

Direct and Observational Learning by Redwinged Blackbirds (Agelaius Phoeniceus): The Importance of Complex Visual Stimuli

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INTRODUCTION

Redwing blackbirds (*Agelaius phoeniceus*, Mason & Reidinger, 1983a), European starlings (*Sturnus vulgaris*, Schuler, 1980), house sparrows (*Passer domesticus*; Greig-Smith & Rowney, 1987), and a variety of other avian species (e.g., Japanese quail, *Corturnix japonica*; Czaplicki, Borrebach, & Wilcoxin, 1976) learn to avoid visual cues associated with sickness. For redwings, visual stimuli appear relatively more important than taste in avoidance acquisition (Mason & Reidinger, 1983a), and certain colors seem to be more effective conditioned stimuli than others. For example, avoidance generalization is broad for hues of red, but relatively narrow for hues of green (Mason & Reidinger, 1983b). Ecologically, the differential effectiveness of color is predictable, since red is used frequently by animals to advertise unpalatability (*aposematic coloration*; Terhune, 1977). Green serves this function rarely, if ever, and is more often associated with the *cryptic* coloration used by palatable prey for concealment from predators (Brower, Cook, & Croze, 1967; Wickler, 1968).

Besides direct acquisition of avoidance, red-wings will learn by observing conspecifics or other birds such as common grackles (*Quiscalus quiscula*; Mason, Arzt, & Reidinger, 1984a). Such vicariously acquired avoidance closely resembles avoidance acquired as a function of direct experience. For example, vicarious learning occurs in a single trial, and resistance to extinction is usually similar to

that exhibited when birds learn directly. These findings have clear implications for theories of mimicry that make the assumption that avian predators learn to avoid unpalatable prey (Alcock, 1969a, 1969b; Avery, 1985; Mason & Reidinger, 1983b). One implication is that not all predators need to experience the unpleasant and potentially lethal consequences of attacking unpalatable aposematic prey in order to learn to avoid them (Mason et al., 1984a).

Given the ease with which avoidance responses are vicariously acquired, it is not surprising that preferences can be acquired through observation as well. For example, in the laboratory, redwings will prefer color-food combinations that they have seen presented to demonstrator birds (Mason & Reidinger, 1981). In a similar vein, chaffinches (*Fringilla coelebs*), white wagtails (*Motacilla alba*) and Tennessee warblers (*Vermivora peregrina*) are more likely to sample new foods when exposed to conspecifics doing so (Davies, 1976; Rubenstein, Barnett, Ridgely, & Klopfer, 1977; Tramer & Kemp, 1979).

One potentially important difference between vicariously acquired preference and avoidance responding is that, for the former, aposematic colors (e.g., orange) do not appear to be more effective stimuli than cryptic colors (e.g., green), at least in terms of resistance to extinction (Mason & Reidinger, 1981). Another difference is that several training trials are often necessary to elicit vicarious color preference responding, whereas avoidance is usually elicited in a single trial. These findings suggest that preferences may be acquired more slowly or with greater difficulty than aversions. Nevertheless, the existence of reliable observational acquisition of color preferences raises the issue of whether observationally acquired preferences or aversions exert greater control over behavior. The answer to this question is important with regard to mimicry, since predators are likely to observe attacks by conspecifics on both models and their mimics, and, in some cases, observed attacks on the latter may exceed observed attacks on the former, since mimics are more numerous (Brower, 1960). In the case of observed attacks on models, observers should learn avoidance, but in the case of attacks on mimics, preference should accrue. If avoidance and preference were to exert equal control over behavior, and mimics were more numerous than models, then observers should develop preferences for both models and mimics.

At least one experiment has addressed this issue (Mason et al., 1984a). As conspecifics watched, individual redwings were trained to prefer or avoid food paired with yellow. During subsequent tests, the demonstrators and half of the observers were assessed in visual isolation. The remaining observers were tested in visual contact with another observer that had watched a demonstrator exhibit behavior opposite to that exhibited by its own demonstrator. For demonstrators and observers tested in isolation, color aversions were more resistant to extinction than color preferences. For the observers tested together, avoidance was again more resistant to extinction than preference. Moreover, once preferences had extinguished, they were replaced by avoidance. Such findings suggest that obser-

tionally acquired avoidance may exert relatively greater control over behavior than observationally acquired preference.

