EPAULET COLOR AND SEXUAL SELECTION IN THE RED-WINGED BLACKBIRD: A FIELD EXPERIMENT

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Abstract. The epaulets of male Red-winged Blackbirds (*Agelaius phoeniceus*) function in both intersexual and intrasexual contexts, but there is little evidence that they covary with reproductive success in this well-studied species. We used path analysis of male/territory traits, mating success, and reproductive success of unmanipulated males to estimate current directional selection. Territory size had a positive effect on number of within-pair mates. Number of extra-pair mates had a positive effect on number of extra-pair fledglings, and number of within-pair and extra-pair fledglings had positive effects on total number of fledglings. We also reddened epaulets of free-living territorial males to determine whether manipulated and control males differ in territorial behavior, mating success, or reproductive success. Compared with control males, males with reddened epaulets incurred elevated rates of trespassing and territorial challenges, lost their territories more often, and were unable to produce extra-pair offspring. Despite these differences, however, the realized reproductive success of experimental and control males did not differ significantly, perhaps because males with reddened epaulets devoted more time to anti-predator vigilance and were more aggressive toward a simulated predator than were control males. An apparent lack of current sexual selection on epaulet color may be a form of counter-balancing sexual selection in which male aggression against redder epaulets opposes female preference for redder epaulets, or it might be the result of males compensating for lost extra-pair fertilizations by increasing their parental care.

Key words: Agelaius phoeniceus, *extra-pair paternity*, *intersexual selection*, *intrasexual selection*, *realized reproductive success*, *Red-winged Blackbird*, *within-pair paternity*.

Color de la Mancha Alar y Selección Sexual en *Agelaius phoeniceus*: un Experimento de Campo

Resumen. La mancha alar en los machos de *Agelaius phoeniceus* funciona tanto en el contexto intra-sexual como inter-sexual, pero existe poca evidencia de que ésta covaríe con el éxito reproductivo en esta especie, que ha sido bastante estudiada. Utilizamos un análisis de pasos usando caracteres territoriales de los machos, éxito de apareamiento y éxito reproductivo de los machos no manipulados para estimar la selección direccional actual. El tamaño de los territorios tuvo un efecto positivo sobre el número de compañeros de una pareja. El número de compañeros adquiridos fuera de la pareja tuvo un efecto positivo sobre el número de polluelos extra-pareja, y el número de polluelos volantones intra- y extra-pareja tuvo un efecto positivo sobre el número total de volantones. También intensificamos el rojo de la mancha alar de machos territoriales silvestres para determinar si los machos manipulados y control diferían en su comportamiento territorial, éxito de apareamiento o éxito reproductivo. En comparación con los machos control, los machos manipulados incurrieron en tasas más altas de traspaso de límites y de disputas territoriales, perdieron sus territorios más frecuentemente y no fueron capaces de producir crías extra-pareja. Sin embargo, a pesar de estas diferencias, el éxito reproductivo alcanzado por los machos control y manipulados no difirió significativamente, probablemente debido a que los machos con las manchas rojas intensificadas asignaron más tiempo a comportamientos de vigilancia anti-depredatorios y fueron más agresivos ante un depredador simulado que los machos control. Una falta aparente de selección sexual actual sobre el color de la mancha alar puede ser una forma de contrarrestar la selección sexual en la que la agresividad hacia machos con manchas más rojas se opone a la preferencia por parte de las hembras de manchas más rojas, o puede ser el resultados de que los machos compensan la pérdida de cópulas extra-pareja al aumentar su cuidado parental.

INTRODUCTION

The possibility that sexually dimorphic traits might enable males to compete for access to females or to convince females to mate has attracted a tremendous amount of interest since Darwin (1859, 1871) first proposed sexual selection as an evolutionary mechanism (Andersson 1994). For example, sexual selection on male ornaments has been clearly demonstrated in

both the Red-shouldered Widowbird (*Euplectes axillaris*) and the Red-collared Widowbird (*E. ardens*). Males with redder and larger wing or throat ornaments have an advantage over males less well endowed in competition for dominance status and territory ownership (Andersson et al. 2002, Pryke et al. 2002, Pryke and Andersson 2003a, b). Despite the continued interest, however, many topics remain poorly understood, even in thoroughly studied species such as the Red-winged Blackbird (*Agelaius phoeniceus*) (Searcy and Yasukawa 1995, Westneat 2006).

Sexual selection occurs when differences in reproductive success result from competition over mates (Andersson 1994), but we must distinguish between a sexually selected adaptation and sexual selection in progress (Searcy and Yasukawa 1995, Badyaev and Martin 2000). As discussed by Grafen (1988), an adaptation (sensu Williams 1966) is a trait that serves a function and is a result of past selection. A trait may therefore be an adaptation even if selection is not currently acting on it. In contrast, selection is occurring when variance in reproductive success results from individuals' differences in trait values. Current selection may thus cause an existing adaptation to evolve further (Badyaev and Martin 2000).

Andersson (1994) and Searcy and Yasukawa (1995) cited the epaulet of the male Red-winged Blackbird as an example of a sexually selected plumage ornament. Males expose their epaulets during territory defense and courtship, and experimental manipulation of epaulet conspicuousness affects both territory defense and female choice of mate (Beletsky 1996, Searcy and Yasukawa 1995, Yasukawa et al. 2009), demonstrating that epaulets evolved by sexual selection and function in territory defense and mate attraction.

To demonstrate sexual selection in progress (Grafen 1988), however, we must show that epaulet conspicuousness varies with reproductive success. In some species of birds such covariance has been demonstrated for red plumage. For example, redder male Northern Cardinals (*Cardinalis cardinalis*) acquire better territories, have mates that begin nesting sooner, and have higher reproductive success than less red males (Wolfenbarger 1999a). Redder males also have redder mates (Jawor et al. 2003), although there is no evidence that females prefer redder males as mates (Wolfenbarger 1999b). The reddest male House Finches (*Carpodacus mexicanus*) are preferred by females, attract older, more experienced females, acquire mates faster, and have higher reproductive success than drab males (Hill 2002). Male Red-backed Fairy-wrens (*Malurus melanocephalus*) in the bright breeding plumage sire more offspring as a result of higher extra-pair paternity than males in the dull plumage (Webster et al. 2008).

