

## Intersexual and intrasexual consequences of epaulet colour in male red-winged blackbirds: an experimental approach

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We conducted experiments on the intersexual and intrasexual consequences of epaulet colour in male red-winged blackbirds, *Agelaius phoeniceus*. In the female choice experiment, we gave captive females a choice between males with normal or dulled epaulets, and between males with normal or reddened epaulets. Females tended to associate more with normal males than with dulled males, but were equally likely to perform precopulatory displays to the two types of males. Females associated significantly more with redder-than-normal males and were more likely to perform precopulatory displays to reddened males. In the male–male competition experiment, we presented free-living territorial males with a male model to which we could attach wings with dulled, normal or reddened epaulets. Presence of the model with reddened epaulets resulted in significant increases in display rates by territory owners, but the increase in display rates was probably in response to males other than the territory owner flying through and trespassing rather than to the reddened epaulet model per se. Normal epaulets produced a significant decrease in song rates and approach distances of owners. Responses of territorial and other males did not differ significantly during normal and dulled epaulet presentations. These results support the hypothesis that epaulets of male red-winged blackbirds are salient inter- and intrasexual signals: unusually red epaulets were attractive to females and attracted more attention and aggression from male conspecifics than normal epaulets. Epaulet colour may thus be an example of intrasexual selection opposing intersexual selection.

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Studies of coloration in avian signalling have received much attention (e.g. Hill & McGraw 2006a, b), especially colour signals that may have evolved by sexual selection (e.g. Andersson 1994; Searcy & Nowicki 2005; Hill 2006; Senar 2006). Colour displays provide many well-known examples of intrasexual signals of aggression and dominance (see Senar 2006) as well as intersexual signals used in mate choice (see Hill 2006). For example, Senar (2006) listed 26 avian species in which plumage traits have been associated with success in agonistic encounters, and 18 avian species for which a relationship between plumage traits and status signalling has been tested experimentally. Interest in the importance of colour in mate choice in birds is even more widespread. Hill (2006) listed more than 50 avian species that have been studied (some multiple times) for the relationship between colour and mate choice. The red-winged blackbird, *Agelaius phoeniceus*, is one

species that has received considerable attention with respect to both inter- and intrasexual selection (see Searcy & Yasukawa 1995).

The common name ‘red-winged blackbird,’ refers to an extensively studied feature of the male’s plumage: the red-and-yellow epaulet at the wrist of the wing. Observational evidence is consistent with the hypothesis that the epaulet functions intrasexually in territory defence. Territory owners display their epaulets in response to male intruders, but trespassing and newly establishing males keep their epaulets covered (Nero 1956b; Orians & Christman 1968; Hansen & Rohwer 1986). Some experimental evidence also supports the territory defence hypothesis. Males whose epaulets were experimentally blackened (‘black-winged blackbirds’) experienced elevated rates of trespassing, had difficulty evicting trespassers and were more likely to lose their territories than sham-manipulated controls (Peek 1972; Smith 1972; Morris 1975). On the other hand, males whose epaulets had been reduced in size were able to defend their territories (Westneat 2006). Thus, despite a number of published studies, the territory defence function of male red-winged blackbird epaulets remains unclear.

There is also some evidence that the epaulet functions intersexually in attracting females. Male red-winged blackbirds display their epaulets conspicuously during courtship and precopulatory

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display (Nero 1956a; Orians & Christman 1968). Epaulet blackening experiments have inconsistent effects on mating success, however. In some cases black-winged males are able to retain mates (Smith 1972; Morris 1975), but Peek (1972) describes cases in which experimental males were unable to attract mates until the black wore off their epaulets. Surprisingly, despite the continued interest in sexual selection on red-winged blackbirds in general, and on their epaulets in particular, to our knowledge there have been no experimental tests of the effects of male epaulets on female mate preferences.

If the epaulets of the male red-winged blackbird function in territory defence and perhaps in mate attraction as well, as is often the case for carotenoid-based ornaments (Searcy & Nowicki 2005; Hill 2006), then it is reasonable to ask whether there are constraints (e.g. Hill et al. 2002; Evans 2004) or counterbalancing selection (Promislow et al. 1992) on them. For example, conspicuous 'badges' (Dawkins & Krebs 1978; Rohwer 1982) such as epaulets may increase the risk of predation and therefore reduce survivorship (Senar 2006). Male red-winged blackbirds are able to reduce this risk to some extent by covering the red portion of the epaulet. Possession of a 'coverable badge' (Hansen & Rohwer 1986) may therefore represent an adaptation to minimize survival disadvantages (Metz & Weatherhead 1992). In addition, male red-winged blackbirds show 'delayed plumage maturation' (Rohwer et al. 1980), in which the epaulets of 1-year-old males are more orange than red and contain at least some black within them (Yasukawa & Searcy 1995). Perhaps the benefits of a conspicuous badge are insufficient to compensate the fitness costs for young males, although other explanations are certainly tenable (e.g. Rohwer & Butcher 1988; Senar 2006). Even with delayed plumage maturation and a coverable badge, however, there may be other limits imposed on the expression of the male red-winged blackbird's epaulets, so that the degree of expression is bounded on both ends: an epaulet that is too small or inconspicuous is ineffective, but one that is too big or showy is too costly. As we discuss below, some experiments with male red-winged blackbirds suggest such limits.

Experiments using mounts with small, normal or enlarged epaulets provide some evidence for a 'self-limiting' sexual selection (Searcy 1979a; Searcy & Yasukawa 1983) on red-winged blackbird epaulet size. Mounts with enlarged epaulets are more effective in 'defending' otherwise empty territories than mounts with normal or no epaulets (Røskaft & Rohwer 1987), but these mounts also receive more aggression from territory owners than mounts with normal epaulets (Hansen & Rohwer 1986). In addition to studies of epaulet size, Westneat (2006) examined epaulet colour. He found that males with dulled epaulets do not differ from those with normal epaulets in territory defence or reproductive success. To our knowledge, however, there have been no studies of red-winged blackbirds with epaulets of enhanced colour.

In our study we conducted separate experiments to investigate the intersexual and intrasexual consequences of epaulet colour. An experimental approach is necessary in this case to disentangle the inter- and intrasexual functions of epaulet colour (e.g. Hill 2006; Griffith & Pryke 2006). In one female choice experiment, we gave wild-caught, captive female red-winged blackbirds the choice of a male with dulled epaulets or one with normal epaulets. In a second experiment females were given the choice of a male with normal epaulets or one with reddened epaulets. If more showy epaulets are advantageous in female choice, then females should prefer normal to dulled males, and reddened to normal males. On the other hand, if female preference has produced epaulets of optimum showiness, then females should prefer normal to dull epaulets, and normal to reddened epaulets. In the male–male competition experiment we presented a model of a male red-winged blackbird with reddened, normal or dulled epaulets to assess the responses of free-living territorial males. If epaulet

showiness is advantageous in male–male competition, then aggression by conspecific males should decrease from dull to normal to reddened epaulets of mounts. If epaulet showiness is constrained by disadvantages imposed by intrasexual aggression, however, then aggression from conspecific males should increase from dull to normal to reddened epaulets.

