

OBSERVATIONAL LEARNING OF FOOD AVERSIONS IN RED-WINGED BLACKBIRDS (*AGELAIUS PHOENICEUS*)

J. RUSSELL MASON AND RUSSELL F. REIDINGER¹

Monell Chemical Senses Center, 3500 Market Street, Philadelphia, Pennsylvania 19104 USA

ABSTRACT.—Recent work has demonstrated that Red-winged Blackbirds (*Agelaius phoeniceus*) display food preferences as a result of observational learning. Also, individual birds learn to avoid food the ingestion of which has been paired with sickness. Such preferences or aversions depend on visual cues associated with the food. A related but unanswered question is whether observational learning is sufficient for birds to associate visual cues with sickness. In the present experiments, Red-wings observed a conspecific consume a food paired with a color cue (CS) and toxin-induced illness (UCS). The observers were subsequently given two-choice preference tests between a food (either the food consumed by the gavaged bird or another food) paired with the CS or with another color. The birds avoided consumption of any food paired with the CS (but not of the other color) during all tests. Such results are consistent with the notion that opportunistic foragers, such as Red-wings, readily learn to avoid conspicuous foods paired with aversive consequences. Moreover, the results support the notion that Batesian model-mimic systems could be maintained, at least in part, by observational learning of models and subsequent generalization of that learning to mimics. Observational learning could provide an efficient strategy to protect against the ingestion of potentially dangerous food. *Received 15 July 1981, accepted 12 December 1981.*

RECENT work has demonstrated that Red-winged Blackbirds (*Agelaius phoeniceus*) readily display food preferences as a consequence of observational learning (Mason and Reidinger 1981). That finding is consistent with earlier work showing that other avian species imitate conspecifics (e.g. Duecker 1976), a factor that could help to promote flocking. For example, Chaffinches (*Fringilla coelebs*) commence feeding and sample new foods when exposed to other Chaffinches doing so. Such behavior may permit Chaffinches to locate and switch to new feeding sources readily. Likewise, Starlings (*Sturnus vulgaris*) probably increase feeding efficiency while minimizing energy expenditure through social feeding (Hamilton and Gilbert 1969). Overall, the feeding seems to be guided by visual cues associated with the food, although tactile/gustatory stimuli from the food and the positive, long-

term after-effects of food ingestion may play a role (Hogan-Warburg and Hogan 1981).

Individual birds have also been shown to use visual cues to avoid foods the ingestion of which has been associated with sickness. For example, Red-wings (Mason and Reidinger MS), Starlings (Schuler 1980), and Japanese Quail (*Coturnix coturnix japonica*) (Czaplicki et al. 1976) readily learn to associate visual cues with sickness. The strength of such aversions is, in part, a function of the salience of the visual cue (Czaplicki et al. 1976).

An important assumption of the theory of Batesian mimicry is that predators learn to avoid unpalatable prey items and their mimics by experiencing the consequences of attacking the unpalatable models and developing conditioned aversions (Mason et al. in press). That assumption has been supported by observations of various caged and wild predators (e.g. Brower 1958a, b, c; Duncan and Sheppard 1965; Morell and Turner 1970; Rettenmeyer 1970). In most cases, visual cues are a critical component of the predator's behavior.

A further question is: will birds associate visual cues with sickness as a consequence of observational learning? There is evidence consistent with this notion (Klopfer 1959). Klopfer

¹ The second author is assigned to the Monell Center from the U.S. Fish and Wildlife Service, Denver Wildlife Research Center, Section of Supporting Sciences, Building 16, Federal Center, Lakewood, Colorado 80225 USA.

(1957) trained Muscovy (*Cairina moschata*) and Mallard (*Anas platyrhynchos*) ducks to avoid a particular feeding dish associated with electric shock. The shock produced an intense alarm response, and other ducks observing that response subsequently avoided the feeding dish, even though they had not experienced the shock. Likewise, Coombes et al. (1980) have reported that, if two rats consume a flavored solution and one is poisoned, the unpoisoned rat will also exhibit a flavor aversion during later preference tests. A sufficient condition for this aversion is that the poisoned partner be present with the unpoisoned rat after it has consumed the flavored solution.

In Experiment 1, Red-wings observed a conspecific consume a novel food associated with a color cue (conditioned stimulus: CS) and toxin-induced illness (unconditioned stimulus: UCS). The observers were then given two samples of the food, one paired with the CS and the other paired with a novel color.