In the Red-winged Blackbird, Searcy and Yasukawa (1995), Weatherhead and Boag (1995), and Westneat (2006) could find no evidence for direct or correlated current selection on male epaulet size or color, and a recent experimental attempt to separate the intrasexual and intersexual effects of male Red-winged Blackbirds' epaulet color seemed to show that the two modes of sexual selection oppose one another (Yasukawa et al. 2009). In a mate-choice experiment females preferred males with epaulets that were reddened, but reddened epaulets also seemed to confer a disadvantage in male–male competition. In this study we used a path analysis of unmanipulated males to identify potentially important components of male reproductive success and an experimental manipulation (reddening the epaulets) to study the effect of reddened epaulets on the mating and reproductive success of free-living territorial male Red-winged Blackbirds.

In species in which extra-pair paternity is substantial, reproductive success comprises within-pair and extra-pair components (Webster et al. 1995). In the Red-winged Blackbird, realized reproductive success depends on both components, although within-pair success is more important than extra-pair success (Gibbs et al. 1990, Weatherhead and Boag 1995, 1997, Westneat 2006). Reproductive success thus depends on (1) territory ownership, (2) mating success, (3) ability to sire offspring with social mates, and (4) ability to sire offspring with extra-pair mates.

As summarized by Searcy and Yasukawa (1995) and Beletsky (1996), territory ownership enables males to acquire both within-pair and extra-pair mates. The vast majority of extra-pair young have been shown to have sires from neighboring territories, although there is some indirect evidence (Weatherhead et al. 1994, Weatherhead and Boag 1995) that nonterritorial males may occasionally gain some extra-pair paternity. Mating success depends on territory and male quality as well as the male's ability to interact with extra-pair females, especially from neighboring territories. Success with social mates (within-pair success) depends on the number of nesting attempts, clutch size, hatching success, and nestling survival. Male parental care in the form of anti-predator behavior can have an important effect on both hatching success and nestling survival (Yasukawa et al. 1992). Extra-pair success depends on access to and interactions with extra-pair females, often from neighboring territories.

To assess these components of reproductive success, we observed aspects of male Red-winged Blackbirds' territorial and anti-predator behavior, we located and determined the outcomes of nesting attempts on focal territories, and we used multi-locus DNA fingerprints to assign paternity to all nestlings from which we obtained blood samples (Parker et al. 1999). In most cases we were able to identify the extra-pair sire when the territorial male was excluded, although in some cases we were unable to find the true sire.

If sexual selection currently favors redder (more conspicuous) epaulets in males, then the realized reproductive success of males with experimentally reddened epaulets should exceed that of normal males. A lack of such an effect, however, can have several explanations, which we explore in this study.

METHODS

STUDY POPULATION

We conducted our observations and experiment at Newark Road Prairie in south-central Wisconsin (42° 32′ N, 89° 08′ W) during the breeding seasons of 1996 and 1997. The study area was a wet-mesic prairie and sedge meadow habitat that supported 20–35 Red-winged Blackbird territories and has been described in more detail by Yasukawa (1989).

FIELD METHODS

The Beloit College Institutional Animal Care and Use Committee approved all methods used in this study (IACUC protocol 92-01). All territorial male Red-winged Blackbirds and all females whose nestlings reached 3 days of age were captured and banded with U. S. Geological Survey numbered aluminum bands and a unique color combination of plastic wrap-around bands (USGS banding permit 20438). Males and some females were captured in Potter traps placed on feeding platforms and baited with nonviable sunflower seed. Capturing and handling of birds and the presence of bands had no apparent effect on their behavior or site fidelity. Most females were captured in Potter traps placed over nests with nestlings; females were captured when they attempted to feed the nestlings. The trap was placed over a nest only once for no longer than 30 min to minimize disturbance. In only one case in 68 attempts did capture, handling, and banding cause a female to abandon her nest.

We observed male Red-winged Blackbirds' territorial behavior from sunrise until 12:00 CDT in random order. During each 10-min observation, we identified the territory owner and noted each song so we could calculate rates for each subject male. Song is the long-range component of territory defense (Nero 1956), and song rate has been frequently investigated as an estimate of territory defense (Searcy and Yasukawa 1995, Beletsky 1996). We identified territory boundaries by plotting the locations of males' territory-defense displays and territorial encounters (Nero 1956, Orians and Christman 1968) on maps of the study area. Plotting was aided by a 20-m grid of marker posts throughout the study area. Territory sizes were measured with NIH Image (National Institutes of Health 1996) on the basis of the convex polygons constructed from display locations. We noted all occurrences of extra-territorial males perching within a focal male's territory, and we used these data to calculate the trespass rate (hr^{-1}). We also noted all occurrences of territorial challenges (Nero 1956) by extra-territorial males. In a territorial challenge both the territory owner and challenger fly upward in a spiral above the defended area, with the territorial male maintaining a position above the challenger. Most challenges lasted from one to several minutes, with the spiral flights being repeated several times in lengthy challenges. We never observed fighting as a direct result of these challenges, although we did find evidence of physical combat (see below).

As male Red-winged Blackbirds that disappeared from their territories did so over a period of 0–7 days following capture and manipulation, in some cases we were able to estimate song and trespass rates for males that subsequently lost their territories. For this reason and because most nests failed before we could collect blood samples from nestlings, samples sizes varied with the comparison being made.

EPAULET MANIPULATIONS

All males used in the epaulet-manipulation experiment were captured prior to the arrival of females, and each was removed from the trap as quickly as possible. We conducted our experiment over two breeding seasons. In each year the first newly captured male was randomly assigned to either the experimental or control group and the second male was assigned to the other group; this assignment procedure was then repeated for all subsequent newly captured males. To verify the effectiveness of our randomization, we compared flattened wing lengths and years of breeding experience on our study area of the control and experimental males. Neither wing lengths (control = 129.5 ± 0.7 [SE] mm, reddened = 129.6 ± 0.7 mm; $t_{26} = 0.07$, $P = 0.9$) nor breeding experience (control = 1.2 ± 0.5 yr, reddened = 1.9 ± 0.7 yr; Wilcoxon $z = 0.3$, $n_C = n_R = 14$, $P = 0.8$) differed significantly.

The red feathers of the epaulets of manipulated males were "painted" with an Eberhard Faber (Lewisburg, TN) Design 2 red art marker (value 3, D-18), immediately reddening the epaulets with no adverse effect on feather texture or strength. Epaulets of control males were sham-painted with a cotton swab. Subject males were then released immediately after treatment.