## METHODS

### *Intersexual Selection (Female Choice) Experiment*

#### *Capture and housing*

Red-winged blackbirds were captured with mist nets and grain-baited Potter traps at two breeding sites in east-central Illinois, U.S.A. The first site, an upland alfalfa field near the University of Illinois, Champaign County, Illinois (40°8'N, 88°12'W), supported approximately 30 territories. The second site, located 45 km south of the first in a cattail marsh near the town of Arcola, Douglas County, Illinois (39°41'N, 88°18'W), supported more than 50 territories. Males were captured beginning in late March as they arrived on the sites; females were captured upon their arrival beginning approximately 3 weeks later. Upon capture, all birds were weighed and morphological measurements (bill length, flattened wing length, tail length, tarsus length) taken. Birds were held in captivity up to 6 weeks (U.S. Fish and Wildlife Service, USFWS permit nos 06507 and prt-759043). Males were housed in individual cages to control for effects of dominance status (Eckert & Weatherhead 1987b). Females were housed in groups of two to three.

Birds were housed in a large outdoor aviary (17.8 × 12.2 × 6.1 m) at the Illinois Natural History Survey, on the campus of the University of Illinois. The aviary consisted of 42 separate holding cages (2.4 × 0.15 × 2.4 m). Outside walls and walls on an inner hallway (2 m wide) as well as half of the ceiling of each cage were made of 1.25 cm<sup>2</sup> plastic-coated hardware cloth. Walls between holding cages were made of sheets of 8-mil (0.2 mm) black plastic on wood frames. Thus birds were exposed to ambient light and weather conditions. Natural perches and a shelter area were provided in each cage, and cages were protected from predators by an electric fence. Birds were fed ad libitum a grain diet (Eckert & Weatherhead 1987b) supplemented with a mixture of boiled eggs, soy flour and vitamin supplement. Twenty larvae (mealworms, wax worms, or fly maggots) were provided to each bird daily, and chopped fruit was provided occasionally. Water was available ad libitum and, because we found captive redwings to be susceptible to coccidiosis, birds were treated with a coccidiocide (in drinking water) for the first 10 days of captivity.

#### *Experimental protocol*

Choice experiments were conducted in an indoor aviary at the University of Illinois, Department of Animal Biology. Mate choice experiments consisted of a series of trials in which we assessed the preferences of single females for one of two simultaneously presented males, one with unaltered epaulets and the other with either dulled (experiment 1) or reddened (experiment 2) epaulets. Each set of males was used to assess two to four females. Two choice experiments were conducted in 1996 (experiment 1: 25 March–24 April; experiment 2: 8–31 May). Experiment 2 was repeated in 1998 (24 March–20 April) because of concerns that male and female hormonal condition, and so behaviour, may change with the season and prolonged captivity, and that the behaviour of the birds may change with repeat exposures to the choice protocol.

Studies of female choice of mate in birds typically use exogenous oestradiol to potentiate copulation solicitation display (e.g. Searcy et al. 1981; Møller 1988; Enstrom et al. 1997; Beguin et al. 2006),

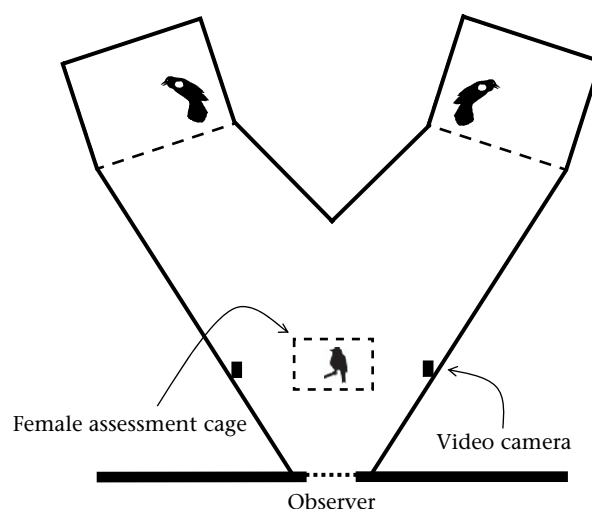
which is used as a female preference bioassay (King & West 1977; West et al. 1979). Administration of oestradiol results in performance of the display (e.g. Searcy et al. 1981; Searcy 1984; Searcy & Capp 1997), but does not alter mate preferences (Enstrom et al. 1997; Searcy & Capp 1997; Hosoi et al. 2005). In our study, female red-winged blackbirds received oestradiol in 20-mm-long silastic® implants (1.47 mm inner diameter, 1.96 mm outer diameter, Dow-Corning, Midland, MI, U.S.A.) sealed with silastic® adhesive (Dow-Corning) to make them receptive to the males during the experiments (Searcy 1988, 1989, 1990; Searcy & Brenowitz 1988; Searcy & Capp 1997). Our implants were sized to produce circulating levels at the upper end of the normal physiological range (see Searcy & Capp 1997). We anaesthetized each female with Methoxyflurane (Pitman-Moore Pharmaceuticals, Kansas City, KS, U.S.A.), then extended the left leg to expose the area above the thigh, cleared the area of down feathers ( $\leq 10$ ) and washed it three times with alcohol and Betadine® (Purdue Pharma L.P., Stamford, CT, U.S.A.). We then made a small (2–3 mm) incision with scissors and opened a channel for the implant using a blunt probe. Once the implant was in place, the leg was allowed to assume its normal position, and the incision was naturally held closed; no sutures or skin adhesives were necessary.

Following implantation, the female was placed in a small dark cage for 20–30 min to allow the effects of the anaesthetic to wear off. The female was then returned to the aviary when she appeared to be alert. Implants were closely examined daily until the incision was completely healed, and were checked again on the day each female was used in preference trials. Implants were removed several days before the females were released into the wild using the same protocol outlined above. The animals were held in the aviary until the incision healed fully.

Male stimulus sets were made up of individuals from a single capture site. Each set was matched as closely as possible for morphological measurements, as well as for epaulet size and colour. Members of each pair were assigned to treatment (altered or control epaulets) randomly, and females were always presented with a stimulus set from the opposite collection site to eliminate effects of familiarity. As we were attempting to determine the effects of epaulet colour rather than the extent to which males display their epaulets, we trimmed the scapular feathers of all experimental males to ensure that their epaulets were exposed to the females throughout the experiment (see Metz & Weatherhead 1992).

