COMPARATIVE ASSESSMENT OF FOOD PREFERENCES AND AVERSIONS ACQUIRED BY BLACKBIRDS VIA OBSERVATIONAL LEARNING

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Abstract.—Red-winged Blackbirds (*Agelaius phoeniceus*) can acquire food preferences and aversions merely by observing conspecifics. In Experiment 1, red-wings were trained to prefer or avoid food paired with yellow, as conspecifics watched. After training, all birds were given two-choice tests between food paired with yellow or green for 12 days. Trainers were tested in visual isolation, whereas watchers were tested either in visual isolation or in visual contact with birds who had observed the opposite behavior during training. Food aversions were more resistant to extinction than food preferences ($P < 0.05$), and, among watchers, social cues facilitated avoidance ($P < 0.05$). In Experiment 2, red-wings were trained to avoid food paired with yellow, as Common Grackles (*Quiscalus quiscula*) and red-wings watched, or vice versa, and then two-choice tests were given between yellow and green. Both grackles and red-wings exhibited observational learning, regardless of the training species (P's < 0.05).

Social interactions among avian predators may influence how predator abundance affects the Batesian model-mimic complex. We speculate that avoidance learning, which occurs when a predator observes the ingestion of a model, is stronger than preference learning, which occurs when a mimic is ingested. Relatively few models would be needed for the model-mimic complex to operate successfully, and the number of mimics could exceed the number of models without jeopardizing the mimetic advantage. *Received 4 November 1983, accepted 12 March 1984.*

RED-WINGED Blackbirds (*Agelaius phoeniceus*) can learn food preferences and aversions by observing conspecifics feed and without necessarily ingesting food themselves (Mason and Reidinger 1981, 1982a). Such observational learning is guided by the visual characteristics of the food (Mason and Reidinger 1983a), although tactile and gustatory stimuli, as well as the long-term consequences of ingestion, may become important. Such findings are consistent with results obtained from other species (Klopfer 1959, Duecker 1976).

Regarding preferences, Common Chaffinches (*Fringilla coelebs*), for example, are more likely to commence feeding and to sample new foods when exposed to conspecifics doing so (Rubenstein et al. 1977). White Wagtails (*Motacilla alba*) and Tennessee Warblers (*Vermivora peregrina*) behave in a similar fashion (Davies 1976, Tramer and Kemp 1979), and European Starlings (*Sturnus vulgaris*) may increase feed-

ing efficiency while minimizing energy expenditure through social feeding (Hamilton and Gilbert 1969). This social feeding is discriminative, and individuals in the flock tend to choose foods that other birds in the flock are choosing (Murton 1974, Williamson and Grey 1975).

Regarding aversions, many insectivorous species learn to avoid visual stimuli associated with prey whose ingestion has sickened them (e.g. Brower 1958a, b, c; Duncan and Sheppard 1965; Wickler 1968; Morell and Turner 1970; Rettenmeyer 1970). Some investigators have suggested that observational avoidance learning may also have implications for Batesian mimicry (e.g. Alcock 1969a, b), a phenomenon in which predators learn to avoid noxious prey by developing conditioned aversions (Mason et al. 1982) and generalize this learning to mimics of the unpalatable items. One such implication is that predator pressure on prey, at least in some instances, may not increase linearly with the number of predators. Instead, social interactions among predators may ultimately determine how predator abundance affects the Batesian complex (Avery 1983). An unanswered question relevant to this issue is

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the strength (i.e. resistance to extinction) of observationally learned aversions in comparison with similarly acquired preferences. Avian predators are likely to observe attacks by conspecifics on both models and mimics, and, in some cases, observed attacks on mimics should exceed observed attacks on models, because mimics are more numerous (Brower 1960). In the former case, the observer should learn approach, or preference, but, in the latter instance, learned avoidance, or aversion, should accrue. In Experiment 1, we assessed which sort of observational experience would exert greater control over behavior.