An unanswered question is the importance of stimulus complexity as a variable influencing direct and observational acquisition of responding. In Batesian mimicry, the importance of this variable is suggested by the fact that unpalatable or toxic models (e.g., Monarch butterflies, *Danaus plexippus*) and their palatable mimics (e.g., Viceroy butterflies, *Limenitis archippus*) employ both aposematic coloration (e.g., orange) and patterns (e.g., stripes) as warnings to potential predators. Aposematic coloration and striping may have even greater importance in Mullerian mimicry, in which both models and "mimics" are unpalatable (Wickler, 1968), and in Mertesian mimicry, in which direct encounters between a predator and a model or mimic are usually fatal for the predator (Wickler, 1968).

The present experiments were designed to assess the relative importance of color and pattern cues in food aversions and food preferences exhibited by birds. Both direct and vicarious acquisition of responding were examined, and for avoidance learning, an attempt was made to manipulate the intensity (malaise, mere unpalatability) of the unconditioned stimulus. One assumption was that, together, pattern and color cues would produce avoidance that was more resistant to extinction than that produced by either of these cues alone. Another assumption was that "complex" stimuli (colors and stripes) might not facilitate preference learning, insofar as aposematic cues are rarely used by palatable prey (outside the context of mimicry).

EXPERIMENT 1

Experiment 1 was performed to test the proposition that, together, color and pattern cues would enhance the resistance to extinction of a directly acquired avoidance response, relative to either color or pattern cues alone.

Method

Thirty decoy-trapped experimentally naive adult male red-wing blackbirds (mean weight: 70.2 ± 2.3 g) were individually housed (cage dimensions: 61 cm \times 36 cm \times 41 cm), and a 6:18 hr light/dark cycle was used to maximize feeding, without reducing the total quantity of food consumed (Mason et al., 1983a, 1983b; Rogers, 1974, 1978). Water was always available. Before the experiment began, the birds were permitted free access to food (Purina Flight Bird Conditioner [PFBC]) presented in hoppers attached to the center of the fronts of the cages.

On each of the 4 days prior to conditioning, food hoppers were removed from the cages for the first 2 hr following light onset. This induced mild food deprivation, because redwings consume the greatest portion of their daily ration during this period (Mason, Dolbeer, Arzt, Reidinger, & Woronecki, 1984c). During the third hour of light, each bird was presented with a food cup (7.5 cm diameter) containing 20 g of PFBC. After 60 min, the cups were removed from the cages, and the amount of PFBC remaining was recorded. Food hoppers were then returned to the cages, and the birds were left undisturbed until light onset of the following day.

Birds were assigned to six matched groups ($n = 5/\text{group}$) on the basis of mean pretreatment consumption. The bird with the highest consumption was assigned to the first group, that with the next highest to the second group, and so on. On the day of conditioning, all groups were food deprived for 2 hr, and then presented with cups containing 20 g of PFBC. White rectangles (17.5 cm \times 12.5 cm) on which four evenly spaced vertical black stripes (1 cm width) had been drawn were attached to the backs of the cups presented to Groups S-E (stripe-experimental) and S-C (stripe-control). These training stimuli are depicted in Fig. 5.1A. Orange rectangles (17.5 cm \times 12.5 cm) were attached to the backs of cups presented to Groups O-E (orange-experimental) and O-C (orange-control). Orange rectangles (17.5 cm \times 12.5 cm) with four evenly spaced vertical black stripes (1 cm width) were attached to the backs of cups presented to Groups SO-E (striped orange-experimental) and SO-C (striped orange-control).

After each bird had consumed 1 g of food, or after 30 min had passed, the food cups were removed, and Groups O-E, S-E and SO-E were gavaged (i.e., orally intubated) with methiocarb solution (2 mg/kg). As a control, Groups O-C, S-C and SO-C were gavaged with propylene glycol, the carrier for the methiocarb

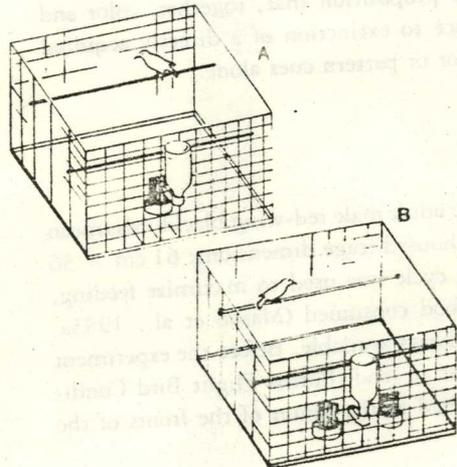


Figure 5.1. Diagram showing stimuli and food cups presented to birds in Groups S-E and S-C on the day of conditioning (A) and during testing (B). All other groups were treated similarly, except that stimulus cards differed.