The experimental aviary was designed to allow females to see and hear both stimulus males while preventing males from seeing each other (Fig. 1). Fluorescent lighting in the aviary was kept on the local sunrise–sunset cycle, and food and water were provided ad libitum to all birds throughout the experiments. Males were located in chambers ( $1.2 \times 1.5 \times 2.4$  m) in opposite arms of the aviary, and were separated from each other by plywood walls and from the female portion of the aviary by  $1.25 \text{ cm}^2$  plastic-coated hardware cloth, through which males and females could interact (Fig. 1). Perches were provided in abundance throughout all three chambers. Males were placed in the aviary (position randomly chosen) the afternoon (approximately 1600 hours Eastern Standard Time) before they were to be used in trials. The following morning (starting about 0615 hours) each male was monitored for 30 min (pretrial period) before the introduction of the female. Up to four trials were conducted per day. During the pretrial period we noted the number of perch changes, songs and calls of each stimulus male.

Each trial consisted of a 20 min ‘assessment’ period and a 30 min period of ‘choice’ (Enstrom et al. 1997). At the start of each trial the female was placed in a small holding cage ( $1 \times 0.5 \times 0.5$  m) suspended 2.2 m in front of the male cages and 2 m from the aviary floor (Fig. 1). From this position, females could



**Figure 1.** Schematic overhead view of choice arena used to test female red-winged blackbird preference for males with dulled versus normal epaulets, or normal versus reddened epaulets.

see and interact vocally with both males. During this assessment period we noted the number of perch changes and vocalizations (songs and calls) of each stimulus male as well as the vocalizations of the subject female. The female was then released into the larger chamber, beginning the period of ‘choice’, during which females were free to spend time with either male in designated choice areas (perches along the shared border with the males, and the hardware cloth wall itself) or in neutral areas (the rest of the aviary). The floors of the male chambers were raised 0.5 m from the floor of the larger aviary so that females had to come up from the floor to ‘spend time’ with the males. During this choice period, males performed song spread displays when females interacted with them. Song spreads are characterized by spreading of the wings and tail while thrusting the head forward and upward (Nero 1956b; Orians & Christman 1968).

After each trial, males were moved to the opposite arm of the test aviary to control for position effects. We waited at least 30 min before introducing the next female.

We observed trials from a room adjoining the choice arena through a  $1 \text{ m}^2$  pane of one-way glass and we could hear interactions through speakers attached to video cameras. We had two estimates of female preference: attendance time (the time that each female spent in each male’s choice area) and the number of precopulatory displays given by the female when in a male’s choice area (Searcy 1988; Enstrom et al. 1997). Only females that spent at least 25% of the choice period ( $\geq 7.5$  min) with one or both males were included in our analysis. Females that did not meet this criterion were retested up to twice more. We classified a male as ‘chosen’ if the female spent at least 20% more time in his choice area than in the choice area of the other male. We considered a trial to have ended in a tie if the female did not spend at least 20% more time with one of the males.

In experiment 1, subject female red-winged blackbirds were given a choice of a male with epaulets of unaltered colour and a male with dulled epaulets. The epaulets of all males were swabbed with alcohol and air-dried. Epaulets of experimental males were then dulled using Nyanzol D black dye (Smith 1972), which was rinsed off with water as the red epaulet feathers began to darken. Control males were treated similarly, but with water rather than dye. Prior to treatment, male epaulets had a red hue (8.75–10R) with value of 4–9 and chroma of 14–16 on the Munsell scale (X-Rite Inc., Grand Rapids, MI, U.S.A.). Dyeing produced a more orange (2.5–5YR), less saturated (chroma = 8–10) colour with

a slightly lower value (4–5). Dulled epaulets were thus at or just below the low end of natural variation for males in the definitive breeding plumage.

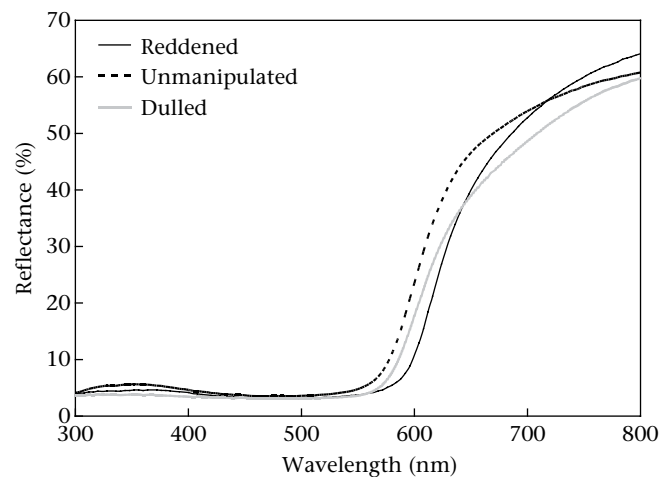
In experiment 2, females were presented with a male with normal epaulets and a male with reddened epaulets. The red feathers of the epaulets of males to be enhanced were 'painted' with a Berol® (Sanford U.K.: London) Prismacolor PM-6 carmine red art marker, resulting in an immediate reddening. Epaulets of control males were 'painted' with a cotton swab. Prior to manipulation, epaulets were 5YR–8.25R in hue, 4–7 in value and 14–16 in chroma on the Munsell scale. Increased redness was accomplished by changing the hue of the epaulet to a redder (7.5R), more saturated (chroma = 16) colour with a consistent value (4) on the Munsell scale. Experimentally reddening thus produced epaulets that were uniformly colour-enhanced and outside the normal range of variation.

Because we used a forced-choice design, we used pairwise comparisons for time spent with each of the stimulus males. The nonparametric Wilcoxon signed-ranks test was used because the data were not normally distributed (Sokal & Rohlf 1995). Copulation solicitation was compared using Pearson tests of independence. We used a Wilcoxon two-sample test to compare dulled males from experiment 1 to reddened males from experiment 2. We used binomial probabilities to test the null hypothesis that females randomly associated with males in our trials. Analyses were performed using JMP v. 6.0 (SAS Institute, Cary, NC, U.S.A.) and statistical significance was accepted at  $\alpha = 0.05$ . The methods used in the intersexual selection experiment were approved by the University of Illinois Institutional Animal Care and Use Committee (IACUC protocol no. 01174).