EXPERIMENT 1

COMPARATIVE ASSESSMENT OF LEARNED FOOD PREFERENCES AND AVERSIONS

METHOD

Subjects.—Twenty-one male Red-winged Blackbirds were decoy-trapped in Sandusky, Ohio during June 1982. The birds were brought to the laboratory during the last week of June and individually housed (cage dimensions: 36 cm × 61 cm × 41 cm) in a room with an ambient temperature of 23°C. A 6:18 light : dark cycle was used to maximize the feeding rate of the birds without reducing the quantity of food consumed (Rogers 1974, 1978). Water was always available, and, before the experiment began, the birds were permitted free access to Purina Flight Bird Conditioner (PFBC) in unpainted metal food cups (7.5-cm diameter). Each food cup was placed within a larger cup (11.3-cm diameter), which caught spillage from the smaller one during feeding.

Procedure.—The birds were assigned to seven groups (n = three/group). The cages of the birds in Groups 1, 2, and 3 were placed adjacent to and in view of one another but in visual isolation from other birds in the laboratory. Similarly, the cages of birds in Groups 4, 5, and 6 were placed in view of one another but in isolation from other birds in the laboratory. The birds in Group 7 were placed in adjacent cages but were visually isolated from one another as well as from other birds in the laboratory.

On days 1–4 of the experiment, Group 2 was trained to prefer food paired with the color yellow (Mason and Reidinger 1981). Preference training involved food deprivation during the dark period of each light cycle and then, during the first hour following light onset, the presentation of 20 g of PFBC in a yellow food cup. After 1 h, the cups were removed, and consumption was measured. Spillage was not assessed, because in previous work it merely reflected consumption (Mason and Reidinger 1983a). During the remaining 5 h of light on each training day, the birds

in Group 2 were left undisturbed and were permitted free access to PFBC in plain food cups and to water. Groups 1 and 3 were visually exposed to the preference training of Group 2 (i.e. they were in cages adjacent to those of Group 2) but were otherwise left undisturbed and had free access to food and water. For clarity, Groups 1, 2, and 3 are referred to below as Groups OPI (Observational Preference Learning, Isolation Testing), PI (Preference Learning, Isolation Testing), and OPN (Observational Preference Learning, Not Isolation Tested), respectively.

On day 4, Group 5 was trained to avoid food paired with yellow (Mason and Reidinger 1982a). Avoidance training involved 18 h of food deprivation (i.e. the dark period of day 3) and then, during the first hour following light onset, the presentation of 20 g of PFBC in a yellow cup. When 1 g was consumed, the cups were removed, and the birds received oral intubations (gavages) of methiocarb [3,5-dimethyl-4-(methylthio)phenol methylcarbamate], a bird repellent that produces conditioned color aversions similar to those produced by lithium chloride (Mason and Reidinger 1983a). One hour after gavage, PFBC in plain unpainted food cups was replaced in the cages. Groups 4 and 6 were visually exposed to the avoidance training of Group 5 but were otherwise left undisturbed and had free access to food and water. Group 7 was given pairings of PFBC in yellow cups, with intubations of propylene glycol, the non-toxic carrier for methiocarb. These pairings served as a control for the gavage procedure, per se. Groups 4, 5, 6, and 7 are referred to below as groups OAN (Observational Avoidance Learning, Not Isolation Tested), AI (Avoidance Learning, Isolation Testing), OAI (Observational Avoidance Learning, Isolation Testing), and CT (Control), respectively.

After completion of the training phase, the birds in Groups OPI, PI, AI, and OAI were visually isolated from one another and from other birds in the laboratory. The birds in Groups OPN and OAN were placed adjacent to and in view of one another but in visual isolation from other birds in the laboratory.

Testing began on the fifth day and continued for 12 consecutive days. On each day, all birds were given two-choice tests between food in yellow or green cups. Previous work had shown that red-wings do not respond differentially to these colors without training (Mason and Reidinger 1981). The two cups were located 5 cm apart at the front of the cages, and each contained 20 g of PFBC. Testing occurred during the first hour of light; the birds were food deprived during the 18-h dark phase of each light cycle. After 1 h, the cups were removed from the cages, and consumption was measured. During the remaining 5 h of light on test days, the birds were left undisturbed and had free access to water and to PFBC in plain metal cups.

