

Correlations between Ontogenetic Change in Color Pattern and Antipredator Behavior in the Racer, *Coluber constrictor*

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Abstract

Differences in snake color pattern have been demonstrated to affect behaviors involved in antipredator defense. Snakes with blotched or banded color patterns are concealed when not moving, and tend to rely on concealment and aggression for defense. In contrast, snakes with uniform or striped color patterns are easily seen when stationary, but their speed and direction are difficult to track when moving. They tend to rely on flight for protection. Some snake taxa exhibit ontogenetic change in color pattern, but the behavioral consequences of this change have not been investigated. I present results of a behavioral study in the racer, *Coluber constrictor*, which has a blotched juvenile color pattern but is uniformly colored as an adult. Hatchling racers were significantly more likely than adults to show aggressive behavior when confronted with a model predator, whereas adults were more likely to flee. This supports the hypothesis that changes in behavior and color pattern are correlated in this species to provide effective antipredator defense at different stages of life history. I also examined sprint speed, which may be an important factor in antipredator defense. Juvenile and adult racers showed a similar relationship between length and speed, a pattern also seen in other species that lack color change. This result suggests that sprint speed is not a causal factor in the evolution of ontogenetic color change.

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Introduction

The manner in which phenotypic traits function to fit an organism to its environment is a central concern of evolutionary biology and ecology. The importance of color pattern to defense against visually oriented predators is a well-studied example (Cott 1940; Endler 1978; King 1992). More recently, studies have focused on the integration of multiple aspects of an organism's phenotype to achieve a specific function (Irschick & Garland 2001; Ghalambor et al. 2003). For

example, color pattern, antipredator behavior, and reproductive strategy have repeatedly co-evolved in guppy populations exposed to different suites of predators (Endler 1994). Covariation between color morph and food-plant choice protects stick insects from predators (Sandoval 1994), whereas color, behavior, thermoregulation, and sprint performance interact to defend pygmy grasshoppers (Forsman & Appelqvist 1999; Civantos et al. 2004), and color pattern, flight performance, and flight behavior are correlated in neotropical butterflies, giving rise to two distinct antipredator strategies (Srygley & Dudley 1993).

Animal color is frequently subject to significant ontogenetic change, and these changes may often have adaptive consequences (Booth 1990; Garcia et al. 2003). Little has been done to determine how such change may affect correlated suites of characters that function to provide antipredator defense, an area of study that holds obvious potential for understanding life history evolution. Certain snakes possess traits that lend themselves to such study.

Jackson et al. (1976) and Pough (1976) first proposed a correlation between the dorsal color patterns of snakes and their antipredator behavior, arguing that snakes with disruptive patterns (blotches, spots or irregular crossbands) tend to rely on concealment and aggression for defense against predators, whereas snakes with striped, finely speckled, and uniform patterns tend to be more active and rely on flight for defense. Jackson et al. (1976) based their conclusions on subjective observations of field biologists, which allowed them to survey a wide variety of taxa on an interspecific level. Brodie (1989, 1992) found a similar pattern in an intraspecific study of garter snakes (*Thamnophis ordinoides*), which have color patterns that range from heavily spotted to distinctly striped. These studies found a distinct difference in the flight behavior of juvenile snakes correlated with the degree of blotched or striped marking of the color pattern. Snakes with more blotched patterns were more likely to exhibit a behavior termed 'reversal', a sudden change in direction thought to permit a fleeing snake to return to a cryptic defense after having been detected by a predator.

While the above studies considered only fixed color patterns, a number of snake taxa exhibit a marked ontogenetic change in color pattern (Burghardt 1978). Where color pattern undergoes a significant change during development, typically juveniles exhibit a blotched or crossbanded pattern, while adults are uniformly colored or possess longitudinal stripes. Antipredator behavior is also known to change with age in a variety of snake taxa (Greene 1988). Possible correlation between these traits has not previously been investigated. Sprint speed in snakes also changes as a function of age and size (Arnold & Bennett 1988; Jayne & Bennett 1990a), and is likely to be involved in predator defense along with color and behavior.