EXPERIMENT 1

METHODS

Subjects.—Eighteen adult male Red-winged Blackbirds were decoy-trapped during May 1981 at Sandusky, Ohio. The birds were brought to the laboratory during the last week of May and individually housed in large (36 cm long \times 61 cm wide \times 41 cm high) cages in a room with an ambient temperature of 23°C. A 6:18 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 apples.

Procedure.—Twelve of the 18 Red-wings were randomly assigned to 4 groups ($n = 3$). The cages of the individual birds in each group were placed adjacent to one another, and then each group 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 following day, the birds in the center cage of each of the 4 groups were given 20 g of steel-cut rolled oats (a preferred food of Red-wings in our laboratory) in a cup (7.5 cm diameter) with a red or white plastic rectangle (CS) (17.5 cm high \times 12.5 cm wide) attached. The other birds in each of the groups were given 20 g of their familiar food, Purina Flight Bird Conditioner, in a similar cup with no colored rectangle attached. To collect spillage during the normal feeding activity, each of the food cups was placed within a larger cup (11.3 cm diameter) (Rogers 1974).

When the 4 birds in the center cages had consumed at least 1 g of oats (approximately 1 h of feeding), 2 were intubated with a methiocarb solution (2 mg/kg) and 2 were intubated with propylene glycol (2 mg/kg) as a control for the traumatic consequences of intubation *per se*. 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 MS). The stock solution of methiocarb was prepared by dissolving 3 mg of methiocarb in 25 ml of propylene glycol. The other 8 birds (2 in each of the groups) were not intubated. Intubation was completed in all 4 cases within 10 min of the end of the feeding trial. The rolled oats and CS were removed 1 h after intubation and the birds left undisturbed with familiar food during the remaining hours of light.

During the first 2 h of light on the 6 days immediately following the day of gavage, all of the birds in each group were visually isolated from one another with pieces of cardboard (36 cm long \times 61 cm wide) and given two-choice preference tests (Dragoin et al. 1971). During preference tests, each bird was presented with two food cups (7.5 cm diameter), each containing 20 g of rolled oats. The two food cups were located 5 cm apart at the front of the cages, and attached to the back of one of the cups was the CS color. Attached to the back of the other cup was a rectangle of another color (i.e. red if white were the CS or vice versa). At the beginning of the third hour of light, the two food cups were removed from each of the cages and consumption was measured. Spillage was not measured, because in all previous work it merely reflected consumption (Mason and Reidinger 1981, Mason and Reidinger MS). For the remaining hours of light on the test days, all birds were permitted free access to Purina Flight Bird Conditioner and apples.

RESULTS

Measurements of consumption during preference tests were assessed using three-way analyses of variance (ANOVA) with repeated measures on two of the factors. The independent factor in the analyses was groups of birds, while the repeated factors were color cue and preference tests. The ANOVAs indicated a significant interaction between groups and consumption of oats paired with the CS or the other color cue for both intubated and observer birds [intubated: $F(1,2) = 20.2$, $P < 0.05$; observer: $F(1,6) = 7.34$, $P < 0.05$]. There were no differences among groups in the total amounts of oats consumed ($P > 0.25$) or among the six preference tests ($P > 0.25$). Bonferroni *post*