(Mason & Reidinger, 1982a; Mason & Reidinger, 1983a, 1983b). Methiocarb (3,5-dimethyl-4-[methylthio] phenol methylcarbamate) is a bird repellent that reliably elicits one-trial avoidance learning similar to that elicited in redwings by 0.15 M lithium chloride (Mason & Reidinger, 1983b). Intubation was completed in all cases within 15 min of the end of the feeding trial. Thirty minutes later, food hoppers were replaced on the cages, and the birds were left undisturbed until light onset of the following day.

On each of the 4 days immediately following conditioning, the birds were food deprived for 2 hr, and then given two-choice tests. Testing involved the presentation of two food cups, each containing 20 g of PFBC, spaced 5 cm apart at the center of the front of each cage. For Groups S-E and S-C, white S+ rectangles with vertical stripes were attached to the back of one of the cups in each pair. Attached to the back of the other cup was a white So rectangle with horizontal stripes. These test stimuli are depicted in Fig. 5.1B. For Groups O-E and O-C, orange (S+) rectangles were attached to the back of one of the cups in each pair. Attached to the back of the other cup was a red (So) rectangle. For Groups SO-E and SO-C, vertically striped orange S+ rectangles were attached to the back of one of the cups in each cage; horizontally striped red So rectangles were attached to the back of the other cup.

After 1 hr, the cups were removed from the cages, and the amount of PFBC remaining was recorded. Food hoppers were then replaced on the cages, and the birds were left undisturbed until light onset of the following day.

Results and Discussion

All experimental groups (O-E, S-E, SO-E) avoided food paired with S+ stimuli during testing ($ps < .05$). However, there were significant differences among groups in resistance to extinction ($ps < .05$). Groups S-E and O-E extinguished after 2 or 3 days of testing, respectively, whereas Group SO-E exhibited conditioned avoidance on all 4 test days ($p < .05$; Figure 5.2). None of the control groups (O-C, S-C, SO-C) exhibited differential consumption ($ps > .25$).

The results of Experiment 1 are consistent with prior findings (Mason & Reidinger, 1983a, 1983b). As in these other investigations, birds learned avoidance after a single pairing of visual cues and malaise. Also, as previously reported for scrub jays (*Aphelocoma coerulescens*; Terhune, 1977), color alone appeared to elicit relatively more durable avoidance than stripes. The present findings extend these observations by suggesting that complex stimuli appeared to enhance resistance to extinction (Group SO-E), relative to that elicited by color (Group O-E) or pattern (Group S-E) alone. Such differential effectiveness suggests that increasing discriminability (e.g., by use of multiple cues) offers an advantage to aposematic prey by increasing their discriminability to potential predators (Guilford, 1986).

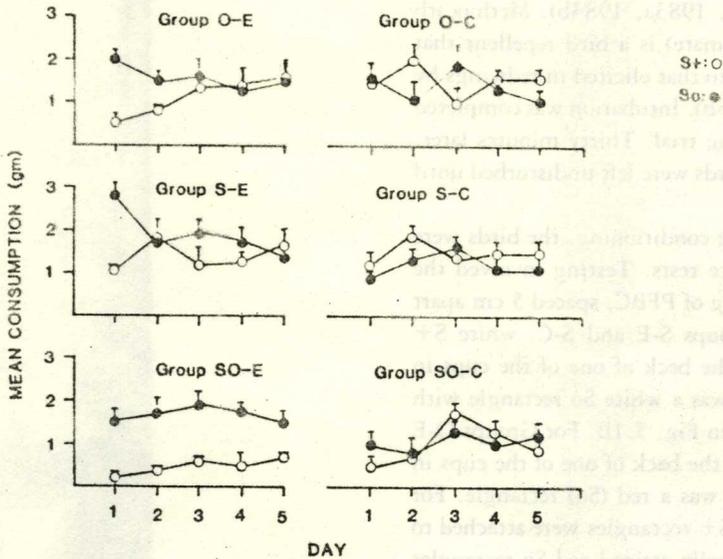


Figure 5.2. Experiment 1 two-choice test results. All experimental groups showed conditioned avoidance. However, Groups O-E and S-E extinguished by test day 3, and Group SO-E exhibited avoidance on all test days. Control groups (O-C, S-C, SO-C) failed to exhibit differential behavior. Capped vertical bars represent standard errors of the means.

