vocalization we used was the "teer" call (Beletsky's (1983a) type II song) which is usually given as part of the song spread display. Because we occasionally used decoy traps to attempt to capture newly-settled females, we quantified

**Table 1.** Ranking scheme for epaulet and chin colors using color swatches from the *Naturalist's Color Guide* (Smithe 1979) and Munsell (1961) color notation. Hue refers to the quality of color (red, yellow, blue, green), value is the lightness (dark = 1, 2, 3 and light = 8, 9, 9.5) and chroma is the purity or intensity of color (low # = weak gray and high # = intense, saturated)

Our score	Smithe color name	Munsell notation		
		Hue	Value	Chroma
<b>Epaulets:</b>				
1	vivid orange	2.2 YR	5.90	16.0
2	strong reddish orange	0.1 YR	5.37	12.3
3	moderate reddish brown	0.7 YR	4.00	5.3
4	brownish orange	1.2 YR	4.30	9.0
5	brownish orange	3.6 YR	4.50	6.7
6	dark orange yellow	5.0 YR	6.90	6.0
7	dark orange yellow	0.7 Y	5.98	7.4
8	pale orange yellow	0.9 Y	7.77	5.5
9	pale yellow	2.5 Y	8.08	3.5
<b>Chins:</b>				
1	strong yellowish pink	1.9 YR	6.84	8.9
2	moderate yellowish pink	5.0 YR	6.90	6.0
3	moderate orange yellow	9.0 YR	7.97	7.5
4	pale orange yellow	0.9 Y	7.77	5.5
5	pale orange yellow	8.8 YR	7.55	4.3
6	moderate yellow	2.6 Y	7.89	6.1
7	light yellow	1.5 Y	8.30	5.5
8	pale yellow	2.5 Y	8.08	3.5

their response to the trap. By always using the same mount in the trap and the same playback we controlled for variation in the stimulus and could relate variation in response to plumage variation of the responding females.

In 1986 we presented decoy traps to 19 females after they had settled but before they began egg laying. Trials were conducted within 4 h of sunrise. The trap was placed on 1 m aluminum poles within 2 m of a perch the female had been observed using. Once the resident female responded by approaching within 10 m of the decoy trap and facing toward it, we recorded her behavior every 5 sec for 10 min with the aid of an electronic metronome (Wiens et al. 1970). We recorded the female's distance from the trap, whether or not she was visible to us, her vocalizations (chit and teer: Beletsky's (1983a) type I and II aggressive vocalizations), displays (song spread and bill tilt), attacks (landing on the trap) and her interactions with the resident male. We terminated the presentation when the female was captured or after 10 min.

To determine if females discriminated between females of various plumages, we presented dull (chin and epaulet scores = 8) and bright (chin score = 2, epaulet score = 3) models to females. All mounts were of comparable size, in upright postures with their epaulets exposed and were presented with playbacks. To standardize when models were presented, we monitored the nesting cycle. When a nest was found we marked a piece of vegetation 1 m away with flagging tape. The nest was then visited every two days to determine the onset of egg laying. We presented a model on the second day after a full clutch was laid. All model presentations took place between sunrise and 1000 h on days when it was not raining and winds were not excessive. If model presentations were scheduled for days when it rained they were postponed until the next clear day. We randomly assigned which model (dull or bright) was to

be presented first by a coin toss. Each model was placed on a 1 m high aluminum pole 5 m from the nest and 1 m from a perch. Model placement involved walking directly from the vehicle (which was parked at the side of the road) into the territory, placing the model and returning to the vehicle (which served as a blind). The entire procedure took less than 1 min. We began recording observations when the female came within 10 m of the model and faced towards it. At 5 sec intervals we recorded the female's position in relation to the model, vocalizations, displays, attacks, and interference by the male. The presentation was terminated when either 10 min had elapsed or the female attacked the model. Two days later the other model was presented.

