BEHAVIOURAL VARIATION IN NATURAL POPULATIONS. III: ANTIPREDATOR DISPLAYS IN THE GARTER SNAKE *THAMNOPHIS RADIX*

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Abstract. Recently born garter snakes (*Thamnophis radix*) were subjected to a variety of threatening stimuli. They would crawl away from the investigator until high levels of lactate were attained, and then adopt one of a variety of antipredator displays. These antipredator behaviours were surprisingly variable between individuals of a single population, but behaviours of individuals were consistent in replicate trials and in response to different stimuli. Snakes became more defensive when simulated predator attacks were more severe, but they became more offensive when tested at a lower temperature. Analysis of behavioural variation within and between 15 litters of full-sibling (172) snakes gave heritability estimates of 0.37 for single trials and 0.45 for the average of two replicate trials. This is the first study to examine the heritability of antipredator behaviour in any terrestrial vertebrate species.

Behaviourists have neglected the study of behavioural variation in natural populations. Because we know so little about the raw material upon which selection acts, our vision of the evolutionary process is very poor. Both phenotypic and genetic studies of natural variation have been neglected. Most estimates of phenotypic variation in behaviour are based on small samples, with no attention to the individual consistency of behaviour. Usually only standard errors are reported and frequency distributions are hardly ever described. Although the prospects for analysing behavioural inheritance have been established by numerous studies (e.g. Ehrman & Parsons 1981), surprisingly few studies have been conducted with natural populations (Arnold 1981a, b; Ayres & Arnold 1983). Estimates of environmental and genetic variance in behaviour for natural populations of vertebrates are exceedingly rare. In this paper we report estimates of repeatability and heritability of antipredator behaviour for a natural population of the garter snake *Thamnophis radix*. The inheritance of antipredator displays has never previously been studied in reptiles, or indeed, so far as we know, in any terrestrial vertebrate species.

We made our observations of antipredator displays in the course of a study of crawling speed in recently born snakes. In the process of

measuring the crawling speed of snakes being chased around a rectangular track, we discovered that they would spontaneously terminate such trials by adopting characteristic antipredator displays. We then conducted locomotory trials under a variety of conditions to determine individual consistency and stimulus effects on behaviour. We estimated the heritability of antipredator displays by analysing variation within and between litters of full siblings.

Materials and Methods

Subjects

The 172 animals used in the trials were the laboratory-born progeny of 15 gravid females collected in July at Wolf Lake, Cook Co., Illinois. After capture these females were maintained on a natural (Chicago) photoperiod in tanks with a timed thermal gradient (20 to > 30°C for 8 h during the day; uniform 20°C at night). Newborn snakes were separated from their mothers within 16 h of birth and individually housed in plastic boxes (Arnold 1981a). The snakes were not fed until the experimental trials were completed.

General Testing Procedures

Locomotory trials were conducted on a rectangular track (116 × 45 cm in inside lane; 10.5 cm wide with 14-cm-high retaining walls), carpeted with artificial, plastic grass (Astroturf) for traction. At each experimental trial a snake was placed at the starting line of the track by

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sliding it directly from its home box down a short 45° ramp. Thereafter the snake was chased by gently prodding its tail with the frayed end of a cotton-tipped swab every 5 s. The trial was concluded when the snake failed to move forward after 10 rapid consecutive taps to its tail, and its behavioural state was recorded.

Behavioural Scores

An open-ended catalogue was used to score the displays that occurred at the end of each trial. We noted the behavioural state of the snake's head, body and tail, adding new categories as they occurred during the experiment. In all we recorded four categories for the head, three for the body and two for the tail. The scores given to each of these display components are listed below.

Head-hide The head is hidden under one or more loops of the body (score = 0).

Head-expose: The head is motionless and flat on the substrate, not hidden under the body (score = 1).

Closed-mouth attack: The snake strikes rapidly forward with the mouth closed (score = 2).

Open-mouth attack: The snake strikes rapidly forward with the mouth open. The mouth is sometimes held open before or after the strike. Usually the snake does not actually bite (score = 3).

Body-ball: The body is loosely rolled into a ball. The body is not dorso-ventrally flattened (score = 0).