To verify that the marker affected epaulet color, we measured reflectance of unmanipulated and altered epaulets of four males by using a Cary 5E spectrometer (Varian, Sunnyvale, CA) and an integrating sphere (model RSA-CA-50D, Labsphere, North Sutton, NH) with a Spectralon surface to produce reflectance spectra from 300 to 800 nm with an interval of 4 nm. As shown in Figure 1, when compared to normal epaulets, reddened epaulets were shifted to the right (shifted to redder hues); the difference in the visual range of birds (300–700 nm) was significant (matched-pairs $t_{100} = 7.4$, $P < 0.0001$; Motulsky and Ransnas 1987). To assess the effectiveness of our manipulation in the field, we used the Munsell tri-stimulus system to score epaulet hue, value, and chroma before and after manipulation (Montgomerie 2006).

MEASUREMENTS OF PATERNAL CARE

Success of nesting attempts on a male's territory depends in part on the male's anti-predator behavior (Yasukawa et al. 1992). We estimated paternal care by quantifying the anti-predator behavior of control and experimental males. We observed territorial males for 30 min each day, weather permitting, from a blind during the incubation stage of each
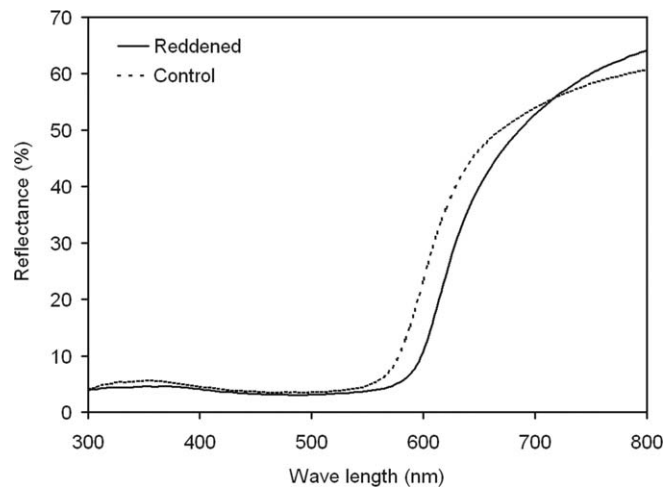
FIGURE 1.   Reflectance spectra of reddened and unmanipulated (control) epaulets of male Red-winged Blackbirds.

male's primary (most advanced) nest. During these observations we noted the amount of time the male spent perching at prominent locations and scanning the territory (time on sentinel; Yasukawa et al. 1992) as well as the amount of time the male spent on the territory (males make frequent forays off territory). Although sentinel behavior may also be a form of territory defense, once nesting begins trespass rates in our study area are low, and the vigilance has been shown to be a component of guarding eggs and young (Searcy and Yasukawa 1995). We also measured the male's response to a simulated predator by placing a model crow (*Corvus* sp.) 20 m from the primary nest for 5 min, then repeating the presentation with the crow 1 m from the same nest. Each presentation was begun while the male was off territory. We chose a direction away from any other active nests on the same territory, used a tape measure to locate the 20-m point, pushed a 2-m-tall pole with the model attached into the ground, and retreated to a position off the male's territory at least 50 m away. We began the 5-min observation when the male returned to the territory. At the end of this first presentation, we then moved the pole to 1 m from the nest and conducted a second 5-min observation, which started when we returned to the observation position. During each of the two observations we noted the male's closest approach to the model, whether the male struck the crow, and the number of strikes. After both presentations were completed we measured the distances of closest approach. We used closest approach and number of strikes to produce a single response score. Males that approached but did not strike the crow were scored with the negative of their measured closest approach (e.g., a male that approached to 25 m was given a response score of −25, whereas a male that approached to 1 m was given a score of −1). Males that struck the crow were given a score corresponding to the number of strikes (e.g., a male that struck once was given a score of 1; a male that struck

10 times was given a score of 10). Thus higher scores indicate more responsive males.

MEASUREMENTS OF MATING AND REPRODUCTIVE SUCCESS

We observed territories and females, located and marked nesting attempts on focal territories, and checked nests daily until each failed or produced fledglings. We used this information to determine the number females nestling on each male's territory (Holm 1973) and used this number to estimate each male's within-pair mating success.

Apparent reproductive success (under the assumption that the territorial male sires all young hatched on his territory) depends on the number of nesting attempts, clutch size, hatching success, and nestling survival on each focal territory. To produce independent estimates of these components of nesting success, we counted the number of nesting attempts (nests receiving eggs) and calculated the number of eggs per nest, number of nestlings per egg, and number of fledglings per nestling on each control and experimental territory. Loss of territory, failure to attract nesting females, and nest failure during the egg and nestling stages resulted in changes in sample sizes from one estimate to the next.

For nests with nestlings at least 3 days old, we also attempted to identify the sire of each nestling by using DNA fingerprinting (Parker et al. 1999), but most nests failed before we could obtain blood samples. Fingerprints were used to estimate the numbers of within-pair and extra-pair fledglings produced by each male. Numbers of extra-pair mates were determined from assignments of extra-pair nestlings to focal males. Numbers of within-pair and extra-pair fledglings were combined to measure realized reproductive success.

Two blood samples of approximately 50 μL each were collected from the wing veins of adult and nestling Red-winged Blackbirds and were immediately stored in lysis buffer. Samples were incubated with 300 μg of Proteinase K for 8 hr at 65°C. DNA was extracted several times in phenol/phenol:chloroform:isoamyl alcohol, then dialyzed against TNE$_2$. Excess Hae III was used to digest 4–5 μg DNA at 37°C. Fragments were separated on a 0.8% agarose gel (22 cm) at 20 V for 65 hr and then transferred to nylon by Southern blot in 10× SSC buffer. The 33.15 probe (Jeffreys et al. 1988) was radiolabeled by random-primer extension with [^{32}P]dCTP. Hybridizations were run overnight at 62°C in 1.5× SSC, 0.1% SDS, 5× Denhart's solution, and 6% dextran sulfate. Hybridized filters were washed 4 × 30 min at 62°C in 1.5× SSC and 0.1% SDS, then exposed to x-ray film at −20°C.