The racer (*Coluber constrictor*), a snake broadly distributed across North America, is an ideal species for investigating these correlations. Throughout the species' range, juveniles are prominently marked with reddish-brown blotches on a tan or light gray background. Adult color varies greatly across the geographic range, but all adults have solid-colored, unmarked dorsal surfaces with few, localized exceptions (Ernst & Barbour 1989). Adult colors vary from light tan and

olive to black, with much of the variation occurring on an east–west gradient. There is no apparent correlation between dark body color and climate in this species, in contrast to other snakes in which dark coloration may be an adaptation for thermoregulation in cold areas (Andrén & Nilson 1981). Adult racers are strictly diurnal and forage actively for prey, which exposes them to visually oriented predators (Fitch 1963; D. A. Creer pers. obs.). The habits of the juveniles are less well known, as their small size prevents the use of radiotransmitters, and they are less frequently encountered in the wild than are adults, relative to their abundance (Fitch 1963, 1999; D. A. Creer pers. obs.). Predators of racers include other snakes, raptors and other predatory birds, and small mammals (Fitch 1963; Ernst & Barbour 1989).

Here, I investigate the antipredator behavior and sprint speed of the racer in both juveniles and adults to determine whether an ontogenetic shift in behavior and sprint speed performance occurs to match the change in color pattern. The hypotheses tested are as follows: (1) juvenile racers are less likely than adults to attempt to flee from a predator, and more likely to mount an aggressive defense, and (2) juvenile racers have lower maximum sprint speed relative to their length than adults.

Methods

Study Animals

I collected adult racers in the field by hand and by the use of drift fences with funnel traps as described by Fitch (1963). All collections were made at Washington University's Tyson Research Center located in St Louis County, Missouri. The study was carried out during the spring and summer of 1998 and 1999, and in the fall of 1998. Collected specimens were marked by clipping of subcaudal scales, measured for snout–vent and tail lengths, and sex was determined by the use of a sexing probe.

All snakes were kept in a building on the Tyson Research Center property. Temperature was not controlled and was similar to, or somewhat higher than ambient temperatures at most times (but not during experiments; see below). The room in which snakes were kept had windows and no alteration was made to the natural light cycle. Specimens were housed in front-opening fiberglass cages (Neodesha Plastics, Kansas, USA), either individually in small cages (60 × 30 × 30 cm) or up to three per cage in larger cages (120 × 60 × 60 cm). All cages were provided with a substrate of newsprint. Water was provided *ad libitum*, but snakes (including hatchlings, below) were not fed during the course of the experiments. Racers usually do not feed under captive conditions (D. A. Creer pers. obs.), and snakes that have recently fed exhibit altered antipredator responses in experiments (Herzog & Bailey 1987). I released male and subadult female snakes at the site of capture immediately following the experimental trials, but retained adult females (except in the fall season of 1998). Gravid females were provided with nest boxes containing a 1 : 1 mixture (by weight) of water and

vermiculite for egg laying; other females were released after a maximum of 40 d in captivity. Females that laid eggs were released within 5 d of oviposition; specimens in which not all tests were completed before the detection of gravidity were tested before release as described below. Gravid snakes do not normally feed, and food was not offered.

Individual egg clutches were maintained separately to permit identification of siblings. Egg clutches were maintained on moist vermiculite until hatching, at which time hatchlings were transferred to individual plastic shoeboxes (30 × 16 × 9 cm). Water was provided *ad libitum*. Hatchling racers do not normally feed before completing the postnatal skin shed (D. A. Creer pers. obs.). No study was performed until after the postnatal skin shed was complete, after which each hatchling was measured for snout–vent and tail length. Because of the small size of the hatchlings, I did not attempt to mark them or determine gender. All hatchlings were released in the wild immediately following experimental work.

Subadult racers (300–500 mm snout–vent length) undergo loss of the juvenile blotched color pattern; snakes in this size range display varying degrees of dorsal blotching. As the sample size in this size class was very small, analyses were restricted to hatchling and adult specimens.

Experimental Conditions

The temperature of experimental venues was regulated with fans and small electric space heaters during the trials. Fitch (1963) determined the body temperature preference of active wild racers to be approx. 29–35°C, with the range from 34 to 35°C being especially favored (an exceptionally high value for a snake species). Body temperature has been shown to have a significant effect on reptile behavior patterns (Heckrotte 1967; Arnold & Bennett 1984; Goode & Duvall 1989). Work with adults took place in the spring (May 14 to Jun. 26, 1998; May 16 to Jun. 16, 1999) and fall (Sep. 19 to Oct. 12, 1998) and was conducted on days when ambient air temperatures were sufficiently high to permit building temperatures to be raised to 31–35°C (as low as 29°C in the fall). Work with hatchlings took place in the summer (Aug. 1–17, 1998; Jul. 24 to Aug. 7, 1999) and was conducted at temperatures of 32–35°C with less regard for outdoor temperatures. All trials took place between approx. 12:00 and 18:00 hours.