#### Model presentations to males

Since male red-winged blackbirds exhibited varying degrees of courtship behavior we wanted to determine if they discriminated between dull and bright females. Therefore, we placed dull and bright models on a male's territory simultaneously. We conducted these presentations in April just after the males had established territories. If a male was present for several days and gave song spreads, we assumed he was the territory holder and models were presented. Models were placed on or near fence posts positioned 5 m apart and located centrally on the territory. Separating the models by 5 m allowed us to distinguish to which model the male was responding while ensuring that the male was aware that both models were present. We used the same observation methods as for the model presentations to females. Observations began when the male came within 5 m of one of the models. Every 5 sec we recorded which model the male was closer to. We continuously recorded all song spreads and to which model they were directed. Trials continued for 10 min or until the male attempted copulation with one of the models.

#### Analysis of model presentations

Male interactions with the resident female affected the amount of time the female spent responding to the model. Therefore, we removed the time the female was chased by the male from the total observation time. From this, we estimated the proportion of time that each female spent (i) at the nest, (ii) less than 1 m from the model, (iii) 1–5 m from the model, (iv) greater than 5 m from the model, and (v) out of sight at these distances. Vocalizations (chit, chit series, teer) per minute were recorded when the female was in sight during the entire presentation. We also recorded whether or not the female attacked the model or solicited the male.

The most aggressive response was for the female to attack the model. Other variables also indicated the level of aggression. An aggressive female would be one that remained within 1 m of the model and gave numerous teer calls and displays. If the female returned to the nest without interacting with the model then it was considered a non-aggressive response. We assumed that females that remained in clear view indicated a more aggressive response than females that remained in the undergrowth.

To test if females responded more to dull or bright models, we performed an analysis of covariance on each of the eight response variables (time at nest, time less than 1 m from the model, time 1–5 m, time out of sight, time chased by male, number of chit calls, number of chit series, number of teer calls). We controlled for female body size and also tested for the effects of the order of model presentation. However, describing a female's behavior using each of these variables separately is difficult because some of the variables are likely to

be correlated. Therefore, we performed a principal component analysis (Aspey and Blankenship 1977). We performed the analysis separately on the decoy trap presentations ( $N=19$ ) and on the dull and bright model presentations ( $N=38$ ). Scores for each female were obtained by multiplying the factor loadings by the standardized value of the female's response for each variable and then summing them for each factor. It was necessary to use standardized values (calculated by subtracting the mean of the variable and dividing by the standard deviation) since all variables were not measured in the same units. Variables that represented proportions (time at nest, time less than 1 m from the model, time 1–5 m from model, time greater than 5 m from model) were transformed using an arcsine squareroot transformation.

## Results

### Plumage patterns

We caught 157 female red-winged blackbirds on roadside territories and in the spring roost in 1986 and 1987. Epaulet color was positively correlated with chin color (Fig. 1,  $r_s=0.253$ ,  $P<0.05$ ), suggesting a pleiotropic effect. However, because the correlation was weak we have analyzed the two plumages separately.

In 1987 we recaptured 13 females we had studied in 1986. With regard to epaulets, nine had be-

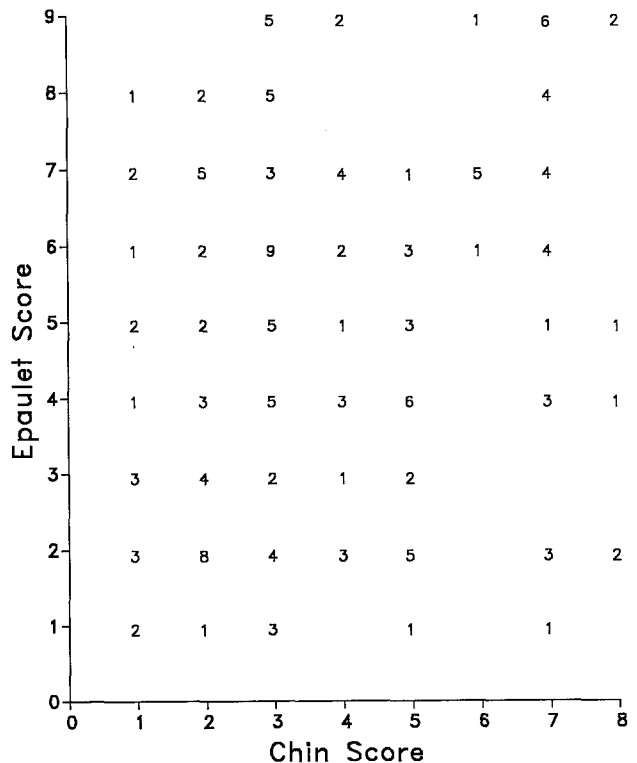


Fig. 1. The relationship between epaulet and chin color for 157 female red-winged blackbirds. The numbers refer to the number of individuals with a particular combination of scores