Samples collected in 1992–1994 were used to develop criteria for assignment. We used thresholds of 0.404 band sharing and two unattributable bands to identify extra-pair fertilizations and applied these thresholds to all nestlings. We ran all territorial males in 1996 and 1997 as potential sires and were

able to assign 51 of 57 (90%) nestlings to specific males. In the remaining six cases the unidentified sires may have defended territories outside our study area or were nonterritorial floaters (see Weatherhead and Boag 1995).

PATH ANALYSIS

We used path analysis (Wright 1934, Kingsolver and Schemske 1991) to estimate directional selection gradients of hierarchically arranged male/territory traits, mating success, and reproductive success. We followed the approach of Westneat (2006), who used path analysis (a nested series of standardized multiple regressions) of data from unmanipulated male Red-winged Blackbirds to identify important components of realized reproductive success. We limited the number of direct paths to effects of interest to us and because our sample of unmanipulated males was only 29. Our path analysis focused on three male/territory attributes (territory size, song rate, and trespass rate), two components of mating success (number of within-pair [social] mates and number of extra-pair mates), and two components of reproductive success (number of within-pair fledglings and number of extra-pair fledglings). We limited direct paths to those between successive hierarchical levels. As we did not examine indirect paths, we used significance tests from the multiple regressions (Kingsolver and Schemske 1991), but these results must be interpreted with caution.

STATISTICAL ANALYSIS

All statistical analyses were conducted with JMP 6.0 (SAS Institute 2006). We used standardized variables to calculate the partial regression coefficients in the path analysis. Although the reproductive-success variables were not normally distributed, normality of fitness is not required for selection gradients to be estimated (Arnold and Wade 1984, Westneat 2006). For comparisons of control and epaulet-reddened males, we used t tests to perform two-group comparisons when assumptions of normality were met and Wilcoxon nonparametric tests otherwise. We also used χ^2 tests of independence to compare territorial challenges and loss of territory of control and reddened-epaulet males and a matched-pairs t test to compare reflectance spectra of unmanipulated and reddened epaulets. Statistical significance was accepted at $\alpha = 0.05$.

RESULTS

PATH ANALYSIS

We used 29 unmanipulated males (16 from 1996 and 13 from 1997) in our path analysis. As shown in Figure 2, at the male/territory level, territory size and song rate were significantly correlated ($P < 0.01$); no other correlations within this level were significant. Territory size had a significant direct positive effect on number of within-pair mates ($P = 0.02$); although trespass rate appeared to have a direct positive effect on number of extra-pair mates, the standardized partial regression coefficient was not significant ($P = 0.06$). Number
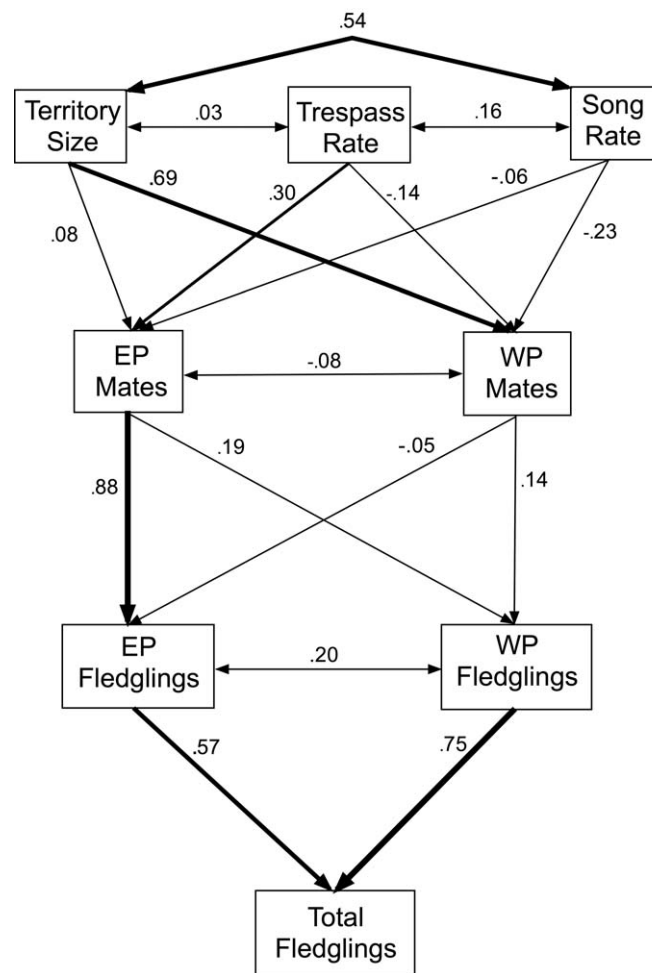

FIGURE 2.   Path analysis of male/territory traits, mating success, and reproductive success of unmanipulated male Red-winged Blackbirds. Numbers on paths with single arrows are standardized partial regression coefficients. Double-headed arrows indicate correlations between variables in the same hierarchical level. Paths in bold were significant in the correlation or multiple regression analysis.

of extra-pair mates had a significant positive direct effect on number of extra-pair fledglings ($P < 0.01$), and both number of within-pair fledglings ($P < 0.01$) and number of extra-pair fledglings ($P < 0.01$) had significant positive direct effects on total number of fledglings. No other path coefficients were significant (all $P > 0.1$).

EPAULET-MANIPULATION EXPERIMENT

We captured 28 male Red-winged Blackbirds for our experiment, 24 in 1996, four in 1997. Prior to manipulation, epaulets were 5YR–8.25R in hue, 4–7 in value, and 14–16 in chroma on the Munsell scale, whereas all manipulated epaulets had a visibly redder hue of 7.5R, more saturated chroma of 16, and a consistent value of 4 on the Munsell tri-stimulus scale. Experimental reddening thus produced epaulets that were uniformly redder and at or just beyond the normal range of variation.

TRESPASS RATE, LOSS OF TERRITORY, AND TERRITORY DEFENSE

Eight of 14 males with reddened epaulets were challenged by other males, whereas only one of 14 control males was challenged (Fig. 3A). Seven of 14 experimental males lost their territories compared with one of 14 control males. Experimental males were thus significantly more likely to be challenged ($\chi^2_1 = 8.0$, $P = 0.005$) and to lose their territories ($\chi^2_1 = 6.3$, $P = 0.01$) than control males.

