

Consistency of individual differences in anti-predator behaviour and colour pattern in the garter snake, *Thamnophis ordinoides*

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Abstract. The importance of individual variation in behaviour as both an ingredient and a consequence of natural selection has only recently received much attention from empirical researchers. The manner in which individual differences change ontogenetically and how such changes may affect an individual's fitness are still largely unknown. This study investigates the development of anti-predator behaviour and colour pattern in the northwestern garter snake, *Thamnophis ordinoides*, during the first 2 years of life under laboratory conditions and in the wild. Several aspects of escape behaviour were examined, including the maximum sprint speed, the distance crawled until an anti-predator display was performed (stamina), and the tendency to perform stereotypical evasive manoeuvres during flight (reversals). These aspects of escape behaviour and the stripedness of colour pattern showed significant changes during this time, although the specific changes varied between laboratory and field conditions. Many of the developmental changes were associated with growth. Traits generally showed strong positive correlations across ages, both in the laboratory and in the field. Individual differences in anti-predator behaviour and colour pattern in this species of snake appear to be relatively consistent throughout the first 2 years of life. Using neonate trait values to estimate selection during this time will provide accurate representations of the form of selection because the ontogenetic trajectories of individuals are parallel.

Individual variation is a critical component of adaptive evolution because it is the substrate on which natural selection acts. Without variation in a trait among individuals, there can be no covariance with fitness and thus no selection. Such variation is observable in a variety of traits in natural populations and often can be shown to have a genetic basis (e.g. Arnold 1981; Arnold & Bennett 1984; Grant 1986; Garland 1988; Brodie & Brodie 1990). Individual differences, especially in behaviour, have also been viewed as adaptations in themselves, either because of social advantages to individuality (Slater 1981, 1983) or because frequency dependent selection operates to maintain variation (Magurran 1986; Clark & Ehlinger 1987).

Behavioural traits, which are especially sensitive to environmental influences, often change over the lifetime of an individual. The proximate causes of developmental change in behaviour have received much attention (Bateson 1978, 1981, 1983; Arnold

1990), but comparatively little effort has been spent on understanding how differences among individuals change ontogenetically (but see MacDonald 1983; Slater 1983; Cheal & Foley 1985; Herzog & Burghardt 1988).

In this study, I examine the ontogenetic change of three aspects of anti-predator behaviour and colour pattern in the northwestern garter snake, *Thamnophis ordinoides*, during the first 2 years of life. These aspects of behaviour, speed, endurance, and evasiveness, are thought to be important in predator escape (Brodie 1989a, b 1991, 1992; Jayne & Bennett 1990a). Each is known to vary among individuals and have a genetic basis in the populations studied (Brodie 1989a, 1991). The development of colour pattern was also examined because it is genetically correlated with evasiveness and selection acts on the combination of colour pattern and behaviour rather than on either one independently (Brodie 1989a, 1991, 1992).

The individual ontogenies of two groups of snakes were followed: one group was held captive in the laboratory for the entire study, the other group was individually marked and free-ranging in

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their home population. Repeated sampling of individuals through time allowed me to examine both the general development of traits as a function of age and growth, and the degree of consistency of individual differences through time.

METHODS

Subjects

Origin

All individuals were born in the laboratory to wild caught females. Pregnant females were captured in July–August 1987 from two localities in coastal Oregon and maintained in the laboratory until parturition in September. A total of 74 individuals from 50 different families were used in this study. Four litters were represented by one individual in both the laboratory and field groups.

Laboratory group

Each individual in the laboratory group was housed in its own plastic shoebox (35 × 17 × 9 cm) at the University of Chicago and maintained on a diet of earthworms. The snakes were communally hibernated (cf. Murphy & Campbell 1987) in a temperature-control room (5–7°C) for 3 months between January and April in 1988 and 1989. Ten neonates from eight families from the Tenmile Creek, Lane Co. (cf. Brodie 1989a, 1991, 1992) and 17 neonates from 13 families from the Clarence Creek, Tillamook Co. (cf. Brodie 1991) populations were used in the laboratory group.