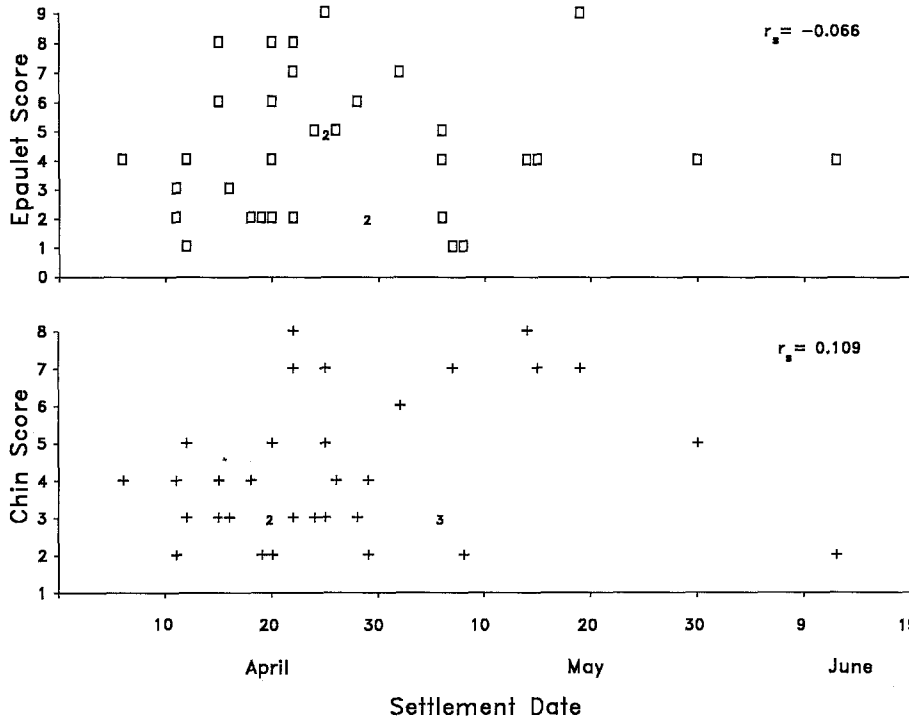


Fig. 2. The relationship between epaulet and chin color and settlement dates for females on roadside territories. Numbers indicate the number of females at a particular point

