

- Rosefinch (*Carpodacus erythrinus*). *Auk* 107:35–44.
- BROWN, J. L. 1975. The evolution of behavior. W. W. Norton, New York.
- BROWN, M. B., AND C. M. BROWN. 1988. Access to winter food resources by bright- versus dull-colored House Finches. *Condor* 90:729–731.
- BURLEY, N. 1981. Sex ratio manipulation and selection for attractiveness. *Science* 211:721–722.
- GAUTHREAUX, S. A., JR. 1978. The ecological significance of behavioral dominance, p. 17–54. In P.P.G. Bateson and P. H. Klopfer [eds.], *Perspectives in ethology*. Vol. 3. Plenum Press, New York.
- HELMS, C. W., AND H. W. DRURY, JR. 1960. Winter and migratory weight and fat field studies on some North American buntings. *Bird-Banding* 31:1–40.
- KALINOSKI, R. 1975. Intra- and interspecific aggression in House Finches and House Sparrows. *Condor* 77:375–384.
- MAXSON, S. J., AND L. W. ORING. 1980. Breeding season time and energy budgets of the polyandrous Spotted Sandpiper. *Behaviour* 74:200–263.
- MAYNARD SMITH, J., AND G. A. PARKER. 1976. The logic of asymmetric contests. *Anim. Behav.* 24: 159–175.
- SAMSON, F. B. 1976. Territory, breeding density, and fall departure in Cassin's Finch. *Auk* 93:477–497.
- SAMSON, F. B. 1977. Social dominance in winter flocks of Cassin's Finch. *Wilson Bull.* 89:57–66.
- SHEDD, D. H. 1990. Aggressive interactions in wintering House Finches and Purple Finches. *Wilson Bull.* 102:174–178.
- SMITH, S. M. 1980. Henpecked males: the general pattern in monogamy? *J. Field Ornithol.* 51:55–63.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman, New York.
- THOMPSON, W. L. 1960a. Agonistic behavior in the House Finch. Part II: factors in aggressiveness and sociality. *Condor* 62:378–402.
- THOMPSON, W. L. 1960b. Agonistic behavior in the House Finch. Part I: annual cycle and display patterns. *Condor* 62:245–271.

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A RETROSPECTIVE ANALYSIS OF RED-BAND EFFECTS ON RED-WINGED BLACKBIRDS¹

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Key words: Red-winged Blackbird; color bands; territoriality; reproduction; survival.

Color bands are probably the most common technique used by ornithologists to identify individual birds at a distance. Burley's (e.g., 1981, 1985, 1986) studies of captive Zebra Finches (*Poephila guttata*) showed that colored bands influenced several important aspects of reproduction and survival. Recent field studies have shown that bands matching the color of prominent secondary sexual traits had a negative impact on reproduction in Red-cockaded Woodpeckers (*Picoides borealis*) (Hagan and Reed 1988) and a positive effect on mate attraction in Rock Ptarmigan (*Lagopus mutus*) (Brodsky 1988), although the latter result may have

been confounded by other factors (Holder 1990). In a field experiment manipulating band color in Red-winged Blackbirds (*Agelaius phoeniceus*), Metz and Weatherhead (1991) found that red bands (matching the males' epaulets) provoked increased aggression from neighbors, which was associated with a higher rate of territory loss. Collectively these studies raise the concern that much of ornithological research could be compromised by the use of colored bands. Here we investigate this possibility using data from our own research on Red-winged Blackbirds.

Because Red-winged Blackbirds have bright red epaulets, the size of which appears to be associated with aspects of social dominance (Eckert and Weatherhead 1987a) and parental behavior (Eckert and Weatherhead 1987b), Metz and Weatherhead (1991) chose red bands as their experimental color. Black bands were used on controls because they matched the color of the rest of the birds' bodies. They found that the red-banded males that lost their territories had larger epaulets than those that retained their territories, indicating that the red bands somehow interacted with the natural epaulet. A further experiment using red, blue and black bands confirmed the importance of red bands (Metz

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TABLE 1. Territory loss by males with^a and without red bands.

Band type ^b	Data ^c	% males losing territories		χ^2 ^d	P
		No red bands (n)	Red bands (n)		
Plastic	All territories	30.6 (108)	39.5 (43)	0.75	0.39
	First year	31.2 (93)	35.9 (39)	0.10	0.75
Aluminum	All territories	11.8 (51)	20.4 (93)	1.17	0.28
	First year	18.5 (27)	21.4 (56)	0.00	0.99

^a Males with one or more red bands.

