Responses of Naive Temperate Birds to Warning Coloration

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ABSTRACT: Eight house sparrows (*Passer domesticus*), seven blue jays (*Cyanocitta cristata*) and two red-winged blackbirds (*Agelaius phoeniceus*), hand-reared on moderately varied diets, were offered a series of colors and patterns painted on wooden dowel models. All three species attacked every color and pattern without measurable hesitation; this included two patterns avoided by similarly hand-reared neotropical omnivores. The temperate birds' attack on aposematic patterns and their tolerance of novelty suggest that there is no widespread mechanism allowing newly fledged birds to reject the first aposematically marked organisms they encounter. The blue jays and red-winged blackbirds attacked a coral snake pattern, even though individuals of both species migrate into coral snake range, and young coral snakes are both prey-sized and potentially lethal. The difference in behavior between these northern migrants and the neotropical omnivores studies earlier may be related to the age at which each can encounter its first coral snake.

INTRODUCTION

Most known mimicry systems involve aposematically colored models. Predators in the wild tend to avoid such prey; Jones (1932, 1934) showed that wild birds strongly rejected insects conspicuously patterned in yellow, orange and red; and Morrell and Turner (1970) and others have shown that such rejection is widespread in wild birds. A question arises: Is learning really necessary for predators such as insectivorous birds to avoid an aposematic color or pattern, or is there perhaps some mechanism allowing them to reject the first aposematic organism they encounter?

While surprisingly little has been done to test this, the available data seem to indicate that some such mechanism exists. Coppinger (1970) hand-reared young blue jays (*Cyanocitta cristata*), red-winged blackbirds (*Agelaius phoeniceus*) and common grackles (*Quiscalus guiscula*) until they were 9-10 months old, and then offered them a variety of stimuli, including certain aposematic butterflies; he concluded that novelty itself is sufficient to cause naive birds to reject a stimulus, and indicated that naive birds would therefore tend to reject any aposematic insects they encountered on the basis of novelty alone. Recently I have found that hand-reared turquoise-browed motmots (*Eumomota superciliosa* and great kiskadees (*Pitangus sulphuratus*) have an inborn aversion to a yellow and red ring pattern (Smith, 1975, 1977). At least in the kiskadees, moreover, this aversion is not simply a rejection of novelty, since the birds had attacked the first contrasting ring pattern they had ever seen (white with green rings) with no hesitation. Both kiskadees and motmots are neotropical snake predators, and I interpret their responses as indicating an innate aversion to a generalized pattern of the deadly coral snake (*Micrurus* sp.). An alternative interpretation, however, is that the birds showed an innate aversion to a generalized aposematic pattern. If so, then other, nonsnake predators might also be expected to avoid yellow and red ring patterns. As Rettenmeyer (1970) pointed out, the hypothesis that insectivorous birds have innate avoidance to aposematic patterns has not been tested. The present experiments were designed to present naive, hand-reared birds, at the age when they would first be investigating potential food items in the field, with various patterns to test: (a) whether they show fear of novelty in color or pattern; (b) whether they show fear of yellow and red rings,

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and (c) whether they show fear of specific aposematic patterns.

MATERIALS AND METHODS

Seven blue jays from two broods and eight house sparrows (*Passer domesticus*) from three broods were removed from their nests in Nassau Co., New York, when they were 4-10 days old and hand-reared under laboratory conditions. At least some of each species were taken before their eyes had opened to ensure that they had had no chance to see any prey prior to their capture. The birds received a varied diet, including stew beef, dog meal, chopped young rat, meal worms and freshly killed crickets, with daily vitamin and mineral supplements. When able to perch and fly (approximately 25 days old), the birds were removed from their cardboard boxes and placed in 92 x 46 x 46 cm hardware cloth cages. The cages held no more than two birds each; only brood mates were held together. Concurrent observations on wild broods, and the hand-reared birds' own exploratory behavior, indicated that the birds were capable of catching insects by the age of 30-35 days; experiments were begun when the birds were 40 days old. In each experiment a wooden dowel model was placed on the cage floor and the number and location of each bird's pecks were recorded for a 5-min period. Blue jay models measured 5.0 x 1.0 cm; sparrow models, 3.0 x 0.5 cm. The models were painted with nontoxic tempera colors in the following five patterns: white with narrow green rings; yellow with narrow red rings; red with narrow black rings; "monarch caterpillar" rings (a complex pattern of yellow, white and black rings); "wasp" rings (yellow with narrow red rings), and "coral snake" rings (red, yellow and black). The birds received two types of model for each pattern: a solid model completely covered with the pattern, and an end-third form having only one end painted, the other two thirds being plain wood (Fig. 1). All birds received the patterns in the above order.