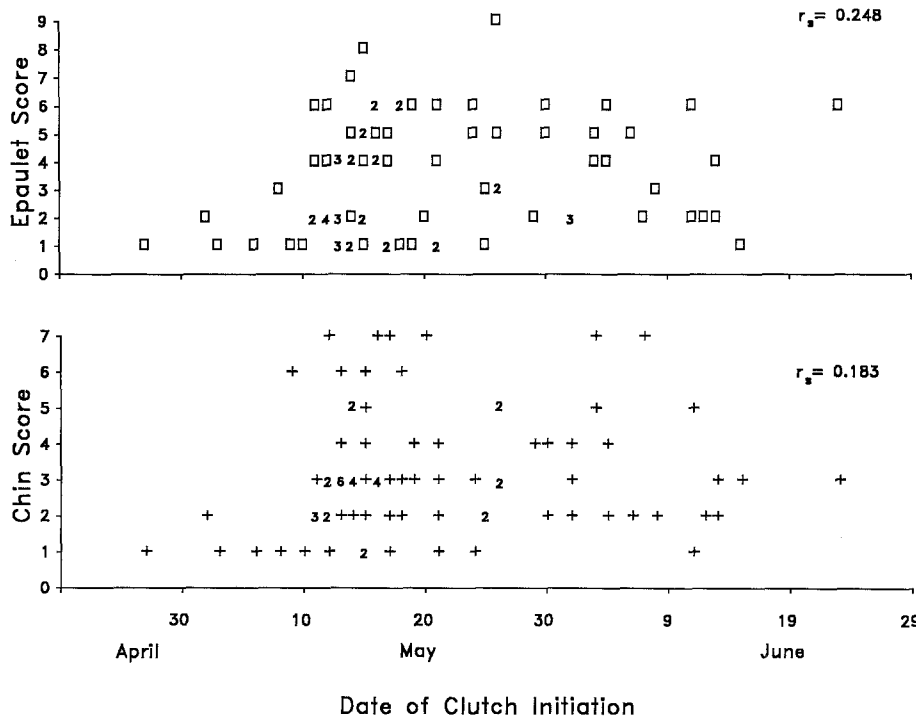


Fig. 3. The relationship between epaulet and chin color and clutch initiation dates for females nesting in marshes. Numbers indicate the number of females at a particular point

come brighter, three remained the same and one was duller. Only three of the females had brighter chins, seven were unchanged and three were duller. These results suggest that variation in epaulet color is at least partly a function of female age.

*Settlement patterns*

There was no correlation between epaulet or chin color and the order females settled on roadside territories (Fig. 2;  $r_s = -0.066$  and  $0.109$ , respec-

tively;  $N=36$ , both  $P$ 's  $> 0.05$ ). In the marsh population there was a weak positive correlation between epaulet color and the order in which females began laying eggs (Fig. 3;  $r_s=0.248$ ,  $N=87$ ,  $P < 0.05$ ), although no correlation was found between chin color and clutch initiation (Fig. 3,  $r_s=0.183$ ,  $N=87$ ,  $P > 0.05$ ).

#### Male feeding

In 1986 eight of 13 males fed nestlings while in 1987, seven of 12 males fed nestlings. Assisted and unassisted females did not differ with regard to either epaulet ( $5.3 \pm 2.2$  vs.  $4.0 \pm 1.9$ ) or chin ( $4.5 \pm 1.6$  vs.  $3.5 \pm 1.5$ ) scores (both  $t$ 's = 1.2, both  $P$ 's  $> 0.10$ ). Therefore, males appear to allocate their assistance independently of their mate's plumage.

#### Model presentations to females

We recorded the responses of 19 females during decoy trap presentations. To compare the plumage of the responding female to the magnitude of her response to the decoy traps we first obtained an index of the response using principal component analysis (Table 2). The first factor accounted for 36.5% of the variation and had high loadings for the number of vocalizations. Neither the brightness of a female's epaulets or her chin was correlated with her score from the first factor ( $r_s = -0.328$  and  $0.179$ , respectively; both  $P$ 's  $> 0.05$ ).

We presented both dull and bright models to 38 females during early incubation. Ten birds gave the maximum aggressive response by attacking the models. Three females attacked both models, five attacked only the bright model and two attacked only the dull model, so the occurrence of attacks

**Table 2.** Unrotated factor loadings from a principal components analysis of decoy trap presentations to 19 female red-winged blackbirds. See text for definition of variables

Variable	Factor 1	Factor 2	Factor 3
Time < 1 m from model	0.361	0.747	-0.068
Time 1-5 m	-0.288	0.067	0.836
Time chased by male	0.345	0.329	-0.377
Time out of sight	-0.491	-0.406	-0.535
Number of chits	0.820	-0.506	0.089
Number of series	0.875	-0.430	-0.098
Number of teers	0.736	0.311	-0.037
Cumulative proportion of variance explained	0.365	0.561	0.726

was independent of the model's plumage. Solicitations to the male can not be considered an act of aggression to an intruding female, but could draw the male's attention away from the intruder. Four females solicited the resident male during the bright model trial, one female solicited during both trials, while no females solicited only during the dull model trial. A larger sample of females responding to the model by soliciting their mates would be required to determine if the trend we found reflects a genuine difference due to the plumage of the model.