EXPERIMENT 2

Experiment 1 demonstrated that color and pattern cues together produce greater resistance to extinction than either cue alone. Experiment 2 was designed to investigate whether similar findings would obtain when avoidance responding was acquired vicariously. Since observational learning by redwing mirrors direct acquisition of color avoidance responding in terms of resistance to extinction (e.g., Mason et al., 1984a) and generalization of responding (personal observation), a reasonable prediction was that a complex stimulus might be more effective than a simple stimulus (e.g., color only) for vicariously acquired avoidance.

Method

Forty decoy-trapped adult male redwings (mean weight 68.5 ± 3.0 g) were adapted to the food deprivation regime and assigned to eight groups ($n = 5/\text{group}$) on the basis of consumption, as previously described.

Groups were paired, and the cages of birds in Groups O-E (orange-experi-

mental) and O-EW (orange-experimental watching); O-C (orange-control) and O-CW (orange-control watching); SO-E (striped orange-experimental) and SO-EW (striped orange-experimental watching); and SO-C (striped orange-control) and SO-CW (striped orange-control watching) were placed adjacent to and in view of one another (Mason & Reidinger 1982a; Mason et al., 1984a). Stripes per se were not used as stimuli because they were the least effective stimuli in Experiment 1.

On the day of conditioning, all birds were food deprived for 2 hr, and then Groups O-E and O-C were given orange S+ rectangles paired with PFBC. Groups SO-E and SO-C were given vertically striped orange S+ rectangles paired with PFBC. The birds in the other two groups (O-C, SO-C) were given food in plain metal cups without colored rectangles attached. When birds in Groups O-E, O-C, SO-E and SO-C had consumed at least 1 g of PFBC, or after 30 min had passed, food was removed from the cages and the birds were intubated. Groups O-E and SO-E were gavaged with methiocarb (2 mg/kg), and Groups O-C and SO-C were gavaged with propylene glycol. Birds in Groups O-EW, O-CW, SO-EW and SO-CW were left undisturbed. One hour following gavage, food hoppers were replaced on the cages. The birds were then visually isolated from one another with pieces of cardboard, and left undisturbed until light onset of the following day.

On each of the next 5 days, all birds were food deprived for 2 hrs, and then given two-choice tests. Groups O-E, O-C, O-EW and O-CW were given tests in which orange S+ and red S₀ rectangles were attached to the backs of food cups. Groups SO-E, SO-C, SO-EW and SO-CW were given tests with vertically striped orange S+ and horizontally striped red S₀ rectangles. After completion of each test period, all birds were left undisturbed with free access to PFBC until light onset of the following morning.

Results and Discussion

Groups O-E and O-EW avoided food paired with orange S+ rectangles for three or two test sessions, respectively ($p < .01$; Figure 5.3). Groups SO-E and SO-EW also avoided food paired with S+ stimuli ($p < .01$), but differential behavior was exhibited by these groups for 5 days. No significant differential consumption was exhibited by birds in the control groups (i.e., Groups O-C, O-CW, SO-C, SO-CW).

The results of Experiment 2 confirm prior observations (e.g., Mason & Reidinger, 1982a). Color avoidance was acquired vicariously after a single conditioning trial. Moreover, resistance to extinction of the observationally acquired response was similar to that of avoidance acquired as a function of direct experience. Finally, regardless of how avoidance was acquired, complex stimuli appeared to enhance resistance to extinction, relative to color alone.

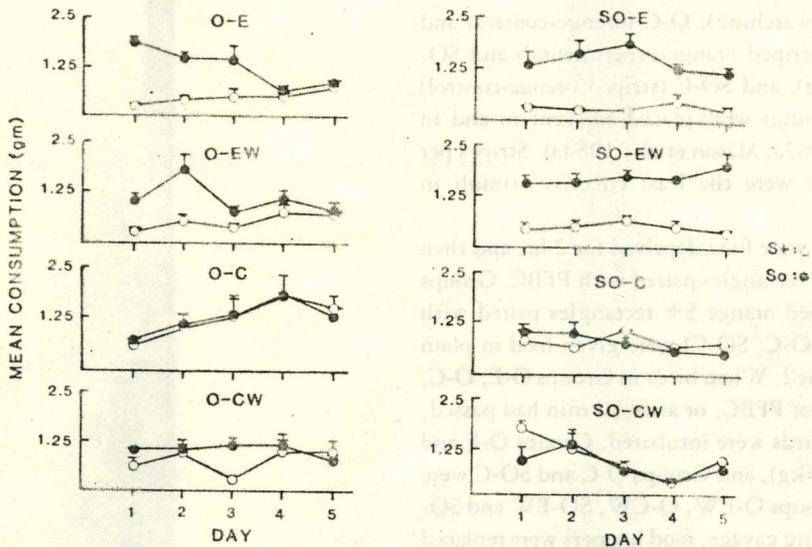


Figure 5.3. Responses exhibited by Groups O-E, O-EW, O-C, O-CW, SO-E, SO-EW, SO-C and SO-CW in two-choice tests in Experiment 2. Groups O-E and O-EW expressed avoidance on test days 1-3 and 1-2, respectively, whereas Groups SO-E and SO-EW expressed avoidance on all test days. Groups O-C, O-CW, SO-C and SO-CW did not exhibit differential consumption. Capped vertical bars represent standard errors of the means.

