The consistency of individual differences in behaviour: temperature effects on antipredator behaviour in garter snakes

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Differences among individuals are necessary for natural selection to occur. The extent and expression of these differences can limit the power of selection to cause evolutionary change. When individuals inconsistently express a trait, selection is less powerful. Labile traits such as behaviour are most likely to be inconsistent in their expression, because of the substantial role of environmental factors in their immediate expression. Previous work has focused on the consistency, or repeatability, of individual behaviour across different environments or within a single environment; little is known about how repeatability within an environment changes across environments. To address this issue, we examined the consistency of antipredator behaviour in juvenile garter snakes in different thermal environments. A group of 59 laboratory-born garter snakes, *Thamnophis ordinoides*, was repeatedly assayed for sprint speed, distance crawled, and number of reversals performed during flight and antipredator display. Antipredator display showed very little variation and could not be analysed. Each individual was tested three times at each of three temperatures chosen to span the range of temperatures that snakes encounter in the field (15, 22.5, 30°C). Temperature had substantial effects on the average expression of each behaviour; snakes crawled more slowly, for shorter distances, and performed fewer reversals at cooler temperatures. Individuals showed significant consistency in their behaviour, and this consistency of expression was not affected by temperature.

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Differences among individuals are the substrate for natural selection. This variation in phenotype is an essential element of the evolutionary process; without differences among individuals, there could be no 'favoured variants' as originally described by Darwin (1859). Modern approaches to understanding natural selection formalize the importance of individual variation by measuring and modelling selection as the covariance between traits and fitness (Price 1970; Lande & Arnold 1983; Brodie et al. 1995).

The perspective of variance and covariance as integral parts of natural selection further reveals the importance of the consistency of individual differences. If an individual always expresses the same value of a trait, the relationship between that character and fitness is predictable; however, if an individual expresses different values of a trait during its lifetime, the relationship between fitness

and the character becomes difficult to define. For example, sprint speed in reptiles is well known to depend on temperature, whereby an individual snake may crawl 25–50% slower at a cool temperature than a warm one. Although this individual may be among the fastest in the population, the speed it expresses at a cool temperature may be insufficient to escape predation. In this scenario, the inconsistency of sprint speed makes it difficult to predict the evolutionary consequences of variation without more knowledge of the environment in which selection occurs and how the environment influences individual phenotypic expression. Individuals might express traits differently across environments, or they might be inconsistent in their phenotypic expression within a single environment. Either source of within-individual variation leads to a weaker covariance between phenotypes and fitness, and therefore weaker selection.

The expression of labile traits such as behaviour is particularly sensitive to environmental effects, which may range from abiotic factors such as temperature (e.g. Hertz et al. 1982; Crowley & Pietruszka 1983; Passek & Gillingham 1997) to less obvious biotic influences such as

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interactions with conspecifics (Boake 1989; Moore et al. 1997). The consistency, or repeatability, of any trait measured across environments will clearly be lower than in any single environment. What is less clear is how the repeatability of a character within an environment differs across the range of environments. Environmental influences can obviously change the average value of a trait expressed (e.g. slower speeds at cooler temperatures in reptiles), but we do not know whether individuals are equally consistent in the expression of their characters in different environments. If repeatability varies among environments, the ability of selection to generate evolutionary change will also depend on the environment; selection will be less effective when individuals are less consistent or traits are less repeatable (Brodie 1993a).

An understanding of the evolution of behaviour is especially dependent on knowledge about repeatability and how it varies. Unlike many morphological traits, which may be developmentally dependent on the environment but are fixed once expressed, behavioural traits may switch back and forth between values depending on the immediate environment. While much attention has been paid to how environments affect the average expression of behaviour (e.g. Crowley & Pietruszka 1983; Arnold & Bennett 1984; Herzog et al. 1989; Passek & Gillingham 1997), little is known about how environments affect the variation or repeatability of behaviour.