All of the males that lost their territories were subsequently resighted at least once on the study area, so their disappearance was not the result of mortality. Most of the experimental males who lost their territories were recaptured later in the same breeding season, and all showed signs of physical combat. They had healed wounds and were missing feathers, especially on the head, which resulted in blackening of the scalp. Despite territorial challenges, loss of territory, and injuries, six of 12 experimental males from 1996 survived and returned the following breeding season, as did seven of 12 control males.

Prior to epaulet manipulation, trespass rates of control and experimental males were not significantly different (Wilcoxon $z = -0.35$, $n_C = n_R = 14$, $P = 0.72$), but, following epaulet reddening, experimental males experienced significantly higher rates of trespass than did control males (Wilcoxon $z = 2.4$, $n_C = 14$, $n_R = 11$, $P = 0.02$; Fig. 3B).

Territory sizes of control and experimental male Red-winged Blackbirds did not differ significantly before ($t_{26} = 0.7$, $P = 0.51$) or after ($t_{23} = 0.33$, $P = 0.74$) epaulet manipulation (Fig. 3C).

As song rate and territory size were significantly correlated in the path analysis and song rate had no significant direct paths to numbers of mates (Fig. 2), we did not compare song rates of control and experimental males.

PATERNAL CARE

Males with reddened epaulets spent significantly more time on sentinel (Wilcoxon $z = 2.5$, $n_C = 13$, $n_R = 6$, $P = 0.01$) and on territory (Wilcoxon $z = 3.3$, $n_C = 13$, $n_R = 6$, $P = 0.0009$) than did control males (Fig. 4A). In addition, experimental males responded significantly more strongly to a crow at 20 m (Wilcoxon $z = -2.7$, $n_C = 13$, $n_R = 6$, $P = 0.007$) and 1 m (Wilcoxon $z = 2.5$, $n_C = 13$, $n_R = 6$, $P = 0.01$) than did control males (Fig. 4B).
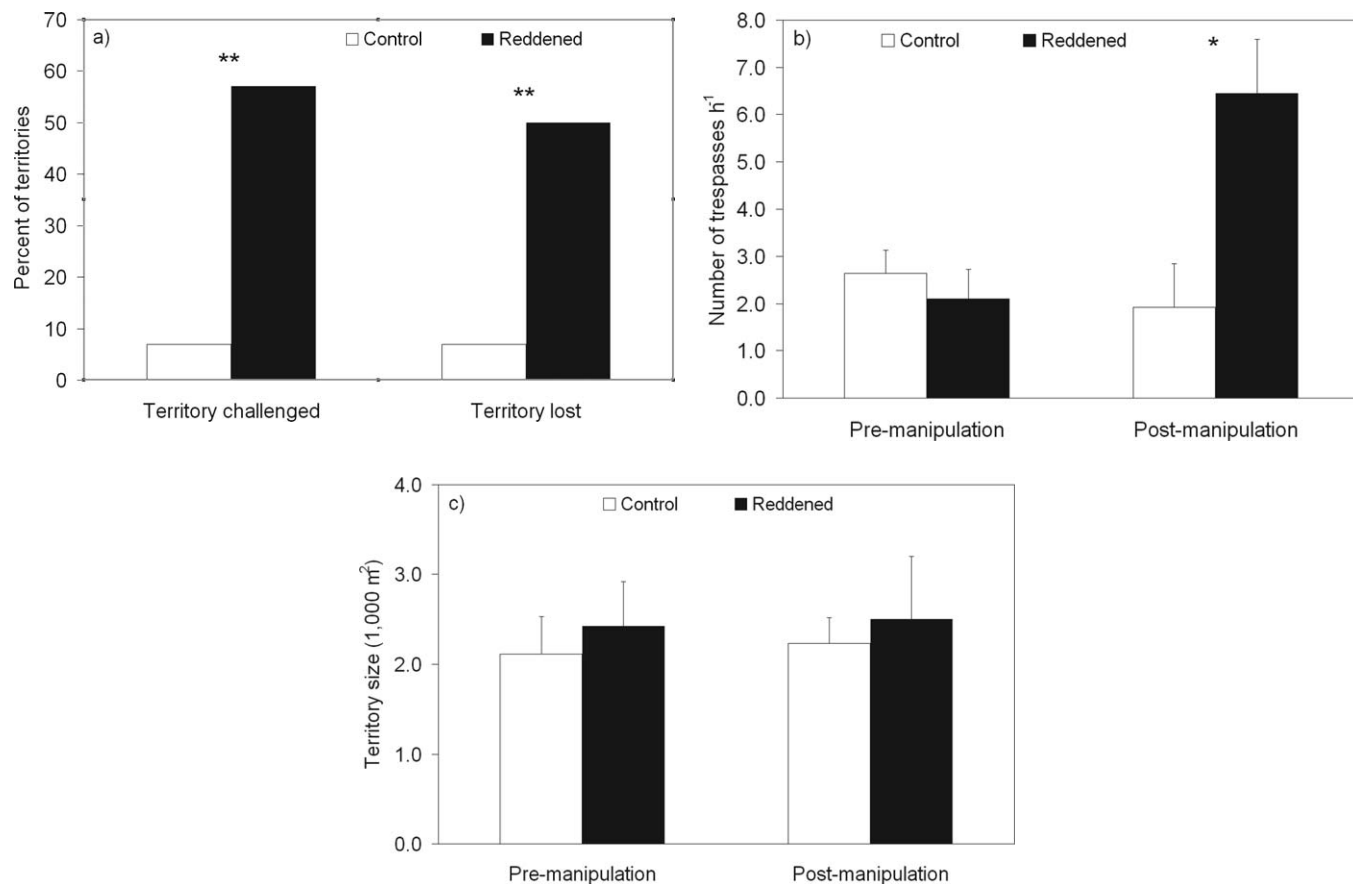
FIGURE 3. Comparison of male Red-winged Blackbirds with control and reddened epaulets before and after epaulet manipulation for (a) territorial challenge and loss of territory, (b) trespass rate, and (c) territory size. $*P < 0.05$, $**P = 0.01$.
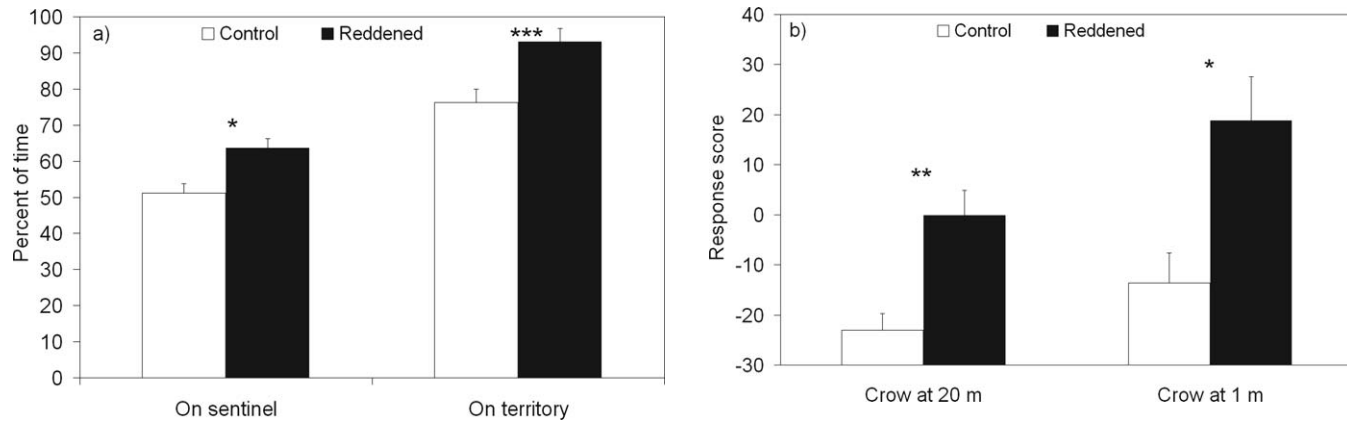
FIGURE 4. Comparison of male Red-winged Blackbirds with control and reddened epaulets for (a) time on sentinel (perching and scanning from prominent locations on territory) and on territory during the incubation stages of primary (most advanced) nests, and (b) response to a model crow (simulated predator) at 20 m and 1 m from primary nests (a high score indicates a strong response). *$P < 0.05$, **$P = 0.01$, ***$P < 0.001$.