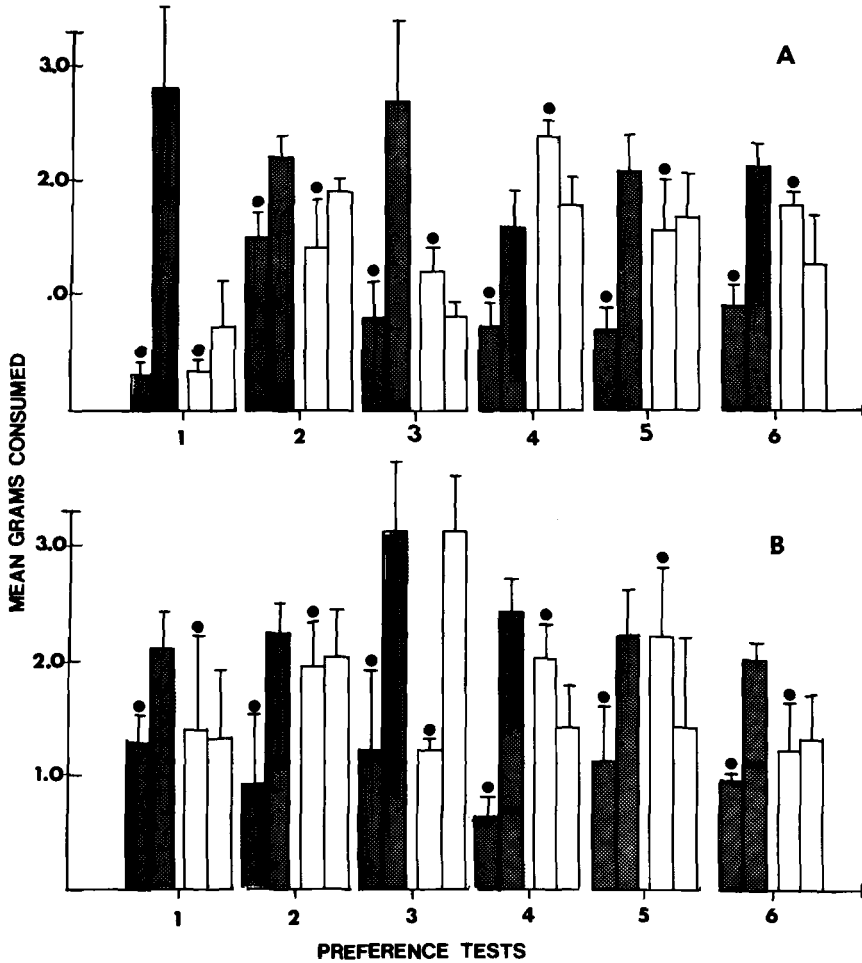


Fig. 1. A. Mean consumption of oats by birds intubated with methiocarb (hatched bars) or propylene glycol (open bars) during each of the six preference tests. B. Mean consumption of oats by observers of the methiocarb-intubated birds (hatched bars) or propylene glycol intubated birds (open bars) during each of the six preference tests. ● = consumption of oats paired with the CS. Standard errors of the means are represented by capped vertical bars.

hoc t-tests (Games 1971) were used to identify significant differences among means ($P < 0.05$). The *t*-tests indicated that birds intubated with methiocarb ate less from the cup paired with the CS than from the other cup. Likewise, observers of the methiocarb-intubated birds ate less from the cup with the CS attached. Red and white were equally effective conditioned stimuli ($P > 0.25$). Birds intubated with propylene glycol and their observers exhibited no differential consumption between the food cups (see Fig. 1).

DISCUSSION

The results of Experiment 1 demonstrate that male Red-winged Blackbirds will learn to avoid foods paired with a distinctive color cue as a consequence of previous observations of a conspecific's aversive experiences. Such aversions appear durable insofar as avoidance of food paired with the CS remained strong over the six preference tests. As such, the results confirm and extend previous demonstrations that some birds readily associate visual cues with

sickness (Schuler 1980, Czaplicki et al. 1976, Mason and Reidinger MS). Also, the results are consistent with work demonstrating that visual cues are relatively more important than taste cues in the formation of conditioned food aversions (but not fluid aversions) by Starlings (Capretta 1961) and Japanese Quail (Gillette et al. 1980).

EXPERIMENT 2

An important unanswered question suggested by the present results is what the relative importance of the food versus that of the color CS is. For example, there may have been an interaction between the novelty of the oats as food and the conditioned stimulus that facilitated expression of the aversion. Taste cues clearly augment the salience of color cues in aversion learning by pigeons (Clarke et al. 1979), and novelty does enhance aversion learning by chicks (Shettleworth 1972). Experiment 2 was designed to assess the importance of the CS when cues presented by the food were irrelevant. Oats paired with the CS were presented to intubated birds during conditioning and preference tests, while familiar Purina Flight Bird Conditioner paired with the CS was given to the observers during preference tests. The familiar food alone was presented to observers on the conditioning day.

METHODS

Subjects.—The remaining six naive Red-wings were used. The birds were maintained as described in Experiment 1.

Procedure.—The procedure of Experiment 2 was identical to that used on methiocarb-intubated birds in Experiment 1, except that during preference tests, the observer birds were presented with two 20-g samples of the familiar food, Purina Flight Bird Conditioner, and were never presented with oats.