Antipredator behaviour in reptiles has been a useful model system for investigating individual variation in behaviour, and a variety of environmental contributions are known to influence the average expression of traits from locomotor performance to aggression. Most commonly studied are the effects of temperature which not only affect speed and endurance, but often modify aggression or defensiveness of antipredator display (Hertz et al. 1982; Crowley & Pietruszka 1983; Schieffelin & de Queiroz 1991; Keogh & deSerto 1994; Scribner & Weatherhead 1995; Passek & Gillingham 1997). Recent feeding history (Garland & Arnold 1983), reproductive status (Bauwens & Thoen 1981; Brodie 1989a; Cooper et al. 1990), nature of threat stimulus (Arnold & Bennett 1984; Burghardt & Greene 1988; Herzog et al. 1989; Burger et al. 1991) and experience (Herzog & Burghardt 1986, 1988; Herzog 1990; Herzog et al. 1992) are also known to alter the expression of antipredator traits. Virtually no information is available on whether or how individual consistency depends on these changes in average behaviour (but see Arnold & Bennett 1984; Brodie 1989a). In particular, temperature might be expected to influence behavioural consistency in reptiles, as it affects virtually every aspect of ectotherm physiology (Lilliwhite 1991).

To examine the repeatability of behaviour under different conditions, we observed antipredator behaviour of juvenile garter snakes at three different temperatures. Employing a standard laboratory testing regime, we assayed individual snakes repeatedly for a variety of performance and behaviour traits. This approach enabled us to investigate both the effect of temperature differences on the average behaviour expressed by juvenile snakes and on the consistency of individual differences.

METHODS

The subjects of this study were 59 neonate ($\sim$30 days old) *Thamnophis ordinoides* born in the laboratory to 11 wild-caught females from the Qualicum Fish Hatchery, Vancouver Island, British Columbia. Females were collected in June 1995 and housed in 40-litre aquaria on a 12:12 h light:dark cycle until parturition. Each individual had access to a thermal gradient ranging from 21 to 32°C. Within 24 h of parturition, we weighed and measured (snout–vent length) all offspring. Subjects were then housed for 10 days and subjected to an initial behaviour and colour-pattern test (cf. Brodie 1989a, 1992, 1993a, b) as part of a separate study. All individuals were subjected to two repeated testings each of sprint speed, distance crawled and number of reversals as described below, but at a single test temperature of 30°C. Upon completion of these tests, we placed subjects into aquaria on an LD 12:12 h cycle at 25°C, in groups of 10–15. All snakes were maintained on a diet of earthworms from birth until testing.

When the majority of individuals reached 30 days of age, we offered them food for 3 successive days and then fasted them for 3 days to clear their guts. We then weighed and measured each snake to determine its condition. Subjects were housed individually in plastic boxes ($18 \times 13 \times 6$ cm) during the 9 days of testing (for locomotor performance and display). All individuals were held at 22.5°C during the 9-day test period except for the 4–6 h before testing, when they were held at the designated test temperature to ensure acclimation. Following the last trial, we weighed the snakes again to determine the amount of body mass lost during the test period. We conducted a second set of tests (for sprint speed) 3 weeks after the conclusion of the first set. Between these two test periods, snakes were fed every other day for 17 days, then fasted for 3 days to clear their guts. Individuals were again weighed before and after the test period to assess condition.

Behavioural Measurements

Twenty-four hours prior to each behavioural trial, we randomly assigned each snake to one of three temperature treatments (15, 22.5, or 30°C) and allowed them to acclimate for 18–24 h. We selected these temperatures to represent the range of temperatures that an active snake might encounter in the wild (based on field observations of this species, E. Brodie III, unpublished data). Each individual was tested at each temperature three times for a total of nine measurements over a 9-day period. We randomized order of testing both within temperatures and within snakes.

In the first set of tests, we examined antipredator behaviour following an established paradigm (cf. Arnold & Bennett 1984; Brodie 1989a; Garland 1994). We placed the snakes on a circular racetrack (294 cm in circumference) lined with astroturf, and stimulated them to flee by

tapping them on the tail with a cotton-tipped swab. We terminated a trial when the snake, while being tapped, either stopped to show an antipredator display or refused to move after 10 consecutive taps to the tail. Behaviours examined included distance crawled, the number of reversals in direction (Brodie 1989a, 1992, 1993a; Brodie & Garland 1993), and the antipredator display (Arnold & Bennett 1984; Brodie 1989b, 1992; Brodie & Garland 1993). Antipredator display is scored on a quasi-continuous scale that sums behavioural elements of the head, body and tail. The scale has been interpreted as reflecting increasing offensiveness of response with increasing values of the score (Arnold & Bennett 1984). These behaviours have been well studied in garter snakes and are presumed to be important in escape from predators (Jayne & Bennett 1990; Brodie 1992; Garland 1994).