MATING AND REPRODUCTIVE SUCCESS

Neither harem size (Wilcoxon $z = 1.6$, $n_C = 13$, $n_R = 6$, $P = 0.1$) nor number of females (Wilcoxon $z = 1.7$, $n_C = 13$, $n_R = 6$, $P = 0.08$) of control and experimental males differed significantly (Fig. 5A).

Control and experimental males did not differ significantly in total number of nesting attempts (Wilcoxon $z = 1.6$, $n_C = 13$, $n_R = 6$, $P = 0.1$), number of eggs per nest (Wilcoxon $z = -0.1$, $n_C = 13$, $n_R = 6$, $P = 0.89$), or number of fledglings per nestling (Wilcoxon $z = -0.5$, $n_C = 13$, $n_R = 6$, $P = 0.65$), but
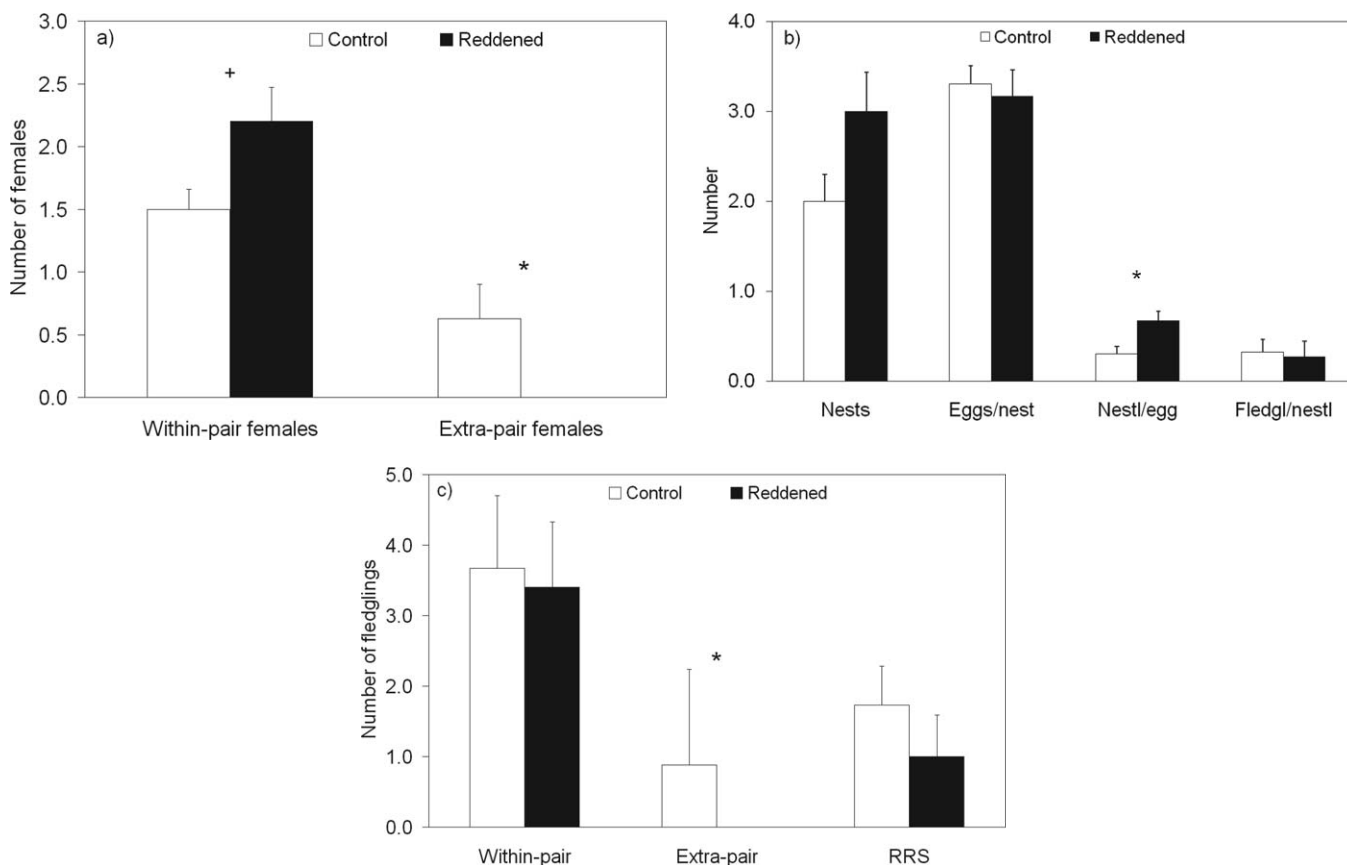

FIGURE 5. Comparison of male Red-winged Blackbirds with control and reddened epaulets for (a) mating success, (b) nest success and (c) reproductive success. Within-pair females = number of social mates. Extra-pair females = number of other females with which a male sired young. Realized reproductive success = number of fledglings produced with both social and extra-pair mates. +$P < 0.1$, *$P < 0.05$.

experimental males produced significantly more nestlings per egg than did control males (Wilcoxon $z = 2.0$, $n_C = 13$, $n_R = 6$, $P = 0.05$; Fig. 5B).