RESULTS

Consumption by the intubated birds during preference tests was assessed using the exact randomization procedure (Edgington 1972). That procedure indicated that the intubated birds ate less of the oats paired with the CS than of the oats paired with the other color ($P < 0.05$). Consumption of food by observers of the intubated birds was assessed using a two-way analysis of variance (ANOVA) with

repeated measures on both factors. The factors were color cue and preference tests. The ANOVA indicated that the observers ate less of the Purina Flight Bird Conditioner paired with the CS than of the Conditioner paired with the other color cue [$F(1,3) = 11.25, P < 0.05$]. As in Experiment 1, there were no differences among measurements of consumption during the six preference tests ($P > 0.25$), and red and white appeared to be equally effective conditioning stimuli (see Fig. 2).

DISCUSSION

The results of Experiment 2 confirmed and extended the results of Experiment 1. Again, the Red-wings exhibited aversions to the CS as a result of observational learning. Unlike the results of Experiment 1, however, the results of the present experiment demonstrated that the type of food associated with the CS was relatively unimportant for the aversion learning. Aversions for the Purina Flight Bird Conditioner were observed only in the presence of the CS. As such, while taste or other cues associated with the oats may have contributed slightly to the aversion learning in Experiment 1, the conditioned aversions exhibited in Experiment 2 seemed as robust as those displayed in the initial experiment.

GENERAL DISCUSSION

In previous work with Red-wings, observational learning of food preferences dissipated over the course of four preference tests (Mason and Reidinger 1981). In contrast, the present experiments demonstrate that observational learning of food aversions is more durable, because robust differential behavior was recorded on each of the test days. Such findings are consistent with evidence suggesting that observational learning is facilitated when food resources are constricted (Hamilton and Gilbert 1969, Wilson 1975) or uncertain (McMillian 1974). As such, the present results support the notion that opportunistic foragers, such as Red-wings (Dolbeer 1980, Orians 1980), readily learn to avoid foods associated with aversive consequences (Klopfer 1958).

More broadly, the present work is consistent with the notion that Batesian model-mimic systems could be maintained, at least in part,