#### *Intrasexual Selection (Male–Male Competition) Experiment*

Mounts were presented at Newark Road Prairie and Diehls Prairie in south-central Wisconsin, U.S.A. (42°32'N, 89°08'W) from 9 April to 13 June 1997 in the early morning. The study area consisted of prairie and sedge meadow habitat, which supported 50–60 red-winged blackbird territories (Yasukawa 1989; Clotfelter 1997). All territorial males used as experimental subjects were captured in grain-baited Potter traps and were banded with U. S. Fish and Wildlife numbered aluminium bands (USFWS permit no. 20438) and unique colour combinations of plastic bands.

We used a complete random blocks design in which each territorial male (block) was to be exposed to all three epaulet treatments. A set of five to six territories was chosen for a round of presentations. The male owners of these territories were observed and their frequently used perches noted. The order in which we conducted presentations within each set was determined such that no contiguous territories were used consecutively. Within each territory a specific location within 10 m of a frequently used perch was chosen and marked with vinyl flagging. This location was used for the three presentations on that territory. On three consecutive days, weather permitting, at about the same time of day, we presented a black balsa wood model of a male red-winged blackbird, to which we could attach with Velcro™ fasteners one of three pairs of wings with reddened epaulets, normal epaulets or dulled epaulets. The epaulets of two pairs of wings were randomly chosen from among seven available pairs and manipulated by colouring them with Eberhard Faber® Design 2 art markers (Lewisburg, TN, U.S.A.): red orange (value 3, D-18) and orange (value 3, D-13). To verify that the markers affected the colour of the epaulets, we used a Cary 5E spectrometer (Varian, Sunnyvale, CA, U.S.A.) using an integrating sphere (model RSA-CA-50D, Labsphere, North Sutton, NH, U.S.A.) with a Spectralon surface to produce reflectance spectra from 300 to 800 nm with an interval of 4 nm. As shown in Fig. 2, the reflectance spectra of the three epaulet types were different. Normal



**Figure 2.** Reflectance spectra of male red-winged blackbird epaulets that were experimentally brightened, unmanipulated and experimentally dulled.

epaulets reflect primarily in the orange–red (600–800 nm), whereas reddened epaulets were shifted to the red (630–800 nm) and were highly reflective above 700 nm (shifted to the right = redder hue). The difference between normal and reddened epaulets was significant (matched-pairs *t* test:  $t_{125} = 5.57$ ,  $P < 0.0001$ ; Motulsky & Ransnas 1987). 'Dull' epaulets did appear to be slightly duller to our eyes, and although their spectra showed orange reflectance similar to that of normal epaulets and red reflectance similar to that of reddened epaulets, the overall reflectance was reduced (shifted downward = less bright). The difference between dulled and normal epaulets was significant (matched-pairs *t* test:  $t_{125} = -12.6$ ,  $P < 0.0001$ ; Motulsky & Ransnas 1987). We assume that male red-winged blackbirds also perceived differences between the epaulet types (note that there does not appear to be a substantial UV component to epaulet colour).

At each location on each day, we first conducted a model-only presentation for 5 min as follows. The balsa wood model was attached to a pole, which was pushed into the ground at the specified location so that the model was about 2 m above the ground and clearly visible from the nearby perch. We began each observation once the subject territory owner was on the territory, in a position to see the model, and oriented towards the model; if the subject left the territory, we stopped the observation and waited for the male's return. The model-only presentation was followed immediately by a model-with-wings presentation for 5 min. We randomly selected the reddened, unmanipulated or dulled epaulets and attached them to the balsa wood model using Velcro™ fasteners and began the presentation using the criteria for the model-only presentation.

During each 5-min presentation we recorded the number of times the territorial male performed song spread displays ('song spreads'; spreading of the wings and tail while thrusting the head forward and upward; Nero 1956b; Orians & Christman 1968) and songs without spreads ('songs'; males often sing without extending the wings and spreading the tail). We also noted the number of times other males flew through the territory ('fly throughs') and perched within the territory ('trespasses'). Whenever possible, we identified the intruding male and his point of origin. After the presentation was completed, we also measured the distance from the model to the territorial male's closest perch ('closest approach').

We performed two sets of statistical comparisons using nonparametric methods. Responses to the model without wings ('pre-experimental') were compared to responses to the model with wings ('experimental') using a Wilcoxon matched-pairs



signed-ranks test. Three such pre-experimental/experimental comparisons (reddened epaulet, normal epaulet, dull epaulet) were performed for each of the five response variables (songs, song spreads, closest approaches, fly throughs, trespasses). These matched-pairs comparisons allowed us to separate the effects of the epaulets from those of the jet-black plumage. Responses to the three experimental treatments (reddened epaulet, normal epaulet, dull epaulet) were compared using a Friedman's test (Sokal & Rohlf 1995). These complete random blocks comparisons allowed us to compare the responses of male red-winged blackbirds to the three treatment groups. Statistical tests were performed with JMP v. 6.0 (SAS Institute, Cary, NC, U.S.A.) and Statview 512+ (BrainPower Inc., Calabasas, CA, U.S.A.); statistical significance was accepted at  $\alpha = 0.05$ . The methods used in the intrasexual selection experiment were approved by the Beloit College Institutional Animal Care and Use Committee (IACUC protocol no. 97001).

