Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae)

THE neotropical coral-snake complex with its contrasting ringed patterns includes true coral snakes, for example. the highly venomous elapid genus *Micrurus*, and many colubrids that are either less strongly venomous or non-venomous[1]. Whether or not this complex involves Batesian and/or Müllerian mimicry has been widely debated[2-8]. Wickler[1] suggested that if mimicry depends on predator learning, true coral snakes are too deadly to be models; rather, they are mimics of the less dangerous colubrids of the complex (Mertensian mimicry). He also claimed that there was no evidence that any predator could recognise a coral snake innately[1]. I have shown that Costa Rican turquoise-browed motmots (*Emomota superciliosa*) need no learning to show strong aversion to a pattern of wide yellow and narrow red rings[9]: this I have interpreted as an innate recognition of a generalised coral-snake pattern. No Costa Rican member of the coral-snake complex has wider yellow than red rings, however, so I had no proof that the motmots were not simply showing an aversion to a general aposematic pattern. I present here evidence that another avian predator needs no learning to avoid not only a pattern of wide yellow and red rings, but also the most common local *Micrurus* pattern of red, yellow and black rings.

The great kiskadee (*Pitangus sulphuratus*) occurs in open and semi-open habitats from southern United States (Texas) to south Argentina. It regularly eats small reptiles[9], and *Micrurus* and many other members of the complex occur over much of its range. These snakes could be dangerous to kiskadees. *Micrurus* in particular may lie partly concealed in leaf litter during the day, often with its head under leaves. A kiskadee attacking the exposed portion of such a snake would be in danger of being bitten, especially if that portion did not include the head. As kiskadees lack heavy protecting scutes on their legs, such a bite could well prove fatal.

Six young kiskadees from three broods aged 12–20 d were removed in May 1976 from their nests in north-western Costa Rica and raised in the laboratory in 91×46×46-cm hardware cloth cages. Two cages each held two birds; the other two held one each. Experiments in these cages were begun when the kiskadees were old enough to catch their own prey, that is, 45 d. In each experiment a wooden dowel model 6 cm long and 1 cm in diameter was placed on the cage floor and the number and location of the birds' pecks

was recorded for 5 min. Models were painted with non-toxic tempera colours in the following five patterns: white with narrow green rings; yellow with narrow red rings; yellow with narrow red stripes; 'coral-snake' rings (wide red, narrow yellow, wide black, narrow yellow); and coral-snake stripes. Two models were made for each pattern: a 'solid' model completely covered with the pattern, and an 'end-third' model having only one end painted, the other two thirds being plain wood (Fig. 1). With the exception mentioned below, all birds received the patterns in the above order.

Each kiskadee had previously attacked solid models of plain white, green, red, yellow and black without hesitation. Of the five patterns on solid models, two were completely avoided, two readily attacked, and one attacked with great caution (Table 1). Although no kiskadee approached either the yellow and red ring or the coral-snake ring model, the responses to the two differed. Only two birds gave mild alarm calls to the former; the same two plus at least two more gave high intensity alarm calls (like those given by a captured bird) to the latter. Their response to the white and green ring model (the first pattern any bird received) shows that they did not fear ring patterns in general. Nor did they hesitate to attack the yellow and red stripe model, which has a relative proportion of yellow and red identical to that of the ring pattern. Unexpectedly, although all six birds approached the solid coral-snake stripe model, all showed great hesitation, and the four birds that finally did attack did so by darting forward with spread wings and contour feathers tightly in.

With the end-third models, the birds directed most of their pecks to the painted third of the white and green ring, the yellow and red stripe, and the coral-snake stripe models, but gave a significant response to the end farthest away from both the yellow and red ring and the coral-snake ring models (Table 1). Kiskadees thus consistently avoid the coral-snake ring and the yellow and red ring patterns, but hesitate to attack the coral-snake stripe pattern only when it covers the entire model.

This aversion to the two ring patterns seems to require no learning. Kiskadees have covered nests, and the three youngest birds barely had their eyes open when they were taken, so it is unlikely that they perceived any patterns in the dim light within their nest before their capture. Coppinger[9] found that naive passerines of three species gave alarm calls and active escape behaviour to a large variety of novel stimuli, the degree of rejection depending on the amount of stimulus change and the birds' previous experience. The order in which the kiskadees received the

Fig. 1 Models used in the experiments. *a*, Solid forms. *b*, End-third forms. The basic patterns were; 1, white and green (or yellow and red) rings; 2, yellow and red stripes; 3, coral snake rings, and 4, coral snake stripes. The three sections of the end-third models were recorded as p, m and u.
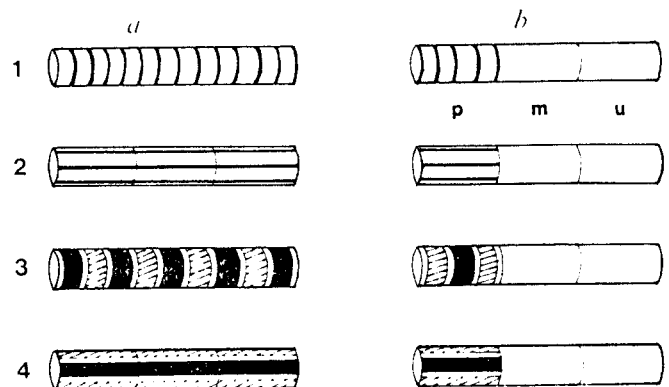
Table 1 Kiskadees' pecks to the ten models

Pattern	Pecks at solid models	Pecks at end-third models % at each area			Total pecks	χ^{2*}
		p	m	u		
White and green ring	59	100	—	—	51	p
Yellow and red ring	—	17.86	—	82.14	28	u
Yellow and red stripe	44	100	—	—	45	p
Coral-snake ring	—	11.11	—	88.89	9	u
Coral-snake stripe	7	100	—	—	23	p

*p indicates a response to the painted third at $P < 0.01$; u indicates a response to the unpainted end at $P < 0.05$.

models was designed to test for such novelty effects. The first pattern given was the white and green ring, which all birds attacked without hesitation: neither fear of patterns themselves nor fear of rings can thus be attributed to novelty. Because the three oldest birds had received the coral-snake ring model before the coral-snake stripe model, however, their hesitation to attack the latter might have been due to their earlier experience. The three youngest birds were therefore given the stripes before the rings. They responded in a manner similar to that of the older birds (Table 1), showing that this hesitation was not caused by previous experience.

The kiskadees' avoidance of the two ring patterns thus seems to be innate. It is unlikely that two separate innate aversions are involved; their stronger rejection of the coral-snake models, both rings and stripes, suggests that great kiskadees have an innate aversion to the coral-snake pattern, yet will generalise to avoid a pattern of wide yellow and narrow red rings.

Pattern generalisation by predators is essential for the functioning and evolution of both Batesian and Mullerian mimicry[1,10]. If mimics evolve by microevolution, broad stimulus generalisation by local predators is necessary to give selective advantage to early divergent phenotypes just beginning to approach the model in pattern. For predators that have learned to avoid a pattern, such generalisation is well documented[11-12]. My results show that generalisation can also occur with an innate aversion. In the presence of such predators, classical Batesion or Müllerian mimics can theoretically evolve even when the model is lethal; furthermore, for Batesian mimics, the model need not be numerically more abundant than the mimic[13]. If innate recognition and generalisation of the coral snake pattern is a common phenomenon, the Mertensian mimicry hypothesis is unnecessary to explain the evolution and maintenance of the coral snake mimicry complex.

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