In addition, observations were made on a single brood of two red-winged blackbirds, treated in the same way as the other 15 nestlings. They were kept in a single cage, and received models measuring 3.7 x 0.6 cm.

Blue jays and red-winged blackbirds are omnivorous, and each is known to take a wide variety of large insects as well as some vertebrate prey (Bent, 1964, 1965; Johnson and Johnson, 1976). Both species are native to North America and locally common in New York, and at least some individuals of each species migrate each winter down into the range of coral snakes (*Micrurus fulvius* and/or *Micruroides euryxanthus*). Young coral snakes hatch in late September (Wright and Wright, 1957), just before the time when migrant birds start arriving in the area. At approximately 20 cm they are well within the prey size range of jays and blackbirds; and

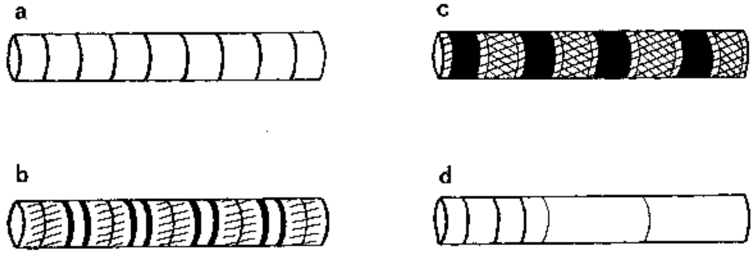

Fig. 1.—Examples of models used in the experiments, showing simple rings (*e.g.*, wasp) (a); monarch caterpillar (b); coral snake (c) and end third form (d). In b and c, single hatching indicates yellow; double hatching indicates red

the bite of even a newly hatched coral snake could probably kill a jay or blackbird in a matter of minutes (Wickler, 1968).

By contrast, house sparrows are not native to North America, having been introduced from Europe only ca. 100 years ago; moreover, there is apparently no record of this species taking vertebrate prey. While primarily granivorous, they eat insects such as beetles, butterflies and moths whenever available, even in the non-breeding season (Bent, 1965). House sparrows encounter a wide variety of aposematic insects, but would never encounter coral snakes.

If innate aversion to yellow and red rings evolved as protection for naive birds against attacking coral snakes, blue jays and red-winged blackbirds might show this aversion, but house sparrows certainly would not. On the other hand, if such an aversion is simply avoiding a generalized aposematic pattern, then all three species might be expected to show it.

RESULTS

Before receiving the patterned models, the birds had been given solid models of plain white, green, red, yellow and black; every bird attacked these plain models with no hesitation. Apparently, therefore, these species have no inborn fear of such classically warning colors as red, yellow or black, nor was the novelty of either their first wooden model or of their first bright color sufficient to cause any measurable hesitation in their attack. In this respect they behaved in the same manner as hand-reared turquoise-browed motmots and great kiskadees (Smith, 1975, 1977).

When given solidly patterned models, every bird attacked each of the five models with no apparent hesitation or alarm calls; their behavior towards yellow and red rings and even toward "coral snake" rings was no different from their response to white and green rings (Table 1). This response contrasts strongly with the behavior of the motmots and kiskadees mentioned above. Each species showed similar distribution of pecks along model length for every pattern given.

When the patterns were presented in end-third form, both the jays and the sparrows gave a significant response to the painted section of all five patterns (Table 2). Again this response is strikingly different from that of the two neotropical snake predators.

Jay and sparrow data were analyzed using X^2. The first step for each species was to run X^2 tests for heterogeneity on the results for each experiment. As there was no significant heterogeneity either among jays or among sparrows, the responses of all individuals of each species could be summed for further analysis.

