

GENERALIZATION OF AND EFFECTS OF  
PRE-EXPOSURE ON COLOR-AVOIDANCE LEARNING  
BY RED-WINGED BLACKBIRDS  
(*AGELAIUS PHOENICEUS*)

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**ABSTRACT.**—We report two experiments designed to assess whether quality of color (and shades) influences food-aversion learning by Red-winged Blackbirds (*Agelaius phoeniceus*). In Experiment 1, Red-wings were given food paired with one of two shades of red or green followed by toxicant-induced sickness. In subsequent tests for generalization of the learned aversions, avoidance of red was generalized broadly to other shades of red, whereas avoidance of green appeared to be relatively stimulus specific. In Experiment 2, we pre-exposed Red-wings to a single shade of red or green in a feeding context for 4 days. Then the birds were conditioned as in Experiment 1 and tested for expression of learned color aversions. Although pre-exposure weakened expression of aversions to both colors, such effects were more pronounced for green. The effects were greater for birds pre-exposed to the conditioning color in close association with the food than for birds pre-exposed to the conditioning color away from food. Generalization of conditioned aversions and resistance to the effects of pre-exposure may reflect adaptations of Red-wings for prey selection. It would appear adaptive for birds to generalize avoidance learning broadly for conspicuously colored, noxious prey and to exhibit such learning regardless of prior experience with the color. Conversely, because few cryptically colored (e.g. green) prey are noxious, it would be adaptive for learning to be specific for the noxious individuals alone. Finally, we believe that the generalization of learned aversions could serve as a useful criterion in selecting appropriate color stimuli for use in bird control (i.e. repellency) and that the methods presented here could provide one empirical means of assessing such generalizations. *Received 24 June 1982, accepted 3 January 1983.*

BIRDS such as Red-winged Blackbirds (*Agelaius phoeniceus*, Mason and Reidinger 1983), Starlings (*Sturnus vulgaris*, Schuler 1980), and Japanese Quail (*Coturnix japonica*, Czaplicki et al. 1976) readily learn to avoid visual cues associated with foods, the ingestion of which has been paired with sickness. Such color aversions are strong and can be acquired directly or through observational learning (Mason and Reidinger 1982). The strength of the aversion learning depends, in part, on the intensity of the color stimulus (Czaplicki et al. 1976, Duncan and Sheppard 1965). For example, quail made ill following ingestion of dark blue water showed a reduced aversion when tested with intensities of blue water that were weaker than

the conditioning intensity. Conversely, birds made ill following ingestion of light blue water showed stronger aversions to dark blue water, suggesting stimulus-intensity dynamism effects (Hull 1952) similar to those observed in taste-aversion learning by rodents (Barker 1976).

An unanswered question of both applied and theoretical interest is whether or not particular colors (or shades of a single color) facilitate broader (i.e. less discriminating) aversion learning. There are reasons to expect that shades of red might produce such effects. Some birds (e.g. Red-wings) attend to red more than to other colors (Royall et al. 1974) and red may facilitate observational learning (Reese 1975). Ecologically, the differential effectiveness of such colors is predictable, because they often serve to distinguish unpalatable from palatable prey (Terhune 1977). Conversely, colors such as green are purported to serve such functions rarely if ever (Wickler 1968). In Experiment 1, Red-wings were conditioned to avoid one of two shades of red or green and then tested for

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generalization of the learned avoidance to other red or green shades. Given the experimental and ecological evidence presented above, one might reasonably expect that generalization around shades of red would be broader (i.e. less discriminative) than generalization around shades of green.