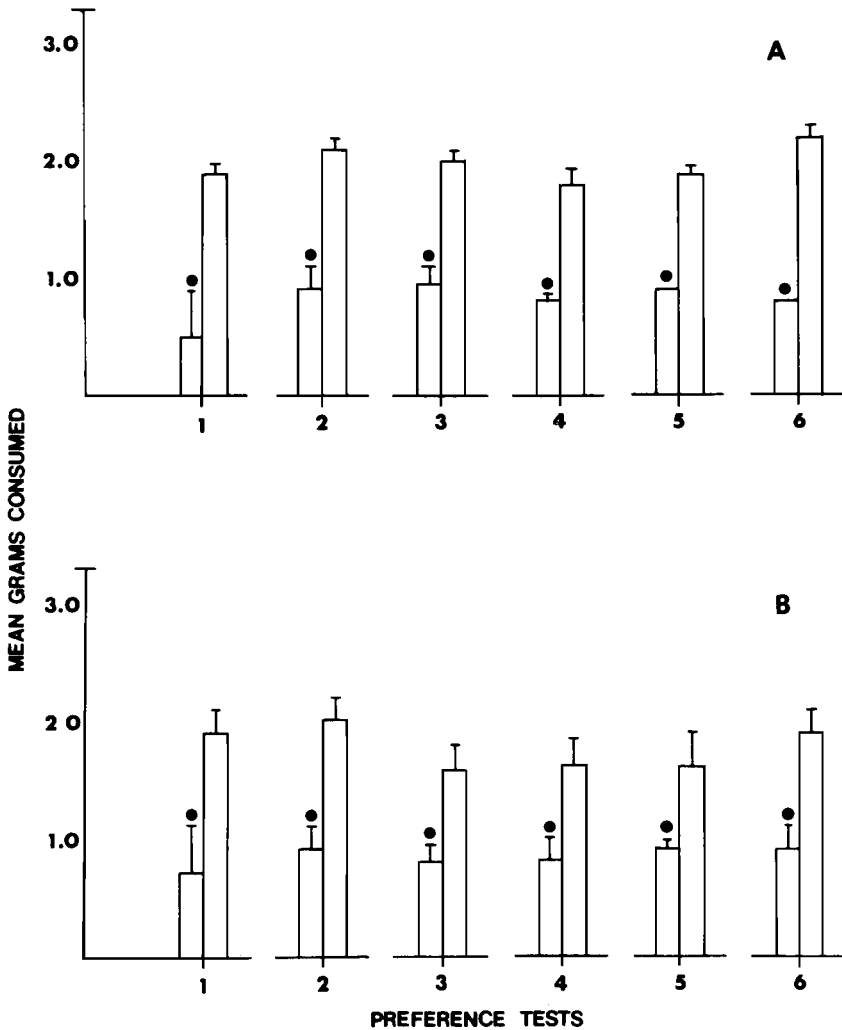


Fig. 2. A. Mean consumption of oats by birds intubated with methiocarb during each of the six preference tests. ● = consumption of oats paired with the CS. B. Mean consumption of Purina Flight Bird Conditioner by observers of methiocarb-intubated birds during each of the six preference tests. ● = consumption of Purina Flight Bird Conditioner paired with the CS. Standard errors of the means are represented by capped vertical bars.

as a consequence of observational learning of models and subsequent generalization of that learning to mimics. In the present experiments, Red-wings that observed methiocarb-intubated conspecifics subsequently avoided foods paired with the appropriate color cue (CS), even though consumption of the food paired with the CS was not followed by aversive post-ingestional consequences. Specifically, during the tests for observational learning of aversions, the food paired with the CS

“mimicked” the “model” food associated with methiocarb intubation. For such learning to be maximally effective for Batesian mimicry, the cues used by models and mimics would probably have to be simple, as were those used here. Many investigators have demonstrated that simple, easily generalized cues are the most effective stimuli in Batesian model-mimic systems (e.g. Duncan and Sheppard 1965, Morrell and Turner 1970, Terhune 1977), and evidence suggests that avian predators learn to

avoid conspicuous prey more readily than cryptic prey (Gittleman et al. 1980). Had complex (e.g. pattern) stimuli been used in the present work, the aversions might have been weaker or might not have occurred. In addition, the particular color cues used in the present experiments may have influenced the results. Red-wings do attend to some colors more than others (e.g. red) (Royall et al. 1974), and, in other species, some colors (e.g. red) result in more efficient observational learning (Reese 1975). On the other hand, the results of the present experiments suggest that white was as effective as red as a CS, and white is not a color typically used by Batesian models and mimics (Wickler 1968). Regardless, observational learning of food aversions could protect Red-wings, and other species, from ingestion of new but potentially dangerous prey items.