Field group

After being tested as neonates, I marked each individual with a unique combination of clip marks on the ventral scutes (Brown & Parker 1976; Arnold 1988) and released it into the maternal population within 10 days of birth. In June of 1988 and July of 1989, I recaptured snakes by hand at the Tenmile locality. No individuals were captured both years, so the two collections will be treated separately and referred to as the 1-year and 2-year groups, respectively. All snakes used in the field groups were from the Tenmile population, although eight subjects were born to females captured in 1988. The 1-year group included 27 snakes from 20 different families. Eight of these (from seven families) were born in 1988 and recaptured in 1989,

the remainder were from the 1987 cohort and were recaptured in 1988. The 2-year group consisted of 20 snakes from 17 families, all from the 1987 cohort. Twenty-eight different families were represented in the two field groups (nine families were represented by one individual in each of the two field groups).

Scoring of Traits

Maximum sprint speed ('speed'), the distance crawled until anti-predator display ('distance'), and the number of reversals of direction during flight ('reversals') were scored at 30°C on a series of racetracks. Speed was measured with a stopwatch on a 1-m linear racetrack lined with AstroTurf (cf. Brodie 1989a). I tapped snakes on the tail with my forefinger to stimulate them to crawl. Each snake was raced three times per trial, and the fastest velocity over a 0.5-m section was taken as the maximum speed. I scored both distance and reversals on a circular racetrack lined with AstroTurf (cf. Brodie 1989a) by tapping the snake on the tail repeatedly with a cotton swab to stimulate the subject to crawl. Trials were terminated when the subject refused to crawl after 10 successive taps to the tail. At this time, I recorded the total distance crawled and the number of reversals during each trial. I scored each of the three types of behaviour twice at each age and used the average of these two measures in subsequent analyses (speed was measured four times on neonates, but only the first two measures were used in this study).

Speed and distance are measures of locomotor performance and may be important in escape from predators (Jayne & Bennett 1990a). Distance is considered a measure of stamina that also reflects an individual's behavioural propensity to sustain flight (Jayne & Bennett 1990a). Reversals are sudden terminations of flight thought to cause a predator to lose sight of its prey, thus allowing the prey to resort to crypsis after initial detection (Pough 1976; Brodie 1989a, b). Each of these aspects of behaviour is known to have moderate to high repeatability over a period of 2 days for both neonates (Brodie 1989a, 1991) and adults (Brodie 1989b).

I scored a number of individual colour pattern components and combined them into an index of overall stripedness ('stripe') of the pattern (cf. Brodie 1989a). These components included (1) the completeness and contrast of the dorsal (DS) and

lateral (LS) stripes scored on a 0–4 scale (0 = absent and 4 = present the entire length of the body), (2) the contrast of the dorsal (DC) and lateral (LC) stripes scored on a 0–3 scale of increasing contrast, and (3) the presence or absence of dorsal and lateral rows of spots (SPOT, 1 = no spots, 2 = one row of spots, and 3 = two rows of spots). I then generated a continuous measure of stripedness of pattern by combining these components into an index: $\text{stripe} = \{(\text{DS} \times \text{DC}) + (\text{LS} \times \text{LC}) + 1\} / \text{SPOT}$. I did not score snakes for colour pattern if the onset of ecdysis was detectable by dullness of the skin or opaque eyes. In these few cases, I scored subjects after shedding was complete. The actual colours of the pattern components are not considered here.

Mass and snout–vent length (SVL) were also measured one day prior to the beginning of each test period. I used these variables as a measure of size at each age.

Schedule of scoring

The same scoring schedule was followed for both the laboratory and field groups at each age (except as neonates). On the first test day, I tested an individual twice for speed, once in the morning and once in the afternoon (no less than 4 h apart). On the second and third test days, I tested each snake once for distance and reversals. I scored colour patterns after the final behaviour test on either the third or fourth test day. As neonates, all individuals were tested on 2 days for sprint speed, so I scored the other aspects of behaviour and colour pattern 1 day later than at other ages.

I began testing all snakes on the third day of life as neonates. At subsequent ages, I began all tests on the same day, so exact ages of individuals varied slightly at each test period. I used the precise age in days of each individual at the start of the first behaviour test for each period as the measure of age in all analyses.