## EXPERIMENT 1: GENERALIZATION OF COLOR AVERSIONS

### METHODS

*Subjects.*—Thirty-two adult male Red-winged Blackbirds ( $\bar{x}$  weight = 70.2  $\pm$  2.6 g) were decoy-trapped during October 1981 at the U.S. Fish and Wildlife Service Ohio Field Station and acclimated to captivity for 6 weeks before the experiment. The birds were individually housed (cage dimensions: 61 cm long  $\times$  36 cm wide  $\times$  41 cm high) in a room with an ambient temperature of 23  $\pm$  2°C. A 6:18-h light-dark cycle was used to maximize the feeding of the birds without reducing the total quantity of food consumed (Rogers 1974, 1978). Water was always available, and, before the experiment began, the birds were permitted to feed *ad libitum* on Purina Flight Bird Conditioner and commercially available blue-colored medicated grit. During the 6th week of adaptation, a white cardboard rectangle (17.5 cm  $\times$  12.5 cm) was attached to the back of the cup containing bird chow during adaptation, and in the center of the upper third of each rectangle was a smaller blue rectangle (4.0 cm  $\times$  10 cm). Presentation of the blue rectangles familiarized birds with the presentation of colored stimuli in association with food. The blue stimuli were of two hues but had the same values and chromas (Munsell hues: 10, 7.5; values: 7, 8; chromas: 10, 8), and each hue was presented to 16 birds. The Munsell system for color description was used to choose stimuli because it plots the visual appearance of a color, not its composition, according to a well-defined nomenclature (Evans 1948). Colors are identified in terms of three attributes: hue, value, and chroma. Hues are the colors per se and are divided into 10 major color groups (e.g. yellow, green, red, blue). Values are the perceived lightness or darkness of a hue in relation to a neutral grey scale extending from black to absolute white. Chromas are the perceived distance of a particular color from a neutral grey of the same value.

*Procedure.*—The birds were assigned in semirandom fashion to 8 groups ( $n = 4$ , i.e. birds exposed to one blue hue were randomly assigned to 4 groups, and birds exposed to the other hue were randomly assigned to the other 4 groups), and then each bird was visually isolated from the others with pieces of cardboard (36 cm long  $\times$  61 cm wide). During the first hour of light on the day following visual isola-

tion, each bird was presented with 20 g of steel-cut oats (a preferred food of Red-wings in our laboratory) in a cup (7.5 cm diameter) attached to the front of the cage. A white cardboard rectangle (17.5 cm  $\times$  12.5 cm) was attached to the back of the cup, and in the center of the upper third of each was a smaller red or green rectangle (4 cm  $\times$  10 cm). These colored rectangles served as the conditioning (CS+) stimuli. Two shades of red (Munsell hues: 10, 7.5; values: 7, 8; chromas: 10, 8) and two of green (Munsell hues: 10, 7.5; values: 7, 8; chromas: 10, 8) were used, and each was presented to two groups.

When each bird had consumed at least 1 g of oats (approximately 30 min of feeding), 4 groups were intubated with methiocarb solution (2 mg/kg), and 4 were intubated with propylene glycol as a control for the traumatic consequences of intubation. We had found in previous work (Mason and Reidinger 1982, 1983) that intubation per se sometimes elicits weak aversion learning. Methiocarb, 3,5-dimethyl-4-(methylthio) phenol methylcarbamate, is a bird repellent that reliably produces conditioned aversions similar to those produced by lithium chloride (Mason and Reidinger 1983). The stock solution of methiocarb was prepared by dissolving 3 mg of methiocarb in 25 ml of propylene glycol. Intubation was completed in all cases within 10 min of the end of the feeding trial. The oats and colors were removed 1 h after intubation, and the birds were left undisturbed with familiar food during the remaining hours of light.

During the first hour of light on the 4 days immediately following the day of intubation, all of the birds in each group were given two-choice feeding tests (Dragoin et al. 1971), according to a Latin Square design. For each test, all food was removed from the cages for 30 min, and then the birds were presented with two cups, each containing 20 g of oats, attached 5 cm apart to the front of the cages. Attached to the back of one of the cups was a card with a red or green rectangle. These rectangles were either the shades presented during conditioning or one of three other shades of varied chroma (4, 6, or 8) but the same hue (i.e. 10 or 7.5) and value (i.e. 7 or 8). Attached to the back of the other cup was a card with a blue rectangle, the hue, value, and chroma of which were matched to those of the red or green rectangles. At the beginning of the second hour of light, the oats and CSs were removed from the cages, and consumption was measured. For the remaining hours of light, the birds were left undisturbed with free access to Purina Flight Bird Conditioner and grit.