^b Plastic bands and aluminum bands were used in separate studies.

^c "All territories" include each territory with a banded male every year of study; "first year" territories include only those occupied by a male the first year he was banded.

^d χ^2 from 2-way contingency table analysis corrected for continuity.

and Weatherhead, in prep.). Using similar reasoning, Beletsky and Orians (1989) looked for a red-band effect in their retrospective analysis using data from Red-winged Blackbirds in Washington State. In contrast to Metz and Weatherhead's (1991) study, Beletsky and Orians (1989) found no effect of red bands on reproduction and concluded that it was unnecessary to avoid using red bands in field studies of Red-winged Blackbirds. The discrepancy between the results of these two studies, and the potential importance of band color effects to ornithology generally, indicates the need for further analysis.

Our data come from two studies conducted in eastern Ontario in the vicinity of the Queen's University Biological Station. The first study was conducted from late March through July 1984 and 1985 (Eckert and Weatherhead 1987a, 1987b). All the males in the study defended territories along roadsides in primarily agricultural habitat. As part of this study some males were removed from their territories prior to the onset of breeding, and their replacements were banded. In addition, some banded males that held territories at the beginning of the season lost their territories by natural means. Analysis of data from this study is restricted to assessing the rates of natural territory turnover within years. While some of these turnovers may represent voluntary territory abandonment rather than territory loss, closely monitored cases indicated that turnovers were usually associated with aggressive conflicts with intruding males, suggesting that most turnovers resulted from territory loss (Eckert and Weatherhead 1987a). All males received a numbered aluminum band and three colored plastic bands. The color of red plastic bands (Munsell renotation 9.2R 3.9/12.1) closely matched the color of the males' epaulets (Metz and Weatherhead 1991). On all males we

measured the length of one epaulet from the bend of the wing to the fullest extent of the yellow plumage.

The second study was conducted from March through July 1986 to 1989 (Weatherhead 1990a, b). Males in this study defended territories in marshes in areas flooded by beavers and along the shore of Lake Opinicon. Each male was banded with a numbered aluminum band and three anodized aluminum bands and had one of his epaulets measured as above. Because red anodized aluminum bands are darker and duller red (Munsell renotation 5.1R 2.8/10.1) than the epaulets, we analyzed data from this study separately. Although no males were removed from their territories in this study, natural turnover of males did occur, particularly early in the season. Reproductive events on those territories are attributed to the males holding the territories at the start of the nesting season. Similarly, return rates of males are based on the males holding territories at the start of the nesting season. We attempted to find all nests on all the territories and to band as many females as possible, again using anodized aluminum bands. We calculated harem size as the maximum number of females nesting at the same time on a male's territory (Weatherhead and Robertson 1977). In all analyses we considered the first year a male was banded separately from subsequent years since the performance of a male in subsequent years may not be independent of his previous performance (following Beletsky and Orians 1989).

Our results gave little indication of any effect, either positive or negative, of red bands on Red-winged Blackbirds. Males with one or more red bands were no more likely to lose their territories than males without red bands, regardless of whether the bands were plastic (i.e., matching the epaulet color) or anodized aluminum (Table 1). Epaulet size did not differ between

TABLE 2. Epaulet length of males holding and losing territories relative to band color (presence or absence of red).

Band type	Color	Mean \pm SD (n) epaulet length (mm)		t	P _{1-tailed}
		Holding territories	Losing territories		
Plastic	with red	44.9 \pm 2.0 (25)	44.5 \pm 2.5 (13)	0.57	0.57
	without red	44.0 \pm 2.5 (65)	43.5 \pm 3.0 (27)	0.79	0.43
Aluminum	with red	44.8 \pm 1.8 (64)	45.3 \pm 2.1 (12)	-0.87	0.39
	without red	44.7 \pm 1.5 (36)	44.6 \pm 1.7 (5)	0.17	0.87

TABLE 3. Within-year breeding success of males and between-year return rate of males and females with and without red bands in the marsh study (i.e., all birds banded with aluminum bands).

