

AN EXPERIMENTAL TEST OF THE CONTRASTING-COLOR HYPOTHESIS OF RED-BAND EFFECTS IN RED-WINGED BLACKBIRDS¹

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Abstract. We performed an experiment to investigate effects of red leg bands on the behavior of male Red-winged Blackbirds (*Agelaius phoeniceus*). We presented models having either black, blue, or red leg bands to territorial male Red-winged Blackbirds to test the hypothesis that any color of band that contrasts with the color of the legs makes an individual appear abnormal or unhealthy and therefore subject to attack. Overall, territorial males responded equally aggressively to the black- and blue-banded models, but spent more time at distances greater than 10 m, displayed at lower intensities, and took longer to attack when the model was given red bands. Thus, red bands appeared to make the model initially more threatening to territorial male Red-winged Blackbirds. These results do not support the contrasting-color hypothesis and suggest that the effect of red bands is attributable to the bands matching the color of the male's epaulets. The failure of the contrasting-color hypothesis also leaves unresolved the different outcomes of one previous experiment showing a negative effect of red bands, and two analyses of long-term banding studies that detected no effect of red bands.

Key words: *Red-winged Blackbird; Agelaius phoeniceus; epaulets; colored bands.*

INTRODUCTION

We recently demonstrated that red leg bands severely reduced the ability of male Red-winged Blackbirds (*Agelaius phoeniceus*) to maintain their territories, unlike black bands which had no noticeable effect on male behavior (Metz and Weatherhead 1991). That study added to growing evidence that colored leg bands can affect bird behavior (Burley 1981, 1985, 1986a, 1986b; Burley et al. 1982; Brodsky 1988; Hagan and Reed 1988; Holder 1990). Because colored leg bands are widely used in ornithological research, it is important that we understand the circumstances that cause color bands to affect behavior. In addition to the practical concerns, understanding color-band effects may also shed light on questions concerning the evolution of colored secondary sexual traits in birds (Burley 1986b). Here, we present an experiment that tests one of the hypotheses proposed to explain the effect of red bands on male Red-winged Blackbirds.

In addition to the general result that red leg bands caused some males to lose territories, we also observed that red-banded males with larger epaulets were more likely to lose their territories

than red-banded males with smaller epaulets (Metz and Weatherhead 1991). The cause of the territory loss appeared to be increased and more persistent intrusion by other males, particularly territorial neighbors. Thus, we proposed that red bands acted as secondary sexual traits in conjunction with the males' red epaulets, the combined effect of which was to make red-banded males appear to be signaling more aggressively than their competitive ability warranted. The inconsistency between signal and ability caused these males to be challenged. This effect was most pronounced in males with large epaulets and was most noticeable to their neighbors. Color-band effects reported by Brodsky (1988), Hagan and Reed (1988) and Holder (1990) also involve colors that matched secondary sexual traits, and in the last two studies, the effect of those bands was also negative.

We also proposed other hypotheses that might explain the negative effect of red bands on male Red-winged Blackbirds (Metz and Weatherhead 1991). Because epaulets are coverable (Hansen and Rohwer 1986) in Red-winged Blackbirds (whereas bands are not), it may have been the exposure of an aggressive signal under inappropriate circumstances rather than the size of the signal per se that made red bands detrimental. An experiment in which feather clipping caused

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male Red-winged Blackbirds to expose their epaulets continuously suggested that the ability to cover epaulets is important for some activities (e.g., trespassing on neighbors' territories), but does not cause males to lose their territories (Metz and Weatherhead 1992). Thus, the inability to cover red bands appears insufficient to explain why red bands are detrimental.

Another hypothesis for the negative effect of red bands, and that which we test here, is that the bands are detrimental simply because they contrast with the color (black) of the legs. A contrasting color may make males appear abnormal or unhealthy and thus, for some reason (e.g., they are less threatening), provoke an attack. If this hypothesis is correct, then any color that contrasts with the color of the legs should provoke attack in Red-winged Blackbirds. This hypothesis could also explain the failure to find any negative effect of red bands in retrospective analyses of two long-term studies of banded populations (Beletsky and Orians 1989, Weatherhead et al. 1991). In both studies, all birds received bands (only some of which were red) that contrasted with the color of their legs. Therefore, regardless of the color of their bands, all birds would have been similarly affected, and no effect specific to red bands would be expected. We test the contrasting-color hypothesis by quantifying the response of territorial male Red-winged Blackbirds to models with either contrasting (red or blue) or noncontrasting (black) color bands.