*Analysis.*—Suppression ratios for consumption of food paired with the CS+ color were calculated by dividing consumption of food paired with the CS+ by consumption of food paired with the CS-. The ratios were then assessed by two-way analysis of variance with repeated measures on the second factor. The independent factor was groups. The repeat-

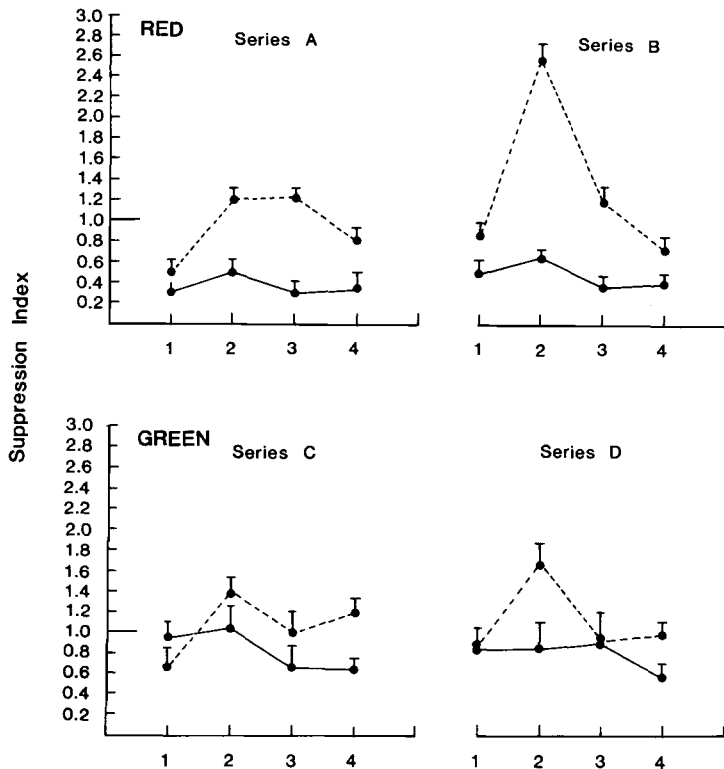


Fig. 1. Suppression index of consumption of oats associated with colored rectangles during two-choice tests. The index values, rather than the actual values per se, are presented for clarity and were obtained by dividing consumption of oats associated with CS+ (i.e. shades of red or green) by consumption of oats associated with CS- (shades of blue). Solid lines represent consumption by birds gavaged with methiocarb, whereas dashed lines represent consumption by birds gavaged with propylene glycol. Series (A) and (B) represent consumption by birds given oats paired with red [(A) hue = 10, value = 10, chroma = 10; (B) hue = 7.5, value = 7, chroma = 8] and intubation. Series (C) and (D) represent consumption by birds given oats paired with green [(C) hue = 10, value = 7, chroma = 10; (D) hue = 7.5, value = 7, chroma = 8] and intubation. For each panel, (4) represents tests with the most intense color stimuli, and (1) represents tests with the least intense color stimuli. Capped vertical bars represent standard errors of the mean.

ed factor was suppression of consumption to each chroma of the CS+ by the birds within each group. Tukey *b* post-hoc comparisons (Winer 1962) were subsequently used to identify significant differences among means.

RESULTS

There were significant differences among groups in overall suppression [ $F(7,24) = 5.3, P < 0.05$ ], and, within groups, suppression was greater for some shades of the CS+ than for others [ $F(3,72) = 4.7, P < 0.05$ ] (Fig. 1). Tukey tests indicated that overall suppression was greater for the birds given pairings of red and methiocarb than for those given pairings of

green and methiocarb, regardless of chroma ( $P_s < 0.05$ ). Those birds trained with the more intense shade of either red or green, however, exhibited greater suppression than those trained with the other shade ( $P_s < 0.05$ ).