Reproduction	Males with		<i>t</i>	<i>P</i> _{1-tailed}
	At least one red band (<i>n</i>)	No red bands (<i>n</i>)		
All years				
Harem size ($\bar{x} \pm$ SD)	2.27 \pm 0.89 (75)	2.02 \pm 0.93 (44)	-1.42	0.16
Young fledged ^a ($\bar{x} \pm$ SD)	3.57 \pm 3.04 (68)	2.51 \pm 2.36 (41)	-1.91	0.06
First year only				
Harem size ($\bar{x} \pm$ SD)	2.07 \pm 0.90 (44)	2.10 \pm 1.00 (21)	0.11	0.91
Young fledged ^a ($\bar{x} \pm$ SD)	3.20 \pm 2.93 (41)	2.57 \pm 2.46 (21)	-0.83	0.41
Return rate (%)				
Females			χ^2	<i>P</i>
All years	37.6 (133)	38.4 (86)	0.00	1.00
First year	35.0 (100)	38.2 (68)	0.07	0.79
Males				
All years	52.9 (68)	68.6 (35)	1.72	0.19
First year	50.0 (50)	61.9 (21)	0.43	0.51

^a An unnatural disturbance (a tractor pull) prevented us from getting complete fledging data on several territories.

males that lost and males that held their territories, for both males with and without red bands and for both types of bands (Table 2). Thus, our data for territory loss show none of the red band effects reported by Metz and Weatherhead (1991). In addition, we found no difference in harem size between males with and males without red bands (Table 3). There was a tendency for more young to be fledged from territories of red-banded males (Table 3). However, the difference was not significant and is opposite to that (also not significant) reported by Beletsky and Orians (1989) and by Metz and Weatherhead (1991). Finally, there was no evidence that having one or more red bands affected the return rate of either males or females (Table 3). Thus, our results both corroborate and extend those of Beletsky and Orians (1989).

Our data support Beletsky and Orians' (1989) conclusion that there is no need to avoid using red bands in studies of Red-winged Blackbirds. However, we suggest three important qualifications. First, Metz and Weatherhead (1991) used six bands per bird (one aluminum plus five colored plastic bands) so that red-banded males received five red bands. We only used three colored bands per bird and very few "red-banded" individuals received three red bands. Although Beletsky and Orians (1989) used from three to five colored bands, no individual received exclusively red bands. It is possible, therefore, that negative effects of red bands may only occur above some threshold amount of red, or the mixture of bands of different colors with red bands may somehow diminish any effect of red (Burley 1985). Second, a negative effect may also be associated with the particular color of red employed. Metz and Weatherhead (1991) used exclusively plastic bands that match the color of the males' epaulets much more closely than the red anodized aluminum bands used predominately by Beletsky and Orians and by us in one of our two studies. Unfortunately, in the study in which we used plastic bands we only had data on territory loss and not on reproductive performance.

Finally, Gibbs et al. (1990) have recently demonstrated that harem size and fledging success are likely to be poor indicators of mating and reproductive success, respectively. This stems from the very high levels of extra-pair fertilizations that they detected using DNA fingerprinting. It is conceivable that red bands could influence female mating behavior but not their choice of nest sites, a situation that would be undetectable by the analyses used here and by Beletsky and Orians (1989). Therefore, we think a more cautious conclusion is warranted at this time. Until additional experiments are conducted to assess the effects of red bands on Red-winged Blackbird behavior, including the use of molecular techniques to assess true mating patterns, we would recommend against the use of multiple red bands, particularly those similar in color to the epaulets. It would also seem prudent for those studying other species to undertake similar assessments of possible band color effects.

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LITERATURE CITED

- BELETSKY, L. D., AND G. H. ORIAN. 1989. Red bands and Red-winged Blackbirds. *Condor* 91:993-995.
- BRODSKY, L. M. 1988. Ornament size influences mating success in male Rock Ptarmigan. *Anim. Behav.* 36:662-667.
- BURLEY, N. 1981. Mate choice by multiple criteria in a monogamous species. *Am. Nat.* 117:515-528.
- BURLEY, N. 1985. Leg-band color and mortality patterns in captive-breeding populations of Zebra Finches. *Auk* 102:647-651.
- BURLEY, N. 1986. Sex-ratio manipulation in color-banded populations of Zebra Finches. *Evolution* 40:1191-1206.