METHODS

We conducted this experiment in three cattail marshes located within 40 km of the Queen's University Biological Station in eastern Ontario from 26 April to 22 May 1990. We presented territorial males with a male Red-winged Blackbird model given red, blue, or black bands. Approximately half the territorial males were "naive," never having been exposed previously to a model blackbird and not used in other experiments. The remaining "experienced" males were also part of another experiment in which we clipped either the black feathers that are used by males to conceal their epaulets, causing the epaulets to be permanently exposed ("experienced-clipped"), or an equivalent number of contour feathers that did not alter the males' appearance ("experienced-controls"). In the course of these treatments these males had been captured using model blackbirds and song playbacks. Although

those models did not have leg bands, previous experience with a model blackbird could reduce the males' aggression in subsequent exposures (Hansen and Rohwer 1986). Therefore, we analyzed their responses separately from those of naive males.

Aggressive territory owners can destroy taxidermic models in a matter of minutes (Rohwer 1978, pers. observ.). This can cause serious problems in keeping the stimulus the same when presenting the model to several males in succession. Therefore, we designed a model that was virtually indestructible by a male Red-winged Blackbird. The model's body was made from black cotton material stuffed with cotton balls. We fastened a male Red-winged Blackbird wing with the epaulet fully exposed to each side of the cotton body. A male Red-winged Blackbird head was covered with the same black material as on the body so that only the bill was exposed and was attached to the body. Pins with round black heads of an appropriate size were used as eyes. Pairs of male Red-winged Blackbird legs given six (three per leg) royal blue, black, or red plastic leg bands could also be fastened with Velcro® to the body. Thus, the only feature of the model that varied when presented to owners was the color of the model's leg bands. The color of the red bands matched the color of the model's epaulets. Red bands and the model's epaulet color were scored as Inter-Society Color Council-National Bureau of Standards (ISCC-NBS) number 36 (Munsell notation 9.2R 3.9/12.1). The color of the blue bands was scored as ISCC-NBS number 182 (Munsell notation 3.0PB 4.3/6.8). The blue bands appeared to us to present the same contrast to the legs as did the red bands. The color of the black bands was ISCC-NBS number 267 (Munsell notation N 0.8). The black bands matched the color of the legs and thus were difficult for us to see at any distance.

Model presentations were conducted between 06:00 to 09:00 hours d.s.t., the time when males were most active. We placed the model near the center of a male Red-winged Blackbird's territory while the owner was present and then observed the response from 30–50 m away for 5 min. Male Red-winged Blackbird songs were not played during the model presentations.

We measured the following aspects of the owners' behavior during the model presentations (after Rohwer 1978): (1) T 1st—the latency in seconds to the first time an owner reacted to the

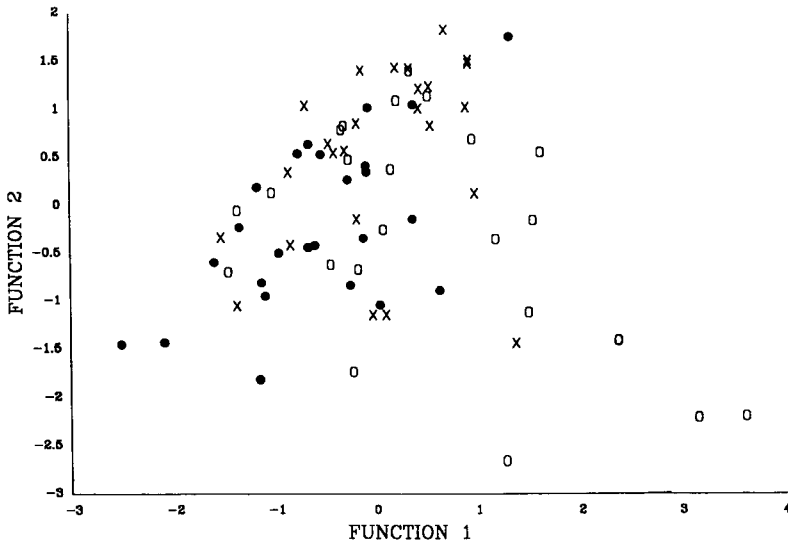


FIGURE 1. Scatterplot of territorial males' responses to the model with red (open circles), black (\times s), or blue (closed circles) bands using the males' discriminant function scores for Function 1 (time to attack; proximity to model) and Function 2 (song spread rate and intensity).