## RESULTS

### Intersexual Selection (Female Choice) Experiment

#### Pretrial versus assessment periods

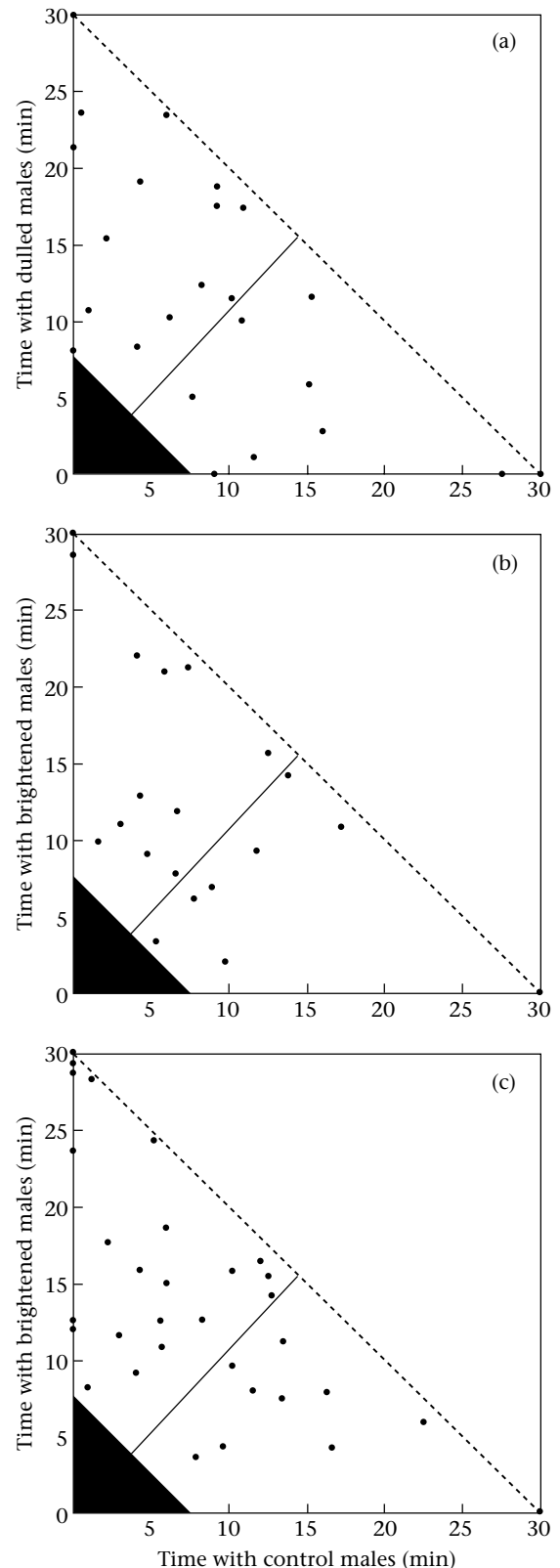
Males changed perches significantly more often during the 20 min assessment period ( $\bar{X} \pm SE = 11.9 \pm 2.55/\text{min}$ ) than during the 30 min pretrial period before females were present ( $5.56 \pm 1.19/\text{min}$ ) when females were confined in the holding cage (Wilcoxon signed-ranks test:  $Z = -5.48$ ,  $N = 21$  stimulus males,  $P < 0.0001$ ). Males seldom sang during the pretrial period, but never sang during the assessment period. Males also gave significantly fewer 'chee' calls (Wilcoxon signed-ranks test:  $Z = -4.74$ ,  $N = 21$ ,  $P < 0.0001$ ) during the 30 min pretrial period ( $\bar{X} \pm SE = 11.9 \pm 2.55/\text{min}$ ) than during the assessment period ( $14.7 \pm 3.13/\text{min}$ ). There were no significant differences in the behaviour of experimental versus control males during either the pretrial period (perch changes: control =  $5.38 \pm 0.49/\text{min}$ , experimental =  $5.49 \pm 0.57/\text{min}$ , Wilcoxon signed-ranks test:  $Z = 0.26$ ,  $N = 21$  stimulus males,  $P = 0.79$ ; songs: control =  $0.19 \pm 0.13/\text{min}$ , experimental =  $0.07 \pm 0.05/\text{min}$ , Wilcoxon signed-ranks test:  $Z = 0.73$ ,  $N = 21$  stimulus males,  $P = 0.47$ ) or the assessment period (perch changes: control =  $11.3 \pm 0.8/\text{min}$ , experimental =  $12.6 \pm 0.7/\text{min}$ , Wilcoxon signed-ranks test:  $Z = 1.1$ ,  $N = 21$  stimulus males,  $P = 0.25$ ) in any of the experiments. During the assessment period, all females moved and vocalized (chip notes) often.

#### Experiment 1: epaulet dulling

We presented seven stimulus sets of male red-winged blackbirds to 28 females (Fig. 3a). Females spent 41% less time with dull males ( $\bar{X} \pm SE = 7.96 \pm 1.47$  min) than with normal males ( $13.6 \pm 1.84$  min), but the difference was marginally nonsignificant (Wilcoxon signed-ranks test:  $Z = 2.05$ ,  $N = 28$ ,  $P = 0.057$ ). The likelihood that females performed precopulatory display for dull (9/28) versus control (12/28) males was not significantly different (Pearson test of independence:  $\chi^2_1 = 0.69$ ,  $P = 0.4$ ). Although control males sang ( $\bar{X} \pm SE = 1.71 \pm 0.32/\text{min}$ ) more often than dull males ( $0.54 \pm 0.10/\text{min}$ ), the difference was not significant (Wilcoxon signed-ranks test:  $Z = -1.11$ ,  $N = 28$ ,  $P = 0.27$ ). We noted, however, that males sang or gave song spread displays only when females were in their choice areas and all female precopulatory displays were given during or immediately after male song spread displays. By our 20% criterion, the difference in preference for control (17) versus dull (9) males (there were two ties) was marginally nonsignificant (binomial test:  $P = 0.084$ ).

#### Experiment 2: epaulet reddening

We presented six pairs of stimulus males to 22 female red-winged blackbirds in 1996 (Fig. 3b). Females spent significantly



**Figure 3.** Female attendance time for control and experimental male red-winged blackbirds. (a) Experiment 1 (1996): control males versus dull epaulet males. (b) Experiment 2 (1996): control males versus reddened epaulet males. (c) Experiment 2 (1998): control males versus reddened epaulet males. Dashed line indicates the maximum attendance time (30 min); shaded area indicates 'no choice' (0–7.5 min); solid line shows the equal attendance function. Points in the upper trapezoid represent females that 'chose' experimental males, whereas points in the lower region are for females that chose control males.

more time with reddened males ( $\bar{X} \pm \text{SE} = 14.2 \pm 1.91$  min) than with control males ( $7.87 \pm 1.44$  min) (Wilcoxon signed-ranks test:  $Z = 2.10$ ,  $N = 22$ ,  $P = 0.036$ ) and were also significantly more likely to direct precopulatory display towards reddened males (14/22) than towards normal males (4/22) (Pearson test of independence:  $\chi^2_1 = 9.40$ ,  $P = 0.002$ ). As in experiment 1, males sang only when females were in their choice areas and all female precopulatory displays were given during or immediately after male song spread displays. Perhaps as a result, reddened males performed song spread displays ( $\bar{X} \pm \text{SE} = 2.27 \pm 0.48/\text{min}$ ) significantly more often than did control males ( $1.13 \pm 0.24/\text{min}$ ) (Wilcoxon signed-ranks test:  $Z = 2.33$ ,  $N = 22$ ,  $P = 0.02$ ). More females chose reddened males (13) than control males (7) (there were two ties), but this difference was not significant (binomial test:  $P = 0.13$ ).