Analysis.—Consumption during preference tests was assessed by a three-way analysis of variance
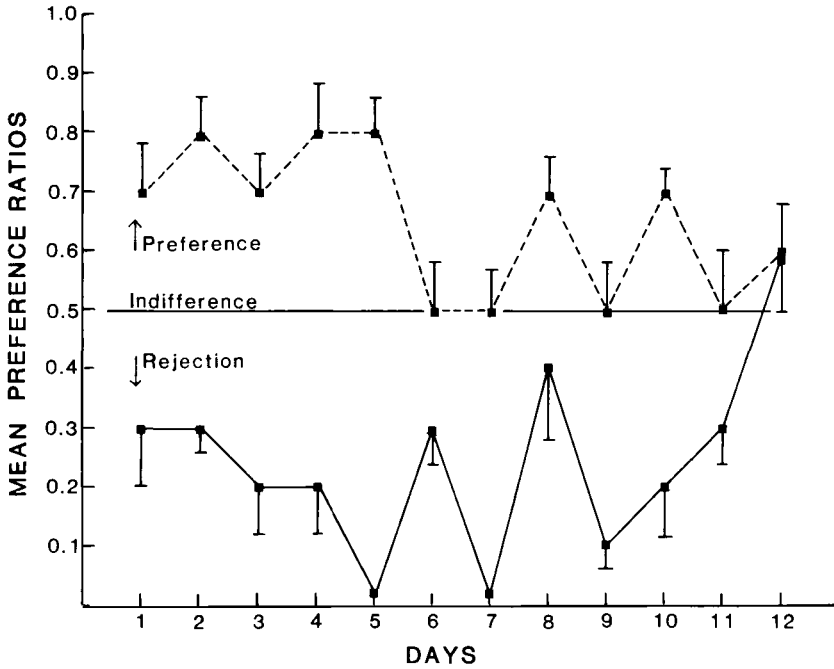
Fig. 1. Mean preference ratios exhibited by birds trained to prefer (Group PI, dotted line) or avoid (Group AI, solid line) PFBC presented in yellow cups. Each bird in both groups was tested in visual isolation. Preference ratios were calculated by dividing consumption of food in yellow cups by total consumption. Vertical bars represent standard errors of the means.

(ANOVA) with repeated measures on two factors. The independent factor in this analysis was groups; the repeated factors were (a) consumption across the 12 test days and (b) consumption of food paired with yellow (CS+) versus consumption of food paired with green (CS−). Subsequently, Tukey b-tests (Winer 1962) were used to identify significant differences among means.

RESULTS

The two-way interactions between groups and days [$F(66,154) = 2.0$, $P < 0.001$], groups and CS+ vs. CS− consumption [$F(6,14) = 26.0$, $P < 0.0005$], and days and CS+ vs. CS− consumption [$F(11,154) = 3.0$, $P < 0.01$] were significant. Because the three-way interaction among groups, days and CS+ vs. CS− consumption was also significant [$F(66,154) = 4.0$, $P < 0.0005$], however, we interpreted the analysis in terms of that higher order effect. Tukey comparisons revealed that on test day 1, groups OPI, PI, and OPN ate relatively more PFBC from yellow cups (P's < 0.05). Conversely, groups OAN, AI, and OAI ate relatively more from green cups (P's < 0.05). Group CT showed no

