EPAULET BRIGHTNESS AND CONDITION IN FEMALE RED-WINGED BLACKBIRDS

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Abstract.—Epaulets of female Red-winged Blackbirds (*Agelaius phoeniceus*) vary in brightness from brown to bright red-orange. We test predictions of the hypothesis that condition at the time of molt determines female epaulet brightness and that females in superior condition produce brighter epaulets. We compared each female's epaulet with a series of color photographs ranked from 1 (dull brown) to 12 (bright red-orange) and considered females to have increased in brightness between years if their color increased by at least two ranks. More first-year females than older females increased in brightness, more older females increased in brightness after low reproductive effort than after high effort, and more first-year females increased in brightness after a year of superabundant food (an emergence of periodical cicadas, *Magicicada* spp.) than after other years. In each case, we expected an improvement in condition. We estimated female condition and regressed condition index on day of the breeding season. During the breeding season, females that later increased in brightness improved in condition relative to females that did not increase in brightness. We confirm a previously reported correlation between age and epaulet brightness, but age does not explain the relationship between change in brightness and either reproductive effort or the emergence of cicadas. We conclude that the most likely explanation for our results is that condition, at least in part, determines epaulet brightness in female Red-winged Blackbirds and that superior condition is reflected by brighter epaulets. Our results support assumptions of the status-signaling hypothesis and mate-choice hypotheses for the evolution of variable plumage. The best explanation for the evolution of variable plumage among female Red-winged Blackbirds is that brightness signals status in female-female aggressive encounters. *Received 21 November 1994, accepted 25 April 1995.*

Epaulet brightness in female Red-winged Blackbirds (*Agelaius phoeniceus*) is highly variable, ranging from brown to a bright red-orange that is similar to the epaulet color of first-year males (Payne 1969). Epaulets sometimes become brighter between years in captive females (Miskimen 1980). In free-living females, brightness is correlated with age. First-year females have epaulets with little or no red-orange (Payne 1969, Crawford 1977), and Blank and Nolan (1983) considered brightness among older females to be positively correlated with age.

Red-winged Blackbirds are polygynous (Orians 1961, Barnard 1979), and males exhibit delayed plumage maturation (Orians 1961, Payne 1969). Muma and Weatherhead (1989, 1991) suggested that variation in female epaulet color is present because it is genetically correlated with changes in male plumage brightness. Several females usually nest simultaneously on a male's territory and sometimes behave aggressively toward one another (Nero 1956, Lenington 1980, Yasukawa and Searcy 1982). Both males (70%; Beletsky and Orians 1987) and females (83%; Picman 1981) are site faithful and, although some males in our study population feed their young, females provide most of the parental care (Patterson 1991). The postjuvenal and prebasic molts are complete (Payne 1969). An incomplete prealternate molt has been reported in females, but does not involve the feathers of the epaulets (Greenwood et al. 1983).

We propose that epaulet brightness in female Red-winged Blackbirds is determined by condition at the time of the postjuvenal or prebasic molt, and that females in superior condition produce brighter epaulets. In mate-choice hypotheses for the evolution of variable plumage (Hamilton and Zuk 1982, Burley and Coopersmith 1987, Andersson 1994), a positive rela-

tionship between condition and plumage brightness is assumed. In the status-signaling hypothesis (Rohwer 1975, 1977, Fugle et al. 1984), plumage brightness is assumed to reflect resource holding potential, which may be influenced by condition.

We make four predictions based on the hypothesis that condition at the time of molt determines epaulet brightness:

(1) Epaulet brightness will increase in more females during their first prebasic molt than during subsequent prebasic molts. If young of the year forage less efficiently than first-year and older females, as is true in certain other species (e.g. American Robins, *Turdus migratorius* [Gochfeld and Burger 1984]; Northern Mockingbirds, *Mimus polyglottis* [Breitwisch et al. 1987]; Yellow-eyed Juncos, *Junco phaeonotus* [Sullivan 1988]), females are expected to be in better condition as yearlings than as young of the year, and their epaulets should become brighter during the prebasic molt following their first breeding season. Young of the year and adults may differ in ways other than foraging efficiency. If age or factors related to age influence epaulet brightness, our first prediction could be confirmed even if condition has no effect on epaulet brightness.