The observations on the blackbirds suggest that they behave similarly to the jays and sparrows, since they attacked every color and pattern immediately, and directed more than 76% of their pecks to the painted section of every end-third model.

TABLE 1.—Responses to solidly patterned models

	Blue jays (7)			House sparrows (8)		
	% pecks at:		Total	% pecks at:		Total
Model	ends	middle	pecks	ends	middle	pecks
Plain wood	92.18	7.82	409	87.41	12.59	302
W & G ring	65.95	34.04	693	68.42	31.58	228
Y & R ring	65.88	34.12	469	67.33	32.67	300
R & BK ring	66.59	33.41	434	64.58	35.42	192
Wasp	68.75	31.25	576	65.53	34.47	264
M. L.	67.22	32.78	662	66.46	33.54	319
C. S.	65.80	34.20	541	63.59	36.41	206

M. L. = monarch larva pattern
C. S. = coral snake pattern

DISCUSSION

All three species showed no hesitation in attacking the yellow and red ring pattern, and directed most of their pecks at the painted third when given this pattern in end-third form. There is thus no widespread innate aversion to such a generalized aposematic pattern that might enable naive young birds to avoid noxious prey on first encounter.

Moreover, none of the three species gave any indication of fear of novelty, either in color or in pattern. This is in marked contrast to the theory that young birds reject novel stimuli. The idea of novelty rejection is widely accepted and appears in most recent reviews of mimicry, *e.g.*, Turner (1977: 165), "Birds do not readily attack novel prey. . ." Yet this seems to be based on very few studies, primarily that of Rabinowitch (1968) who found that 30% of young gulls raised on a severely restricted diet starved to death rather than accept novel foods, and Coppinger's (1970) work on hand-reared blue jays, grackles and red-winged blackbirds mentioned above. It is interesting that my hand-reared blue jays and red-winged blackbirds behaved so differently from Coppinger's. Since the two groups hatched less than 400 miles apart and belong to the same subspecies, it is unlikely that any genetic behavioral differences exist between the two populations; I believe the differences are results of differing experimental techniques.

Probably the most important of these is the timing of experiments. Coppinger's birds were 9-10 months old before they received their first novel food items; this is equivalent to birds hatched in June receiving their first new prey the following March or April. By contrast I timed my experiments to coincide with the period when young birds would first be exploring the wild; this is the age at which they would be most likely to encounter their first aposematic prey naturally. A second difference in experimental technique is the restricted nature of the diet that both Rabinowitch's gulls and Coppinger's jays, grackles and blackbirds were raised on before being offered novel food. My birds received at least a moderate variety of food; similarly, Alcock (1973) raised red-winged blackbirds on a moderately varied diet and found no evidence of novelty rejection. This does not mean that novelty has no effect on a bird's behavior; Shettleworth (1972) found that chicks learn to reject novel stimuli more rapidly than they learn to reject familiar ones. Whether or not novelty is later rejected or even actively chosen by avian predators has recently been debated (Mueller, 1971, 1975, 1977; Kaufman, 1973). Nevertheless, as far as mimicry is concerned, novelty rejection at first sight by newly fledged wild birds now appears unlikely. Hence, there is apparently no general mechanism that allows naive newly fledged birds to avoid aposematic coloration.

It remains possible, however, that naive birds might show certain specific aversions. Most of the particular patterns of warning coloration that the birds received,

TABLE 2.—Responses to end-third models

	Blue jays (7)					House sparrows (8)				
	% pecks at:			Total		% pecks at:			Total	
Pattern:	p	m	unp.	pecks	X^2	p	m	unp.	pecks	X^2
W & G ring	89.41	1.51	9.08	595	**	82.68	2.61	14.71	306	**
Y & R ring	72.64	12.52	14.84	775	**	78.09	1.12	20.79	178	**
R & BK ring	81.65	4.93	13.42	648	**	79.92	4.33	15.75	254	**
Wasp	77.91	5.15	16.94	602	**	84.66	1.84	13.50	163	**
M. L.	86.71	4.77	8.52	582	**	75.35	0.71	23.94	142	**
C. S.	80.66	5.08	14.26	512	**	88.60	3.11	8.29	193	**

M. L. = monarch larva pattern
C. S. = coral snake pattern
** indicates a significant response to the painted third at the 0.01 level

such as the wasp pattern and that of the fifth instar monarch butterfly (*Danaus plexippus*) were of nonlethal aposematic prey. Since the penalty for eating or attempting to eat such prey is mild (Brower, 1969; Reiskind, 1965; Rothschild, 1971), learning is perfectly possible. The present data suggest that naive birds will attack all such patterns without hesitation and learn to avoid them only by experience.

