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Polymorphic Clay Models of *Thamnophis sirtalis* Suggest Patterns of Avian Predation¹

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ABSTRACT. Models of snakes varying in color pattern have been used to test hypotheses about predation and mimicry. In the present study, clay models of the common garter snake were used to test for a difference in attack frequency between adult and juvenile striped and melanistic garter snakes; such difference may indicate a difference in cryptic coloration between the two morphs. The research was performed on the shores of Sandusky Bay and Lake Erie, where polymorphic garter snake populations contain both striped and melanistic garter snakes. There was no difference in attack frequency between the two morphs; however, juvenile snake models were attacked more frequently than adult ones. The study suggests that melanism may not confer a strong disadvantage with respect to visually-oriented predators.

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INTRODUCTION

Color polymorphisms have significant implications for the ecology and evolution of animals because of the importance of color pattern in predator avoidance, physiology, thermoregulation, and intraspecific signaling. A striking form of polymorphism is found in the common garter snake, *Thamnophis sirtalis*. Throughout most of its extensive range, *T. sirtalis* has variable small dorsal “checkers” of tan, white, brown, and black, and sometimes yellow or orange, and a light-colored (ivory to yellow) dorsal stripe running most of the length of the body (see Conant and Collins 1998). In the Lake Erie region, melanism, or extremely dark epidermal coloration, is relatively prevalent (up to 59%, King 1988). Melanistic garter snakes are hypothesized to suffer greater predation than their striped counterparts (Gibson 1978; Gibson and Falls 1979, 1988; Lawson and King 1996). Melanistic snakes may appear less cryptic to predators because they lack disruptive coloration and contrast strongly against natural backgrounds found in the region. However, melanism may provide a thermal benefit which may enhance fitness (Gibson and Falls 1988; Bittner and others 2002). In this study, I used clay models of the common garter snake to test for a difference in attack frequency between adult and juvenile striped and melanistic garter snakes, which may indicate a difference in the level of cryptic coloration (hereafter, crypsis) between the two morphs.

A systematic analysis of a large number of snake taxa concluded that the dorsal pigmentation patterns of snakes (for example, blotched, striped, banded) are strongly influenced by selection for predator avoidance, and patterns tend to be correlated with specific behavioral strategies and ecological niches (Jackson and others 1976). For example, blotched snakes tend to lie motionless and use crypsis to avoid detection but, if detected, rely on defensive behaviors over flight to avoid predation. This association between pattern, ecology,

and behavior strongly suggests that selection favors certain combinations of pattern and behavior over others.

Both uniformly colored (for example, melanistic) and striped snakes tend to rely on a flight-oriented anti-predator strategy because their patterns lack reference points on which predators can focus (Jackson and others 1976). Thus, when moving forward, these patterns create an illusion of immobility or reduced speed. There are two main differences between uniform and striped patterns. First, striped patterns may be more cryptic because the stripe functions disruptively (that is, it breaks up the outline of the body). Second, stripes may augment the illusion of immobility when moving because they make the body appear narrower, and narrow shapes have lower apparent velocities than broad shapes (Jackson and others 1976). In garter snakes, the striped/checked pattern is more disruptive and the coloration matches the background more closely than melanistic coloration. Therefore, melanistic snakes should be at a disadvantage with respect to escaping predators, all else being equal.

Scars found on live snakes have been used to infer predation patterns, but the relationship between predation and observed scar frequencies in live reptiles is ambiguous (Schoener 1979; Jaksic and Greene 1984). Some scars may not be the result of interactions with predators. Even if all scars and tail breaks are attributable to attacks by predators, differences in injury frequency between morphs may be interpreted in one of two ways: 1) one morph was attacked more often than the other, or 2) one morph was better able to survive attacks than the other.