In 1998 we presented eight pairs of stimulus males to 32 females (Fig. 3c). Females again spent significantly more time with reddened males ( $\bar{X} \pm \text{SE} = 13.9 \pm 1.41$  min) than with control males ( $7.91 \pm 1.27$  min) (Wilcoxon signed-ranks test:  $Z = -2.33$ ,  $N = 32$ ,  $P = 0.02$ ). More females performed precopulatory displays to reddened males (17/32) than to control males (13/32), but the difference was not significant (Pearson test of independence:  $\chi^2_1 = 1.00$ ,  $P = 0.3$ ). Although reddened males gave song spreads at a higher rate ( $\bar{X} \pm \text{SE} = 1.44 \pm 0.25/\text{min}$ ) than control males ( $0.78 \pm 0.14/\text{min}$ ), the difference was not significant (Wilcoxon signed-ranks test:  $Z = 1.39$ ,  $N = 32$ ,  $P = 0.16$ ). Significantly more females chose (spent  $\geq 20\%$  more time in one choice area than in the other) reddened epaulet males (20) than control males (8) (binomial test:  $P = 0.018$ ); there were four ties.

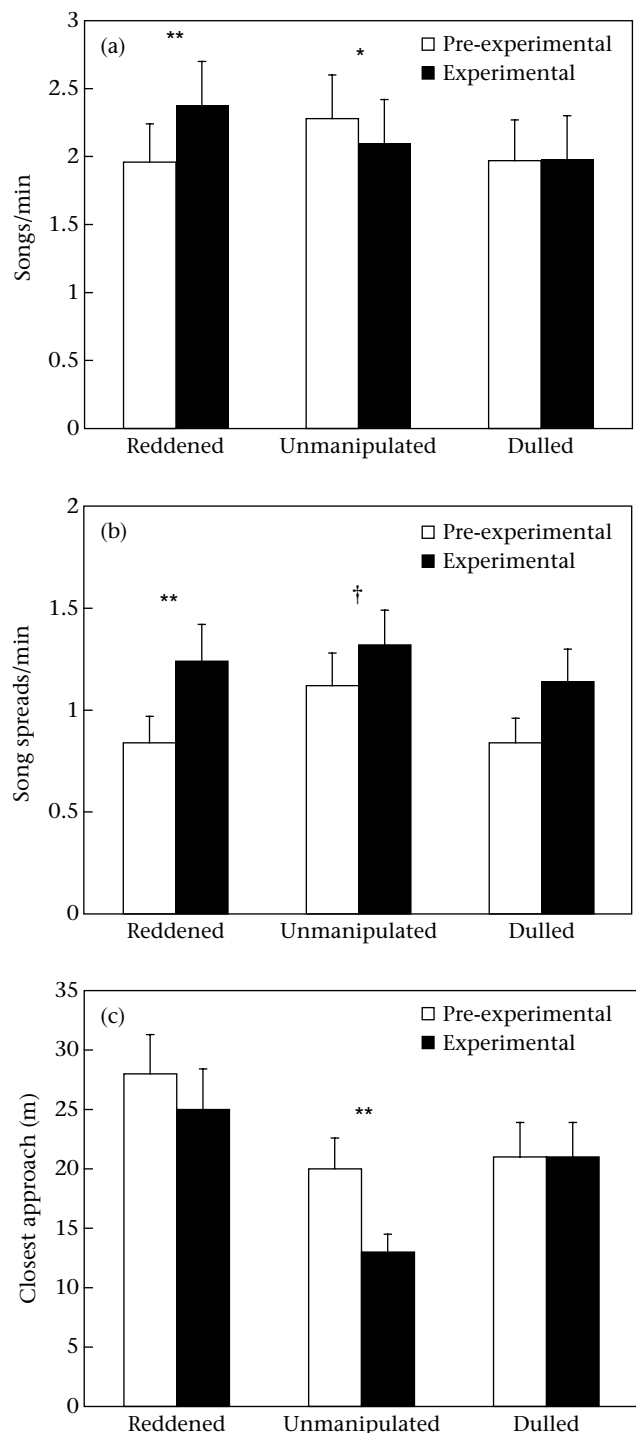
When we compared the results of the two female choice experiments (results of the reddening experiments were pooled), female red-winged blackbirds spent significantly more time with reddened males ( $\bar{X} \pm \text{SE} = 13.9 \pm 1.13$  min) than with dulled males ( $7.96 \pm 1.47$  min) (Wilcoxon two-sample test:  $Z = -3.27$ ,  $N_1 = 28$ ,  $N_2 = 54$ ,  $P = 0.001$ ) and were significantly more likely to perform precopulatory display to reddened males (31/54) than to dulled males (9/28) (Pearson test of independence:  $\chi^2_1 = 4.71$ ,  $P = 0.030$ ).

#### Intrasexual Selection (Male–Male Competition) Experiment

We presented dulled, normal and reddened epaulets to 47 free-living territorial males. Two additional males disappeared from their territories before we could present all three types of epaulets. One of these males was presented with normal and reddened epaulets but not dulled epaulets, and the other male saw only the reddened epaulets. We present means, standard errors and statistical comparisons for all available subject males, so our sample size varies from 47 to 49.

When we compared song rates (Fig. 4a) and song spread rates (Fig. 4b) among the three experimental treatments, neither rate varied significantly with epaulet treatment (Friedman's ANOVA: song rate:  $\chi^2_2 = 3.99$ ,  $P = 0.14$ ; song spread rate:  $\chi^2_2 = 4.18$ ,  $P = 0.12$ ). In contrast, both song rates and song spread display rates were significantly higher during presentations of the model with reddened epaulets than during presentations of the model alone (Wilcoxon signed-ranks test: song rate:  $Z = 2.79$ ,  $N = 49$ ,  $P = 0.004$ ; song spread rate:  $Z = 2.77$ ,  $N = 49$ ,  $P = 0.004$ ). Song rates were significantly lower during presentation of the model with normal epaulets than during presentation of the model alone (Wilcoxon signed-ranks test:  $Z = 2.08$ ,  $N = 48$ ,  $P = 0.036$ ), and song spread rates were marginally higher, but not significantly so ( $Z = 1.74$ ,  $N = 48$ ,  $P = 0.081$ ). Neither song rate nor song spread rate differed significantly between dull epaulet and model-only presentations (Wilcoxon signed-ranks test: song rate:  $Z = 0.06$ ,  $N = 47$ ,  $P = 0.96$ ; song spread rate:  $Z = 1.74$ ,  $N = 47$ ,  $P = 0.15$ ).

Closest approaches of territorial male red-winged blackbirds (Fig. 4c) varied significantly with epaulet treatment (Friedman's



**Figure 4.** (a) Song rates, (b) song spread rates and (c) closest approach distances of territorial male red-winged blackbirds to presentation of mounts without wings (pre-experimental) and with wings (experimental). Epaulets on wings were either unmanipulated, or experimentally reddened or dulled. † $P < 0.1$ ; \* $P < 0.05$ ; \*\* $P < 0.01$  (for comparison of pre-experimental and experimental presentations).