Laboratory group

I rescored behaviour of the laboratory group at approximately 4, 8, and 20 months (± 13 days) of age. These test periods corresponded to 3 weeks prior to the first hibernation, 4 weeks after the first hibernation and 1 week after the second hibernation, respectively. I conducted the 8- and 20-month tests for this group soon after hibernation so that I could travel to the field site and

collect the field groups in early summer. I rescored colour patterns at approximately 1, 3, and 4 months (± 13 days) of age because previous observations suggested that any change in colour pattern occurred prior to the hibernation in the first year.

Field group

I scored both the 1- and 2-year groups within 10 days of capture. I retested the 1-year group at approximately 9 months (± 14 days) of age and the 2-year group at approximately 23 months (± 13 days). I rescored colour pattern and all three aspects of behaviour at these times.

Statistical Analyses

Laboratory group

I examined individual and age effects and individual by age interactions through analysis of covariance (ANCOVA). Individual identity was declared as a random categorical variable with age as the covariate. I repeated this analysis adding mass and snout–vent length as covariates to examine the above effects independent of differences in size. I used the GLM procedure of PC-SAS Release 6-03 (SAS Institute Inc. 1988) for all ANCOVAs and used the type-III sums of squares for all *F*-tests.

To determine the degree of association of an individual's scores for a particular trait through time, I calculated Kendall coefficients of concordance based on individual ranks at each age (Siegel 1956). The same analysis was repeated adjusting each trait for individual differences in growth (see below).

Field group

I analysed the 1-year and 2-year groups separately for individual and age effects in the same manner as the laboratory group. Interactions between individual and age could not be analysed because too few degrees of freedom were present to test for differences among individual slopes.

I examined correlations between an individual's behaviour at birth and at recapture for both the 1-year and 2-year groups. I calculated Spearman rank correlations between the two ages because they are linearly related to Kendall coefficients of concordance (Siegel 1956), which were used to measure concordances over four ages in the laboratory group. Correlations are used to measure associations between two sets of variables while

Table 1. Individual and age effects for the laboratory group

Effect	Unadjusted				Growth-adjusted			
	Speed	Distance	Reversals	Stripe	Speed	Distance	Reversals	Stripe
Mass (1)	—	—	—	—	0.56	1.58	1.76	4.55
SVL (1)	—	—	—	—	3.81	1.26	2.22	5.31
Individual (26)	0.79	1.35	2.37**	82.60****	1.82	2.76***	2.32**	86.66****
Age (1)	5.18*	0.0	7.34**	27.46****	11.20***	14.41***	0.18	2.39
Individual × age (26)	0.95	0.44	0.89	1.23	1.60	0.99	0.92	1.07

Unadjusted and growth-adjusted ANCOVA results (*F*-values). Degrees of freedom are shown in parentheses. * $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$.

concordances are used to measure associations between more than two sets. I performed these analyses on growth-adjusted data as well.

Transformations

Speed, distance, mass, and snout-vent length were distributed normally, so they were analysed untransformed. Reversals and stripe were both square-root transformed for all parametric analyses to achieve more normal distributions.

In the growth-adjusted non-parametric analyses, I adjusted the data for individual differences in growth by using the residuals from a regression of the trait on mass and snout-vent length in place of the original score (Garland 1988; Jayne & Bennett 1990a). I performed these regressions separately for each trait at each age.

Adjustment of significance levels

I used the sequential Bonferroni technique to adjust significance levels for the multiple tests performed within a given analysis (Rice 1989). For the ANCOVAs, I adjusted significance levels for the number of effects tested in each model (five for the unadjusted and three for the growth-adjusted laboratory data, four for the unadjusted and two for the growth-adjusted field data). For both the concordance and correlation analyses, I adjusted significance levels for the number of coefficients calculated for each data set (four each for the unadjusted and growth-adjusted data for both the laboratory and field groups).

Statistical significance was taken at $P < 0.05$ for all tests, however, all probabilities less than 0.1 are reported.

RESULTS

Individual Effects

Significant individual differences in reversals and stripe were detectable in all groups. Except for reversals in the 2-year field group, this variation among individuals was present even when size effects were removed (Tables I, II, III). Individuals in the field groups also differed with respect to speed, but only the differences in the 2-year group were independent of size (Tables II, III). Distance did not generally vary among individuals, showing a significant individual effect only when size differences were removed in the laboratory group (Table I).

