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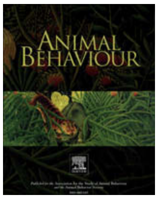

Intersexual and intrasexual consequences of epaulet colour in male red-winged blackbirds: an experimental approach

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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.

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^2 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 coccidiacide (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),