We assessed sprint speed in a second set of tests (cf. Brodie 1989a; Garland 1994). We stimulated the snakes to crawl along a 2-m linear track lined with astroturf by tapping them on the tail with an extended index finger. Interval times were taken every 0.5 m with a stopwatch. The fastest 0.5-m interval during a trial was taken as an individual's maximum sprint speed for that trial. We recorded three measures at each of three temperatures for a total of nine measures of sprint speed per individual.

Statistical Analyses

Snakes that were judged to be in poor physical condition during the test were removed from the data set prior to any analysis of the behaviours. We obtained a condition index by regressing the pretest weight on snout–vent length and using residual weight as an indicator of condition. Individuals with extremely negative residuals (-0.2 or less) were considered to be overly thin for their length and were therefore excluded from further analyses. Five individuals were excluded from the antipredator/locomotor performance analyses due to condition (and a sixth because it was undergoing ecdysis during the test period). Fifty-one individuals were included in the final analysis. For the sprint tests, six additional snakes were judged to be in poor condition using the residual index so the final analysis included 45 individuals.

We examined each behavioural variable for normality. Antipredator display showed little variation and was therefore not analysed statistically. The reversal measure was the only remaining variable that was not normally distributed and was transformed using $[reversals+1]^{0.5}$. We also conducted a regression analysis to determine whether the behaviours were influenced by differences in age and condition. Only speed was affected by condition (30°C: $t=2.69$, $P<0.01$; 22.5°C: $t=2.88$, $P<0.006$; 15°C: $t=3.01$, $P<0.005$). Neither distance nor reversals was significantly influenced by age or condition. As a relative measure of speed uncorrelated with differences in condition (cf. Brodie 1993a; Brodie & Garland 1993; Garland 1994), we used the residuals from the regression of speed on condition in the statistical analyses.

We examined temperature effects on average behaviours using a one-way analysis of variance (ANOVA). We made unplanned comparisons of pairwise differences between mean scores at different temperatures via Tukey's least significant difference procedure with an experimentwise $\alpha=0.05$ (Sokal & Rohlf 1995).

We calculated the repeatability of the behaviours from a one-way ANOVA with individual as the main effect. We calculated observational components of variance from the mean squares (Becker 1984; Lessells & Boag 1987; Falconer & Mackay 1996). We then estimated repeatability as the ratio of among-individual variance (σ^2_A) to the total phenotypic variance (or the sum of within- and among-individual variances, $\sigma^2_W+\sigma^2_A$):

$$R=\frac{\sigma^2_W}{\sigma^2_W+\sigma^2_A}.$$

We calculated repeatabilities separately for each behaviour at each temperature and calculated standard errors for all repeatabilities following Becker (1984). We compared repeatabilities at each temperature using pairwise t tests.

RESULTS

### Temperature Effects on Behaviour

All antipredator behaviours were significantly influenced by temperature (Fig. 1; distance: $F_{2,150}=89.62$, $P<0.0001$; reversals: $F_{2,150}=10.59$, $P<0.0001$; speed: $F_{2,130}=93.62$, $P<0.0001$). In general, snakes crawled faster and further at higher temperatures, and also performed more reversals. Within each behaviour, all pairwise comparisons between temperatures (i.e. 30°C versus 22.5°C, 22.5°C versus 15°C, and 30°C versus 15°C) were significant at $P=0.05$ with the exception of the comparison of number of reversals between 30 and 22.5°C (Fig. 1).

Little variation in antipredator display was observed at any temperature. On the quasi-continuous scale proposed by Arnold & Bennett (1984), individuals typically scored a 2 (an outstretched body with tail undulating). A few individuals deviated from this pattern by either hiding the head (display=1) or not undulating the tail (display=3). Variation at any temperature was insufficient to analyse antipredator display further.