(2) Epaulet brightness of females will more often increase during the prebasic molt following a season of low reproductive effort (few young fledged) than of high reproductive effort (many young fledged). Females with experimentally enlarged broods lose more mass than controls (e.g. Lapland Longspurs, *Calcarius lapponicus* [Hussell 1972]; Snow Buntings, *Plectrophenax nivalis* [Hussell 1972]; Pied Flycatchers, *Ficedula hypoleuca* [Askenmo 1977]; and Blue Tits, *Parus caeruleus* [Nur 1984]), probably because of increased reproductive effort (but see Högstedt 1980, 1981), and this may be associated with inferior physical condition at the time of the prebasic molt.

(3) More females will increase in epaulet brightness during the prebasic molt in a year in which resources are abundant and the environment conducive to good condition than in other years. Therefore, in the following year, the population will consist of females that have brighter epaulets than in other years.

(4) Female physical condition during the breeding season will influence the increase, or the failure to increase, in epaulet brightness during the prebasic molt.

METHODS

Female condition and epaulet brightness.—We captured adults in baited Potter traps and banded each with a U.S. Fish and Wildlife Service numbered band and a unique combination of colored bands. We weighed each to the nearest 0.1 g with a Pesola spring scale and measured the flattened wing to the nearest 1 mm. As an index of female condition at the time of capture, we divided mass by the cube of wing length (Searcy 1979) and then multiplied this number by 10^5.

When a female was captured during the breeding season, we scored the color of her right epaulet by comparing it with a series of ranked photographs of increasingly bright epaulets (from 1 [dull brown] to 12 [bright red-orange]; see Blank and Nolan 1983). When more than one of us scored a female in the same year, our scores usually were consistent. For example, in 1985 Hengeveld and Johnsen independently scored three females, and their rank scores were: 5.5 and 4; 1.5 and 1.5; and 7 and 7. When scores did vary, we used the more frequent score or averaged scores when frequencies were equal (a female whose epaulet was ranked as 1 and 2 in the same year would be given a brightness score of 1.5). We pooled scores to create three categories: "dull" (1–5.5), "medium" (6–8.5), and "bright" (9–12). To determine change in epaulet brightness between consecutive years, we assigned females that increased by at least two ranks to a category of "increased brightness." All other females were placed in a category of "no increase in brightness."

Study site and data collection.—Our study site at the northern end of Yellowwood Lake in Brown County, Indiana (39°10′N; 86°20′W) has been described by Yasukawa (1979, 1981). We gathered data from 1978 through 1988. Approximately 20 territorial males and 60 breeding females were present each year. When nests failed between early May and mid-June, females typically renested within a few days, and some renested after rearing an early brood. We associated females with nests when they were observed entering or leaving the nest and we could identify them by their colored bands.

Of 359 banded females in our study, 8 had been banded as nestlings and, thus, were of known age. We assigned other females a minimum age of one year at first capture. Because we had predicted that more females would increase in brightness during their first prebasic molt than during later prebasic molts, we could not use the reported correlation between female age and epaulet brightness (Payne 1969, Blank and Nolan 1983) to assign age.

We estimated a female's seasonal reproductive effort by counting the number of her young that fledged and classified the production of zero to three fledglings per year as "low effort," and four to seven fledglings as "high effort." We found nests by searching the marsh every two to six days and then checked their contents every one to three days. We assumed

young had fledged if they were alive on the last nest check before age 10 days (day 1 = day of hatching), provided they were not later found dead and the nest was intact on or after day 10.

In 1987, 17-year periodical cicadas (*Magicicada septendecim, M. cassini,* and *M. septendecula;* see Young 1971) emerged on our study site between 18 May and 15 June, providing a natural experiment in which food abundance was increased. Densities of periodical cicadas in Indiana are high; often there are hundreds in each tree or shrub (Young 1971, Nolan and Thompson 1975). Red-winged Blackbirds eat cicadas and feed them to their young (pers. obs.), and a cicada emergence reduces nestling mortality in Red-winged Blackbirds (Strehl and White 1986).