EXPERIMENT 3

An unanswered question is whether complex stimuli are generally more effective than simple stimuli, or whether they enhance avoidance responding alone. Just as aposematic colors (e.g., orange) are no more effective than cryptic colors (e.g., green) in preference learning, it may be that complex stimuli are no more effective than simple stimuli outside aversive contexts. Experiment 3 was designed to assess this possibility.

Method

Twenty decoy-trapped adult male redwings (mean weight: 70.2 ± 2.0 g) were adapted to the food deprivation regime, and assigned to four groups (5/group) on the basis of consumption.

Birds in Group O-EW (orange-experimental watching) were placed in cages adjacent to birds in Group O-E (orange-experimental). Birds in Group SO-EW (striped orange-experimental watching) were placed in cages adjacent to birds in Group SO-E (striped orange-experimental). At the beginning of the third hour of light on each of the next 4 days, Groups O-E and SO-E were given

PFBC in cups with orange or vertically striped orange rectangles attached. Birds in Groups O-EW and SO-EW were given PFBC in plain metal cups. After 60 min, the amount of PFBC remaining was recorded. After each trial, the birds were left undisturbed with free access to PFBC until the following morning.

Immediately following training, all birds were visually isolated from one another, and given two-choice tests during the third hour of light for 4 days. Birds in Groups O-E and O-EW were given food in two cups with orange S+ or red S_o rectangles attached. Birds in Groups SO-E and SO-EW were given food in cups with vertically striped orange S+ or horizontally striped red S_o rectangles attached. After 60 min, the cups were removed from the cages and consumption was measured. After each test, the birds were left undisturbed with free access to PFBC until light onset of the next day.

Results and Discussion

During testing, all groups preferred PFBC paired with their respective S+ ($p < .05$; Figure 5.4). However, differential consumption extinguished rapidly. By the third test session, only Group O-EW continued to exhibit color preference responding. No group exhibited differential consumption during the fourth or fifth test session.

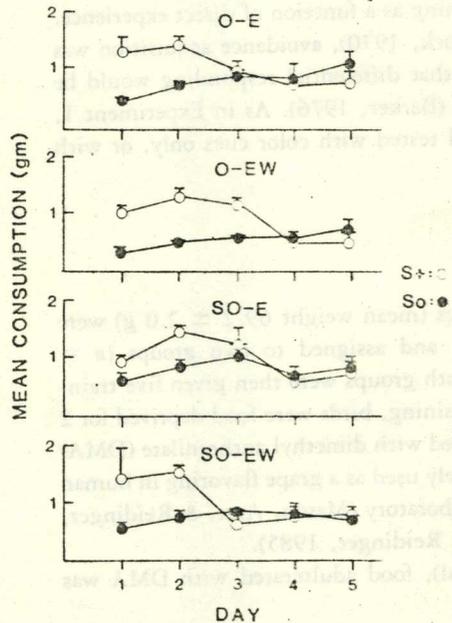


Figure 5.4. Preferences expressed by Groups O-E, O-EW, SO-E, and SO-EW in two-choice tests in Experiment 3. All groups showed preference acquisition, but only Group O-EW exhibited differential consumption for more than 2 days. Capped vertical bars represent standard errors of the means.

The results of Experiment 3 are consistent with other observations. Redwings (Mason & Reidinger, 1981), wood pigeons (*Columba palumbus*; Murton, 1971) and European starlings (Williamson & Grey, 1975) are capable of developing food preferences, either as a result of direct experience or observation. However, unlike the results of Experiments 1 and 2, no evidence was obtained to suggest that color and pattern cues together facilitated preference, relative to color alone. Although it is arguable that complex stimuli might have been more effective than simple stimuli if an "appropriate" color such as green had been used, previous work (e.g., Mason & Reidinger, 1981) has suggested that aposematic colors are no more effective than cryptic colors for resistance to extinction of a color preference response.