I used two venues for experimental testing. One was a linear track, constructed by laying a double layer of heavy-gauge black plastic along the building hallway with the sides attached to freestanding wooden supports and the middle portion covered with gravel to form a trackway 7 m long and approx. 1 m wide, with raised sides approx. 1.4 m high. The second consisted of a circular metal tank, 60 cm high and 1.5 m in diameter, with its floor covered with gravel.

Testing of a given specimen, as described below, began not less than 1 d following measurement and sexing. In addition, specimens that were in a pre-shed condition (determined by ‘opaque’, cloudy skin) were not tested until after skin shedding, and obviously gravid females were not tested until after egg laying. In three cases, gravid females were tested for behavior (but not sprint speed) before

their condition became apparent. Sprint speed trials for these specimens were completed following oviposition.

Behavioral Tests

Initial tests determined a specimen's response to approach by a model predator. I used a stuffed raccoon (*Procyon lotor*) as a model. Herzog et al. (1989) found the use of a similar predator model to be effective in studies of garter snakes. The tests were conducted first on the linear and then the circular track. In both cases, the snake was placed under a wooden board measuring 53 cm × 30 cm, with a 1-cm flange placed around the edge to provide a space for the snake to rest. Snakes were left under the board for a period of 10 min before commencement of the test. On rare occasions when a specimen emerged from beneath the board before the start of testing, it was replaced and the time count was restarted from the beginning. A thermometer was placed on top of the board to provide an individual record of temperature for each trial. At the commencement of each trial, the board was lifted suddenly, the raccoon (held in the hand by the hindquarters) was immediately brought toward the snake, and the snake was tapped with the raccoon's snout. In eight of the initial trials (involving adults) a cloth bag was used in place of the board, and the snake was simply released from the bag at the beginning of the trial. In the linear-track trials, the snake was pursued with the raccoon as long as it did not flee out of reach, and its immediate reaction to the model was recorded.

In the trials on the circular track, where a specimen was unable to flee out of reach, the snake was pursued repeatedly with the raccoon until it stopped attempting to flee, or for a maximum of 4 min. I noted whether the snake struck at or attempted to bite the model, or if it fled out of reach without aggressive behavior. The snakes were divided into two categories based on this criterion. I used a hand-held audio tape recorder to record responses. Snakes were classified in this trial by whether they repeatedly attempted to flee from the model, sprinting a distance greater than one body length at least twice following the initial response, or quickly settled into an aggressive defense without flight attempts.

I tabulated all results and tested differences between groups using Fisher's exact test. Because of the sibling relationships of hatchling snakes, I also used a t-test to compare hatchling clutches with the adult snakes. In these tests, I took the proportion of hatchlings in each egg clutch having more than 10 individuals showing aggressive behavior in a given trial, and compared these sibling groups with the adults. I treated each adult as an independent group, and assigned it a proportion of 0 or 1.0 for non-aggressive and aggressive animals, respectively. Specimens from both years were combined in the t-tests to get adequate statistical power.

Sprint Speed Tests

Tests of maximum sprint speed were conducted on the linear track. Snakes were placed in individual cloth bags at the forward end of the track, and permitted

to rest a minimum of 5 min before the first trial. I then released each snake from the bag and pursued it down the track, using a stopwatch to record the time between two marks at the beginning and end of the course. I avoided making physical contact with the snakes (such as tapping their tails) as this tended to cause specimens to stop, turn, and strike, which negated the trial. Adults were tested on a 5-m course to permit sufficient time to record trials with a stopwatch. Hatchlings were tested on a 1-m course; this corresponds to the distance used by Arnold & Bennett (1984) and subsequent studies for measuring maximum sprint speed in juvenile snakes. Each adult snake was tested a minimum of three, but usually four times. Hatchlings were tested six times; those that failed to complete the course satisfactorily after four trials were dropped from the sprint speed tests and not examined further. Specimens were rested a minimum of 10 min between trials, and for most of the hatchlings the total trials for a given individual were spread over ≥ 2 d. Analysis was based only on the trials in which a given specimen displayed its greatest speed. I generated regression lines to show the relationship between body length and speed, and used analysis of covariance (ANCOVA) and analysis of variance (ANOVA) to evaluate the significance of the results. Because hatchlings from different clutches did not differ significantly in relative sprint speed (see results, below), I did not account for clutch assignment in analyzing the test results.