As shown in Figure 5C, control and experimental males did not differ significantly in number of fledglings produced with social mates (Wilcoxon $z = -0.9$, $n_C = 7$, $n_R = 4$, $P = 0.38$). Success in siring young with extra-pair females was significantly higher for control than for reddened males (Wilcoxon $z = 2.0$, $n_C = 8$, $n_R = 7$, $P = 0.04$); experimental males sired no extra-pair young. Although males with reddened epaulets were more likely to lose their territories and sired no extra-pair young, realized reproductive success of control and experimental males did not differ significantly (Wilcoxon $z = -0.9$, $n_C = n_R = 14$, $P = 0.36$), perhaps because experimental males were more vigilant (Fig. 4A), responded more aggressively to predators in the area (Fig. 4B), and had higher hatching success (Fig. 5B) than did control males.

DISCUSSION

PATH ANALYSIS

Our path analysis demonstrated that the ability to sire young with social mates and with extra-pair females both contributed significantly to males' realized reproductive success but that within-pair success was relatively more important. Although the path coefficient from extra-pair mates to extra-pair fledglings showed a strong, positive effect, we interpret the strength of this relationship with caution because we estimated the number of extra-pair mates from identified sires of extra-pair young. We had no way of determining the numbers of extra-pair females with which males copulated but did not produce fledglings. The weak relationship between within-pair mates and within-pair fledglings demonstrates that many other factors such as predation, male parental care, and female quality affect reproductive success. Finally, the positive direct effect of territory size on within-pair mating success demonstrates that, on our study area, males with large territories were able to attract many social mates. Given this result, the lack of a significant difference in territory sizes of control and experimental males means that territory size was not responsible for any differences in mating success in our epaulet experiment.

EPAULET EXPERIMENT

Our attempt to redden epaulets in the field was clearly effective. Epaulets "painted" with a red marker reflected redder wavelengths, were visibly redder and more uniformly red to our eyes than unmanipulated epaulets, and were at or just beyond the extreme end of the normal range of variation. Our experimental males also showed effects of the manipulation. Territories defended by males with reddened epaulets were challenged and trespassed upon more than territories defended by control males, and males with reddened epaulets

were more likely than control males to lose their territories. Males who lost their territories and were subsequently recaptured showed evidence of wounds from combat. We conclude, therefore, that unusually red epaulets are costly in male–male competition for territories, primarily as a result of aggression from neighboring territorial males.

Given that female Red-winged Blackbirds have been shown to prefer males with reddened epaulets (Yasukawa et al. 2009), one explanation for the intrasexual cost of exaggerated epaulet color is that neighboring males were striking pre-emptively to guard their own paternity. In this species most extra-pair sires are territorial neighbors (Gibbs et al. 1990, Westneat 1993, Weatherhead et al. 1994, Gray 1996), so if a neighbor is, or in this experiment becomes, very attractive to a male's mates, it is to that male's advantage to drive the neighbor from the territory to protect his within-pair paternity. Olendorf et al. (2004) found that male Red-winged Blackbirds maintained vigilance against, and were aggressive toward, sexually attractive neighbors that were successful at extra-pair fertilizations. These authors speculated that it is unlikely that males directly observe neighbors copulating with their mates but rather are more likely to assess a neighbor's ability to achieve extra-pair copulations from surrogate cues that correlate with success in extra-pair fertilizations. Epaulet color might be such a cue. It is also possible that males with reddened epaulets were more threatening to their neighbors and those neighbors therefore responded with increased aggression. Although relevant information is generally lacking, Searcy (1979a) concluded that epaulet color does not function as a signal of dominance in adult male Red-winged Blackbirds (but see Eckert and Weatherhead 1987).

Our experimental males were also unable to fertilize extra-pair females. Perhaps male Red-winged Blackbirds with reddened epaulets are more conspicuous to their neighbors (epaulets are exposed during flight) and therefore have difficulty trespassing to fertilize extra-pair females, or perhaps neighbors are more vigilant when a male has reddened epaulets. We should note that in 1997 there was one brood of three nestlings of which we identified the sire, but we were unsure whether this male was the female's social mate or the owner of a neighboring territory. To be conservative, we classified the sire as the female's social mate, but our conclusions would be the same even if this assignment were reversed because it would have increased the extra-pair success of control males, which was already significantly greater than that of experimental males.

Despite their difficulties in territory defense and their inability to produce extra-pair young, our males with reddened epaulets did not appear to suffer an overall disadvantage in reproductive success. One explanation is that males with reddened epaulets were "making the best of a bad situation." If males with enhanced epaulets are truly disadvantaged in seeking extra-pair copulations, then they could compensate

by allocating more effort to paternal care. We found that experimental males spent more time on territory, allocated more time to anti-predator vigilance, and were more aggressive toward a simulated predator than were control males. Perhaps males with reddened epaulets, which were more vigilant and more aggressive than control males, were better able to warn their mates of danger (Beletsky 1996, Burton and Yasukawa 2001) and drive away predators (Knight and Temple 1988), and, as a result, their eggs were more likely to survive and hatch than eggs of control males.

In some ways our results paralleled results of the experiments of Metz and Weatherhead (1991, 1992, 1993). Male Redwinged Blackbirds given five red bands incurred high rates of aggression from neighbors and lost their territories more often than males with five black bands. In addition, males whose epaulets were "uncovered" by removal of the black scapular feathers had more difficulty than controls in trespassing onto neighboring territories.

Our results also seemed to parallel those of experiments that manipulated the size of Red-winged Blackbird epaulets. Hansen and Rohwer (1986) found that territory owners were more aggressive toward mounts with half epaulets than toward black-winged blackbirds and more aggressive toward mounts with larger epaulets than toward mounts with smaller epaulets. In addition, Røskaft and Rohwer (1987) found that trespassing males avoided mounts with normal or enlarged red epaulets and were more likely to approach mounts with normal epaulets than mounts with triple-sized epaulets.