When Experiments 2 and 3 are compared, visually mediated avoidance appears more resistant to extinction than visually mediated preference. This impression is consistent with previous work (Mason et al., 1984a). Not only are direct and vicariously acquired avoidance responses more resistant to extinction, but in addition, avoidance responses are more likely to affect the behavior of conspecifics.

EXPERIMENT 4

In the preceding experiments, avoidance responding was mediated by the experience or observation of malaise in association with visual cues. Experiment 4 was designed to assess whether a merely unpalatable flavor (one not associated with sickness) would elicit color avoidance learning as a function of direct experience. On the basis of other evidence (e.g., Alcock, 1970), avoidance acquisition was predicted, although it also was expected that differential responding would be less durable than that elicited by sickness (Barker, 1976). As in Experiment 1, different groups of birds were trained and tested with color cues only, or with color and pattern cues together.

Method

Twenty decoy-trapped adult male redwings (mean weight 69.2 ± 2.0 g) were adapted to the food deprivation regime, and assigned to two groups ($n = 10$ /group) on the basis of consumption. Both groups were then given five training trials (one trial/day). On each day of training, birds were food deprived for 2 hr, and then given stimulus rectangles paired with dimethyl anthranilate (DMA) adulterated food (0.8% w/w). DMA is widely used as a grape flavoring in human foods, but is unpalatable to birds in the laboratory (Mason, Arzt, & Reidinger, 1984b) and in the field (Mason, Glahn, & Reidinger, 1985).

For Group O-E (orange-experimental), food adulterated with DMA was

presented in a cup with an orange S+ rectangle attached. Group SO-E (striped-orange experimental) was treated similarly, except that vertically striped orange S+ rectangles were attached to food cups. On each of the 5 days following training, both groups were food deprived for 2 hr, and then given two-choice tests. Group O-E was given food cups with orange S+ and red So rectangles attached, and Group SO-E was given cups with vertically striped orange S+ and horizontally striped So rectangles attached. All food cups contained plain (unadulterated) PFBC. After 2 hr, consumption was measured. PFBC was returned to the cages in plain metal cups, and the birds were left undisturbed until light onset of the following day.

Results and Discussion

Both groups exhibited avoidance of PFBC paired with their respective S+ ($p < .05$; Figure 5.5). However, as in Experiments 1 and 2, color and pattern together (Group SO-E) elicited avoidance that appeared more resistant to extinction than avoidance exhibited toward color alone (Group O-E).

That DMA was as effective as methiocarb was not expected, and this result is inconsistent with previous reports. Alcock (1970) found that chickadees (*Parus atricapillus*) showed stronger avoidance of mealworms when ingestion was paired with malaise, than when ingestion merely was associated with an unpleasant taste (i.e., an unspecified concentration of NaCl). Possibly, the discrepancy between avoidance elicited by NaCl and that elicited by DMA reflects the sensory modalities stimulated by the latter compound. Dimethyl anthranilate is an olfactory and trigeminal stimulant for birds, and it also may have gustatory properties

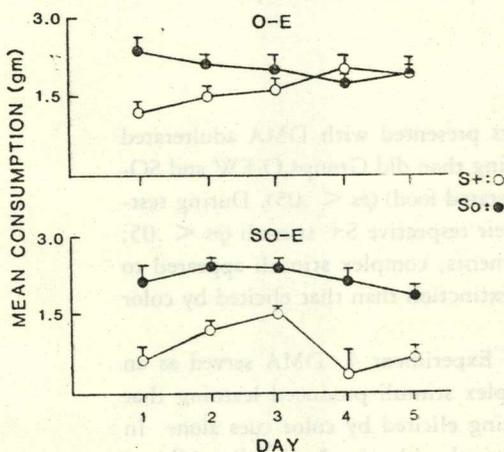


Figure 5.5. Avoidance expressed by Groups O-E and SO-E in two-choice tests in Experiment 4. Group SO-E showed greater resistance to extinction than Group O-E. Capped vertical bars represent standard errors of the means.

(Mason, Adams, & Clark, 1987). Sodium chloride is primarily a taste stimulus. In our laboratory, DMA has been found to be 200%, 150%, and 125% more effective than 0.1 M NaCl, 0.0001 M quinine HCl, and 0.001 M sucrose octaacetate in reducing or eliminating consumption of foods by redwing black-birds (Mason, unpublished observation).

EXPERIMENT 5

Because DMA elicited color avoidance responses that were as resistant to extinction as those elicited by methiocarb, Experiment 5 was designed to test whether observers of birds given DMA paired with a visual stimulus would also exhibit visually mediated avoidance. As in previous experiments, different groups of birds were trained and tested with color cues only, or with color and pattern cues together.