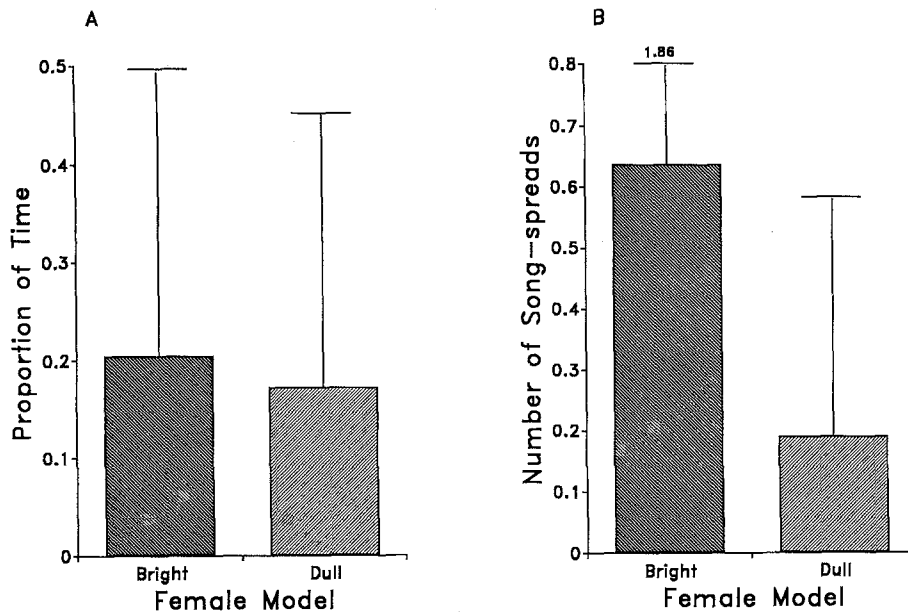
Of the 24 females presented models in 1987, eight gave bill tilt displays to both bright and dull models while three displayed only to the bright model and three displayed only to the dull model. Since the bill tilt is an aggressive display in blackbirds, aggression and model plumage were independent. This conclusion is also supported by the analysis of covariance for all behaviors (all  $F$ 's  $< 3.70$ , all  $P$ 's  $> 0.05$ ).

Since the brightness of the model's plumage had no effect on the females' responses, we used the mean of each female's response to the two models in our analysis to determine whether the female's own plumage affected her response. Again, we used principal components analysis to produce orthogonal factors from all our independent variables. The first two factors accounted for 34% and 26% of the total variation, respectively (Table 3).

Both involved heavy loadings of vocalizations, and the time spent less than 1 m from the model loaded heavily on the second factor. Thus, both factors appear to reflect a response to the model. By contrast, the third factor appears to reflect lack of response as indicated by the heavy positive loading of the amount of time spent at the nest. There

**Table 3.** Unrotated factor loadings from a principal components analysis for dull and bright female model presentations to 38 female red-winged blackbirds. Factor loadings were calculated by taking the average score for the bright and dull models

Variable	Factor 1	Factor 2	Factor 3
Time at nest	-0.652	-0.215	0.661
Time < 1 m from model	-0.006	0.776	-0.497
Time > 5 m from model	0.662	-0.576	0.007
Time chased by male	0.534	-0.351	-0.136
Time out of sight	0.571	-0.367	-0.542
Number of chits	0.801	0.266	0.499
Number of series	0.775	0.365	0.493
Number of teers	0.186	0.788	-0.048
Cumulative proportion of variance explained	0.344	0.602	0.780



**Fig. 4.** Male response to dull and bright female models. Figure A is the proportion of time spent less than 1 m from each model. Figure B is the number of song spreads per minute directed toward each model

was no significant correlation between either epaulet color and factors 1 or 2 ( $r_s = 0.009$  and  $-0.164$ , respectively; both  $P$ 's  $> 0.05$ ) or between chin color and either factor ( $r_s = 0.151$  and  $-0.163$ , respectively; both  $P$ 's  $> 0.05$ ). Therefore, these results are consistent with those from the decoy trap study, in that a female's response to a simulated intruder appears to be independent of her plumage.