differential consumption ($P > 0.25$). Except for group OAN (given observational avoidance training and tested while visually exposed to group OPN) and group CT, patterns in consumption changed over test days. Group PI (given preference training) continued to eat relatively more from the yellow cups on test days 2–4 (P's < 0.05) but manifested no consumption preferences on days 5–12 (P's > 0.10; Fig. 1). Likewise, group OPI (given observational preference training) displayed relatively higher consumption of PFBC in yellow cups on days 1–6 (P's < 0.05) but not on days 7–12 (P's > 0.10; Fig. 2). The birds in groups AI (given avoidance training) and OAI (given observational avoidance training) ate relatively more from green cups on test days 1–10 (P's < 0.05) but did not avoid food in yellow cups on days 11 and 12 (P's > 0.10; Figs. 1 and 2, respectively). Finally, group OPN (given observational preference training and tested while visually exposed to group OAN) exhibited relatively higher consumption from yellow cups on days 1 and 2 (P's < 0.05), no differential consumption on days 3–6 (P's > 0.10), and relatively
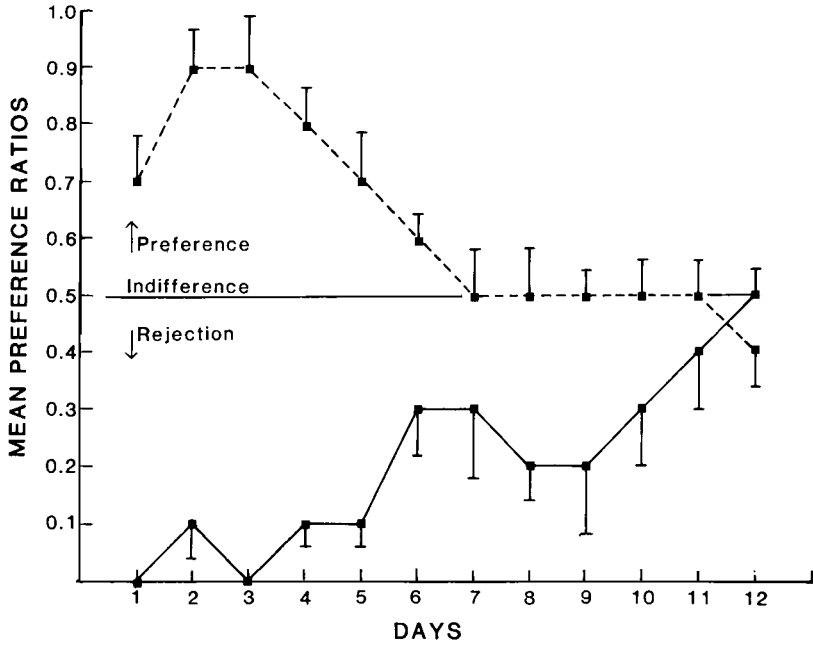
Fig. 2.   Mean preference ratios exhibited by birds that learned preference (Group OPI, dotted line) or avoidance (Group OAI, solid line) via observation. Each bird in both groups was tested in visual isolation. Vertical bars represent standard errors of the means.

higher consumption from green on days 7–12 (P's < 0.05; Fig. 3).

DISCUSSION

The results of Experiment 1 confirm and extend previous findings obtained in our laboratory with Red-winged Blackbirds (Mason and Reidinger 1981, 1982a). Color preferences and aversions were acquired either through direct experience with a food-color combination (Groups PI and AI) or as a consequence of observation (e.g. Groups OPI and OAI). Even though more preference training (4 trials) was given than aversion training (1 trial), preferences, once formed, were less durable (i.e. less resistant to extinction) than aversions, and, when birds that had acquired observational preferences for yellow (Group OPN) were visually exposed to birds that had similarly acquired aversions (Group OAN), preferences dissipated and were replaced by avoidance. Subsequently, a synergistic interaction developed between Groups OPN and OAN, and the avoidance behavior these groups exhibited was more durable than that displayed by birds tested

in visual isolation (Groups AI and OAI). Such results suggest the robust nature of aversion learning by Red-winged Blackbirds and the extent to which such learning might exert control over the behavior of conspecifics. An unanswered question is the extent to which such learning might occur interspecifically (e.g. among red-wings and other birds in mixed-species flocks). Experiment 2 was performed to address this question. We used Common Grackles (*Quiscalus quiscula*), a species that often flocks with red-wings (Dolbeer 1980).