Temperature Effects on Repeatability

Repeatabilities of behaviours were generally intermediate in value, ranging from 0.32 to 0.66 (Table 1). Number of reversals was the least repeatable of the behaviours, with values ranging between 0.3 and 0.4. The locomotor performance traits were somewhat more repeatable, with values between 0.45 and 0.65.

Repeatabilities did not vary significantly among temperature treatments (Table 1). None of the pairwise comparisons between temperatures was significant within behaviours, and no general trend relating temperature to repeatability was observed. Because the null hypothesis could not be rejected, we investigated the power of the t test to detect significant differences between repeatabilities. Assuming a standard error for the repeatability
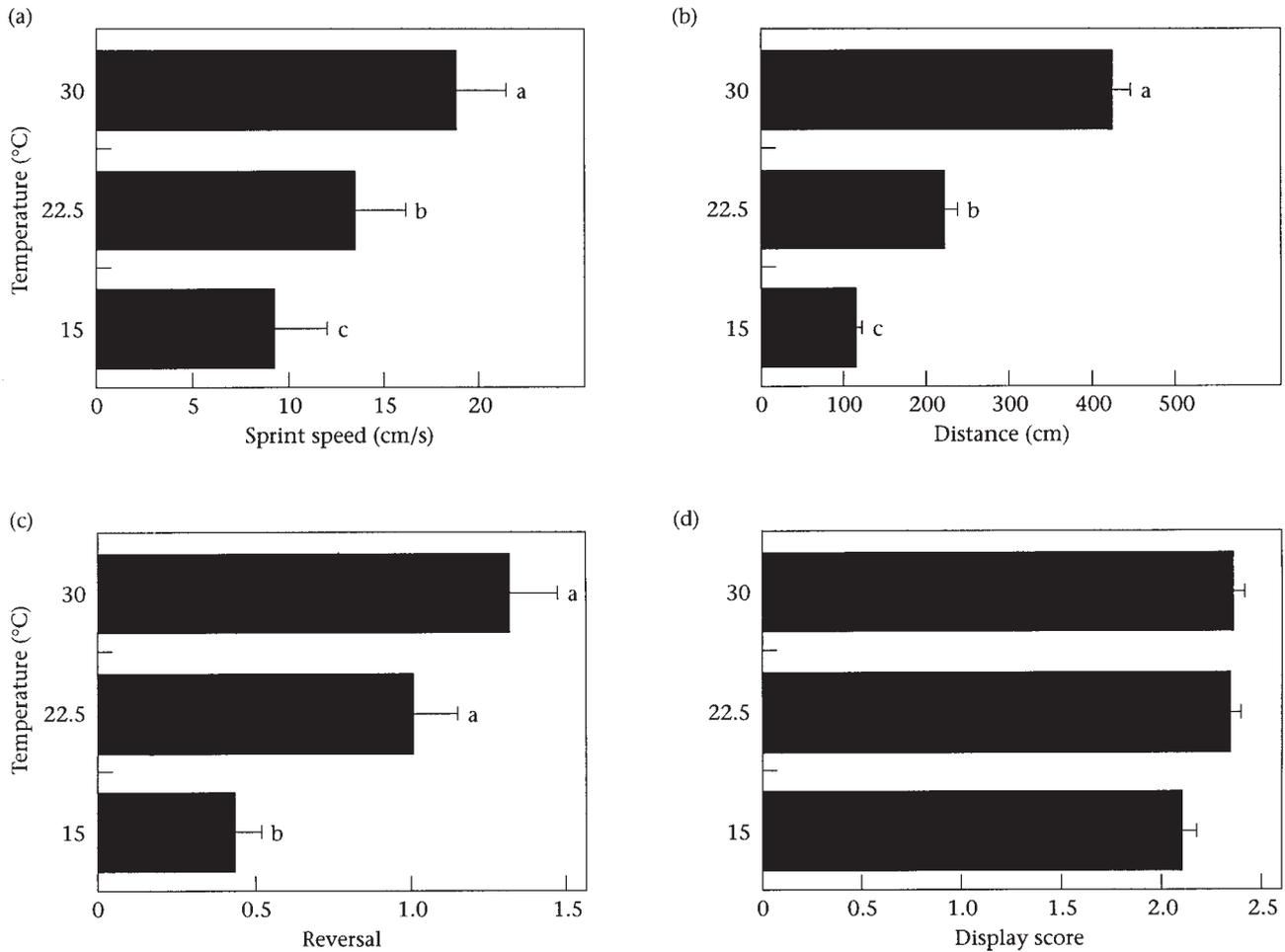
Figure 1. Average (±SE) behaviours at three temperatures. (a) Sprint speed (cm/s), (b) distance crawled (cm), (c) number of reversals and (d) antipredator display of snakes tested at each of three temperatures. Mean scores at different temperatures that were judged significantly different by Tukey's LSD (P<0.05) are denoted with different letters.