Age Effects

Over the course of the study, stripedness increased slightly while reversals decreased (Figs 1, 2). This was apparently explained by size differences rather than age alone (Tables I, II, III). Stripe showed a significant age effect in all groups, but never when adjusted for growth. Similarly, reversals changed with age in the laboratory and 1-year field groups, but not if growth differences were removed. The general age trend in all three data sets suggested that most of the change in both traits occurred in the first year, with little or no additional change in the second year (Figs 1, 2).

Qualitative inspection of colour pattern components showed that any changes in colour pattern were the result of slight initial increases in the contrast and or completeness of the dorsal and lateral stripes. The presence or absence of spots did not change ontogenetically. Consequently, unstriped snakes changed little if at all, while striped snakes

Table II. Individual and age effects for the field groups

Effect	Unadjusted				Growth-adjusted			
	Speed	Distance	Reversals	Stripe	Speed	Distance	Reversals	Stripe
1-year group								
Mass (1)	—	—	—	—	1.18	0.08	0.29	0.0
SVL (1)	—	—	—	—	2.73	1.14	0.04	0.20
Individual (26)	2.38**	1.45	2.86***	12.99****	1.57	1.38	2.87**	12.35****
Age (1)	12.40**	1.04	4.40**	9.34***	0.42	3.61	2.45	2.64
2-year group								
Mass (1)	—	—	—	—	0.37	1.18	0.27	0.01
SVL (1)	—	—	—	—	0.05	1.85	0.78	0.37
Individual (19)	4.44***	1.93*	2.76**	9.76****	4.13**	2.08	2.32	8.18****
Age (1)	268.9****	42.09****	0.68	16.78****	8.07**	0.11	0.66	1.84

Key as for Table I.

Table III. Coefficients of concordance between ages

	Speed	Distance	Reversals	Stripe
Unadjusted				
Laboratory (27)	$W = 0.453***$	0.617****	0.527****	0.757****
1-year field (27)	$r_s = 0.416*$	0.046	0.566***	0.924****
2-year field (20)	$r_s = 0.596**$	0.512**	0.633***	0.826****
Growth-adjusted				
Laboratory (27)	$W = 0.519****$	0.603****	0.536****	0.682****
1-year field (27)	$r_s = 0.152$	0.134	0.647****	0.888****
2-year field (20)	$r_s = 0.465**$	0.509**	0.551**	0.739***

Kendall coefficients of concordance (W , laboratory group) and Spearman rank correlation coefficients (r_s , field groups) for unadjusted and growth-adjusted data. Sample sizes are shown in parentheses.

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$.

underwent an initial increase in stripedness and then stabilized. This effect was the result of a general lightening of the pattern during the first few months of life, causing stripes to become brighter and to contrast more greatly with the background colour. Snakes without stripes also lightened but did not become striped.

An overall increase of speed with age was seen in both field groups and was suggested ($P < 0.08$) in the laboratory group. This change was independent of growth in the laboratory and 2-year field groups (Tables I, II, III). Distance increased with age in the 2-year field group, but was not independent of growth. In the laboratory group, changes in distance were only detected when values were adjusted for size differences (Tables I, II, III).

In the field groups, both locomotor performance traits increased with age, but primarily between the first and second years (Fig. 2). The speed and distance ontogenies of the laboratory group were more complex, indicating an initial increase in performance through the first 8 months but a marked decrease between the 8-month and the 20-month trial (Fig. 1).

Consistency of Individual Differences

Heterogeneity of individual ontogenies could only be investigated statistically in the laboratory group. No interactions between individual and age were detected for any trait in this data set (Table I). Qualitative assessment of individual ontogenies from the two field groups did not indicate any