Data analysis.—We used contingency tables (*G*-tests with Williams' correction; Sokal and Rohlf 1981) to test for independence between change in epaulet brightness and minimum age, reproductive effort, and the cicada emergence. We also used a *G*-test to test for independence between the presence or absence of a cicada emergence and female epaulet brightness in the following year. Because it was not possible for females with scores of 11 or 12 in the earlier year to increase in brightness, we excluded females with bright epaulets in the earlier year from the analyses of change in brightness between years. In the analysis of change in brightness with reproductive effort, first-year females were excluded because we expected they would increase in brightness as the result of improved foraging efficiency, and first-year females fledge fewer young than older females (Crawford 1977). In comparing the year that followed the cicada emergence with other years, we included only first-year females because the sample size of older females was too small. Similarly, in the analysis of epaulet brightness associated with the emergence of cicadas, we included only females that were at least two years old.

We used a *t*-test to compare the slopes of least-squares linear regressions of condition index on day of breeding season for females that returned in the following year with increased epaulet brightness and females that returned with no increase in brightness. Many females were captured several times, and we randomly selected one data point per female for each year. For each female, we used the day she laid her first egg of the breeding season as day 1. To avoid including mass associated with egg formation, we excluded data from females caught before day 6 and from females caught during formation of eggs for a replacement clutch (from five days before to five days after laying the first replacement egg; see Ricklefs 1974, Ricklefs and Hussell 1984).

The statistics that directly tested predictions of the hypothesis were one-tailed (Sokal and Rohlf 1981). All existing theory predicts a positive relationship between condition and plumage brightness. We would draw the same conclusion from data showing that females in poor condition had brighter plumage as we would if we found no relationship between condition and plumage brightness.

RESULTS

Epaulet brightness increased more often between a female's first and second year than between subsequent consecutive years. Of 63 females scored in both their first and second breeding seasons, epaulets increased in brightness in 34 (54.0%) and did not increase in 29 (46.0%). Of 60 older females scored in two consecutive years, the corresponding numbers were 16 (26.7%) and 44 (73.3%). In a *G*-test, there was a significant effect of age on change in epaulet brightness ($G = 9.54$, df = 1, $P < 0.003$). In addition, females older than one year increased in brightness more often than they decreased (16 increased, 4 decreased; sign test, $P = 0.012$).

Epaulet brightness increased more often between years after a year of low reproductive effort than after a year of high effort. Of 35 females that were two years old or older whose reproductive effort was low, epaulet brightness increased in 13 (37.2%) and did not increase in 22 (62.8%). Of 23 females whose effort was high, the corresponding numbers were 3 (13.0%) and 20 (87.0%). In a *G*-test, there was a significant effect of reproductive effort on change in epaulet brightness ($G = 4.18$, df = 1, $P < 0.025$).

Female epaulet brightness increased more frequently after the cicada emergence in 1987 than after all other years combined. Of 14 first-year females whose epaulet brightness was recorded in 1987 and 1988, 11 (78.6%) increased in brightness and 3 (21.4%) did not increase. Of the 63 first-year females whose change in epaulet brightness was recorded between other consecutive years, the corresponding numbers were 34 (54.0%) and 29 (46.0%). In a *G*-test, there was a significant effect of the presence or absence of a cicada emergence on change in epaulet brightness ($G = 2.94$, df = 1, $P < 0.05$).

Furthermore, females in the breeding population had brighter epaulets in 1988 than in other years combined. Of 30 females scored in 1988 that were two years old or older, 14 (46.7%) had bright epaulets, 13 (43.3%) had medium epaulets, and 3 (10.0%) had dull epaulets. Of 191 older females scored in other years, the corresponding numbers were 62 (32.5%), 64 (33.5%), and 65 (34.0%). In a 2 × 3 *G*-test, there was a significant effect of the presence or absence of a cicada emergence on female epaulet bright-

ness in the following year ($G = 8.24$, df $= 2$, $P < 0.013$).