Table 1. Repeatabilities of antipredator behaviour at three temperatures

Speed	Temperature (°C)	Repeatability	versus 22.5°C	versus 15°C
	30	0.527±0.080	| t | =0.910	| t | =0.119
	22.5	0.659±0.065		| t | =0.789
	15	0.546±0.078		
Distance				
	30	0.444±0.086	| t | =1.060	| t | =0.178
	22.5	0.611±0.071		| t | =0.879
	15	0.474±0.084		
Reversals				
	30	0.392±0.089	| t | =0.086	| t | =0.317
	22.5	0.376±0.090		| t | =0.789
	15	0.319±0.092		

t statistics refer to the comparison of repeatabilities between two temperatures. All values were nonsignificant at a testwise P>0.05.

estimates of 0.082 (the average for the nine repeatabilities estimated in this study), we calculated the minimum difference in repeatability that would be judged signifi-cant at the testwise $\alpha=0.05$. We found that a 33% difference in repeatability (e.g. repeatabilities of 0.34 and 0.67) would be detected.

DISCUSSION

Temperature Effects on Behaviour

Many conditions, stimuli and environments are known to influence antipredator behaviour. Especially in reptiles, these changes in behaviour are generally thought to reflect a combination of adaptive changes and physiological limitations. As expected, temperature had a dramatic effect on the expression of antipredator behaviours in this study. Speed and distance, both measures of locomotor performance, and the number of reversals, a measure of evasiveness, were all depressed at lower temperatures (Fig. 1). This relationship between organismal performance and temperature is well documented (e.g. Arnold & Bennett 1984; Lilliwhite 1991; Scribner & Weatherhead 1995; Passek & Gillingham 1997), and emphasizes the physiological constraints on the expression of some behaviours.

Many studies that have detected decreased locomotor performance as a result of environment or condition have noted a corresponding increase of behaviours that presumably compensate for this reduced escape ability. Reduced performance at low temperatures is accompanied by increased aggression (Hertz et al. 1982; Crowley & Pietruszka 1983) or 'shyness' (Rand 1964) in lizards. In snakes, antipredator displays are usually more exaggerated (either more passive or offensive) at low temperatures (Schieffelin & de Queiroz 1991; Scribner & Weatherhead 1995). Pregnancy also results in lower locomotor abilities and is accompanied by a variety of compensatory behavioural changes (Bauwens & Thoen 1981; Brodie 1989a; Cooper et al. 1990). In fact, T. ordinoides is known to increase the number of reversals performed during pregnancy, presumably to alleviate selection pressure by switching to a less locomotor-dependent escape strategy (Brodie 1989a). Contrary to these observations, the number of reversals performed by T. ordinoides in this study decreased along with speed and distance, possibly indicating a physiological limitation to performing this behaviour.

As in previous studies of T. ordinoides from other populations (Brodie 1989a, b, 1992, 1993a, b), antipredator display showed little variation. The typical display expressed by T. ordinoides is an outstretched body with undulating tail (Brodie 1989a, 1993a). Comparable studies of other garter snake species have detected much more variation in antipredator display (T. radix, Arnold & Bennett 1984; T. sirtalis, Garland 1994). The greater variation expressed by some taxa may reflect additional behavioural elements in the threat display such as use of the head and mouth. Threat displays are rarely seen in T. ordinoides, especially in juveniles, perhaps because of their small body size (neonates are typically small, 120–160 mm total length).