This leaves only consideration of responses to lethal patterns. Since a generalized aposematic aversion apparently does not exist, or at least is not universal among birds, it is now clear that the aversion to yellow and red rings shown by motmots and kiskadees (Smith, 1975, 1977) is indeed rejection of a generalized coral snake pattern. Yet neither of the two omnivores whose range potentially overlaps with the coral snake (jays and blackbirds) showed any hesitation in attacking either the yellow and red ring pattern or even the coral snake pattern itself. Why does their behavior differ so markedly from that of naive motmots and kiskadees raised and handled in the same manner?

The answer may lie in the difference in age at which young birds first encounter a coral snake. Jays and blackbirds from northern populations generally do not arrive in coral snake range until October or November, *i.e.*, when they are approximately 4-5 months old. By contrast, Costa Rican kiskadees and motmots hatch in coral snake range, and thus potentially could encounter their first lethal snake as soon as they fledge. This age difference might affect how dangerous a coral snake is to a potential predator in several ways.

One of these is levels of curiosity. Newly fledged birds show very high levels, readily pecking at any prey-sized object such as twigs that they encounter. However, this curiosity level declines markedly with age, and would be considerably lower by the 4th month (Vince, 1960; Smith, 1973, 1974). The danger of pecking at a coral snake simply out of curiosity would thus be far greater to birds hatched in coral snake range than to individuals arriving at the age of 4 or more months.

A second factor that might cause older birds to be less likely than younger ones to attack their first coral snake is novelty rejection. Thus far, the only evidence for this in passerines is Coppinger's work; since my 50-day-old jays and blackbirds did not reject novelty whereas his 270-day-old birds did, perhaps the likelihood of novelty rejection increases with age. More work with birds raised on more natural diets is necessary to see whether or not this is really so.

The third way in which age of first encounter can influence how dangerous its first coral snake is to a bird is perhaps the most important. The older a bird is, the more time it has had to encounter nonlethal aposematic insects. Schuler (1974) has shown that at least certain bird species have excellent memories, since after an interval of 133 days without tests his starlings (*Sturnus vulgaris*) still avoided an aposematic model as frequently as they had before the interval. Similarly, crows (*Corvus*) can remember aposematic insects for at least 9 months, and two species of tits (*Parus*) refused to eat an aposematic moth 12 months after their last experience with aposematic insects (Rettenmeyer, 1970). The careful work of Brower, *et al.* (1971) and others clearly demonstrates that birds in the field can and do generalize to avoid patterns other than those they have experienced previously. Finally, many studies have shown that wild birds strongly reject brightly colored prey in the field (*e.g.*, Jones, 1932, 1934; Allen and Clarke, 1968; Morrell and Turner, 1970). The red, black and yellow of a coral snake are among the most universal of aposematic colors, and a ring pattern is among the most common aposematic patterns (Wickler, 1968). Northern populations of jays and blackbirds will have plenty of time to experience nonlethal aposematic insects and to generalize to avoid other brightly colored organisms before arriving in coral snake range.

Clearly much work needs to be done to see whether any or all of these do, in fact, affect migrants' responses to their first coral snake pattern. The most southern populations of both jays and red-winged blackbirds breed within the range of coral snakes. It would be very interesting to see whether naive young birds from these areas differ behaviorally from those of more northern populations.

LITERATURE CITED

ALCOCK, J. 1973. The feeding response of hand-reared Red-winged Blackbirds (*Agelaius phoeniceus*) to a stinkbug (*Euschistus conspersus*). *Am. Midl. Nat.*, **89**:307-313.

ALLEN, J. A. AND B. CLARKE. 1968. Evidence for apostatic selection by wild passerines. *Nature*, **220**:501-502.