Within groups, generalization of suppression was influenced by the chroma of the conditioning stimulus. Birds trained with the more intense red shade exhibited suppression toward all of the chromas presented during testing (i.e. less was eaten of food paired with CS+ than of food paired with CS-). Likewise, birds trained with the less intense red shade exhibited suppression toward three of the four chromas presented during testing. In contrast, suppression of consumption by birds trained

TABLE 1. Mean suppression ratios for consumption of CS+ food. Suppression ratios represent consumption of CS+ divided by consumption of CS-. Values greater than 1 indicate no suppression (i.e. greater consumption of CS+ than CS-).

	Mean suppression to test stimuli chromas			
	10 (CS+)	8	6	4
<b>Red</b>				
Chroma 10 + Methiocarb	0.40	0.25	0.44	0.30
Chroma 7.5 + Methiocarb	0.45	0.40	0.70	0.50
Chroma 10 + Propylene Glycol	0.80	1.20	1.20	0.50
Chroma 7.5 + Propylene Glycol	0.80	1.20	2.70	0.90
<b>Green</b>				
Chroma 10 + Methiocarb	0.65	0.70	1.05	0.95
Chroma 7.5 + Methiocarb	0.60	0.95	0.90	0.90
Chroma 10 + Propylene Glycol	1.20	1.00	1.40	0.65
Chroma 7.5 + Propylene Glycol	1.00	1.00	1.70	0.90

with the shades of green was relatively stimulus specific. Birds trained with the more intense shade exhibited suppression toward the conditioning stimulus per se and the chroma closest to it (i.e. chromas 10 and 8) ( $P$ s < 0.05). Birds trained with the other shade of green showed suppression ( $P$  < 0.05) only toward the conditioning stimulus (Table 1).

None of the groups intubated with propylene glycol exhibited suppression of feeding relative to the appropriate experimental groups. Birds trained with the more intense shade of red, however, ate less CS+ than CS- food when the conditioning stimulus per se was presented ( $P$  < 0.05). No such differential consumption was observed with the birds trained with green.

#### DISCUSSION

As in previous work, methiocarb intubation elicited strong aversion learning, whereas propylene glycol intubation elicited weak or no learning. Although both red and green elicited reliable aversions, red was the more effective stimulus, insofar as avoidance of red generalized broadly, whereas avoidance of green appeared relatively stimulus specific. Such avoidance was facilitated by neophobia, because birds presented with the more intense shades of red ate less than the other birds regardless of intubation condition. Moreover, avoidance of red was apparently a function of stimulus intensity (i.e. the more intense red stimulus elicited broader generalization), whereas intensity did not influence avoidance of green. Such results are consistent with evidence sug-

gesting that predators learn to avoid conspicuously colored (e.g. red) prey more readily than cryptically colored (e.g. green) prey (Gittleman et al. 1980, Wickler 1968). The results are also consistent with evidence suggesting the importance of stimulus-intensity dynamism effects in color-avoidance learning (Czaplicki et al. 1976). For the shades of red, the strength of avoidance (i.e. the degree of differential consumption) was related to stimulus intensity (i.e. the more intense the stimulus color, the stronger the avoidance behavior).

Identification of colors that elicit stronger avoidance has practical significance in that visual cues enhance the repellency of bird repellents (e.g. Mason and Reidinger 1982, 1983). We have speculated that once birds have been conditioned to avoid sprayed fields, the mere presence of color cues might be sufficient to prevent bird damage. In our prior work as well as in the present experiment, color was associated with intubation only once, and yet birds continued to avoid food associated with color cues over successive preference tests. Eventually, the aversions disappeared, but that required several exposures to the food previously associated with the toxicant. Blackbirds in the field may avoid the toxicant-treated crop entirely after ingesting the repellent and not have opportunities to learn that the food is safe when the repellent is no longer present. The possibility of such effects might be maximized if salient color stimuli (e.g. red rather than green for Red-winged Blackbirds) are used.