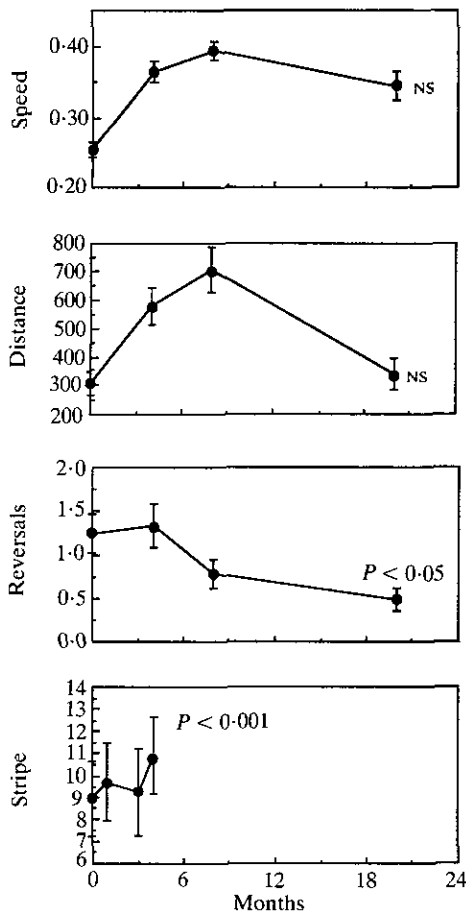


Figure 1. Average (\pm SE) ontogenies of anti-predator behaviour and colour pattern for the laboratory group (unadjusted for growth). Significance levels are for age effects in the unadjusted ANCOVAs (see Table I).

major differences among snakes in the way any of the traits changed with age.

Kendall coefficients of concordance demonstrated a moderate to high ($W=0.453-0.757$) degree of association among an individual's scores through time in the laboratory group (Table III). This was true for all traits, even when adjusted for size differences. This test was based on ranked data and suggested that snakes generally retained their relative ranking over the course of the study. Spearman rank correlations indicated similar results for all traits in the 2-year field group and for stripe and reversal in the 1-year field group (Table III). Individuals' ranks for the two locomotor performance traits were generally not correlated in the 1-year group (unadjusted speed showed a marginally

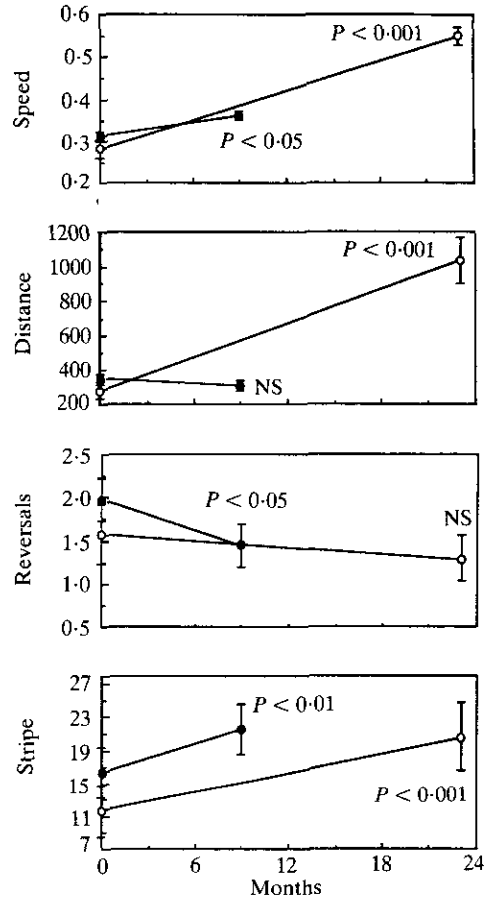


Figure 2. Average (\pm SE) ontogenies of anti-predator behaviour and colour pattern for the field groups (unadjusted for growth). ●: 1-year group; ○: 2-year group. Significance levels are for age effects in the unadjusted ANCOVAs (see Table II).

significant correlation). This could be an artefact of little variation in these scores in this group (no individual differences were detected except for unadjusted speed), so that ranked data did not reflect important variation.

DISCUSSION

Individual Differences

Moderate to high heritabilities previously demonstrated for both of the study populations (Brodie 1989a, 1991) contribute to individual differences in all the traits examined. Individual variation for locomotor performance was not consistently detected in all of the data sets in this study.

However, larger samples from these populations indicate substantial variation in these characters and high repeatability within individuals (Brodie 1989a, 1991). Where individual variation was observable in the present data sets, it was generally independent of size differences. Individual differences in these traits probably reflect the genetic variation commonly found in quantitative characters (Falconer 1981).