EXPERIMENT 2

INTERSPECIFIC TRANSFER OF VICARIOUSLY ACQUIRED FOOD AVERSIONS

METHOD

Subjects.—Fifteen male Common Grackles and 15 male Red-winged Blackbirds were decoy-trapped in Sandusky, Ohio during September 1982 and brought to the laboratory during the first week in October. The birds were individually housed and maintained as described in Experiment 1.

Procedure.—The grackles were randomly assigned to Groups 1–3 (n = five/group), and the red-wings
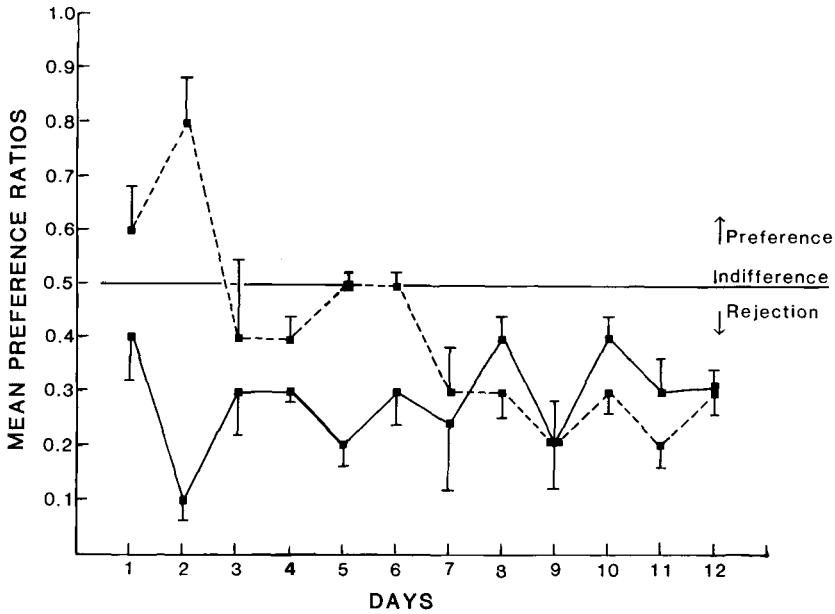
Fig. 3. Mean preference ratios exhibited by birds that learned preference (Group OPN, dotted line) or avoidance (Group OAN, solid line) via observation. The birds in these groups were tested while visually exposed to one another. Vertical bars represent standard errors of the means.

were assigned to Groups 4–6 (n = five/group). Groups 4 (red-wings) and 1 and 2 (grackles) were visually exposed to one another but isolated from other birds in the laboratory. Similarly, Groups 3 (grackles) and 5 and 6 (red-wings) were visually exposed to one another but otherwise were visually isolated. Below,

Group 2 is referred to as Group GOG (grackle observing grackle), Group 1 as Group GT (grackle trainer), Group 4 as Group ROG (red-wing observing grackle), Group 3 as Group GOR (grackle observing red-wing), Group 6 as Group RT (red-wing trainer), and Group 5 as Group ROR (red-wing observing red-
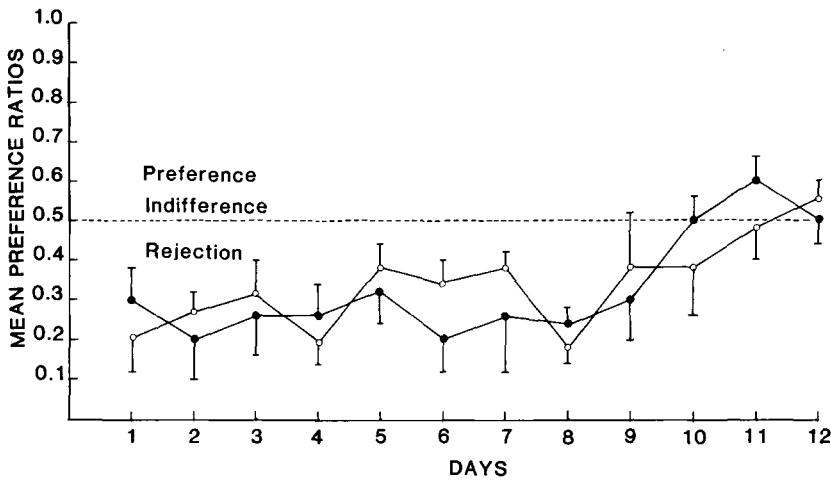