Method

Twenty decoy-trapped redwings (mean weight: 69.2 ± 2.0 g) were adapted to the food deprivation regime, and assigned to four groups ($n = 5/\text{group}$) on the basis of consumption. Groups O-E (orange-experimental) and SO-E (striped orange-experimental) were given training (4 days) identical to that described in Experiment 4. Birds in Groups O-EW (orange-experimental watching) were placed in cages adjacent to those of group O-E, and birds in Group SO-EW (striped orange-experimental watching) were placed in cages adjacent to those of Group SO-E. After conditioning, all birds were visually isolated, and given two-choice tests identical to those described in Experiment 4 for 5 days.

Results and Discussion

Groups O-E and SO-E (i.e., demonstrators presented with DMA adulterated food) showed less consumption during training than did Groups O-EW and SO-EW (i.e., observers presented with unadulterated food) ($ps < .05$). During testing, all groups avoided food paired with their respective S+ stimuli ($ps < .05$; Figure 5.6), and as in the previous experiments, complex stimuli appeared to elicit avoidance that was more resistant to extinction than that elicited by color alone.

The present results confirm those of Experiment 4. DMA served as an effective unconditioned stimulus, and complex stimuli produced learning that was more resistant to extinction than learning elicited by color cues alone. In addition, observers of birds given DMA paired with visual stimuli exhibited avoidance, although the cues used by observers remain unclear. Demonstrators

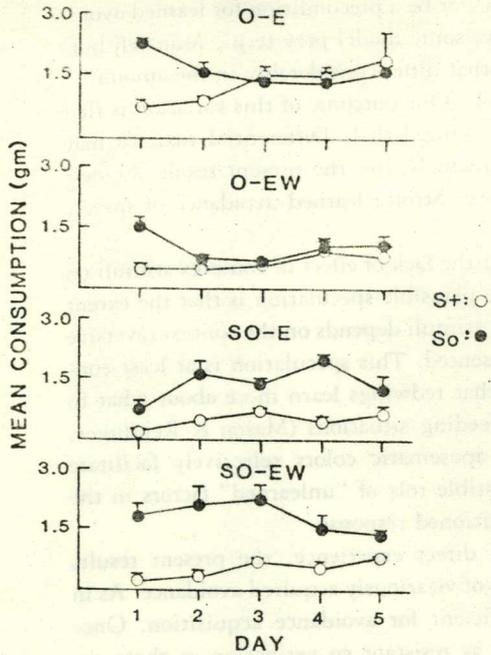


Figure 5.6. Avoidance expressed by Groups O-E, O-EW, SO-E and SO-EW in two-choice tests in Experiment 5. Groups SO-E and SO-EW expressed greater resistance to extinction than Groups O-E and O-EW. Capped vertical bars represent standard errors of the means.

exhibited few signs of discomfort (only bill wiping was observed occasionally). Possibly, the demonstrator's decreasing consumption of DMA adulterated food during training provided sufficient information to observers. Alternatively, it may be that "vicarious" learning in the present experiment was actually learning through direct experience. Observers may have detected DMA volatiles from the demonstrators' food and associated the volatiles with the S+ cue.

GENERAL DISCUSSION

Various passerine species learn to avoid visual cues associated with sickness. Moreover, prior investigations have demonstrated that the breadth of response generalization depends, in part, on the intensity (Czaplicki et al., 1976; Duncan & Shepherd, 1965) and color (Mason & Reidinger 1983b) of the conditioned stimulus. The present experiments extend these observations by suggesting that stimulus complexity influences the resistance to extinction of an avoidance response. Experiments 4 and 5 further suggest that this facilitative effect may not depend on malaise.

That complexity should facilitate learned avoidance is predictable on an ecological basis, because black stripes against an aposematic background (e.g., red, orange) are used by animals to advertise unpalatability (Cott, 1940). In this

regard, the observation that malaise may not be a precondition for learned avoidance is interesting, because, in mimicry, some model prey (e.g., Monarch butterflies) sequester toxicants from plants that differ considerably in the amount of toxicant contained (Fink & Brower, 1981). One outcome of this variation is that models range from being palatable to being lethal. Differential toxicity may result in greater predation on toxic individuals, but the present results suggest that this may not necessarily be the case. Strong learned avoidance of merely unpalatable individuals may occur.