Ontogenetic Trends in Behaviour

A variety of factors might explain the change in behaviour over time, including differences in genetic control from one age to another, changes in performance ability due to changes in body size or physiology, and experiential modifications (Bateson 1978, 1981, 1983; Arnold 1990). The current study does not address the genetics of behavioural ontogeny but does provide some data concerning the alternative proximate hypotheses.

Changes in locomotor performance in both field groups were seen to be primarily associated with growth, although speed also changed independently of size in the 2-year group. Similarly, ontogenetic changes in reversals in both the laboratory and field groups could be attributed to growth effects. Dependence of locomotor performance on allometry has been demonstrated previously in other species of garter snakes using both longitudinal and cross-sectional data (Jayne & Bennett 1990b). Also, physiological capacities of juvenile snakes are known to be lower than those of adults and this has been related to locomotor ability (Pough 1977).

The correlated change of locomotor performance and reversals in opposite directions (Figs 1, 2) may reflect a switching of anti-predator strategy as snakes grow. Sprint speed has never been shown to correlate with fitness in neonate snakes (Jayne & Bennett 1990a; Brodie 1991, 1992), but does affect survivorship of older age classes (Jayne & Bennett 1990a). The absolute speed attainable by juvenile snakes may not be sufficient to escape predators, thus rendering alternative anti-predator mechanisms more important. Reversals are a behavioural component of crypsis that are employed after initial detection by a predator (Pough 1976; Brodie 1989a, b, 1992) and are an example of a defensive tactic that does not rely heavily on speed. When locomotor performance is low, such as in neonates, selection may favour defensive strategies that are

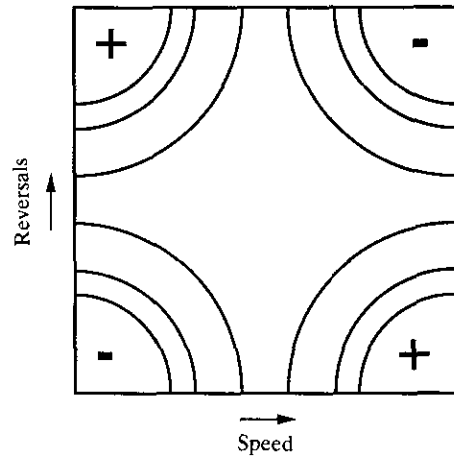


Figure 3. Contour view of a hypothetical correlational selection surface for the combination of speed and reversals. Lines indicate contours of equal fitness. Higher fitness corresponds to higher contours and plus and minus signs indicate relative peaks and valleys, respectively. Individuals with opposite values of speed and reversals have higher fitness. Young snakes are slow and would have higher fitness if they performed more reversals (upper left corner), whereas older snakes are faster and would have higher fitness if they performed fewer reversals (lower right corner).

independent of locomotor capacity. As the snake increases in size and physiological performance, flight would become more effective, and selection would favour a shift toward locomotion-dependent anti-predator tactics. This process can be envisioned as a correlational selection surface where selection favours opposite combinations of speed and reversals (Fig. 3). When a snake is young and slow, selection would favour a high tendency to perform reversals. As a snake grows and can attain greater speeds, it enters the region of the selection surface that favours fewer reversals (Fig. 3). A similar explanation has been offered for the change in anti-predator behaviour associated with pregnancy in *T. ordinoides* (Brodie 1989b).

The genetic ability to respond to such hypothetical selection has not yet been demonstrated, but would involve heritable variation for the ontogenetic trajectories of both speed and reversals. Methods for measuring heritability of and selection on growth trajectories have recently been developed (see Kirkpatrick et al. 1990). These techniques require the repeated measurement of family groups throughout the period that ontogenetic change is being examined. Sampling should be especially frequent during periods of critical change, such