I examined snakes during each trial to see whether they failed to run the course in a straight line, stopped or hesitated during the trial, or otherwise gave evidence of completing the course at less than their maximum possible speed. Such trials were not considered for analysis, but trials in which I observed no clear evidence of submaximal performance were included. This was done to separate maximal physiological performance from behavioral tendencies that affect actual speed in an experimental trial. This issue is discussed at length in Losos et al. (2002); these authors recommend exclusion of trials in which individuals can be determined to be performing submaximally by objective criteria (not including actual speed).

In addition to the sprint speed tests on the linear track, I attempted to repeat Brodie's (1989, 1993) tests on garter snakes (*T. ordinoides*) for stamina and reversals on the circular track. However, the measurement of these parameters in *C. constrictor* is confounded by the tendency of this species to stop and show aggressive behavior before becoming exhausted by flight. I therefore abandoned this approach.

Results

In 1998, I captured 18 adult racers (10 males, eight females), three of which (two males, one female) were captured in the fall. All of these were tested for both antipredator behavior and sprint speed performance. Three adult females captured in the spring proved gravid, but most eggs were infertile. I tested 14 resulting hatchlings, of which one, two, and 11 came, respectively, from the three clutches. Only the clutch of 11 was treated as a group for analytical purposes because of the small numbers of the others.

I captured 13 adult racers (six males, seven females) in the spring of 1999. Four adult females proved gravid, producing three clutches of 16, 16, and 22 hatchlings, respectively, as well as a fourth clutch which proved inviable. All animals were tested for both behavior and sprint speed. In both years, adult snakes represented an approximately equal mix of animals caught in drift fence traps or discovered in the open, and those taken by hand while resting under cover. Thus, the collecting protocol was unlikely to have been biased in favor of active or sedentary snakes.

Hatchling snakes frequently struck at the model when tested on the linear track (Table 1). Two adults also struck at the model, and both were females that later proved to be gravid (Table 1); all other adults fled without striking. The difference between hatchlings and adults is significant ($p = 0.005$; Table 2). Snakes that did not strike usually fled in a straight line down the track at high speed, but occasional specimens attempted to flee behind the board or otherwise sought cover. Approximately half of all specimens that struck at the model eventually fled, but did not do so immediately and were classified for purposes of this trial as exhibiting aggressive behavior. The remainder made no attempt to flee and continued to strike as often as approached.

When tested on the circular track, a variety of behaviors were exhibited including rapid flight, aggressive striking at the model, slow crawling in an apparent threat posture (head elevated, neck vertically flattened, tongue frequently extended in a rigid position), and poking at the wall and gravel substrate in attempts to locate an escape route. Typically, snakes fled across the

Table 1: Numbers of specimens collected by age and year, with category of performance in each of the behavioral trials

	Total number	Linear track		Circular track	
		Flight	Aggressive	Flight	Aggressive
Adults	31	29	2	24	7
1998	18	18	0	15	3
1999	13	11	2	9	4
Total gravid	2	0	2	0	2
Total postgravid	5	5	0	2	3
Hatchlings	68	46	22	34	34
1998					
Total	14	7	7	3	11
Clutch A	1	0	1	0	1
Clutch B	2	1	1	1	1
Clutch C	11	6	5	2	9
1999					
Total	54	39	15	31	23
Clutch A	16	11	5	10	6
Clutch B	16	8	8	4	12
Clutch C	22	20	2	17	5

Table 2: Results of Fisher's exact tests between adults and all hatchlings, and among adults and hatchlings from various egg clutches for behavioral trials on the linear track

	Adults	1998 clutch C	1999 clutch A	1999 clutch B
Total hatchlings	0.005*			
1998 clutch C	0.009*			
1999 clutch A	0.036*	0.687		
1999 clutch B	0.001*	1.000	0.473	
1999 clutch C	1.000	0.027*	0.108	0.008*