ANOVA:  $\chi^2_2 = 8.06$ ,  $P = 0.018$ ); models with unmanipulated epaulets elicited the closest approaches. A comparison of pre-experimental and experimental periods showed that territorial males approached significantly closer to the model with normal epaulets than to the model without epaulets (Wilcoxon signed-ranks test:  $Z = 2.46$ ,  $N = 48$ ,  $P = 0.01$ ), but neither the presence of reddened epaulets (Wilcoxon signed-ranks test:  $Z = 0.67$ ,  $N = 49$ ,  $P = 0.51$ ) nor dulled epaulets (Wilcoxon signed-ranks test:  $Z = 0.22$ ,

$N = 47$ ,  $P = 0.83$ ) had a significant effect on closest approach compared with approach to the model alone.

Fly-through rates of male red-winged blackbirds other than the territory owner (Fig. 5a) did not vary significantly among the epaulet treatments (Friedman's ANOVA:  $\chi^2_2 = 3.64$ ,  $P = 0.16$ ), but fly-through rates were significantly higher during reddened epaulet presentations than during model-only presentations (Wilcoxon signed-ranks test:  $Z = 3.14$ ,  $N = 49$ ,  $P = 0.001$ ). Presentation of normal or dulled epaulets did not result in significantly different fly-through rates than did presentation of the model without wings (Wilcoxon signed-ranks test: normal epaulets:  $Z = 1.31$ ,  $N = 48$ ,  $P = 0.25$ ; dull epaulets:  $Z = 1.04$ ,  $N = 47$ ,  $P = 0.33$ ).

Trespassing by male red-winged blackbirds other than the territory owner (Fig. 5b) varied significantly with epaulet treatment (Friedman's ANOVA:  $\chi^2_2 = 6.25$ ,  $P = 0.044$ ), and trespass rates were significantly higher in response to the reddened epaulet model than in response to the model alone (Wilcoxon signed-ranks test:  $Z = 2.54$ ,  $N = 49$ ,  $P = 0.014$ ). Trespass rates did not differ significantly when model-only presentations were compared with normal epaulet treatments (Wilcoxon signed-ranks test:  $Z = 1.81$ ,  $N = 48$ ,  $P = 0.12$ ) or dulled epaulet treatments ( $Z = 1.41$ ,  $N = 47$ ,  $P = 0.29$ ).

Singing, especially song spread display, is a common response to territorial intruders, so the significant increases in singing rates during presentation of the mount with reddened epaulets could

either be in response to the presence of the model, or to intruders attracted by the presentation. In an attempt to separate the effects of intruders from those of the model itself, we restricted comparison of song and song spread rates for model-only versus model-with-wings to those presentations in which both the fly-through rates and trespass rates were the same. With this subset, singing rates during model-only and model-with reddened epaulet presentations did not differ significantly (Wilcoxon signed-ranks test: song rate:  $Z = 0.69$ ,  $N = 26$ ,  $P = 0.49$ ; song spread rate:  $Z = 1.24$ ,  $N = 26$ ,  $P = 0.22$ ). Significant increases in singing rates during reddened epaulet presentations thus appear to be the result of increased trespassing rather than a response to the model itself.

## DISCUSSION

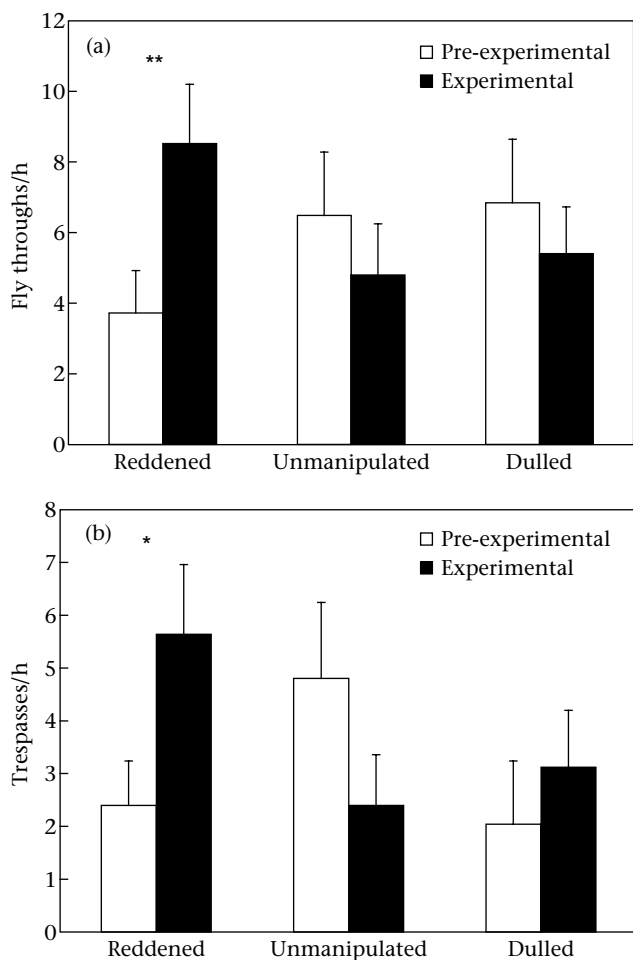
Experimental manipulations are used to good advantage in studies of visual signals in general and of sexual selection in particular. Andersson (1994), Searcy & Nowicki (2005), Senar (2006) and Hill (2006) reviewed experimental studies of sexual selection and size or colour of badges. Senar (2006) concluded that three decades of research support the hypothesis that colours can act as reliable signals of fighting ability in birds, and Hill (2006) noted that over 100 studies made it clear that mate choice is an important selective agent in the evolution of colour displays.

The epaulet of the red-winged blackbird is a trait that would seem to be a product of sexual selection, and many studies have been published, but perhaps surprisingly, there is little evidence that epaulet size and colour affect reproductive success (Westneat 2006; Yasukawa et al., in press). In discussing the general lack of evidence of current sexual selection in red-winged blackbirds, Westneat (2006) noted that confounding variables and counterbalancing selection make it difficult to interpret this result (see also Hill 2002), and he pointed out that experimental manipulation is necessary to decouple interacting variables.

Our two experiments were designed to decouple intersexual and intrasexual components of sexual selection. Our female choice experiment showed that female red-winged blackbirds spent significantly more time with reddened epaulet males than with males with normal epaulets and they were more likely to solicit copulation from males with redder-than-normal epaulets. We also found marginally nonsignificant evidence of discrimination against duller-than-normal epaulets. These results suggest that female choice results in directional selection for epaulet colour (Searcy & Yasukawa 1983).