On the other hand, a number of studies have found no relationship between male Red-winged Blackbirds' epaulet size or color and mating or reproductive success (Searcy 1979b, Searcy and Yasukawa 1995, Weatherhead and Boag 1995, 1997, Westneat 2006), and Dufour and Weatherhead (1998) found no relationship between epaulet symmetry and either mating or reproductive success. In a meta-analysis of studies of Red-winged Blackbird epaulet size and color Yasukawa et al. (2010) found that selection on epaulet size was weak at best and on color was nil. Why are Red-winged Blackbird epaulets currently experiencing little or no directional selection? A number of explanations have been proposed, including methodological complications, evolutionary constraints, and counter-balancing selection.

Westneat (2006) discussed methodological complications such as insufficient sample size, nestling starvation and predation, and spatial and temporal variation in selection, all of which might obscure directional selection on epaulet expression in this and other studies.

Epaulet color could be limited by constraints. In the Redwinged Blackbird epaulet color is produced by both carotenoid pigments and melanin deposited in the upper marginal coverts (McGraw et al. 2004), so epaulet color might also be limited by access to dietary carotenoids (Hill 2002). In addition, female Red-winged Blackbirds also possess epaulets, although

their size and color vary considerably (Yasukawa and Searcy 1995). Muma and Weatherhead (1989, 1991) investigated possible functions of epaulets in female Red-winged Blackbirds and concluded that genetic correlation was the most likely explanation for their existence. Such a genetic correlation could limit the evolution of epaulets in males (Chenoweth et al. 2008), but the magnitude of the correlation is unknown. In addition, Searcy and Yasukawa (1995) speculated that sexual selection on epaulets in Red-winged Blackbirds is constrained by a lack of heritable variance (Badyaev and Martin 2000).

Natural selection has long been thought to counter-balance sexual selection (Searcy and Yasukawa 1983, 1995), and predation is often assumed to limit Red-winged Blackbird epaulets (Metz and Weatherhead 1992), but there is little evidence to support this assumption (Searcy and Yasukawa 1995).

Searcy (1979c) proposed a self-limiting process in his discussion of intrasexual selection on male body size in Redwinged Blackbirds. Large males may have an advantage in physical contests during territory establishment and defense, but small males may have an advantage in territorial contests requiring endurance. Although self-limiting intrasexual selection on epaulet color predicts that males with reddened epaulets pay an intrasexual cost, there is no evidence that normal epaulets are more effective in territory defense than less red epaulets (Westneat 2006, Yasukawa et al. 2009).

In contrast, we have evidence that benefits from female preference for reddened epaulets are limited by the intrasexual costs of reddened epaulets (Yasukawa et al. 2009, this study). A similar tradeoff has been identified in the Spotted Bowerbird (*Chlamydera maculata*), in which males build and decorate bowers to attract females (Borgia 1995). Madden (2003a, b) found that mating success was predicted by the number of *Solanum* berries decorating the bower, which male preferentially proffer to females. Although bower destruction by neighbors was usually rare (Borgia and Mueller 1992), when the number of *Solanum* berry decorations was artificially increased, enhanced bowers were destroyed by owners of neighboring bowers (Madden 2002).

Counter-balancing sexual selection proposes that intersexual advantages of extreme expression are opposed by intrasexual disadvantages. For example, male Red-winged Blackbirds with showy epaulets may be preferred as mates by females but may be attacked disproportionately by other territorial males as a form of mate defense. At this point, only one study provides results to test this hypothesis. Yasukawa et al. (2009) demonstrated that females prefer male Red-winged Blackbirds with epaulets reddened just beyond the range of natural variation over males with normal epaulets. This hypothesis can also explain why epaulets are favored in intrasexual selection if epaulets are necessary territory-defense signals, so males whose epaulets are eliminated (black-winged blackbirds) are unable to establish or defend territories. The results of epaulet-blackening experiments are consistent with this

explanation (Peek 1972, Smith 1972, Morris 1975, Hansen and Rohwer 1986). Finally, the hypothesis of counter-balancing sexual selection may also account for the lack of covariance between epaulet expression and reproductive success if only the extremes of expression are disadvantageous. The meta-analysis of Yasukawa et al. (2010) shows that directional selection on epaulet expression is very weak at best, but several experimental tests are still lacking. A female-preference experiment like those of Yasukawa et al. (2009) but comparing males with epaulets near the lower and upper ends of color or size expression, or comparing males just below and within the natural range of expression, would be informative tests of the hypothesis of counter-balancing sexual selection for epaulet expression in male Red-winged Blackbirds.

As observational and experimental results to date show evidence that the Red-winged Blackbird's epaulets evolved in response to sexual selection, but no evidence for current sexual selection on the epaulets, an examination of epaulet phylogeny might be informative. Johnson and Lanyon (2000) performed a phylogenetic analysis of the evolution of carotenoid plumage patches, and of epaulets in particular, in the clade that includes the Red-winged Blackbird. They concluded that a shift to breeding in marshes by an all-black ancestor coincided with the evolution of carotenoid plumage patches in general and epaulets in particular. Among the hypotheses they discussed to explain why marsh breeding would favor the evolution of epaulets were (1) direct female choice on plumage, (2) elevated intensity of sexual selection, (3) more frequent territorial encounters among males, (4) the nature of carotenoid signals per se, and (5) the signaling environment of marshes. Colorful plumage patches have evolved multiple times within the blackbird lineage, so studies of sexual selection in these other species, using the methods developed to study the Red-winged Blackbird, would be valuable.

The epaulet of the Red-winged Blackbird is a well-studied coverable badge that has both intrasexual and intersexual functions (Andersson 1994, Searcy and Yasukawa 1995, Beletsky 1996, Yasukawa et al. 2009). As a result, there have been many attempts to determine whether epaulets are under current sexual selection and therefore affect reproductive success (Searcy and Yasukawa 1983, 1995, Westneat 2006, Yasukawa et al. 2009, this study). We conclude that, despite the many observational and experimental studies, there is no evidence for current sexual selection on the epaulets of male Red-winged Blackbirds. These male ornaments may be holdovers from past sexual selection (Møller and Pomiankowski 1993).

ACKNOWLEDGMENTS

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