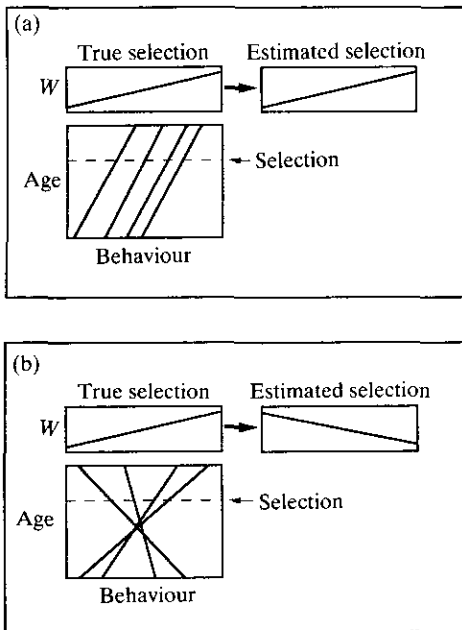


Figure 4. The effects of different patterns of ontogeny on the estimation of selection by mark-recapture techniques. Selection is measured at the oldest age shown in the figure (the top of the ontogeny plots), but the major selective event occurs at the time indicated by the dashed line. Diagonal lines in the ontogeny plots show ontogenetic trajectories of different individuals for a given behaviour. The true form of selection (where W = fitness) is shown above each ontogeny plot. In this example, the true form of selection favours higher values of the behaviour (directional selection). The estimated form of selection based on neonate scores will be accurate if individual ontogenies are parallel (a) but will be a misrepresentation if individual differences change before the major selective event (b).

as the point at which absolute speed becomes an efficient anti-predator mechanism in this example. At these times, genetic variances and covariance are expected to change rapidly (Cheverud et al. 1983; Atchley 1984). A negative genetic correlation between speed and reversals at the age when speed becomes important is an expected outcome of the correlational selection hypothesized above (Lande 1980, 1984).

Interpretation of the laboratory ontogenies of locomotor performance is more problematic. Both speed and distance increased through the first year but were depressed, almost to neonatal levels, at the post-hibernation test in the second year (Fig. 1). Because of this subsequent drop in performance, no effect of age was detected in linear slope tests. Because body size increased over this time, an

analysis of covariance adjusting for size effects suggested a negative relationship between performance and age. This outcome is probably an artefact of the timing of testing. The 8-month test was performed 4 weeks after the snakes emerged from hibernation while the 20-month test was conducted only 1 week post-hibernation. All snakes ate and passed at least two meals before the 8-month test, whereas no snakes were fed between hibernation and the 20-month test. It is likely that snakes in the latter test were still recovering from the physiological changes associated with emerging from hibernation and had no opportunity to recoup energy lost during hibernation. Additionally, these animals had been largely immobile for a period of 3 months prior to the test and were probably suffering from minor muscle atrophy. No information is available regarding the timing of physiological and behavioural recovery from hibernation in reptiles. Studies of this kind promise to be especially interesting because emergence from hibernation is a time of high local population densities and mating in many species, and is therefore probably a period of especially strong selection on many traits.

This study did not include control subjects without testing experience, so no direct test of the effect of experience on escape behaviour was possible. Short- and long-term habituation and long-term sensitization of defensive response to artificial threat stimuli in a variety of *Thamnophis* species have been demonstrated (Herzog & Burghardt 1988; Herzog et al. 1989; Herzog 1990). It is possible that a similar effect could explain the decrease in reversals and locomotor performance observed in the laboratory group. This is an unlikely explanation, however, in that the decreases seen in this study occurred after 8 or 20 months, whereas the experiential effects found in other studies occurred within 2 weeks or 2 months. Also, previous studies of lizards found no effect of repeated testing on locomotor performance (Gleeson 1977; Garland et al. 1987).

Ontogenetic Trends in Colour Pattern

Little is known about the specifics of ontogenetic colour pattern change in snakes, particularly in polymorphic species. Many species have different patterns as juveniles and adults, but the details of the timing of changes are unknown (Wright & Wright 1957). In some polymorphic species, differences in pattern frequencies between juveniles and

adults have been observed, but this may be due to ontogenetic change or differential selection (Camin & Ehrlich 1958; Gregory et al. 1983; King 1987). In one species of *Elaphe* that has been followed longitudinally, neonates may be striped or blotched but converge on the striped pattern between 1 and 4 years (Hadley & Gans 1972). Differences in behaviour of juveniles and adults may accompany such pattern shifts (Gans 1961; Burghardt 1978).