Body-extend: The body lies flat and extended on the substrate. It may be linear or kinked, and there is no dorso-ventral flattening (score = 1).

Body-flat coil: The body is coiled with the tail on the outside and the head near the centre of the coil. The body is dorso-ventrally flattened by protraction of the ribs, giving the impression of a larger or stockier snake (score = 2).

Tail-wave: The tail is elevated by dorsal flexure near the cloaca and moved sinuously from side to side. The movement ranges from a slow wave to a rapid wiggle, and may be accompanied by discharge of cloacal contents, which may be smeared over the body (score = 0).

Tail-flat: The tail lies flat on the substrate (score = 1).

We assigned a total score to each snake's display by summing the scores of the head, body and tail components of the display (Fig. 1). Thus a snake that hid its head (score 0) with its body

in a ball (score 0) while waving its tail (score 0) was given a total score of zero (Fig. 1, top). The rationale for this ordering of display behaviours is given in the results section.

Testing Schedule

We devised new tests for the snakes born and tested later in the experiment so that we could learn something about the stimulus control of the displays. These new tests were simply added to the original protocol (two trials) so that snakes born later were used in three or five trials. All trials were conducted in the afternoon (1300–1700 hours) to control for diel effects. All snakes were subjected to the first two trials, which were intended as replicates and conducted on consecutive days, beginning when the snake was 14–15 days post-partum. At each trial behaviour was scored when no further locomotor movement
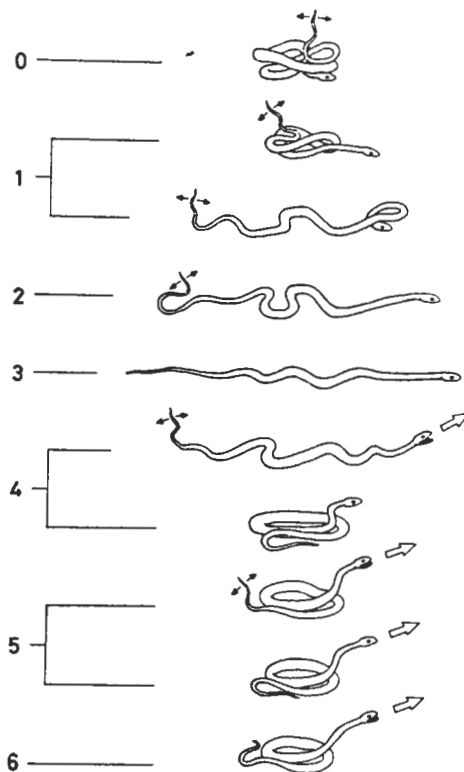

Fig. 1. The antipredator displays of the garter snake *Thamnophis radix* form a continuum from defensive (top) to offensive (bottom). The total scores (left) were assigned to each display by summing scores given to the behavioural characteristics of the snake's head, body and tail (see text for details). Illustration by T. R. Halliday.

occurred after 10 consecutive taps to the tail. After the second trial the snake was immediately tapped five times on the head: its behavioural response constituted trial 3. These first three trials were conducted at a room temperature of 27–28° C. Trials 4 and 5 took place in a controlled temperature room at 15–16° C on the day after trials 2 and 3. The snakes were moved to this lower temperature immediately after trial 3 and were kept there for 24 h. Trials 4 and 5 followed the same protocol as trials 2 and 3, except for the difference in temperature: tail-tapping followed by head-tapping. Trials 3–5 were added to the experiment after several litters had already been tested, so sample sizes for these trials are smaller.

Cloacal temperatures were determined directly with a Wescor thermocouple thermometer to verify that the snakes had equilibrated to room temperature. Mean body temperatures (and their standard errors) were $26.5° C \pm 0.1$ SE ($n = 45$) after the first and third trials and $15.1° C \pm 0.2$ SE ($n = 20$) after the fifth trial. These test temperatures are ecologically relevant. The preferred body temperature of *Thamnophis* is about 28° C, but snakes that have just emerged can have body temperatures as low as 15° C (Brattstrom 1965; Peterson 1982; Scott et al. 1982).