Consistency of Individual Behaviour

The levels of individual repeatability observed in this study are comparable to those reported by other authors. In garter snakes, the repeatability of locomotor perform-

ance characters like speed and endurance are generally in the range of 50–80%, while the repeatability of other antipredator behaviours is somewhat lower at 35–65% (e.g. Arnold & Bennett 1984; Brodie 1989a, b; Brodie & Brodie 1990; Garland 1994). It is not surprising that behaviours often have relatively low repeatability, given the possible sources of variance within individuals, including factors such as condition, motivation, and unknown, uncontrolled aspects of the testing protocol.

Individual consistency did not appear to be affected by environment, even though the environment had substantial effects on the average behaviour expressed. One might have expected temperature to affect the consistency of behaviours, because it alters the basic physiology of the individual (Lilliwhite 1991; Garland 1994). None the less, while speed, distance crawled, and the numbers of reversals all increased with temperature, an individual's ability to perform consistently did not change. It is important to keep in mind the statistical difficulty in detecting differences in repeatability estimates. As indicated by the power analysis, only large differences in repeatability could be recognized with a study of the scale reported here. However, large sample sizes reduce the standard error of the repeatability estimate, providing much greater opportunity to recognize small differences. Standard errors reported by Brodie (1993b) for repeatability estimates of the same behaviours investigated in this study (all tested at 30°C) ranged from 0.014 to 0.029 for a population of T. ordinoides where 393 individuals were examined. Standard errors of this magnitude would allow the detection of differences in repeatability of 17–20%, even after conservatively adjusting significance levels for multiple comparisons. Even at this scale, none of the repeatability differences found in this study would be judged significant.

The Importance of Individual Differences

The ability of natural selection to drive adaptive change is determined in part by the amount and stability of individual differences. The repeatability of individual differences can be viewed as an upper bound on the genetic variation between individuals that determines the reponse to selection (Boake 1989; Brodie & Garland 1993; Falconer & Mackay 1996) because differences within an individual cannot be due to genetics. Thus, two behaviours with different patterns of repeatability might evolve differently under the same strength of selection. Behaviours with low repeatability cannot have a high heritability and so are likely to respond to selection more slowly than behaviours that are highly heritable and highly repeatable.

Repeatability also directly affects the relationship between expected fitness and phenotype. A highly repeatable trait will be expressed the same in different instances, and therefore will have predictable fitness consequences. However, traits that have low repeatabilities may take on different values when expressed multiple times. A character that is inconsistently expressed could generate a range of possible fitness consequences (Brodie 1993a),

thus weakening the covariance between phenotype and fitness that is selection.

The same scenario holds for behaviours expressed in different environments. Several studies have examined the consistency of individual differences across environments and ages and found that individuals generally maintain at least their rank order of difference (Herzog & Burghardt 1988; Herzog et al. 1989; Herzog 1990; Brodie 1993a). This result implies that selection acting at multiple ages or in multiple environments will have the same qualitative effect on the distribution of traits (Brodie 1993a). If repeatabilities of behaviours are consistent across the same range of environments or ages, as in this study, then the quantitative effect of selection should also be the same.

While patterns of repeatability can provide some insight into the potential for selection to affect a trait, the interpretation of repeatability remains complex. Any estimate of repeatability is specific to the conditions and individuals that are being examined. Thus, while low repeatability does imply a low level of genetic variation, aspects of the experimental protocol or the ability of the observer to accurately detect differences may render the trait observed less relevant to selection. For example, sprint speed may be highly repeatable under a condition of controlled temperature and stimulus, but unrepeatable if these aspects are not carefully standardized. Sprint speed as assayed under these variable conditions has relatively little genetic variation (compared with environmental variation), but this does not imply that sprint speed is not influenced by genetics, nor that heritability of sprint speed could not be large under conditions that reduce the environmental sources of variation. Alternatively, responses to environmental cues may be variable, and the response itself affected by selection. In order to truly understand the relationship between selection and patterns of character variation (phenotypic and genetic), it is essential that the appropriate context and scale of environmental variation be examined.

Acknowledgments

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