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LITERATURE CITED

- BROWER, J. V. Z. 1958a. Experimental studies of mimicry in some North American butterflies. Part I. The Monarch, *Danaus plexippus* and the Viceroy, *Limenitis archippus archippus*. *Evolution* 12: 32-47.
- . 1958b. Experimental studies of mimicry in some North American butterflies. Part II. *Battus philenor* and *Papilio trailus*, *P. polyxenes* and *P. glaucus*. *Evolution* 12: 123-136.
- . 1958c. Experimental studies of mimicry in some North American butterflies. Part III. *Danaus gilippus herenice* and *Limenitis archippus floridensis*. *Evolution* 12: 273-285.
- CAPRETTA, P. J. 1961. An experimental modification of food preferences in chicks. *J. Comp. Physiol. Psychol.* 54: 238-242.
- CLARKE, J. C., R. F. WESTBROOK, & J. IRWIN. 1979. Potentiation instead of overshadowing in the pigeon. *Behav. Neural. Biol.* 25: 18-29.
- COOMBS, S., S. REVUSKY, & B. T. LETT. 1980. Long-delay taste aversion learning in an unpoisoned rat: exposure to a poisoned rat as the unconditioned stimulus. *Learn. Motiv.* 11: 256-266.
- CZAPLICKI, J. A., D. E. BORREBACH, & H. C. WILCOXIN. 1976. Stimulus generalization of an illness-induced aversion to different intensities of colored water in Japanese Quail. *Anim. Learn. Behav.* 4: 45-48.
- DOLBEER, R. A. 1980. Blackbirds and corn in Ohio. U.S. Fish and Wildlife Serv. Res. Publ. 136.
- DRAGOIN, W. B., G. E. MCCLEARY, & P. A. MCCLEARY. 1971. A comparison of two methods of measuring conditioned taste aversions. *Behav. Res. Method. Instru.* 3: 309-310.
- DUECKER, G. 1976. Learning of three different positions in birds. *Z. Tierpsychol.* 42: 301-314.
- DUNCAN, C. L., & P. M. SHEPPARD. 1965. Sensory discrimination and its role in the evolution of Batesian mimicry. *Behaviour* 24: 270-282.
- EDGINGTON, E. S. 1972. Statistical inference and nonrandom samples. Pp. 146-149 in *Statistical issues: a reader for the behavioral sciences* (R. E. Kirk, Ed.). Monterey, California, Brooks-Cole.
- GAMES, P. A. 1971. Multiple comparison of means. *Amer. Ed. Res. J.* 8: 531-565.
- GILLETTE, K., J. D. IRWIN, D. K. THOMAS, & W. P. BELLINGHAM. 1980. Transfer of coloured food and water aversions in domestic chicks. *Bird Behav.* 2: 37-47.
- GITTLEMAN, J. C., P. H. HARVEY, & P. J. GREENWOOD. 1980. The evolution of conspicuous coloration: some experiments in bad taste. *Anim. Behav.* 28: 897-899.
- HAMILTON, W. J., & W. M. GILBERT. 1969. Starling dispersal from a winter roost. *Ecology* 50: 886-898.
- HOGAN-WARBURG, J. A., & J. A. HOGAN. 1981. Feeding strategies in the development of food recognition in young chicks. *Anim. Behav.* 29: 143-144.
- KLOPFER, P. H. 1957. Empathetic learning in ducks. *Amer. Natur.* 91: 61-63.
- . 1958. Influence of social interactions on learning rates in birds. *Science* 128: 903.
- . 1959. Social interactions in discrimination learning with special reference to feeding behavior in birds. *Behaviour* 14: 282-299.
- MASON, J. R., & R. F. REIDINGER. 1981. Effects of social facilitation and observational learning on feeding behavior of the Red-winged Blackbird (*Agelaius phoeniceus*). *Auk* 98: 778-784.
- , M. D. RABIN, & D. A. STEVENS. In press. Taste aversions used as a biological defense mechanism by tiger salamanders (*Ambystoma tigrinum*). *Copeia*.
- McMILLIAN, J. C. 1974. Average uncertainty as a determinant of observing behavior. *J. Exp. Anal. Behav.* 22: 401-408.
- MORELL, G. M., & J. R. G. TURNER. 1970. Experi-

- ments on mimicry: 1. The response of wild birds to artificial prey. *Behaviour* 36: 116-130.
- ORIAN, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton, New Jersey, Princeton Univ. Press.
- REESE, N. C. 1975. Imprinting as an independent variable in the modeling of a low-probability behavior in ducks. *Bull. Psychon. Sci.* 6: 28-30.
- RETTENMEYER, C. W. 1970. Insect mimicry. *Ann. Rev. Entomol.* 15: 43-74.
- ROGERS, J. G. 1974. Responses of caged Red-winged Blackbirds to two types of repellents. *J. Wildl. Mgmt.* 38: 418-423.
- . 1978. Some characteristics of conditioned taste aversions in Red-winged Blackbirds. *Auk* 95: 362-369.
- ROYALL, W. C., J. C. GUARINO, & O. E. BRAY. 1974. Effect of color on retention of leg streamers by Red-winged Blackbirds. *Western Bird Bander* 49: 64-65.
- SCHULER, W. 1980. Factors influencing learning to avoid unpalatable prey in birds re-learning new alternative prey and similarity of appearance of alternative prey. *Z. Tierpsychol.* 54: 105-143.
- SHETTLEWORTH, S. J. 1972. The role of novelty in learned avoidance of unpalatable prey by domestic chicks (*Gallus gallus*). *Anim. Behav.* 20: 29-35.
- TERHUNE, E. C. 1977. Components of a visual stimulus used by Scrub Jays to discriminate a Batesian model. *Amer. Natur.* 111: 435-451.
- WICKLER, W. 1968. *Mimicry in plants and animals*. New York, McGraw-Hill.
- WILSON, E. O. 1975. *Sociobiology: the new synthesis*. Cambridge, Massachusetts, Belknap Press.