Three litters (83 snakes) were subjected to a sixth trial at room temperature (27–28° C), during which their tails were held firmly against the substrate. In this trial, each snake was gently moved from its home box onto an arena carpeted with Astroturf and then chased with periodic prodding of the tail, as in the locomotion trials, for 10–15 s. Then the snake's tail was held firmly to the substrate with the tip of the cotton-tipped swab, applying just enough force to hold the snake in place. Tail-pinning ruled out scoring the behavioural state of the tail, but we did score the behaviour of the snake's head and body. All snakes used in this trial were tested on the same day. The snakes had previously experienced only trials 1–2 or 1–3. The tail-pinning trial occurred 19–23 days later and was the last trial.

Physiological Methods

Intense bursts of activity in ectothermic vertebrates are fuelled primarily by anaerobic metabolism, measured by the production of lactic acid (Bennett 1978, 1982). To measure whole-body lactic acid content at the end of locomotory trials, six naive snakes were chased with a protocol identical to that of trial 1. When an animal ceased locomoting, its antipredator display was recorded, and it was frozen immediately in liquid nitrogen. The carcass was then broken into pieces and homogenized in 10 times its volume of 0.6 N perchloric acid with a Polytron tissue homogenizer. The anaerobic capacity, the total amount of lactate an animal is capable of forming during a burst of activity to exhaustion (Bennett & Licht 1972), was estimated by analysing the lactate contents of two other groups of snakes. Six animals were frozen without chasing and their lactate contents were used as resting, unexercised controls. Six other animals were stimulated constantly by hand for 30 min, after which the snakes were limp and had generally lost their righting response. This group was used to estimate the maximal lactate levels the animals were capable of forming. All animals were frozen and homogenized in an identical manner after rest or exercise at 27–28° C. Homogenates were stored at 4° C and later analysed for lactate content on a Hitachi spectrophotometer, using an enzymatic analysis kit manufactured by Boehringer-Mannheim Corp. (Bennett & Licht 1972).

Field Observations

Antipredator displays of *T. radix* were also observed in the field. Juvenile snakes, discovered under cover objects, were chased with periodic tapping as in the laboratory protocol. We used a proportionally similar but absolutely larger stimulus to evoke antipredator responses from adult snakes; tapping them with an extended finger.

Statistical Methods

Inter-class correlations, rather than intra-class correlations (Falconer 1981), were used to measure repeatability or individual consistency of antipredator behaviour across trials, because means were often demonstrably different at two different trials and variances were often slightly different.

Heritability of the sum of scores at trials 1 and 2 was estimated by an analysis of variance within and between the 15 full-sibling families. Heritability was estimated only for the first two trials, since far fewer families participated in later trials. Families were weighted in the calculations because of the substantial variation in family size (mean family size = 11.47 ± 10.08 SD; range = 1–37). A procedure outlined by Bulmer (1980, page 84) was used which has the convenient feature of also yielding confidence limits for

the estimate. In Bulmer's procedure, the heritability estimate is based on a between-family variance in which the contribution of each family is weighted in inverse proportion to the expected variance of its mean, rather than by family size. After calculating the components of variance within and between the full-sibling families, we estimated heritability as twice the intra-class correlation (Bulmer 1980; Falconer 1981).

Results
Deciding on a Measurement Scale

We decided to order the displays as shown in Fig. 1, using two different kinds of logic. First, two displays (top and bottom of Fig. 1) seem to represent the end-points of a defensive–offensive scale. A snake that rolls its body into a ball while hiding its head and smearing its body with excrement is apparently using a defensive tactic to avoid predation. The greatest contrast to such behaviour was shown by snakes that struck at the investigator with open mouth while flattening the body: clearly these snakes employed an offensive tactic. If we view these two categories as extremes, then a response with extended body and exposed, motionless head (middle, Fig. 1) can be taken as intermediate. We applied such a scale to each behavioural component (head, body and tail) and assigned the scores indicated in the Methods section.