We compared the least squares linear regressions of condition index on the day of the breeding season for females whose epaulets increased in brightness between years with females whose epaulets did not increase in brightness (Fig. 1). The slope of the regression line for females whose epaulets increased in brightness between years was positive ($Y = 3.55 + 0.0045X$; $r = 0.16$; $t = 0.77$, df $= 23$, $P < 0.50$). The slope for females whose epaulets did not increase in brightness was negative ($Y = 3.78 - 0.0064X$; $r = 0.30$; $t = 2.07$, df $= 45$, $P < 0.05$), and the slopes differed significantly from each other ($t = 1.77$, $n_1 = 47$, $n_2 = 25$, $P < 0.05$). The difference in slope suggests that females that returned in the following year with brighter epaulets improved in condition during the previous breeding season relative to females that returned with no increase in epaulet brightness.

DISCUSSION

Overall, our results support predictions of the hypothesis that epaulet brightness in female Red-winged Blackbirds is determined by condition at the time of molt, with superior condition reflected by a brighter epaulet. Some of our tests of the hypothesis are not completely independent of each other. First, we used the same population of females to measure change in epaulet brightness between years associated with the emergence of cicadas and to measure the distribution of bright, medium, and dull epaulets. Second, many females in our analysis of condition index as a function of the number of days after their first egg also were included in analyses of change in epaulet brightness with differences in age and reproductive effort. However, our tests of the change in epaulet brightness as a function of age, reproductive effort, and the presence or absence of an emergence of cicadas are independent of each other. Therefore, we believe that our predictions provide several independent tests of the condition hypothesis.

The high frequency of females whose epaulets became brighter between their first and second year as compared with older females could be interpreted as delayed plumage maturation, perhaps as a genetically correlated trait with males (Muma and Weatherhead 1989, 1991), whose first-year plumage is duller than in older
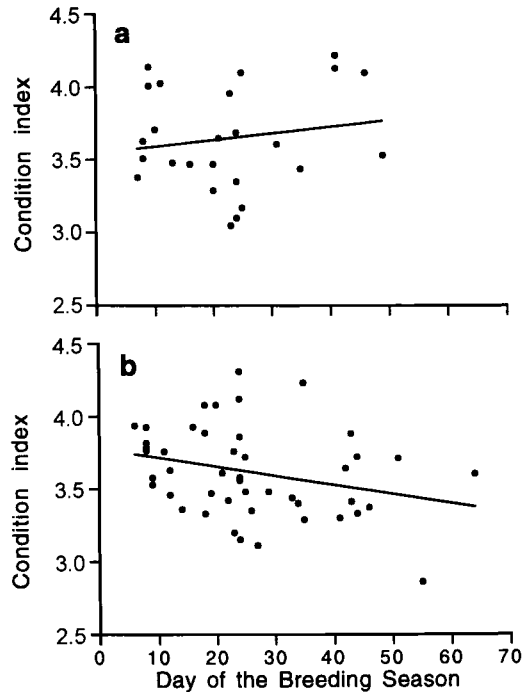

Fig. 1. Linear regressions of condition index on number of days after each female's first egg of season (first egg = day 1): (a) females whose epaulets increased in brightness between years ($n = 25$); and (b) females whose epaulets did not increase in brightness between years ($n = 47$).

males (Payne 1969). Although we cannot reject this hypothesis, Muma and Weatherhead (1991) predicted that plumage brightness should not be correlated with reproductive performance, and the relationship between condition and epaulet brightness suggests that such a relationship may exist.

The relationship between age and epaulet brightness in females older than one year also indicates that age may be a factor determining brightness. However, an alternative explanation is that winter mortality is higher for females whose condition has deteriorated during the breeding season and, according to the condition hypothesis, these are females whose epaulets should decrease in brightness. Age-related hypotheses fail to explain the occasional decrease in epaulet brightness (6.6%), the relationship between the change in epaulet brightness and reproductive effort, and the change associated with the emergence of cicadas. Although we cannot reject age as a factor influencing epaulet brightness, our data sug-

gest that the age-brightness relationship may simply result from an improvement in average condition with age. We conclude that the most likely explanation for our results is that condition, at least in part, determines epaulet brightness in female Red-winged Blackbirds and that brighter plumage reflects superior condition.