#### *Model presentations to males*

We presented paired models to 18 territorial males. Males did not spend a disproportionate amount of time close to either model (Fig. 4, Wilcoxon matched-pairs signed-ranks test,  $P = 0.83$ ). Although a disproportionate number of song spreads were directed toward the bright model, the difference was not significant (Fig. 4, Wilcoxon matched-pairs signed-ranks tests,  $P = 0.40$ ). Finally, five males attempted copulation with the bright model while four other males attempted copulation with the dull model, again showing a clear lack of preference for the model's plumage.

#### **Discussion**

Epaulets in female red-winged blackbirds are appropriate for testing the genetic correlation hypothesis because epaulets in males are an obviously sexually-selected trait. Variation in chin brightness is more problematic in that male chins are uniformly black. However, Nero (1954) documented that males occasionally exhibit a pinkish tinge to chin, throat and breast and suggested that this

color may be present in most males but is masked by black pigments. This observation, and the positive correlation we found between epaulet and chin color are consistent with there being some pleiotropic relationship between them. The fact that the correlation between them was weak may be due at least in part to our subjective ordering of brightness of the epaulet and chin not accurately reflecting how they truly covary. However, because epaulet and chin brightness did not differ in their effects on male and female behavior, and because they are positively correlated, we consider them jointly as 'plumage brightness' for much of the discussion.

Before considering the effects of plumage brightness on behavior, we consider the effect of age on plumage brightness. Females we encountered in both years of our study tended to be brighter the second year, particularly their epaulets. In a captive study, Miskimen (1980a, b) found that 84% of females acquired bright epaulets after their first molt and that all females had bright epaulets after their second molt. Among free-living females, Blank and Nolan (1983) noted that the size and brightness of female epaulets increased with age. Meanly and Bond (1970) noted that young females had little salmon coloration on their chin when compared to older females. Thus, it seems to be generally the case that females get brighter when they get older. This pattern is similar to that exhibited by males (Greenwood et al. 1983; Greenwood 1985). In their first potential breeding season, males exhibit plumage generally intermediate to that of females and older males, with sub-

stantial individual variation. The following year and thereafter, all males exhibit the typical adult male plumage. Thus the age-related changes in female plumage are consistent with both the direct and indirect sexual selection hypotheses. If direct competition between females has selected for bright plumage, young females being less competitive (as are young males), may delay plumage maturation. If female plumage brightness is due to genetic correlation with the same trait in males, then again the expectation is that plumage should get brighter with age. Thus, age effects do not allow us to distinguish between the hypotheses, although both hypotheses would have been weakened had our results been different.

A similar situation arises with our data on the initiation of nesting. Although we found no correlation between settlement and plumage brightness in the roadside population, we did find a weak trend for brighter females to initiate nests earlier in the marsh population. Since settlement and nest initiation are weakly correlated in this population (Teather et al. 1988), there may be a correlation between settlement and plumage brightness in the marsh population. Dolbeer (1976) found that the same percentage of females with bright epaulets nested during the first and second half of the breeding season in an upland population. However, Crawford (1977) and Blank and Nolan (1983) found that dull females began nesting later than bright females in marsh populations. Among male red-winged blackbirds, older individuals migrate back earlier in the spring than younger males and abandon communal roosts to occupy territories well before breeding begins, presumably due to the strong competition for breeding sites (Greenwood and Weatherhead 1982). Thus, earlier settlement and nesting by older (brighter) females would be consistent with either direct selection on females due to competition for breeding sites, or due to genetic correlation with an age-related trait in males. The possibility that sexually-selected male behaviors could be expressed by females due to genetic correlation was recently proposed by Halliday and Arnold (1987).

The predictions of the direct and indirect sexual selection hypotheses are distinct regarding the effect of female plumage brightness on other breeding birds. If sexual selection is direct and bright plumage signals competitive ability, both males and females should act differently toward dull and bright females. If bright plumage in females is due to genetic correlation with the male trait, no effects of plumage variation were predicted. Females did not respond to the decoy trap and playback differ-

ently according to their plumage. Nor did the plumage of the responding female correlate with her response to a taxidermic mount of a female. The plumage of the female mount did not affect the response of breeding females and finally, males did not distinguish between dull and bright female models when presented with them both simultaneously. These results can not be attributed to an inability to distinguish between individual females. Females are more aggressive to non-resident than to resident females (Searcy 1986) and males risk more defending nests of their primary females (Knight and Temple 1988). Thus, both sexes make distinctions among individual females, but our results indicate that they do not distinguish among females based on the brightness of their plumage. Thus, the results of the model presentations consistently support the hypothesis that bright plumage in females is not functional, but rather is due to genetic correlation with the trait in males.