Results are shown as p-values; significant results are indicated by an asterisk.

track immediately or shortly after release (often striking at the model first), although the most aggressive did not. The aggressive snakes then exhibited combinations of the behaviors described above except rapid flight. The less aggressive repeatedly fled across the middle of the track or around its edge, usually showing other behaviors between attempts to flee. With few exceptions, specimens behaved aggressively at the end of trials and ceased any attempts at flight, but one adult displayed the 'head-hide' behavior described in Arnold & Bennett (1984) and a few other adults persisted in attempting to flee; these behaviors were not observed in hatchlings. As noted in the methods, specimens were categorized according to whether they made repeated attempts to flee at any time during the trial, regardless of the aggression displayed at the end of the trial. Hatchlings were significantly less likely than adults to make repeated attempts at flight ($p = 0.015$; Table 3).

With only two exceptions, snakes that struck at the model in the trials on the linear track behaved aggressively on the circular track; however, a number of snakes that failed to strike on the linear track also behaved aggressively on the circular track. The overall results were similar in both cases.

I observed significant differences among hatchlings from different egg clutches (Tables 2 and 3). One clutch gave results similar to those obtained from adults.

Four clutches of hatchlings were included in the t-tests, excluding those that contained only one or two individuals. I compared these four groups with the 31

Table 3: Results of Fisher's exact tests between adults and all hatchlings, and among adults and hatchlings from various egg clutches for behavioral trials on the circular track

	Adults	1998 clutch C	1999 clutch A	1999 clutch B
Total hatchlings	0.015*			
1998 clutch C	0.001*			
1999 clutch A	0.318	0.047*		
1999 clutch B	0.001*	1.000	0.073	
1999 clutch C	1.000	0.002*	0.471	0.003*

Results are shown as p-values; significant results are indicated by an asterisk.

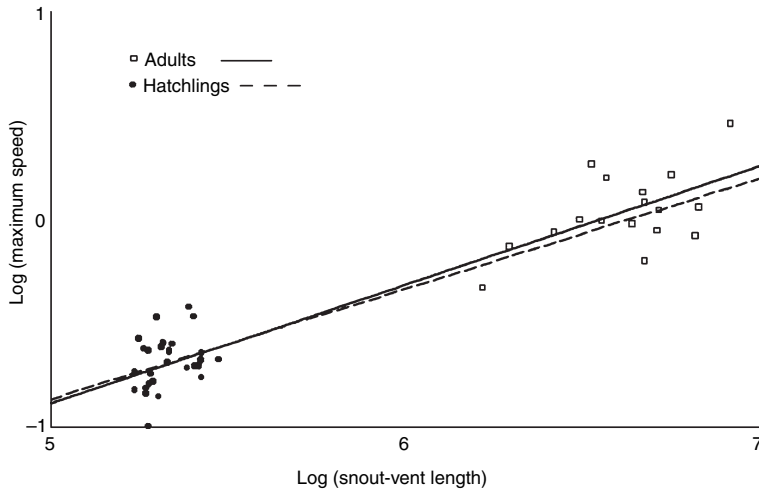


Fig. 1: Graph plotting log (maximum sprint speed, m/s) vs. log (snout-vent length, mm). See text for description of included data. Regression lines are shown for adults and hatchlings separately

adults as described in the methods. The difference in mean values between hatchlings and adults for aggression on the linear track is significant ($t = -2.119$, $df = 33$, $p = 0.042$). The difference is not significant for aggression on the circular track ($t = -1.439$, $df = 33$, $p = 0.160$).

I obtained results for 17 adults and 30 hatchlings in the sprint speed trials (Fig. 1); other specimens failed to complete any trial meeting the criteria described in the methods. The regression lines for hatchlings and adults are not significantly different in slope (ANCOVA; $n = 47$, $f_{1,43} = 0.009$, $p = 0.924$) or intercept ($f_{1,44} = 0.001$, $p = 0.977$). Body size (measured as snout-vent length) is significantly correlated with maximum sprint speed ($p = 0.001$). If adults are analyzed separately, the correlation remains significant (ANOVA, $n = 17$, $f_{1,15} = 7.111$, $p = 0.018$); if hatchlings are analyzed separately, the correlation is not significant ($n = 30$, $f_{1,28} = 2.773$, $p = 0.107$). The different clutches of hatchlings did not significantly differ from each other when analyzed separately (ANCOVA, slope: $n = 30$, $f_{2,24} = 0.053$, $p = 0.154$, intercept: $n = 30$, $f_{2,26} = 0.050$, $p = 0.186$).