Fig. 4. Mean preference ratios exhibited by grackles (Group GT, O) and red-wings (Group RT, ●) trained to avoid food paired with yellow. Vertical bars represent standard errors of the means.
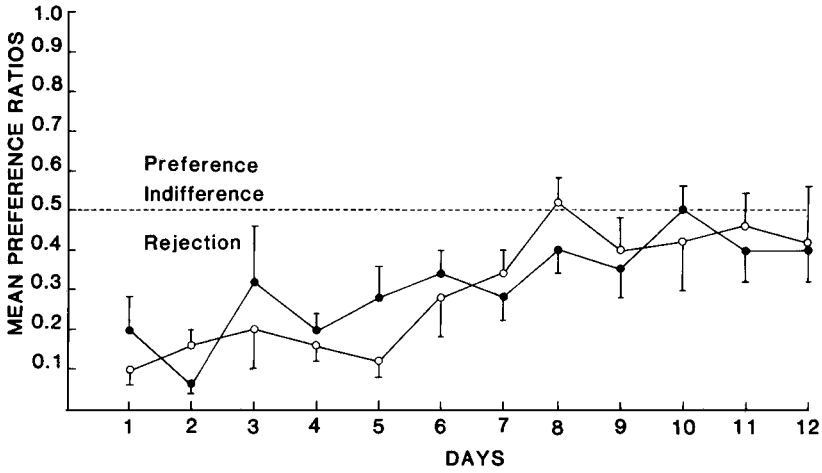
Fig. 5. Mean preference ratios exhibited by grackles (Group GOR, O) and red-wings (Group ROR, ●) that observed red-wings being trained to avoid food paired with yellow. Vertical bars represent standard errors of the means.

wing). Groups GT and RT were then trained to avoid food paired with yellow, as described in Experiment 1. Groups GOG and ROG and GOR and ROR were visually exposed to the avoidance training of Groups GT and RT, respectively, but otherwise were left undisturbed. On the day after training, each bird was visually isolated, and 12 days of testing began. On each day, two-choice tests were given between food in yellow or green cups. The grackles, like red-wings, did not prefer yellow or green before training (pers. obs.). As in Experiment 1, the birds were food deprived for 18 h (1 dark cycle) before each test session, and testing occurred during the first hour of light.

Analysis.—A three-way ANOVA with repeated measures on two factors was used to assess the test results. The factors of this analysis were identical to the factors of the analysis used in Experiment 1. Tukey *b*-tests were used to isolate significant differences among means.

RESULTS

There were no significant differences among groups in overall consumption ($P > 0.10$), although there were differences in consumption
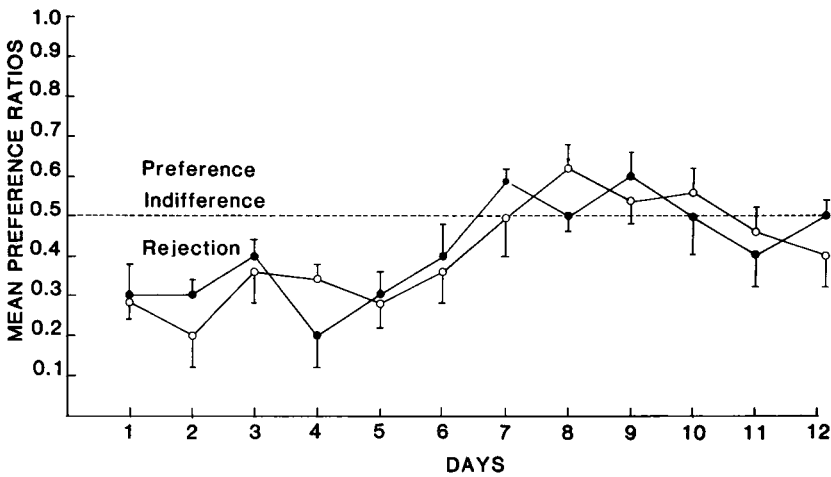