- ECKERT, C. G., AND P. J. WEATHERHEAD. 1987a. Owners, floaters and competitive asymmetries among territorial Red-winged Blackbirds. *Anim. Behav.* 35:1317-1323.
- ECKERT, C. G., AND P. J. WEATHERHEAD. 1987b. Male characteristics, parental quality and the study of mate choice in Red-winged Blackbirds (*Agelaius phoeniceus*). *Behav. Evol. Sociobiol.* 20:35-42.
- GIBBS, H. L., P. J. WEATHERHEAD, P. T. BOAG, B. N. WHITE, L. M. TABAK, AND D. J. HOYSAK. 1990. Realized reproductive success of polygynous Red-winged Blackbirds revealed by DNA markers. *Science* 250:1394-1397.
- HAGAN, J. M., AND J. M. REED. 1988. Red color bands reduce fledgling success in Red-cockaded Woodpeckers. *Auk* 105:498-503.
- HOLDER, K. R. 1990. Ornamental traits in Rock Ptarmigan: morphology, behaviour and mating success. Unpublished M.S. thesis, Queen's University, Kingston, Ontario, Canada.
- METZ, K. J., AND P. J. WEATHERHEAD. 1991. Color bands function as secondary sexual traits in male Red-winged Blackbirds. *Behav. Ecol. Sociobiol.* 28:23-27.
- WEATHERHEAD, P. J. 1990a. Nest defence as shareable paternal care in Red-winged Blackbirds. *Anim. Behav.* 39:1173-1178.
- WEATHERHEAD, P. J. 1990b. Secondary sexual traits, parasites and polygyny in Red-winged Blackbirds. *Behav. Ecol.* 1:125-130.
- WEATHERHEAD, P. J., AND R. J. ROBERTSON. 1977. Harem size, territory quality, and reproductive success in the Red-winged Blackbird (*Agelaius phoeniceus*). *Can. J. Zool.* 55:1261-1267.

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MITOCHONDRIAL DNA VARIATION AND THE TAXONOMIC STATUS OF THE LARGE-BILLED SAVANNAH SPARROW¹

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Key words: Savannah Sparrow; *Passerculus sandwichensis*; mitochondrial DNA; species limits; biogeography.

The Savannah Sparrow (*Passerculus sandwichensis*) is widely distributed in North America (AOU 1983). The species includes several phenotypically distinct and geographically restricted forms, some of which were once considered species, as well as a more "typical" or familiar form that is found throughout much of the continent (van Rossem 1947, AOU 1957). We assessed mitochondrial DNA (mtDNA) differentiation between one of the divergent forms, the large-billed Savannah Sparrow (*P. s. rostratus*), and representatives of more "typical" forms of the species. Although van Rossem (1947) proposed that Savannah Sparrow morphology changed gradually from typical (interior North American forms) to large-billed forms (coastal Mexican forms), we suggest that the large-billed Savannah Sparrow is a distinct taxon and not merely the end-point of a gradual cline. The mtDNA of *rostratus* differed considerably from that of "typical" Savannah Sparrows. Although we do not plan an extensive survey of mtDNA variation in the Savannah Sparrow at this

time, we suggest that further study will support our hypothesis of species status for *rostratus*.

The large-billed Savannah Sparrow, once considered a species (AOU 1931), differs (Bent 1968) from more typical Savannah Sparrows in having: a thicker and longer bill with a more decurved culmen; reduced dorsal streaking and an absence or near absence of yellow lores and supercilium (contrary to some field guides); darker tarsi and toes; different rectrix shape; proportionately shorter wings; and, larger body size. The bill differences are particularly striking, especially considering that bill size and shape vary little among other Savannah Sparrow populations (Rising 1987). Furthermore, after breeding in salt marshes along the northern and eastern coasts of the Gulf of California many adults and immatures migrate north to winter in saline marshes in southwestern California, unlike other Savannah Sparrows, which migrate south or are sedentary. Migratory behavior likely has a genetic basis, which suggests genetic differences in addition to those controlling morphological variation.

MtDNA analysis is being used with increasing frequency to document genetic variation within avian species (Ball et al. 1988, Avise and Nelson 1989, Shields 1990, Fleischer et al. 1991, Moore et al. 1991, Zink et al. 1991b). In contrast to most allozymic analyses, mtDNA surveys sometimes reveal considerable differentiation among closely spaced North American bird populations (Avise and Nelson 1989, Fleischer et al.

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