Possible alternative explanations of Experiment 1 are (a) that the findings could reflect

differences in spectral sensitivity rather than differences in stimulus effectiveness per se, (b) that red elicited relatively stronger avoidance behavior because of the importance of that color in the social behavior of Red-wings, or (c) that red might not have been more effective than green, but rather that decoy-trapped birds had had more experience with green than red prior to capture. The first criticism seems unlikely, for although the spectral thresholds of passerines are higher than those of pigeons and humans (e.g. Adler and Dalland 1959) and the perception of shades of blue and violet is sometimes poor (Donner 1953), discrimination among shades of other colors is acute (Portmann 1950). The second criticism also seems unlikely: the use of red in social contacts among Red-wings is ambiguous in that it sometimes elicits avoidance but more often elicits approach (i.e. red provokes agonistic behavior, Rohwer 1978, Searcy 1979). The third criticism is plausible, however, insofar as pre-exposure to (i.e. familiarity with) color cues has been shown to weaken learned food avoidance in laboratory experiments (Elkins 1974) and has been implicated as an important variable affecting the efficacy of bird repellents for crop protection (Dolbeer 1980). In Experiment 2, we pre-exposed birds to color cues at various distances from food to determine whether warning colors (e.g. red) are more resistant to familiarity effects than are colors such as green. Although the procedure did not control for experience prior to capture, the effects of recent exposure to the test colors could be systematically investigated in this manner.

## EXPERIMENT 2: THE EFFECT OF COLOR PRE-EXPOSURE ON CONDITIONED AVERSIONS

### METHODS

*Subjects.*—Thirty-two adult male Red-wings were decoy-trapped and adapted to our laboratory as described in Experiment 1.

*Procedure.*—The Red-wings were randomly assigned to eight groups and each bird was visually isolated. The birds in four groups were exposed to a red rectangle (4 cm × 10 cm) on a white rectangular background (17.5 cm × 12.5 cm, as in Experiment 1) for 5 days prior to the day of conditioning. Birds in the other four groups were exposed to green rectangles for 5 days. For two of the groups exposed to each color, the rectangles were attached to the back of the food cups. For the other two groups exposed

to each color, the rectangles were attached to the sides of the cages next to a perch about 30.5 cm from the front of the cages and 20.5 cm above the floor. Such positioning exposed the birds to color stimuli away from food but in a location frequented by the birds as they flew back and forth in the cages.

During the first hour of light on the 6th day, each bird was presented with 20 g of steel-cut oats in a cup (7.5 cm diameter) with a colored (red or green) rectangle attached. For half of the birds, the color was that to which they had been previously exposed. For the other birds, the color was novel (i.e. green for birds exposed to red, and vice versa).

When each bird had consumed at least 1 g of oats (approximately 40 min of feeding), 4 groups (1 previously exposed to red behind the food cup, 1 to red on the side of the cage, 1 to green behind the food cup, and 1 to green on the side of the cage) were intubated with methiocarb solution (2 mg/kg). The other 4 groups were intubated with propylene glycol as a control for the effects of intubation per se. The oats and color stimuli were removed from the cages 1 h after intubation, and the birds were left undisturbed with familiar food during the remaining hours of light. All intubations occurred within 10 min of the end of the feeding trial.

During the first hour of light on each of the 4 days immediately following the day of intubation, all of the birds in each group were given two-choice feeding tests. These tests were similar to the feeding tests given in Experiment 1, except that only the conditioning hues of red and green were presented.

*Analysis.*—Suppression ratios for consumption of food paired with the CS+ were calculated by dividing consumption of food paired with the CS+ by consumption of food paired with the CS-. The ratios were then assessed by two-way analysis of variance with repeated measures on the second factor. The independent factor was groups, while the repeated factor was test days. Tukey *b* comparisons were used to isolate significant differences among means as detected by the omnibus procedure.