Discussion

More study is needed to understand the significance of ontogenetic color change with respect to antipredator defense (Booth 1990). Although considerable work has been carried out on snake color patterns and predation, the present study is the first to examine the antipredator behavior of a snake species with an ontogenetic change in color pattern such that individuals exhibit different pattern types at different stages of life history. Ontogenetic change in antipredator behavior has been examined in some cases involving garter snakes (Herzog & Burghardt 1986, 1988; Brodie 1993). Brodie (1993) found that the tendency to flee

from threats intensifies in older striped individuals of *T. ordinoides* in a case in which the striped pattern becomes more apparent with increasing size. However, this does not involve a change across the color pattern categories defined by Jackson et al. (1976), and none of these studies show a switch from primarily aggressive behaviors to reliance on flight, as is hypothesized for a color-changing species. Madsen (1987) found evidence that bright head collar markings in juvenile *Natrix natrix* are aposematic and protect young snakes from bird predation, but this system involves neither specific antipredator behaviors nor a change in color pattern category.

The hypothesis that juvenile racers should show more aggressive defensive behavior than adults, and that adults should tend to flee a perceived threat, is strongly supported. This result was found in both behavioral trials, and indicates that antipredator behavior in this species is correlated with color pattern in a manner that may contribute to alternate strategies for antipredator defense at different stages of life history. Similar correlations between color and behavior are known in other taxa, where different individuals or populations possess different antipredator strategies (Endler 1994; Forsman & Appelqvist 1999). In the present system, however, different strategies involving both traits appear to characterize different life stages of each individual. Understanding how the correlation between color and behavior is maintained during development may therefore have implications for life history evolution.

While hatchlings as a group differ significantly from adults, the aggressive behavior observed in these specimens is not seen in all clutches of siblings when these are considered individually. Studies of different species of garter snakes (*Thamnophis*) have consistently found both individual variation and significant differences between litters of snakes (Arnold & Bennett 1984; Herzog & Burghardt 1988; Brodie 1993; see Burghardt & Krause 1999, for an exception). The present study is typical in this regard (Tables 1–3). The differences between the clutches raise the issue of independence of the hatchlings for statistical purposes. However, the results of the t-tests (especially as applied to the linear-track trials) seem to indicate that the results are robust to this potential problem. Particularly noteworthy is the fact that hatchlings frequently displayed aggressive behavior in the linear-track trials, but this was never observed in a nongravid adult.

Studies in garter snake species have shown age-related differences in antipredator behavior, involving a reduced number of strikes in aggressive behavior or lesser tendency to employ evasive maneuvers in flight with increasing age during the first year of life (Herzog & Burghardt 1988; Brodie 1993). These changes do not appear to be of the magnitude of those observed in the present study, and do not show a shift from primarily aggressive to primarily evasive defense. Herzog & Burghardt (1986) not only found antipredator behavior to be similar between juveniles and adults of three species of garter snakes, but also significant differences between species. This seems to indicate that the ontogenetic change in behavior observed in racers is not widespread, and is evidence that this change is indeed a correlate of the change in color in this species. Some species of

whipsnakes (*Masticophis*), the sister taxon to *C. constrictor*, do not show any ontogenetic change in overall color pattern. Quantitative information on their behavior, allowing interspecific comparison, would permit a further test of the association between color pattern and behavior.

Previous studies have noted significant behavioral differences between gravid female snakes and other adults, with more aggressive behavior being noted in gravid females (Goode & Duvall 1989). Physiological differences have also been noted; Jayne & Bennett (1990a) found that gravid female *Thamnophis* showed significantly lower maximum sprint speed and endurance in comparison with nongravid adults. The fact that the only two adults to show aggressive behavior in the trials on the linear track were gravid females is suggestive in this regard. In addition, while the five postgravid females that were tested following oviposition all fled from the predator model on the linear track, three of the five showed an aggressive response on the circular track. The difference between these five females and the aggregate of male and nongravid female adults is significant (Fisher's exact test, $p = 0.024$). The physiological burden of reproduction has been reported to persist past oviposition in a study of the lizard *Uta stansburiana* (Miles et al. 2000); the above results suggest that racers may be similar in this regard.