In *T. ordinoides*, dorsal pigmentation patterns appear to brighten slightly before their first summer, but individuals' patterns do not change qualitatively. Snakes that are predominantly unstriped or spotted remain so while those with stripes simply become more obviously striped. This brightening of colour pattern with growth may be partially a result of the production of diet-dependent pigments such as carotenoids that are responsible for the reds and oranges present in many animals (Rossotti 1983). Pattern morphs in *T. ordinoides* are known to be genetically correlated with the tendency to perform reversals, presumably because selection favours particular combinations of colour pattern and behaviour (Brodie 1989a, 1991, 1992). Ontogenetic convergence of colour pattern would not be expected as long as correlational selection acts in this manner.

Consistency of Individual Differences

Although all of the traits examined in this study showed some change over time, either in the laboratory or the field or both, individuals retained their relative differences throughout the first 2 years of life. The possible exception to this trend is locomotor performance in the 1-year field group, but no individual differences were detectable in this group as neonates. The strong correlations between ages in the field groups suggest that experiences in nature are either similar for all individuals or are of relatively minor importance in determining behavioural expression at a later age. The work of Herzog and colleagues (Herzog & Burghardt 1988; Herzog et al. 1989; Herzog 1990) suggests that experience does effect some aspects of anti-predator behaviour in juvenile garter snakes, but that individual and family differences are robust to this effect.

The stability of individual differences through time suggests that positive genetic correlations exist between the expression of a behaviour at different ages. This could result either from the same genes controlling a behaviour throughout ontogeny, or

from linkage between genes that are expressed at different ages (Falconer 1981). The pattern of genetic covariance of behaviour at different ages will affect the short-term evolution of ontogenies in the same manner that genetic covariances among meristic traits affect their evolutionary trajectories (Lande & Arnold 1983; Arnold 1990). Longitudinal studies of family groups can provide the data both for estimating genetic covariances among traits at different ages (Arnold 1990), and for estimating heritabilities of and genetic correlations between the actual functions that represent ontogenies of traits (Kirkpatrick et al. 1990). This information is necessary to predict the evolutionary response of ontogenies to natural selection (Arnold 1990).

That individual differences observable as neonates are retained at least throughout juvenile development also lends credence to the growing wealth of studies that use quantitative genetic techniques to examine a variety of traits in natural populations of reptiles (e.g. Arnold 1981; Arnold & Bennett 1984, 1988; Huey & Dunham 1987; Garland 1988; Herzog & Burghardt 1988; Brodie 1989a, 1991; Brodie & Brodie 1990, 1991). Typically, such studies seek to draw conclusions about the ecological importance of individual and heritable variation based on measurements of neonates. If individual ontogenies interacted with age so that an individual's behaviour as a neonate was not necessarily a good predictor of its behaviour as a 1- or 2-year-old, then the interpretation of neonatal variation would be sorely complicated. However, the results of this and other studies of juvenile reptiles indicate that individual ontogenies of many aspects of behaviour are parallel, at least for the first 1–2 years of life (Huey & Dunham 1987; Herzog & Burghardt 1988; van Berkum et al. 1989).

Mark-recapture studies typically consider selection over some window of time, but are unable to determine the precise time of a selective event (e.g. Arnold 1988; Jayne & Bennett 1990a). If phenotypes are changing during this period, it will similarly be impossible to determine the exact value of a trait at the time of selection. If variation among neonates disappears or if the relative rankings of individuals change before an important period of selection, then fitness functions estimated from neonatal scores may be inaccurate representations of true selection. An extreme example would be if relatively slow and fast snakes traded ranks before some critical period that favoured faster snakes. If selection was measured by survival past this period,

it might appear, based on neonate data, that slow snakes were at an advantage (Fig. 4). However, if all individuals changed in a parallel fashion, such a study would accurately represent the form of selection, even though the exact scale might be shifted because each individual's absolute speed increased before selection (Fig. 4).

Selection acts on individual variation and creates an evolutionary response through the inheritance of such variation. Information on the genetic control and pattern of individual variation in ontogenies is critical for evaluating adaptive hypotheses about the development of behaviour (Arnold 1990). Studies of individual ontogenetic trajectories can suggest underlying genetic mechanisms, but are not a substitute for longitudinal studies of family groups. It is phenotypic variation, however, that selection acts upon, and the ontogenetic change of individual differences is an important consideration in longitudinal studies of selection.

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