There are no ready explanations for the lack of effect of complex stimuli on food preference extinction, although one plausible speculation is that the extent to which some passerines attend to visual stimuli depends on the context (aversive or appetitive) in which the cues are presented. This speculation is at least consistent with laboratory demonstrations that redwings learn more about what to avoid than what to approach in some feeding situations (Mason & Reidinger, 1982b). Regardless, the finding that aposematic colors selectively facilitate avoidance responding highlights the possible role of "unlearned" factors in the development and maintenance of a conditioned response.

Beyond learning as a function of direct experience, the present results confirm and extend previous observations of vicariously acquired avoidance. As in other work, one training trial was sufficient for avoidance acquisition. Once established, conditioned responses were as resistant to extinction as those acquired directly, and complex cues appeared to be more effective conditioned stimuli than color alone. One implication of such durable vicariously acquired avoidance is that social interactions among predators (even predators of different species; Mason et al., 1984a) may influence the frequency of attacks on aposematic prey. A second implication is that the use of redundant aposematic cues (i.e., pattern, color) by prey could provide extra protection from predators by enhancing resistance to extinction of the avoidance response. In the simplest case, fewer observed attacks on unpalatable prey would be needed to maintain avoidance of both model and mimic organisms.

From the perspective of an avian predator, socially acquired avoidance, albeit imperfect (e.g., the occasional rejection of a palatable mimic of an unpalatable model) could lead to more efficient foraging than learning by direct experience. In the case of Batesian mimicry (unpalatable model, palatable mimic), observationally acquired avoidance would allow the predator to reject models without wasting limited foraging time. Of course, mimics would also be avoided at the cost of rejecting harmless prey. Presumably, the disadvantages of mistakenly rejecting mimics is outweighed by the advantages of avoiding models. In the case of Mullerian mimicry, the advantage of observational learning to the predator is more clear, since both models and mimics are unpalatable. However, vicariously acquired avoidance would be of the greatest advantage to predators in Mertesian mimicry (deadly models and mimics), because any direct encounter between a predator and a model or mimic is lethal to the predator. Indeed, in the

absence of observational learning, it is difficult to conceive how Mertesian mimics might evolve.

Broadly, the present experiments suggest that a knowledge of stimulus effectiveness in laboratory studies of direct and vicarious avoidance learning will further understanding of aposematic signals used in model-mimic systems. Provided that laboratory experiments of visually mediated avoidance learning fit within a broader ecological context, one might predict that the stronger the avoidance response (e.g., the greater the resistance to extinction) in the laboratory, the more effective (and, perhaps, the more common) the stimulus complex in nature. This prediction is consistent with the observation that aposematic animals use both color and pattern cues to deter potential predators (Cott, 1940). Strong avoidance acquisition after experience with a model prey (or after observation of prey sampling by a conspecific) could deter even brief sampling excursions by birds, thus decreasing the likelihood of encountering a mimic (and weakening the learned association). Strong acquisition might also permit the number of mimics to exceed the number of models without damage to the mimetic complex (Brower, 1960).

SUMMARY

Learned avoidance and preference by birds for some foods is mediated by visual cues. Learning can occur either through direct experience or observation. For avoidance, *aposematic* colors such as red are more effective conditioned stimuli than *cryptic* colors such as green. For preference, both red and green appear to be equally effective. Ecologically, the differential effectiveness of color is predictable, because the aposematic colors are used frequently by animals to advertise unpalatability, whereas the cryptic colors serve this function rarely. An unanswered question is the importance of pattern cues as a variable influencing direct and observationally acquired preference and avoidance. The potential significance of striping is suggested by the observation that aposematic animals often are striped as well as brightly colored. The present experiments were designed to address this issue using redwinged blackbirds as subjects. Experiments 1 and 2 assessed whether complex stimuli (pattern and color cues) elicited greater resistance to extinction than simple stimuli (pattern or color cues) in avoidance learning. Experiment 3 investigated whether complex stimuli might facilitate resistance to extinction of color preference responding. Experiments 4 and 5 assessed whether complex stimuli would enhance learned avoidance of visual stimuli associated with merely unpalatable food. Both direct and vicariously acquired avoidance were more resistant to extinction when complex stimuli were employed. Resistance was enhanced regardless of whether the unconditioned stimulus was malaise or unpalatability. Conversely, resistance to extinction of color preferences was not affected by the use of complex stimuli. These results

suggest that the strength of visually mediated food avoidance learning depend on the number of available discriminative cues. Ecologically, such findings are consistent with the observation that the use of multiple aposematic cues may confer greater protection from predators than the use of simple cues, such as color, alone.

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