Because it is so difficult to assess predation on live snakes, a common approach is to offer snake models to predators. Wooden, clay, plaster, plastic, and rubber models have been used in studies of predation and mimicry (Smith 1975, 1977; Andren and Nilson 1981; King 1987; Brodie 1993; Brodie and Janzen 1995; Hinman and others 1997). In the field, clay models provide an advantage over other types because clay clearly records beak or tooth marks, whereas predation attempts on hard models can be detected only by displacement from their original locations; the agent of

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displacement is unknown. Of course, model snakes do not exhibit antipredator behaviors nor do they flee from predators; therefore, only the effect of color, pattern, and body size on initial detection by predators can be tested. Because many visual predators "cue" on movement, motionless models may escape the notice of some predators. In this study, the focus was on avian predators because they generally hunt using visual cues, whereas many mammals rely more heavily on auditory and olfactory cues.

Selective pressures may change through ontogeny, but most studies have focused on adult snakes. The difference in crypsis between morphs may have a greater effect on juvenile than adult garter snakes because they may fall prey to a larger variety of predators, chiefly birds (Brodie 1992). In addition, predators may be more efficient in their attacks on young snakes (Willis and others 1982; Mushinsky and Miller 1993). However, juveniles are usually underrepresented in field studies of snakes, thus making it difficult to test predictions or draw conclusions about the relative selective pressures on them (Willis and others 1982; King 1987; Parker and Plummer 1987; Mushinsky and Miller 1993). For these reasons, juvenile-sized models were included in this experiment.

MATERIALS AND METHODS

Clay model snakes were used to determine the effects of color pattern and snake size on the frequency of predation attempts. Models were formed by hand from Sculpey-III® modeling compound (Polyform Products, Schiller Park, IL). This material remains soft enough to retain beak marks of birds and tooth marks of mammals, which are easily distinguished. Models had realistic proportions, heads, and tapering tails, unlike clay models used in other studies, which were cylindrical (Brodie 1993; Brodie and Janzen 1995; Hinman and others 1997; Pfennig and others 2001). Models fell into one of four categories: adult (50.0-55.0 cm total length, mass 25.0-30.0 g), striped or melanistic; and juvenile (20.0-25.0 cm total length, mass 2.0-3.0 g), striped or melanistic. Melanistic models were made from plain black modeling compound, and striped models from a medium-brown blend of several colors. For the stripe, a mid-dorsal indentation was filled with tan-colored clay. To further assess realism, I measured the percent reflectances of models and live striped and melanistic garter snakes over the visual spectrum (400-700 nm) using a fast spectral scanner.

The experiment was conducted at two mainland sites in Ohio where potential avian predators are plentiful: Winous Point Shooting Club, bordering Sandusky Bay, and Metzger Marsh, bordering Lake Erie. Potential avian predators seen at these sites included gulls, herons, egrets, raptors, crows, and a variety of smaller birds such as sparrows, blackbirds, and sandpipers. Each site had a raised dike topped by a dirt road which separates a wetland from a larger body of water. Since there may be differences in predation intensity between the two sides of the road, I placed equal numbers of each type of model along transects on each side. At Winous Point,

models were placed between the grass and dirt along the marsh side of the road and on the exposed tops of large rocks 1.0-2.0 m above the water line on the bay side of the road. At Metzger Marsh, models were placed in a mixture of small- to medium-sized rocks and dirt with scant vegetation on the marsh side of the road and on the tops of large rocks 3.0-5.0 m above the water line on the lake side of the road. In general, the rocks were very light-colored and models were quite visible on the bay/lake transects, whereas the vegetation and dirt on the marsh transects provided a more cryptic environment.

The experiment was repeated four times. Models were placed in various natural curved positions at 2.0-4.0 m intervals along these two transects. Model placement alternated regularly along the transect in a set pattern (adult melanistic, juvenile striped, adult striped, juvenile melanistic). After an interval ranging from 4 to 7 days, models were scored and picked up. Multiple beak marks were scored as a single predation attempt, and a single lost model (an adult striped model) was conservatively scored as unattacked (see Brodie and Janzen 1995). Between experiments, models were reshaped and damaged models were replaced to maintain the desired sample size for each trial. In each of the first three experiments, 120 models (30 per category) were used. In the final experiment, only juvenile models were used, alternating placement of striped and melanistic. Sixty juvenile models of each morph were used, for a grand total of 480 models (Table 1). Because attack rates were expected to be low based on previous studies (see Discussion), the large sample size per trial was chosen in order to obtain adequate data.