model (up to 300 sec). Reactions included flying closer to the model, or directing a song spread display at the model; (2) T HIT—the latency in seconds to the first time an owner struck the model (up to 300 sec); (3) N HITS—the number of times the owner struck the model; (4) 0–2 m—the amount of time in seconds an owner spent within two meters of the model; (5) > 10 m—the amount of time in seconds an owner spent greater than 10 meters from the model; (6) Total SS—the total number of song spread displays directed by the owner toward the model; (7) The intensity of song spread displays given by the owner that were directed toward the model. We classified the intensity of song spread displays based on the body postures of singing males. We considered a display not to be a song spread when singing males' wings remained at their sides and their tails were not fanned (SS1). A low intensity song spread involved males slightly arching their wings out from their sides, and holding their tails down but not fanned (SS2). In a medium song spread the wings were arched out and down and the tail was slightly fanned (SS3). In a high intensity song spread (SS4), the feathers of the epaulet were ruffled, the wings fully arched out and down and the tail completely fanned.

We presented the model only once to each owner. This minimized the possibility that owners would become familiar with the model and

respond differently upon subsequent presentations. We randomly assigned whether an owner was presented with the red-, blue-, or black-banded model. We usually performed 5–12 model presentations per morning. This normally resulted in all three band colors being presented each morning. Thus, potential variation in behavioral responses caused by weather or other factors were randomized.

RESULTS

Prior experience did not affect the response of males to the model. Thirteen of 31 (41.9%) experienced males attacked the model and 20 of 42 (47.6%) naive males attacked the model ($\chi^2 = 0.23$, $df = 1$, $P = 0.63$). There was also no significant difference between naive and experienced males in how vigorously they responded to the model (t -tests for each variable; all P s > 0.05). Among experienced males, clipped and control individuals were just as likely to attack the model; 10 of 15 clipped males attacked the model, and 8 of 16 control males attacked the model ($\chi^2 = 0.88$, $df = 1$, $P = 0.35$). The behavior of clipped and control males was also similar when reacting to the model (t -tests for each variable; all P s > 0.05). Since prior experience with the model and our clipping treatments did not affect how males responded to the model, we

TABLE 1. Discriminant function analysis of behavioral differences of owners to a conspecific model that had red, black, or blue colored bands during 5-min activity budget recordings. Variables are defined in the text.

Variable	Red <i>n</i> = 23 \bar{x}	Black <i>n</i> = 25 \bar{x}	Blue <i>n</i> = 25 \bar{x}	Significant variables		Entered at step
				Wilks' λ	<i>P</i>	
T 1ST	42.57	56.16	37.84			
T HIT	274.61	230.52	234.60	0.718	0.034	6
N HIT	1.87	3.92	1.68			
0–2 m	105.43	172.32	110.56	0.814	0.028	3
>10 m	77.43	26.08	29.84	0.912	0.039	1
Total SS	14.83	14.32	17.16	0.740	0.026	5
SS1	0.70	0.00	0.08			
SS2	0.87	0.12	0.04	0.859	0.032	2
SS3	1.57	1.16	0.76	0.781	0.031	4
SS4	7.78	10.16	11.40			

Function 1 Wilks' Lambda $\chi^2 = 22.35$, $P = 0.034$.
Function 2 Wilks' Lambda $\chi^2 = 8.67$, $P = 0.12$.

combined all males in our analysis of their response to the red-, black-, or blue-banded model.

To determine whether males reacted differently to the models we first considered each behavioral variable separately. Seven of 23 males attacked the model with red bands, 14 of 25 males attacked the model with black bands, and 12 of 25 males attacked the model given blue bands. Thus, territorial males were just as likely to attack the model when it was given red, black, or blue bands ($\chi^2 = 3.28$, $df = 2$, $P = 0.20$). We used analysis of variance to analyze the remaining response variables. We found no significant differences in the responses to the red-, black-, or blue-banded model (all $F_s < 2.37$, all $P_s > 0.10$). We then used discriminant function analysis to see if we could differentiate the males presented with the red-, black-, or blue-banded model from their response to the model. The discriminant functions were able to correctly classify the response of owners to red, black, and blue bands with 53.4% accuracy using song spread rate and intensities, distance from the model, and time to first hit (Wilks' Lambda Function 1: $\chi^2 = 22.35$, $df = 12$, $P = 0.03$; Function 2: $\chi^2 = 8.67$, $df = 5$, $P = 0.12$, Table 1). For the first, second, fourth and sixth variables to enter the discriminant function, responses to the model with red bands appeared to be different from responses to the model with either blue or black bands (Table 1). Owners spent more time farther than 10 m from the red-banded model, gave more low and intermediate intensity song spreads, and took longer to hit the model. For the third variable to enter the discriminant function (time spent <2 m from the model), the response appeared