As a second approach to deciding on a scale of measurement, we used the criterion of individual consistency across trials. If there is any degree of individual consistency in behaviour, then we should prefer that measurement scale that gives the greatest measure of repeatability. If the individuals lie on some actual behavioural scale and move slightly along it from one trial to the next, we will get a poorer measure of repeatability if we arrange the behaviours in the wrong order and a better measure of repeatability as we approach the correct ordering. Pursuing this course, we calculated the repeatability of behaviour at replicate trials 1 and 2 using different orderings of behaviour (Table I). Only two categories of tail behaviour were recorded, so repeatability gives no grounds for deciding on a scale for this component. The three categories of body posture yield three orderings with different repeatabilities. The ordering suggested by the defensive–offensive scale (ball, extend, coil) gives a better or comparable repeatability compared with the other two orderings. We calculated repeatabilities for only three of the possible orderings of head behaviour, since one of the four behavioural states (closed-mouth attack) was extremely rare. Again, the ordering suggested by the defensive–offensive scale (hide, expose, attack with closed or open mouth) gave comparable or higher repeatability than the other two orderings. The worst scales from the standpoint of repeatability are those that placed snakes with extended bodies or exposed heads into extreme categories. Thus the ordering we used for behavioural components gave a higher repeatability than some other orderings (or certainly no worse), and had a relatively clear interpretation as a defensive–offensive scale. The resulting total scores assigned to the displays (Fig. 1) were used in all subsequent data analysis.

A slightly more complicated score was also tried, in which each of the three behavioural components had equal ranges, so that they

Table I. Repeatabilities using Different Scoring Schemes for Display Components

Component	Scoring scheme	Repeatability, r*
Tail	1 = flat, 0 = wave	0.66
Body	0 = ball, 1 = extend, 2 = coil	0.60
	0 = extend, 1 = ball, 2 = coil	0.62
	0 = ball, 1 = coil, 2 = extend	0.47
Head	0 = hide, 1 = expose, 2 = attack with closed mouth, 3 = attack with open mouth	0.64
	0 = expose, 1 = hide, 2 = attack with closed mouth, 3 = attack with open mouth	0.63
	0 = hide, 1 = attack with closed mouth, 2 = attack with open mouth, 3 = expose	0.37

*All correlations are statistically significant at the 0.01 level.

would more equally contribute to the total score. However, this more cumbersome sum gave the same repeatability for trials 1 and 2 as the more simple sum. Accordingly we decided not to pursue more complicated schemes for weighting the three component variables (e.g. discriminant functions), particularly since the three variables covaried strongly and produced only three behavioural classes that accounted for most of the observations (Table II). We also tried an extremely simple dichotomous coding, in which scores 0–3 in Fig. 1 were assigned a value of zero and scores 4–6 a value of one. This coding gave the same repeatability (and heritability) as the sum coding, but had the disadvantage that it suppressed a considerable amount of the behavioural variation.

The Effects of Different Stimuli on Antipredator Displays

Snakes gave a more defensive response to head-tapping and tail-holding than to tail-tapping. Thus by shifting the stimulus from tail- to head-tapping, we caused the snakes to adopt a more defensive posture at both experimental temperatures (Table III). When snakes with an extended body posture (score 2) were tapped on the head, they tended to form a ball (score 0 or 1, Table II). The effect of tail-holding was evaluated by comparing trials 2 and 6 using just the sum of head and body scores: mean difference $= -0.83 \pm 0.21$ SE, correlation $= 0.50$, $n = 83$. Thus tail-holding had an even more dramatic effect than head-tapping in eliciting defensive response. The effect is more than twice as great,

Table II. Frequency of Behavioural Scores at Each of Five Trials*

	Trial Number				
	1	2	3	4	5
Day:	1	2	2	3	3
Temperature:	Warm	Warm	Warm	Cold	Cold
Stimulus:	Tail-tap	Tail-tap	Head-tap	Tail-tap	Head-tap
Score:					
0	0.22	0.12	0.30	0.02	0.10
1	0.06	0.06	0.15	0.02	0.16
2	0.30	0.33	0.09	0.20	0.02
3	0	0	0	0.04	0
4	0.02	0.02	0.01	0	0
5	0.02	0.01	0	0	0
6	0.37	0.46	0.44	0.72	0.72
n	172	172	97	50	50
Mean $\pm$ SE	3.10 ± 0.19	3.62 ± 0.18	3.04 ± 0.28	4.86 ± 0.27	4.52 ± 0.34

*Displays corresponding to each score are illustrated in Fig. 1.