A two-tailed *t*-test was used to determine whether the average proportion attacked differed significantly from zero. Because proportions are not normally distributed, I first transformed the total proportion attacked for each trial ($n = 4$ trials) using the arcsine transformation.

The data were pooled across all four experiments for analysis. I used SPSS for Windows version 7.5 to perform general loglinear analysis as in King (1987). Loglinear analysis is appropriate because it can test the influence of two variables (morph and size) simultaneously, and it is not affected by contingency table cells with small expected frequencies (contrast Chi-square goodness-of-fit). The null hypothesis is statistical independence among morph, size, and attack score. The test statistic, *G*, is acquired by comparing a statistical model containing a particular interaction to one lacking it. For example, to test the independence of morph and attack score, the *G*-value of a model containing the morph by attack interaction was subtracted from the *G*-value of a model containing only the main effect of morph. *P*-values are obtained from the Chi-square distribution and independence is rejected if $P < 0.05$.

Because the number of days of exposure and the number of juvenile and adult models differed, relative attack rates (# attacked/# exposed/# of days) were also calculated for each category. Statistical tests were not performed on the relative attack rates, but they illustrate the basic pattern of the data.

TABLE 1

Number of models attacked by birds over number offered in each experiment.

Date	Site*	Duration	Size	Striped	Melanistic	Total
May 1996	1	5 days	juvenile	9/30	8/30	17/60
			adult	6/30	2/30	8/60
June 1996	1	7 days	juvenile	2/30	2/30	4/60
			adult	0/30	0/30	0/60
August 1996	2	4 days	juvenile	3/30	1/30	4/60
			adult	1/30	3/30	4/60
May 1997	2	5 days	juvenile	5/60	8/60	14/120
Total				26/240	24/240	50/480

*1 = Winous Point Shooting Club, 2 = Metzger Marsh

Mammal attacks were counted and relative attack rates were calculated, but no loglinear analysis was performed for mammal attacks.

RESULTS

Spectral scanner data showed that clay models were very similar in reflectance to live snakes. Melanistic snakes ranged from 1.75-5.4% while black clay was 1.7%. When comparing the sides of the dorsum (at mid-body, excluding the dorsal stripe), live snakes ranged from 3.5-12.8% and models ranged from 7.0-11.1%.

The average proportion attacked by birds over the four trials was significantly greater than zero ($t = 5.035$, $0.01 < P < 0.02$). The relative attack rates were identical for striped and melanistic juveniles (6.03×10^{-3} models attacked per day). The adults had lower relative attack rates (striped: 4.86×10^{-3} ; melanistic: 3.47×10^{-3} models attacked per day). Statistically, there was no difference in attack frequency between the two morphs (morph by score interaction, $G = 0.0989$, $P > 0.75$). There was a significant difference in attack frequency between the two sizes of models (size by score interaction, $G = 4.5200$, $P < 0.05$, Table 1). In other words, a model's chance of being attacked is independent of its color, but not independent of its size. As illustrated by the relative attack rate, juvenile models were attacked more frequently than adult models, regardless of morph.

Attacks by mammals showed a similar pattern. There was no difference in attacks between striped and melanistic morphs, but many more mammal attacks occurred on juvenile models than on adult models. Relative mammal attack rates were: juvenile striped and melanistic (both), 7.3×10^{-3} ; adult striped, 1.38×10^{-3} ; adult melanistic, 2.08×10^{-3} .

It was very easy to distinguish between bird beak marks and mammal teeth marks on the clay. The size of the marks also indicated the relative size of the predator. Most of the beak marks appeared to belong to smaller species such as sparrows and blackbirds, but a few

marks were from much larger birds, possibly great blue herons. In some cases the tail was completely severed. The mammal marks belonged to small rodents; none appeared to belong to carnivores.

DISCUSSION

Avian predators do not seem to discriminate between striped and melanistic garter snake models; they attacked each morph with equal frequency. This suggests that the melanistic models were no less cryptic than the striped models on backgrounds found in the region. Both morphs were conspicuous on the light-colored limestone found on shorelines; however, I placed half of the models on vegetated/soil transects where morph differences in crypsis were more likely.