Does condition determine plumage brightness in other species?—Variable breeding plumage has been reported in male Pied Flycatchers (Røskaft and Järvi 1983), Great Tits (*Parus major*; Järvi and Bakken 1984), Yellow Warblers (*Dendoica petechia*; Studd and Robertson 1985), Darwin's Medium Ground Finches (*Geospiza fortis*; Price 1984), House Sparrows (*Passer domesticus*; Møller 1987a), Black-headed Grosbeaks (*Pheucticus melanocephalus*; Hill 1988), and House Finches (*Carpodacus mexicanus*; Hill 1990). These species may provide a basis for judging whether the relationship between condition and plumage brightness is a more general phenomenon. In some of these species, males with brighter plumage have higher survivorship and arrive earlier on the breeding grounds (Järvi et al. 1987), defend territories in superior habitat (Studd and Robertson 1985, Hill 1988, Møller 1988), and/or are more successful in attracting and retaining mates (Røskaft and Järvi 1983, Price 1984, Alatalo et al. 1986, Lifjeld and Slagsvold 1988a, Møller 1988, Hill 1988), even when habitat is homogeneous (Lifjeld and Slagsvold 1988b). Further, in male Pied Flycatchers, mass at fledging is positively correlated with first-year plumage brightness (Slagsvold and Lifjeld 1992). These findings are consistent with the view that brighter plumage reflects superior condition, and they suggest that the relationship between condition and plumage brightness should be investigated more closely in other species with variable plumage.

Variable plumage in female Red-winged Blackbirds.—The maintenance of variable plumage depends both on the cost, either of producing the signal or the social consequences of displaying the signal (Zuk 1991), and the benefits to individuals in poor condition of producing bright plumage. According to the status-signaling hypothesis, variable plumage can be maintained through aggressive encounters if aggression is more common among those signaling dominance than among dominant and subordinate individuals (Ketterson 1979, Møller 1987b). According to the mate-choice hy-

pothesis, maintenance of variable plumage depends on the assumption that brightness carries a cost, either energetic or increased risk of predation (Andersson 1982, 1994). However, plumage signals may be inexpensive to produce (Krebs and Dawkins 1984), and at least male Red-winged Blackbirds can conceal their epaulets and become less conspicuous to predators (Hansen and Rohwer 1986).

The individual-recognition hypothesis (Whitfield 1986) explains the evolution of variable plumage by proposing benefits to both potential winners and losers of avoiding fights. Although our data do not directly test this hypothesis, we would expect epaulet brightness to be random with respect to age or reproductive performance if individual recognition were the only selecting agent for variable plumage. Our results are consistent with both the status-signaling (Rohwer 1975, 1977) and mate-choice hypotheses (Andersson 1994) because we find a positive relationship between condition and plumage brightness.

Variability in plumage brightness will be maintained in a population if carotenoids are scarce in the diet or are otherwise expensive to acquire (Hill 1990), and if cicadas are richer in carotenoids than the Red-winged Blackbird's food sources in other years, the increased brightness associated with the emergence of periodical cicadas could be explained by the increased access to the pigments that color the epaulets. If the signal is expensive, the cost of the signal should prevent females in poor condition from having bright plumage, and we must explain why bright females invest in the signal. If the signal is not expensive, all females could potentially benefit by having bright plumage, and we must explain why dull females do not "cheat" and display bright plumage. In a polygynous mating system (up to seven females mated to one male in our study population), intersexual selection on females should be especially weak. A mating preference by males for bright females would not explain the benefit to females in good condition of displaying bright plumage. However, female-female aggression (Nero 1956, Lenington 1980, Yasukawa and Searcy 1982) and a dominance hierarchy among females nesting on a male's territory (Roberts and Searcy 1988, Langston et al. 1990) may select for the maintenance of variable plumage. Dominant females with bright plumage may benefit by delaying nest starts of other females

and reducing competition for resources and male parental care (Langston et al. 1990). Bright plumage in females in poor condition would be selected against if red color is expensive (Hill 1990), or if females are aggressive at the beginning of the breeding season (Langston et al. 1990, Cristol and Johnsen 1994), and the display of bright plumage is tested in aggressive encounters.

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