Our results may have implications for the question of why females are aggressive. For some time, observations such as reproductive success decreasing with nesting density (Weatherhead and Robertson 1977a) have been interpreted as the reason females are aggressive toward new settlers (e.g. Weatherhead and Robertson 1981). However, recent experiments have cast doubt on this interpretation. Searcy (1988) found that removal of females from some territories did not increase the rate of subsequent settlement on those territories, nor did it enhance the reproductive success of the females that settled on those territories. In another experiment where the first females to settle were allowed to remain and later settlers were removed, the success of the first females was not improved by removal of later females (Searcy ms). Finally, Searcy (1988) could find no effect of female aggression on settlement patterns. Thus, female red-winged blackbirds are aggressive but it is not clear why. Halliday and Arnold (1987) proposed that females of some species may copulate with multiple males even though it is not adaptive for them to do so. Because selection favors multiple matings in males, the female behavior may be due to genetic correlation with the male trait. Given the support we have obtained for the genetic correlation hypothesis regarding plumage brightness, it is tempting to speculate that aggressive behavior in female red-winged blackbirds might also be due to genetic correlation with a trait that is clearly selected for in males.

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## References

- Aspey WP, Blankenship JE (1977) Spiders and snails and statistical tales: application of multivariate analysis to diverse ethological data. In: Hazlett BA (ed) Quantitative methods in the study of animal behavior. Academic Press, New York. NY
- Beletsky LD (1983a) An investigation of individual recognition by voice in female red-winged blackbirds. *Anim Behav* 31:355–362
- Beletsky LD (1983b) Aggressive and pair bond maintenance songs of female red-winged blackbirds. *Z Tierpsychol* 62:47–54
- Blank JL, Nolan Jr V (1983) Offspring sex ratio in red-winged blackbirds is dependent on maternal age. *Proc Natl Acad Sci* 80:6141–6145
- Crawford RD (1977) Breeding biology of year-old and older female red-winged and yellow-headed blackbirds. *Wilson Bull.* 89:73–80
- Darwin C (1871) *The descent of man and selection in relation to sex.* John Murray, London
- Dolbeer RA (1976) Reproductive rate and temporal spacing of nesting red-winged blackbirds in upland habitat. *Auk* 93:343–355
- Eckert CG, Weatherhead PJ (1987a) Ideal dominance distributions: a test using red-winged blackbirds (*Agelaius phoeniceus*). *Behav Ecol Sociobiol* 20:43–52
- Eckert CG, Weatherhead PJ (1987b) Male characteristics, parental quality and the study of mate choice in the red-winged blackbird (*Agelaius phoeniceus*). *Behav Ecol Sociobiol* 20:35–42
- Fisher RA (1958) *The genetical theory of natural selection.* Dover, New York, NY
- Greenwood H (1985) Sexual selection and delayed plumage maturation in the sub-adult male cohort of the red-winged blackbird (*Agelaius phoeniceus*). Ph. D. thesis, McGill University
- Greenwood H, Weatherhead PJ (1982) Spring roosting dynamics of red-winged blackbirds: biological and management implications. *Can J Zool* 60:750–753
- Greenwood H, Weatherhead PJ, Titman RD (1983) A new age- and sex-specific molt scheme for the red-winged blackbird. *Condor* 85:104–105
- Halliday T, Arnold SJ (1987) Multiple mating by females: a perspective from quantitative genetics. *Anim Behav* 35:939–941