Avian predators seem to distinguish between juvenile and adult model snakes as prey items because the attack frequency on adult models was significantly lower than on juvenile models, regardless of morph. This could be due to the small size of most birds which attacked the models. The fact that small birds stayed away from the adult models suggests that models were perceived as real snakes. Although a small snake may provide food for a small bird, a large snake may prey upon a small bird, so selection would favor avoidance of large snakes. Interestingly, small rodents also seemed to avoid the adult models. However, it is not clear why more large birds did not attack the models.

I assumed that snakes would be attractive prey for large birds, but most of the bird species observed near the transects are aquatic predators and scavengers feeding on fish; snakes onshore may not represent a common food item for them. The specific bird species attacking the models should be identified, perhaps using triggered cameras. Future studies using clay models should test the assumption that models are perceived as real snakes, perhaps by placing "control" shapes among the snake models. These controls would be the same color and size as the snake models, but would not

resemble snakes or other potential food items, and should not be attacked. The results would help to distinguish whether birds are merely pecking at a new substance in their environment.

Similar predation studies fall into two general categories: testing intraspecific or interspecific color pattern variation. To facilitate comparison among studies, the phrase "attack frequency" will be used to refer to the percentage of models attacked during the time frame of the study. However, the time frame varies among studies from several hours to 6 days. Furthermore, some studies included mammalian as well as avian attacks.

Intraspecific studies like this one test for predation differences between morphs in a polymorphic population. Andren and Nilson (1981) used plastic models to test for differences in predation between normal and melanistic morphs of the adder *Vipera berus* on an island in Sweden. They found a significantly higher attack frequency on the melanistic morph, suggesting that the normal morph (a disruptive "zig-zag" pattern) is more cryptic. The Lake Erie water snake is also polymorphic, ranging from banded to unbanded (uniform) gray coloration. Although unbanded individuals are hypothesized to be more cryptic on limestone shorelines, King (1987) found no difference in attack frequency on painted models at the extremes of the color pattern continuum. Two sizes of models were tested, neonates and juveniles, and the frequency of attacks was the same for both sizes. Despite finding no difference between morphs in predation on snake models, King (1993) concluded that banded neonates do suffer significantly greater predation, based on a selection survey in which live neonates were released and survivors were counted one year later. The mean number of dorsal and lateral blotches was significantly lower in the survivors, suggesting natural selection favors neonates with reduced pattern.

Interspecific model studies also detect differences in predation on a variety of real and imagined color patterns. For example, avian predators seem to avoid models having coral snake ringed patterns (Smith 1977; Brodie 1993) and certain other ringed patterns (Smith 1975; Brodie and Janzen 1995; Hinman and others 1997) when compared to uniformly colored models. However, Beckers and others (1996) suggested that animals (in general) are likely to perceive the difference between model and real snakes and found that a mammalian predator (coati, *Nasua narica*) did not avoid live coral snakes or their mimics, as suggested by Greene and McDiarmid (1981) based on rubber snake models.

In the current study, total avian attack frequency (10.4%) was well within the range of attack frequencies found in other studies of predation on model snakes. Frequencies on model snakes in Costa Rica ranged from 2.2-21.8% (Brodie 1993; Brodie and Janzen 1995; Hinman and others 1997), in the southern US from 5.2-6.8% (Pfennig and others 2001), and in Sweden 18.8% (Andren and Nilson 1981). My attack rate is most similar to the 9.8% on plaster and rubber model Lake Erie water snakes (*Nerodia sipedon insularum*) on the Lake Erie islands (King 1987).

Further studies should utilize other approaches to the study of predation on live striped and melanistic garter snakes. Computer graphics capabilities may allow direct measurement of crypsis, perhaps from photographs of snakes in the field. A second approach is to compare escape speed between the morphs. However, if morphs do not differ in speed, they may differ in escape ability due to the illusion of reduced speed, which is augmented by stripes. Therefore, a third approach is to test escape ability with live predators. Trained birds could peck at video images of fleeing snakes to measure the birds' accuracy with respect to each morph (for example, Clark and others 1997).

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