Mate choice can be defined as differential mating (an outcome) that is a result of mating preferences (Heisler et al. 1987), sampling strategies and environmental conditions (Wagner 1998). Many studies of mating preferences use forced-choice designs and a variety of response variables to infer choice (see Wagner 1998; Adkins-Regan 2005). In birds, attendance time (e.g. Burley et al. 1982; Hill 1990; Enstrom et al. 1997) and copulation solicitation (e.g. King & West 1977; Searcy et al. 1981; Enstrom et al. 1997) are frequently used to study the effects of acoustic and visual signals on female preferences. Attendance time predicts mating success (West et al. 1981; Burley 1986; Zuk et al. 1990) and fertilization success (Burley et al. 1996), and copulation solicitation occurs when females are fertile (Drevon & Slagsvold 2005) and it predicts copulation success (West et al. 1981), so these estimates of preference are valid indicators of choice.

Our male–male competition experiment showed that reddened epaulets had the greatest effect on territorial male red-winged blackbirds, normal epaulets elicited some response and dull epaulets had no significant effect. We also found that a model male red-winged blackbird with epaulets that were redder than normal elicited more interest from males other than the territory owner than a model with normal, dull or no epaulets. Fly throughs and



**Figure 5.** Rates of intrusion by male red-winged blackbirds other than the territory owner in response to presentation of a model without wings (pre-experimental) and with wings (experimental): (a) fly throughs; (b) trespasses. Epaulets on wings were either unmanipulated, or experimentally reddened or dulled. \* $P < 0.05$ ; \*\* $P < 0.01$  (for comparison of pre-experimental and experimental presentations).

trespasses by males other than the territory owner were significantly more frequent during reddened epaulet presentations than during model-only presentations.

Territorial male red-winged blackbirds are known to take interest in male–male conflicts on neighbouring territories (Nero 1956b; Freeman 1987; personal observation), so perhaps males flew through and trespassed from neighbouring territories in an attempt to gather information about the contestants (Freeman 1987). In many cases we could not identify the intruding male, but in most cases when we were able to see bands or the origin of the intruder's flight, the intruders did not appear to be immediate neighbours. Both nonterritorial 'floaters' and owners of poor territories are known to prospect for breeding opportunities (Beletsky 1996), however, so the trespassing males we observed may have been attracted to our simulated confrontation while searching for territories. Our reddened epaulet mount may have attracted more attention because it was visible over greater distances than the normal and dull epaulet mounts. Hailman (1977) suggested that animal colour signals should use the wavelengths that penetrate best and he speculated that the epaulet colour of red-winged blackbirds uses long wavelengths to penetrate early morning mist, but little is known about the effect of epaulet colour on visibility. Dale & Slagsvold (1996) presented caged male pied flycatchers, *Ficedula hypoleuca*, some of which were experimentally 'brightened', to unmated territorial males and concluded that contrasting coloration enhances conspicuousness in birds. McNaught & Owens (2002) used comparative methods to determine that 'bright' plumage increases contrast over long distances in open habitats. 'Colourful' signals are not necessarily more conspicuous, however (e.g. Macedonia et al. 2004).

Taken together, our results and those of previous studies of epaulet manipulation (Hansen & Rohwer 1986; Røskaft & Rohwer 1987; Metz & Weatherhead 1992) provide evidence for a disadvantage of epaulets that are too conspicuous, although the evidence is somewhat equivocal. Metz & Weatherhead (1992) found that males whose scapular feathers were removed, and, thus, that were unable to cover their epaulets, not only had difficulty evicting their neighbours, which trespassed frequently, but also had difficulty trespassing onto their neighbours' territories. Metz & Weatherhead (1993) also found that territorial males wearing multiple red bands were more likely to encounter aggression from neighbours and were more likely to lose their territories than males wearing multiple black bands. Other evidence suggests that territory owners attack mounts with enlarged epaulets, although trespassers tend to avoid such mounts (Hansen & Rohwer 1986; Røskaft & Rohwer 1987), and that multiple red bands reduce the likelihood of attack by a territory owner (Metz & Weatherhead 1991). In our study, a model with unusually red epaulets attracted the attention of males other than the territory owner, who flew through and perched within the territory where the model was presented. Territory owners, however, were reluctant to approach a model with unusually red epaulets. In another study, Yasukawa et al. (in press) reddened epaulets of free-living territorial male red-winged blackbirds and found that these males incurred more trespassing and lost their territories more often than did control males, suggesting that males with reddened epaulets appear to incur an intrasexual cost.

Given that possession of unusually showy epaulets might be advantageous in attracting mates or extrapair copulations, perhaps male–male aggression counterbalances female choice and thus constrains epaulet colour in male red-winged blackbirds. For example, showy territory owners might risk increased intrasexual aggression from neighbours and other territorial challengers, which would reduce their realized reproductive success. One example of a signal that is intersexually advantageous but intrasexually disadvantageous is the 'high potency' song of the male

brown-headed cowbird, *Molothrus ater*. Male brown-headed cowbird song functions both intra- and intersexually (Dufty 1986). High potency song is attractive to females, but elicits aggression from males (West & King 1980, 1986).

An alternative way to examine the evolution of badges of status and female preference ornaments is to use phylogenetic methods. Irwin (1994) used this method to test hypotheses for the evolution of sexual dichromatism in the Icterinae, a clade that includes the red-winged blackbird. Irwin (1994) concluded that changes in blackbird dichromatic plumage, including epaulets, more often result from changes in female plumage conspicuousness than from changes in male showiness. It may therefore be worthwhile to determine whether epaulets serve an inter- or intrasexual function in female red-winged blackbirds, although Muma & Weatherhead (1989, 1991) used both observational and experimental methods and concluded that the epaulets of female red-winged blackbirds do not have such functions.

Our study provides no information on the direct or indirect benefits of female red-winged blackbird preference for showy epaulets. Eckert & Weatherhead (1987a) found a correlation between male red-winged blackbird epaulet size and nest defence, but found no evidence that epaulet colour provides a direct benefit. Westneat et al. (2003) found no relationship between epaulet size and immune response in red-winged blackbirds, and Weatherhead et al. (1993) found little evidence for a relationship between epaulet size or colour and parasite loads. Our results also do not demonstrate an intrasexual advantage of epaulet showiness. Eckert & Weatherhead (1987c) found no consistent difference in epaulet size between territory owners and floaters, and Searcy (1979b) concluded that epaulet size and colour do not function as signals of dominance in adult male red-winged blackbirds.

Our study does not examine potentially counterbalancing effects of natural selection on males or females (e.g. Promislow et al. 1992; Huhta et al. 2003), nor does it provide information on the balance between presumed intersexual advantages and putative intrasexual disadvantages of large, showy epaulets. Perhaps counterbalancing selection explains the lack of evidence that epaulet colour affects reproductive success (Westneat 2006; Yasukawa et al., in press). Clearly, more information is needed on potential costs and benefits of epaulet colour.

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