- Hurly TA, Robertson RJ (1984) Aggressive and territorial behaviour in female red-winged blackbirds. *Can J Zool* 62:148–153
- Hurly TA, Robertson RJ (1985) Do female red-winged blackbirds limit harem size? *Auk* 102:205–209
- Knight RL, Temple SA (1988) Nest-defense behavior in the red-winged blackbird. *Condor* 90:193–200
- LaPrade HR, Graves HB (1982) Polygyny and female-female aggression in red-winged blackbirds (*Agelaius phoeniceus*). *Am Nat* 120:135–138
- Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:292–305
- Lande R, Arnold SJ (1985) Evolution of mating preference and sexual dimorphism. *J Theor Biol* 117:651–664
- Meanley B, Bond GM (1970) Molts and plumages of the red-winged blackbird with particular reference to fall migration. *Bird-Banding* 41:22–27
- Miskimen M (1980a) Red-winged blackbirds: I. Age-related epaulet color changes in captive females. *Ohio J Sci* 80:232–235
- Miskimen M (1980b) Red-winged blackbirds: II. Pigmentation in epaulets of females. *Ohio J Sci* 80:236–239
- Muldal AM, Moffat JD, Robertson RJ (1986) Male parental care of nestlings by red-winged blackbirds, *Agelaius phoeniceus*. *Behav Ecol Sociobiol* 19:105–114
- Munsell AH (1961) *A color notation.* 11th ed. Munsell color Co., Baltimore, Md
- Nero RW (1954) Plumage aberrations of the red-wing (*Agelaius phoeniceus*). *Auk* 71:137–155
- Nero RW (1956a) A behavior study of the red-winged blackbird I. Mating and nesting activities. *Wilson Bull* 68:4–37
- Nero RW (1956b) A behavior study of the red-winged blackbird II. territoriality. *Wilson Bull* 68:129–150
- Orians GH, Christman GM (1968) A comparative study of the red-winged blackbird, tri-colored, and yellow-headed blackbirds. *Univ. of Calif. Publ. in Zoology.* Vol. 84, Univ. of Calif. Press., Berkeley, CA.
- Partridge L, Harvey P (1986) Contentious issues in sexual selection. *Nature* 323:580–581
- Patterson CB (1979) Relative parental investment in the red-winged blackbird. PhD Thesis, Indiana University
- Peck FW (1972) An experimental study of the territorial function of vocal and visual display in the male red-winged blackbird (*Agelaius phoeniceus*). *Anim Behav* 20:112–118
- Picman J (1979) A new technique for trapping female red-winged blackbirds. *N Am Bird Bander* 4:56–57
- Roskaf E, Rohwer S (1987) An experimental study of the function of the red epaulettes and the black body colour of male red-winged blackbirds. *Anim Behav* 35:1070–1077
- Searcy WA (1986) Are female red-winged blackbirds territorial? *Anim Behav* 34:1381–1391
- Searcy WA (1988) Do female red-winged blackbirds limit their own breeding densities? *Ecology* 69:85–95
- Smith DG (1972) The role of epaulets in the red-winged blackbird (*Agelaius phoeniceus*) social system. *Behavior* 41:250–268
- Smithe FB (1975) *Naturalist's color guide.* American Museum of Natural History. New York, NY
- Teather KL, Muma KE, Weatherhead PJ (1988) Estimating female settlement from nesting data. *Auk* 105:196–200
- Weatherhead PJ, Greenwood H (1981) Age and condition bias of decoy-trapped birds. *J. Field Ornithol.* 52:10–15
- Weatherhead PJ, Robertson RJ (1977a) Harem size, territory quality, and reproductive success in the red-winged blackbird (*Agelaius phoeniceus*). *Can J Zool* 55:1261–1267
- Weatherhead PJ, Robertson RJ (1977b) Male behavior and female recruitment in the red-winged blackbird. *Wilson Bull* 89:583–592
- Weatherhead PJ, Robertson RJ (1981) In defense of the “sexy son” hypothesis. *Am Nat* 117:349–356
- Wiens JA, Martin SJ, Holthaus WR, Iwen FA (1970) Metronome timing in behavioral ecology studies. *Ecology* 51:350–352
- Yasukawa K, Searcy WA (1982) Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. *Behav Ecol Sociobiol* 11:13–17