### RESULTS

There were significant differences among groups in overall suppression [ $F(7,24) = 8.3$ ,  $P < 0.05$ ], and, within groups, suppression decreased over days [ $F(3,72) = 6.0$ ,  $P < 0.05$ ]. Because the interaction between groups and days was significant [ $F(21,72) = 3.2$ ,  $P < 0.05$ ], the analysis was interpreted in terms of that higher-order effect. Tukey *b* tests indicated that, for birds intubated with methiocarb, the greatest suppression was exhibited by the birds pre-exposed to red near the perch ( $P < 0.05$ ). The next strongest suppression was exhibited by birds pre-exposed to red near the food cup,

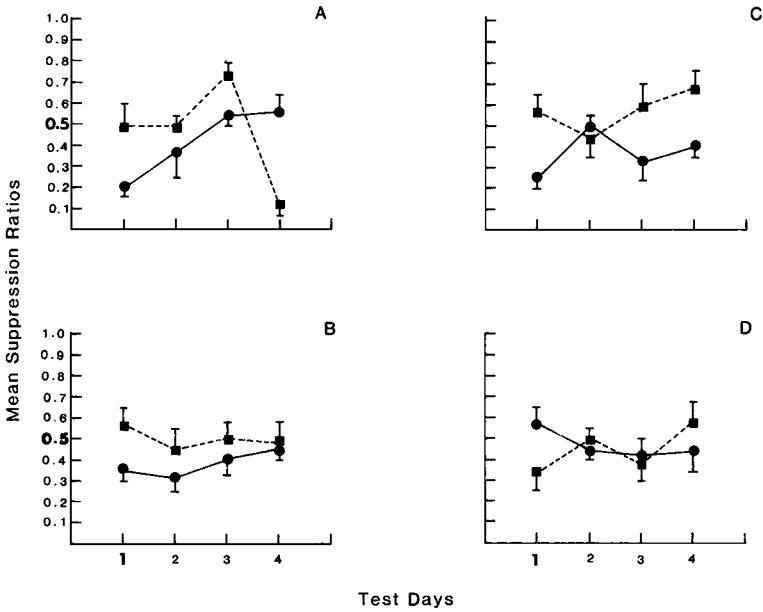


Fig. 2. Mean suppression of consumption of oats associated with CS+ during two-choice tests. In all panels, dotted lines represent suppression by birds intubated with propylene glycol, whereas solid lines represent suppression by birds intubated with methiocarb. Panel A represents suppression by birds pre-exposed to red near the perch and subsequently conditioned with red. Panel B represents suppression by birds pre-exposed to red near the food cup. Panels C and D represent suppression by birds pre-exposed to green near the perch or food cup, respectively. Capped vertical lines represent standard errors of the means.

followed by birds pre-exposed to green near the perch ( $P_s < 0.05$ ). The difference in suppression between these two groups, however, was largely accounted for by the lack of suppression exhibited on the second test day by the birds pre-exposed to green. The least suppression was exhibited by the birds pre-exposed to green near the food cup. For the birds intubated with propylene glycol, no significant suppression of consumption was recorded ( $P > 0.10$ ) (Fig. 2).

When the experimental groups were compared with the appropriate control groups, we found that suppression by the experimental groups dissipated over test days ( $P_s < 0.05$ ) and that such dissipation was influenced by the pre-exposure treatment ( $P_s < 0.05$ ). Dissipation of suppression within groups reflected overall differences in suppression between groups. Birds pre-exposed to red near the perch and intubated with methiocarb showed the least dissipation, whereas birds pre-exposed to red near the food cup were next. Conversely, birds pre-exposed to green, and especially birds pre-exposed to green near the food cup, showed

relatively rapid dissipation of suppression ( $P < 0.05$ ).