Physiological performance is believed to interact with morphology and behavior for functions such as antipredator defense (for discussion, see Arnold 1983; Irschick & Garland 2001). Sprint speed performance has been shown to be correlated (at an interspecific level) with both specific morphological traits and antipredator behavior in studies of butterflies, damselflies, and lizards (Srygley & Dudley 1993; McPeck 1995; Irschick & Losos 1998). Although the relationship between maximum sprint speed and avoiding predation is intuitive, testing this relationship has proven difficult (Bennett & Huey 1990; Miles 2004). In staged encounters in the laboratory, speed is correlated with ability to avoid predators (e.g. Srygley & Dudley 1993). Three field studies to date have shown a correlation between locomotor performance and survival in the wild, all in squamate reptiles (Jayne & Bennett 1990b; Warner & Andrews 2002; Miles 2004). Other studies, including some in squamates, have failed to find such a relationship (Bennett & Huey 1990; Blomberg & Shine 2000; Kingsolver & Srygley 2000). Moreover, such studies cannot distinguish between the effects of predation and success in capturing prey on survival (Miles 2004); however, Irschick & Losos (1998) found that lizards use a greater percentage of maximal sprint capacity in escape behavior than in prey capture. It appears that sprint speed is selected for predator escape in some species but not others, although the reasons are not always clear. Even where sprint speed is selected, the relationship can be complex; significantly, Jayne & Bennett (1990b) found that sprint speed is correlated with survival in garter snakes, but not during the first year of life.

While there is no direct evidence showing that sprint speed is selected for predator escape in racers, this trait is likely to be important in adults. Their reliance on escape behavior when confronted with a predator strongly suggests this. The tendency of adult racers to be found in open microhabitats relatively far

from cover also suggests a dependence on speed to avoid predation (D. A. Creer pers. obs.). Use of open habitats is correlated with higher running performance among mammal species, which supports the intuitive importance of this trait to animals that may encounter predators away from a refuge (Garland et al. 1988).

The purpose of the sprint speed trials was to determine whether juvenile racers show any handicap with regard to performance that might explain their disruptive color patterns and reliance on aggression for defense. Results of the trials indicate that sprint speed in racers is correlated with body length, and that adults and hatchlings fall along essentially the same curve (Fig. 1). Sprint speed performance therefore does not appear to be correlated with color pattern and behavior in this system. The alternative possibility is that absolute, rather than relative, speed is a factor in predator avoidance in this species. While theoretical studies and simulations suggest that relative speed determines vulnerability, this has not been confirmed in field studies (Van Damme & Van Dooren 1999; Domenici 2001). However, juvenile snakes generally have slower absolute speed than adults, yet most lack ontogenetic color change (e.g. Jayne & Bennett 1990a). The present data therefore do not indicate that any difference in sprint speed performance in racers relative to other species explains this species' color change. This in turn suggests that explanations for the suite of defensive characters observed in juvenile racers might best be sought in other factors.

One promising avenue for future research concerns habitat selection and foraging behavior in juvenile racers, whose traits may differ greatly from those of adults. Microhabitat choice affects the manner in which organisms can effectively escape predators (Scribner & Weatherhead 1995), and also has implications for the cryptic value of color patterns. Current radiotransmitter technology cannot be used in snakes as small as juvenile racers (D. A. Creer pers. obs.), but this problem may be overcome by technological advances. Alternatively, a way might be found to simulate natural habitats under captive conditions in such a way as to permit observation of habitat choice.

In conclusion, correlations between behavior, morphology, and physiology that form complex traits are likely to continue to attract interest from biologists. The aspect of ontogenetic change adds a new dimension to such investigations by altering one of the key components of an antipredator defensive strategy during the course of an individual's life history. In racers, color pattern and behavior appear to be correlated as a mechanism for defense against predation, and both traits change significantly during ontogeny in a manner consistent with the maintenance of this mechanism. However, the present study offers no evidence that sprint speed performance is directly correlated with ontogenetic changes in color pattern or behavior.

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