Table III. Effects of Stimulus Treatments on Antipredator Displays

Effect of:	Trials being compared	Number of days between trials	n	Mean difference in score at the two trials $\pm$ SE	Correlation between trials, †r
Replicated trials	2 & 1	1	172	0.52 ± 0.15*	0.65
Head-tapping at warm temperature	3 & 2	0	97	-0.48 ± 0.19*	0.73
Head-tapping at cold temperature	5 & 4	0	50	-0.34 ± 0.22	0.76
Cold temperature on tail-tapping	4 & 2	1	50	0.84 ± 0.27*	0.55
Cold temperature on head-tapping	5 & 3	1	50	0.80 ± 0.31*	0.63

*Denotes significance at 0.05 level.
†All correlations are statistically significant at the 0.01 level.

since the evaluation of the tail-holding effect necessarily excluded the contribution of tail behaviour. As in head-tapping, tail-holding caused a decrease in the incidence of extended bodies and an increase in balling displays.

Cold temperatures apparently caused more aggressive or offensive responses from the snakes. Cold temperature had comparable effects on the responses to tail- and head-tapping (Table III). Unfortunately one cannot be sure that the effects are solely due to temperature. Snakes were also more aggressive at a replicated trial conducted at the same temperature (trials 1 and 2).

Individual Consistency Across Experimental Trials

The behaviour of individuals was remarkably consistent, despite the use of differing stimuli to elicit responses. Repeatabilities between different trials ranged from 50 to 76% (Table III). Pairs of trials that occurred only a few seconds apart, using different stimuli, gave the highest values; those one day apart gave intermediate values, and two trials (2 and 6) that occurred 19–23 days apart gave the lowest values.

Heritability and Repeatability Estimates for the Average of Two Trials

Contamination of the racetrack surface with cloacal secretions is a potential fault in the design, but it did not contribute to behavioural differences across litters. Since littermates were tested on the same day, litters born late experienced a more contaminated surface. However, the average scores of litters at the first trial are not correlated with litter test order ($r = 0.27$, $P > 0.05$).

Families differed greatly in antipredator behaviour (Table IV). The estimate of heritability for the sum of scores at trials 1 and 2 and its 95% confidence limits, using Bulmer's (1980) procedure for weighting of families, was $h_2^2 = 0.45$ (0.19–0.97). This is exactly equivalent to the heritability of the average score at trials 1 and 2.

The previously reported repeatabilities (Table III) were for single trials, and we now need a repeatability measure appropriate to a sum of two observations that we can compare with the heritability just reported. These two repeatabilities are related as the ratio of two readily observed variances, but to see why this is so we will need a simple statistical model.

Suppose that an individual's score at a particular trial, P, is the sum of a value characteristic of its family, F, a value characteristic of that individual, E_1, and a value, E_s, characteristic of that individual at a particular trial, so that

$$P = F + E_1 + E_s$$

F represents genetic and non-genetic effects causing the family mean to deviate from the mean of its population; E_1 represents a permanent environmental and genetic effect, causing variance within families; and E_s represents a special environmental effect that fluctuates from trial to trial.

Since the values of F and E_1 do not change from trial to trial, the variance of the difference in scores at two trials will be equal to twice the special environmental variance, $2V_{E_s}$, assuming no covariance between special environmental effects at the two trials. This will be true, however, only if there is a perfect genetic correlation between antipredator behaviour at the two trials. We tested this genetic proposition by

Table IV. Antipredator Display Scores in Each of 15 Litters of *T. radix* at Trial 1

| | Litter number* | | | | | | | | | | | | | | |
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Score:															
0	9	10		2	4		11	1	2				2		
1		2		1	1		3						1		
2	4	16	1	6	4	1	2	3	1	1	1	5	2	3	1
3															
4						2				1		1			
5								1	2		1				
6	1	2		2	2		21	3	3	1	1	6	11	5	6
Total litter size	14	30	1	11	11	3	37	8	8	3	3	12	15	8	7

*Ordered by average score, not by test sequence.

calculating the heritability of the difference between scores at the first and second trials, using Bulmer's procedure for weighting the families. The estimated heritability and its 95% confidence limits was $h^2 = 0.08$ (0–0.44), which provides no evidence for differences in F at the two trials. Consequently we proceed using our simple model and from the total variance in score differences estimate $2V_{E_8} = 4.09$.