strongest to the model with black bands, and with the fifth variable (total song spreads), the response was strongest to the model with blue bands (Table 1). Overall, however, the response to the model with red bands was most different. A plot of individual discriminant function scores illustrates this difference, particularly with regard to function 1 (time to attack and proximity to the model) (Fig. 1).

DISCUSSION

The results from our experiment provide stronger support for the hypothesis that it is the color of the red bands that is responsible for their effect on males' behavior, than for the hypothesis that any color contrasting with the leg will have a similar effect. Most of the differences we observed, and those most important in discriminating between treatments, were between red bands and the other two colors. Territory owners spent more time farther than 10 m from the red-banded model, gave more low and intermediate intensity song spread displays to the red-banded model, and took longer to attack the model when it had red bands. Thus, red bands appear to make the model more threatening to territory owners, consistent with our hypothesis (Metz and Weatherhead 1991) that red bands enhance the signal provided by the epaulets.

If larger badges are more threatening to other males, why did red-banded males lose their territories in our previous study (Metz and Weatherhead 1991)? The answer may lie in the difference in the duration of exposure of territorial males to males or models with large badges. If selection maintains the reliability of badges, then

a male confronted with a rival with large badges should initially respond cautiously because a large badge signals a dangerous rival. However, if continued assessment of the rival indicates that the badges are too large for the true quality of the rival, an escalated response should follow. In our banding experiment (Metz and Weatherhead 1991), it was the neighbors of red-banded males that were aggressive. These males had previous experience with the red-banded males before they received their red bands, as well as a period of days to continue assessing them following banding. In our model presentations males only had 5 min to both assess and respond to the models. Thus, in the model presentations there may have been insufficient time for males to determine that the red-banded model was not as threatening as it appeared.

The hypothesis proposed above to explain the difference in response we observed to red bands in our two studies may also reconcile our model presentation results with those of Hansen and Rohwer (1986). They demonstrated that models that had epaulets that were double their normal size were attacked more vigorously by owners than models with normal-sized epaulets. In our model presentation study, we only recorded the owners' behavior for the 5 min immediately following placement of the model on the males' territories. Hansen and Rohwer (1986) started their observations after they had moved to their observation post (40–60 m from the males' territory) and after the male first flew at the model. Then they observed the male's behavior for 10 min. Thus, males in their study had more time to assess the quality of the model. If correct, this explanation suggests that males are able to evaluate rivals quite quickly, although that may only be true when the rival is an inanimate model. Our hypothesis also predicts that with longer exposure, red-banded males such as those we presented in this study, should be attacked more vigorously.

Our failure to support the contrasting-color hypothesis leaves unresolved the different outcomes of our experimental study (Metz and Weatherhead 1991) and the retrospective analyses of long term studies of color-banded Red-winged Blackbirds (Beletsky and Orians 1989, Weatherhead et al. 1991). Had we determined that the birds responded differently to a conspecific with any color band that contrasts with their black legs, then we could explain why the birds

respond differently to red versus black bands (i.e., Metz and Weatherhead 1991), but not to red versus other contrasting colors (i.e., Beletsky and Orians 1989, Weatherhead et al. 1991). However, because it appears that the effects we have observed in our experimental studies are specifically attributable to red bands, we must consider other explanations for the lack of a red-band effect in the long-term studies. Possible explanations include a threshold to the amount of red necessary to produce an effect, a need for the color of red to match that of the epaulets fairly precisely, or the possibility that red-band effects occurred in the long-term studies but were too subtle to be detected by the methods used (Weatherhead et al. 1991). Until these hypotheses are explored, we are left with the possibility that one of our basic research tools is compromising the phenomena we study.

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