## DISCUSSION

The results of Experiment 2 indicate that pre-exposure to the conditioning stimulus weakened subsequent expression of color aversions. Such weakening was more pronounced for green than red, and we infer that such results are consistent with the results of Experiment 1 (i.e. that red was intrinsically the more effective stimulus). Moreover, pre-exposure appeared context specific insofar as effects were more pronounced when stimuli were pre-exposed in close association with food. This latter result is consistent with other evidence indicating that Red-wings are sensitive to both locational and visual cues associated with prey (Alcock 1972). In addition, our findings are consistent with those of Logue (1980), who reported that the effectiveness of a visual cue for pigeons' illness-induced aversions is influenced by the spatial coincidence of the cue with the ingested substance.

We believe that the present results extend and clarify the work of others. Czaplicki et al. (1976) reported that pre-exposure to blue water had little effect upon subsequent conditioning. Because pre-exposure effects are usually obtained when taste stimuli are used, Czaplicki et al. speculated that visual cues might be less potent than gustatory cues and possibly more subject to environmental interference. We infer on the basis of the present results that visual cues may not be less potent than gustatory cues but rather that some visual cues may be more effective than others. The implication of blue as a potent stimulus might appear surprising from an ecological point of view (i.e. it is rarely if ever used as a warning color, Wickler 1968), but it is consistent with results showing that naive chicks attend more to blue than to some other colors (e.g. Hess 1956). Had Czaplicki et al. (1976) used other colors, pre-exposure effects similar to those reported here might have been observed. In addition, we infer on the basis of the present results that because the importance of visual cues for avoidance learning is context specific, visual cues, at least in certain situations, may be no more subject to environmental interference than are gustatory cues. That inference is consistent with findings reported by Martin et al. (1977), who noted that varied color experience did not influence chickens' formation of color aversions. Similarly, Barrows et al. (1980) have reported that a period of exploratory feeding (i.e. pre-exposure) with many food types (both conspicuously and cryptically colored) may facilitate learned avoidance of noxious prey types.

#### GENERAL DISCUSSION

Overall, the results of Experiments 1 and 2 suggest that the conditionability of stimuli does not necessarily reflect their effectiveness (here defined as broadness of generalization and resistance to pre-exposure effects). Previous work in our laboratory (Mason and Reidinger 1982, 1983) and in the laboratories of others (e.g. Terhune 1977) suggests that reliable aversions of equivalent strength (i.e. of equivalent resistance to extinction) can be conditioned to many color stimuli. Both the extent to which such avoidance learning generalizes from the CS to other stimuli and the extent to which such learning resists pre-exposure effects, however, are probably different, as is demonstrated here.

Evolutionarily, that possibility appears reasonable insofar as birds should be able to learn to avoid unpalatable or noxious prey regardless of color. Because many noxious prey are brightly colored, however, it would seem particularly adaptive for birds to generalize avoidance learning more broadly for such prey and to be able to exhibit such avoidance learning regardless of prior experience with the color. On the other hand, because only a few cryptically colored prey are noxious, it would seem that avoidance learning should be specific to the noxious individuals alone and should not generalize to other similar but probably palatable prey.

Finally, we believe that the methodology presented here could be useful for the practical application of conditioned color aversions to bird control. As stated above, color cues seem to enhance the efficacy of bird repellents. The particular colors that would be most effective with birds other than Red-wings, however, remain unclear. The techniques presented here provide a basis for the choice of the most effective (i.e. most potent) stimuli for use with various pest species.

#### ACKNOWLEDGMENTS

This research was partially supported by Training Grant #5 T32 NS07176-02 from the National Institutes of Neurological and Communicative Disorders and Stroke and BRSG Grant SO7 RR 05825-02 from the Biomedical Research Support Grant Program, Division of Research Resources, National Institutes of Health. The U.S. Fish and Wildlife Service also provided broad support. We wish to thank Richard Lebowitz for expert technical and statistical assistance and R. A. Dolbeer, W. L. Silver, S. Shumake, and R. H. Stehn for critical comments.

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