The desired repeatability of the sum of scores will be the ratio of variance from all causes except special environmental effects to total variance (Falconer 1981). Our model for the sum of the two trials is $2F + 2E_1 + 2E_8$, and since we assume no covariance between special environmental effects, the variance of the sum will be $4V_F + 4V_{E_1} + 2V_{E_8}$, which was estimated to be 18.67 from the sum of the within- and between-family variance components. Subtracting our estimate of $2V_{E_8}$ from this estimated total variance and dividing by the total variance gives an estimate of the desired repeatability of the average or sum of two scores,

$$r_2 = (V_F + V_{E_1})/(V_F + V_{E_1} + 1/2V_{E_8}) = 0.78$$

Heritability and Repeatability Estimates for Single Trials

We need a heritability estimate for single trials which can be compared with the single-trial repeatability estimates reported in Table III. The heritability of a single trial is estimated as $V_F/V_P = V_F/(V_F + V_{E_1} + V_{E_8})$, whereas the heritability estimate for the sum or average of two trials is $V_F/(V_F + V_{E_1} + 1/2V_{E_8}) = V_F/(V_P - 1/2V_{E_8})$. We can obtain a simple conversion factor for these two heritabilities by noting that $V_P - 1/2V_{E_8} = 0.82V_P$. Thus the heritability estimate for a single trial is 0.82 times the herita-

bility estimate for the average of two trials, or $h_1^2 = 0.37$. We can estimate the corresponding repeatability for single trials as $(V_F + V_{E_1})/(V_F + V_{E_1} + V_{E_8})$ by dividing our estimate of the variance of the sum of scores minus the variance in the score difference by the sum of these two variances, or $r_1 = 0.64$. This intra-class correlation is very similar to the inter-class correlation between the first and second trials (Table III). Thus 36% of the total variance in behaviour at particular trials is due to special environmental variance. The estimates of the variance components (V_F, V_{E_1} and V_{E_8}) are shown in Table V together with their interpretation, using Falconer's (1981) notation.

Physiological Results

Determinations of whole-body lactic acid concentrations indicated that the snakes had reached their anaerobic capacities when they spontaneously assumed antipredator displays at the end of their locomotion trials.

Resting controls and snakes exercised for 30 min had mean lactate contents of 0.30 mg/g body mass (± 0.011 SE, $n=6$) and 0.65 mg/g (± 0.054 SE, $n=6$), respectively. Snakes on the track had an average lactate content of 0.70 mg/g (± 0.075 SE, $n=6$), not significantly different from that of animals exercised for 30 min ($P > 0.5$, Student's t-test). Apparently, snakes in these experiments fled until their capacity to support major activity through anaerobic metabolism was exhausted. Only at that point did the snake switch to antipredator display.

Field Observations

Snakes located in the field showed the same antipredator displays that we observed in the

Table V. Partitioning of Phenotypic Variance in the Antipredator Displays of *Thamnophis radix*: Components of Variance are Expressed as Percentages of Total Phenotypic Variance at a Single Trial

Observed components	Percentage	Expected components*
Between families, V_F	37	$V_A + 1/2V_D + V_{E_c}$
Among individuals within families, V_{E_1}	27	$V_{E_g} + 1/2V_D$
Within individuals (special environment), V_{E_8}	36	V_{E_8}
Total phenotypic, V_P	100	V_P

*V_A=additive genetic variance; V_D=dominance variance; V_{E_c}=common family environmental variance; V_{E_g}=general environmental variance.

laboratory. Our field sample was small (about 20 animals), and we could not detect behavioural differences between juveniles and adults. Animals of all sizes showed the same diversity of displays.

Snakes that assumed defensive postures (scores 0–3, Fig. 1) were very cryptic in the field. After an escape attempt, snakes would poke their heads into small depressions or between the bases of grass stalks. Simultaneously, the body was rolled into a ball over the head, or left extended and twined about vegetation, while the tail was elevated and waved. Snakes assuming the extended body posture were especially difficult to detect, because the body was often entwined through similarly coloured grass stalks. In the laboratory snakes were unable to embed their heads in the substrate or hide themselves when they performed these same displays.