BENT, A. C. 1964. Life histories of North American jays, crows, and titmice. Part 1. *U.S. Natl. Mus. Bull.*, **211**.

———. 1965. Life histories of North American blackbirds, orioles, tanagers, and allies. Dover Publ. Inc., N.Y.

BROWER, L. P. 1969. Ecological Chemistry. *Sci. Am.*, **1969**:22-29.

———, J. ALCOCK AND J. V. Z. BROWER. 1971. Avian feeding behaviour and the selective advantage of incipient mimicry, p. 261-274. *In:* R. Creed (ed.). Ecological genetics and evolution. Appleton-Century-Crofts, New York.

COPPINGER, R. P. 1970. The effect of experience and novelty on avian feeding behavior with reference to the evolution of warning coloration in butterflies. II. Reactions of naive birds to novel insects. *Am. Nat.*, **104**:323-335.

JOHNSON, K. W. AND J. E. JOHNSON. 1976. An incident of Blue Jay predation on a Yellow-rumped Warbler. *Wilson Bull.*, **88**:509.

JONES, F. M. 1932. Insect coloration and the relative acceptability of insects to birds. *Trans. R. Entomol. Soc. Lond.*, **80**:345-386.

———. 1934. Further experiment on coloration and relative acceptability of insects to birds. *Ibid.*, **82**:443-453.

KAUFMAN, D. W. 1973. Shrike prey selection: color or conspicuousness? *Auk*, **90**:204-206.

MORRELL, G. M. AND J. R. G. TURNER. 1970. Experiments on mimicry: I. The response of wild birds to artificial prey. *Behaviour*, **36**:116-130.

MUELLER, H. C. 1971. Oddity and specific searching image more important than conspicuousness. *Nature*, **233**:345-346.

———. 1975. Hawks select odd prey. *Science*, **188**:953-954.

———. 1977. Prey selection in the American kestrel: experiments with two species of prey. *Am. Nat.*, **111**:25-29.

RABINOWITCH, V. E. 1968. The role of experience in the development of food preference in gull chicks. *Anim. Behav.*, **18**:425-428.

REISKIND, J. 1965. Behaviour of an avian predator in an experiment simulating Batesian mimicry. *Ibid.*, **13**:466-469.

RETTENMEYER, C. W. 1970. Insect mimicry. *Annu. Rev. Entomol.*, **15**:43-74.

ROTHSCHILD, M. 1971. Speculations about mimicry with Henry Ford, p. 202-223. *In:* R. Creed (ed.). Ecological genetics and evolution. Appleton-Century-Crofts, New York.

SCHULER, W. 1974. Die Schutzwirkung kunstlicher Batesscher Mimikry abhängig von Modellähnlichkeit und Beuteangebot. *Z. Tierpsychol.*, **36**:71-127.

SHETTLEWORTH, S. J. 1972. The role of novelty in learned avoidance of unpalatable "prey" by domestic chicks (*Gallus gallus*). *Anim. Behav.*, **20**:29-35.

SMITH, S. M. 1973. A study of prey-attack behaviour in young Loggerhead Shrikes, *Lanius ludovicianus* L. *Behaviour*, **44**:113-141.

———. 1974. Factors directing prey attack by the young of three passerine species. *Living Bird*, **12**:55-67.

———. 1975. Innate recognition of coral snake pattern by a possible avian predator. *Science*, **187**:759-760.

———. 1977. Coral-snake pattern recognition and stimulus generalization by naive great kiskadees (Aves:Tyrannidie). *Nature*, **265**:535-536.

TURNER, J. R. G. 1977. Butterfly mimicry: The genetical evolution of an adaptation, p. 163-206. *In:* M. K. Hecht, W. C. Steere and B. Wallace (eds.). Evolutionary biology, vol. 10. Plenum, New York.

VINCE, M. A. 1960. Developmental changes in responsiveness in the Great Tit (*Parus major*). *Behaviour*, **15**:219-243.

WICKLER, W. 1968. Mimicry in plants and animals. McGraw-Hill, New York. 255 p.

WRIGHT, A. H. AND A. A. WRIGHT. 1957. Handbook of snakes of the United States and Canada. Vol. II, p. 565-1105. Comstock Publishing Associates, Ithaca.

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