Fig. 6. Mean preference ratios exhibited by grackles (Group GOG, O) and red-wings (Group ROG, ●) that observed grackles being trained to avoid food paired with yellow. Vertical bars represent standard errors of the means.

among days [$F(3,24) = 4.0$; $P < 0.025$] and between consumption of CS+ vs. CS− foods [$F(1,8) = 38.0$; $P < 0.0005$]. The two-way interaction between days and CS+ vs. CS− foods was also significant [$F(3,24) = 3.3$, $P < 0.05$], and we interpreted the analysis in terms of this higher order effect. Tukey tests indicated that all groups ate less food on the two days following training (P's < 0.05) and that all groups ate more CS+ than CS− food (P's < 0.05) during the initial tests but that this avoidance dissipated over days. Although all groups exhibited avoidance on days 1–7 (P's < 0.05), only groups GT and RT continued to express avoidance until days 9 or 10, respectively (P's < 0.05). No differential consumption was observed on days 11–12 (P's > 0.10). These results are illustrated in Figs. 4, 5, and 6.

DISCUSSION

The results of Experiment 2 demonstrate that reliable observational learning of food aversions can occur between species that typically associate with one another. Such learning, at least in terms of durability, was as strong as learning among conspecifics. This finding is surprising in that the available evidence would have predicted a more effective transfer among conspecifics (e.g. Fleuster 1973). This difference between the expected and obtained results may reflect the fact that only one measure (i.e. resistance to extinction) was used to assess the strength of learning. At least for red-wings, resistance to extinction does not necessarily reflect other measures of learning, such as generalization or resistance to pre-exposure effects (Mason and Reidinger 1983b). Regardless, the present results are consistent with other demonstrations of the social transmission of behavior among avian species in feeding (Short 1961, Thompson and Barnard 1983) and mobbing (Vieth et al. 1980) contexts. They suggest that one benefit of foraging in mixed-species flocks may be that members of one species (e.g. grackles) can learn to avoid noxious foods by observing the effects of ingestion on members of another species (e.g. red-wings).

GENERAL DISCUSSION

The results of Experiment 1 suggest that learned food aversions are more durable than learned food preferences and more likely to af-

fect the behavior of conspecifics vicariously. The results of Experiment 2 suggest that acquired aversions transfer as readily between species as among conspecifics and that, when learned preferences among conspecifics (Experiment 1) are compared with learned aversions between species (Experiment 2), aversions appear to be more resistant to extinction than do preferences. As such, it seems plausible to suggest that vicariously acquired preferences between species would be weaker than similarly acquired aversions. That aversions appear to be relatively stronger than preferences is consistent with (a) the notion that opportunistic foragers, such as red-wings and grackles (Dolbeer 1980, Orians 1980), readily learn to avoid food associated with aversive consequences; and (b) the observation that blackbirds learn more about what to avoid than what to approach in some feeding situations (Mason and Reidinger 1982b). More broadly, relatively higher levels of resistance to extinction of avoidance (in comparison with extinction of preferences) is a commonly reported finding in the psychological literature (Mackintosh 1974).

The present results suggest that predator pressure on prey may not always increase with the number of predators. Social interactions among birds may influence their behavior toward prey and could determine how predator abundance affects the Batesian model-mimic complex. We speculate, for example, that the avoidance learning that occurs when a predator observes the ingestion of a Batesian model is stronger than the preference learning that occurs when a mimic is ingested. As such, relatively few models would need to be encountered for the model-mimic complex to operate successfully, and the number of mimics could exceed the number of models without seriously jeopardizing the mimetic advantage.

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