Discussion

The main contributions of this paper are the demonstrations that (1) snake antipredator displays can be highly variable within populations, (2) that, nevertheless, the behaviour of individuals is consistent, and (3) that the behavioural differences are in part heritable. These results set the stage for more detailed studies of the inheritance, phylogeny and adaptive significance of antipredator displays in snakes.

Ontogenetic changes have been documented in the stamina and activity capacity of snakes (Pough 1977, 1978). Young (small) *Thamnophis sirtalis* and *Nerodia sipedon* exhaust far more rapidly than do adults of the same species. This differential stamina is directly correlated with ontogenetic changes in anaerobic capacity and aerobic scope in these animals. It is shortly after hatching or birth that snakes have the least endurance. They are then especially reliant upon antipredator displays to avoid predation. Young snakes are consequently particularly good models for this type of study.

Families varied greatly in antipredator behaviour. Our analyses gave heritability estimates of 0.37 for single trials and 0.45 for the average of two trials. However, as these estimates were based on full-sibling families, they should be viewed as upper limits on the actual heritability, because the estimates may be inflated by dominance variance and common family environment (Falconer 1981). We probably eliminated postnatal maternal effects and common environment by moving siblings into identical individual cages the day after birth. Nevertheless it would be desirable to obtain less ambiguous heritability estimates by such techniques as offspring–parent regression or the analysis of half-sibling families. Our results indicate that heritable variation for antipredator behaviour probably exists in snake populations, so more sophisticated genetic designs are worth pursuing.

Phylogenetic Considerations

Each of the diverse antipredator behaviours we observed in our *T. radix* population has previously been observed in a wide variety of species from different snake families. Thus rolling of the body into a ball has been documented in a variety of boids, colubrids and elapids, and striking from a coiled body posture is widespread in these same families and in viperids (Mertens 1946; Bustard 1969; Greene 1973). Reports of snakes elevating and waving their tails with the body in an extended posture are less common, but such behaviour has been observed in *Cylindrophis* and *Maticora* (Mertens 1946). Mertens provides a photograph of a *Cylindrophis* that assumed this posture and then, as taunting proceeded, tucked its head under its anterior body, just as we observed in *T. radix*. Since intraspecific variation in snake antipredator behaviour is a neglected topic, we do not know whether our *T. radix* population is exceptionally variable. If we assume that it is not, then the behavioural differences between species and higher taxa of snakes must be quantitative rather than qualitative. Our results that antipredator displays in this one population are both heritable and so variable as to span nearly the entire range of variation seen in higher snake taxa suggest that snake antipredator behaviour is capable of rapid evolution. Greene's (1979) comparative studies also indicate relatively rapid evolution. A more detailed test of fast behavioural divergence could be made by detailed comparison of conspecific populations and closely related species.

Adaptive Significance

Many functional interpretations have been offered for the antipredator displays of snakes (reviewed by Greene 1973), but only a few of the candidates seem especially plausible. Thus the constellation of traits associated with rolling the body into a ball strongly suggests that the behaviour is designed to protect the snake's head during predatory attack. The head is usually hidden under or at the centre of the balled body while the elevated tail is waved, sometimes broad-

casting excrement or foul-smelling secretions. In *Thamnophis*, the body is rolled into a rather disorganized heap on top of the head, but some boids roll the body into a highly organized, rigid ball with their head at the centre (Bustard 1969). In both cases balling behaviour is probably a tactic that minimizes injury to the head during predatory attack.

Tail-waving displays in which the snake's body is extended, rather than balled, have been observed in a variety of snakes (Greene 1973). Some taxa wave their elevated tails while stationary, but a tail-waving display may also accompany a crawling or burrowing escape or saltatory thrashing movements. Mertens (1946) noted that some taxa with distinctively but similarly coloured heads and tails perform tail-waving displays. He proposed that in these taxa the tail is designed to mimic the head and so deflect injurious attack from the vulnerable head to the tail. Bright ventral coloration is commonly exposed during tail-waving displays, and this too may direct attacks away from the stationary or hidden head (Greene 1973). Thus some of the most frequent antipredator displays in *T. radix* (top of Fig. 1) are probably tactics that promote survival under actual predatory attack, particularly by shielding or deflecting attacks away from the head.

The tactic of striking (bottom of Fig. 1) probably deters attack by bluffing the predator. Striking appeared to be bluff in our sample because the snakes seldom attempted to bite. Such sham strikes are common in snakes (Mertens 1946). In a variety of snakes striking is associated with a display in which the snake inflates its coiled body (thereby increasing its apparent size and sometimes revealing bright coloration between its scales), hisses or produces sound in other ways, and repeatedly strikes or jumps towards the potential predator (Mertens 1946; Gans & Richmond 1957). The effect is presumably to startle or intimidate the predator and so stave off attack.

While the foregoing analysis of the adaptive significance of snake antipredator displays raises some important possibilities, it is largely speculative. Almost all reports are based on responses given to human investigators rather than to natural predators (which are thought to be raptors or riparian birds for *T. radix*). Although natural interactions between snakes and their predators are difficult to observe, field studies that focused on their predators, rather than on the snakes themselves, might yield critically needed information. In addition it should be possible to stage encounters between snakes and their predators and record natural behaviour. A third promising approach is to measure the adaptive value of alternative antipredator behaviours directly by diagnosing the behaviours of newborn snakes, marking them for individual recognition, and then conducting a field recapture program to give estimates of survivorship or other aspects of fitness. The theoretical rationale and technical details of this approach are discussed by Arnold (1983) and Lande & Arnold (1983). The present study partially establishes the feasibility of the approach using snakes.

Stimulus Control of Behaviour

The result that simulations of severe predatory attack (i.e. head-tapping and tail-holding) elicited more defensive responses than milder attack (tail-tapping) suggests that snakes change from bluff to active defence as the predatory situation becomes more life-threatening.

The effect of body temperature on antipredator behaviour has received some study in reptiles. Crawling speed is directly dependent upon body temperature in garter snakes and is significantly decreased at $15°$ C as compared to $25°$ C (Heckrotte 1967; Stevenson et al. 1982; Bennett, unpublished observations). Fitch (1965) and Heckrotte (1967) noted that *Thamnophis sirtalis* are more likely to stop and attempt to bite at lower temperatures, just as we observed in *T. radix*. Similar decrements in burst speed with decreased body temperatures over this thermal range have also been observed in lizards (Bennett 1980; Hertz et al. 1982). In agamid and iguanid lizards, colder animals are more likely to attack and bite rather than flee (Hertz et al. 1982; Crowley & Pietruszka 1983). Thus reduced speeds associated with lower body temperatures appear correlated with the assumption of more aggressive defensive postures in many different species of reptiles.

Consistency of Behaviour

The individual personalities of the snakes were preserved across trials even though temperature and the severity of attack affected the average antipredatory response. Displays were repeatable even when stimulus conditions were varied. The good correlation ($r = 0.50$) between responses at tail-tapping and tail-holding trials is especially remarkable. In the former trial the snakes were physiologically exhausted and at the limits of their anaerobic capacities, whereas in the latter

trial the snakes were still capable of locomotion and active escape. Thus while stimulus conditions affect antipredator responses, characteristic personalities are retained irrespective of external conditions and physiological state.

The level of repeatability of antipredator behaviour in *T. radix* is comparable to those reported for a variety of physiological measures in mammals. Thus the repeatability of fleece yield in different years in sheep, milk yield in cattle in successive lactations, and litter size in mice in successive pregnancies all range from 0.45 to 0.74 (Falconer 1981). Individual consistency of behaviour has, however, seldom been studied. In the case of snake antipredator displays, repeatability during a 24-h period is about half due to differences between families and half to consistent differences among littermates (Table IV). It drops as the interval between trials increases from a few seconds to 24 h to several days, but the total range is only 76–50%. This drop probably reflects a growing divergence in motivational state. Whether this trend is due to a slowly fluctuating or gradually maturing motivational state will have to be established by future studies.

Acknowledgments

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