

Genetic correlations between morphology and antipredator behaviour in natural populations of the garter snake *Thamnophis ordinoides*

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THE genetic coupling of morphology and behaviour means that the evolution of the two types of traits will not be independent: changes in behaviour will result in changes in morphology and vice versa^{1,2,3}. This might explain nonadaptive differences in morphology through indirect selection on correlated characters of other categories⁴. Genetic correlations between morphology and behaviour are also the basis for some models of sympatric speciation⁵ and of the stability of polymorphisms⁶. Morphology and behaviour are often correlated in nature^{7–11} and a genetic basis for such couplings has been demonstrated^{12,13}. I present here evidence that colour pattern and antipredator behaviour are genetically coupled in natural populations of the garter snake *Thamnophis ordinoides*. Similar phenotypic correlations between pattern and behaviour exist among species of North American snakes¹⁴, indicating that selection for particular combinations of traits may help to maintain genetic covariances and colour polymorphism in *Thamnophis ordinoides*.

Interspecific studies can provide a basis for predicting patterns of genetic correlations within populations. Dorsal pigmentation patterns of different species of snakes are correlated with specific ecological and behavioural tendencies. Longitudinally striped snakes tend to be more active, wide-foraging and flee when threatened, whereas species with broken colour patterns (blotches or crossbands) are more secretive and rely on crypsis or aggression as their primary defence¹⁴. These relationships probably reflect survival advantages of particular combinations of traits. It is more difficult for the vertebrate eye to detect motion or judge the speed of a moving stripe than a moving heterogeneous pattern¹⁵, so that flight may be a more effective antipredator behaviour for striped snakes than for blotched ones.

The Northwest garter snake, *Thamnophis ordinoides*, exhibits variation in colour pattern within populations similar to that observed across snake species. To determine whether this morphological variation is genetically coupled with behavioural variation, colour patterns and four types of antipredator behaviour¹⁶ were scored for 474 neonates from 77 litters from 3 natural populations of *Thamnophis ordinoides* in coastal Oregon (Table 1). The four behaviours scored (sprint speed, endurance, antipredator display and the number of reversals during flight) were not mutually exclusive, but rather were each present in varying degrees in each individual.

Neither repeatabilities nor heritabilities differed significantly among populations. Pooled estimates and population estimates are given in Table 1. Estimates of repeatabilities indicated significant ($P < 0.05$) variation among individuals for each of the antipredator behaviours scored. The broad-sense heritabilities of all behaviours and the stripe index were significantly different from zero, indicating the existence of significant additive genetic variance for each of these traits (broad-sense heritability estimates also include a fraction of dominance variance²).

Colour pattern was genetically correlated with the number of reversals during flight but not with any other behaviour examined (Table 2). In two populations, significant negative genetic correlations were detected between the stripe index and the number of reversals during flight. In the third population, a significant correlation was observed between the stripe index

TABLE 1 Repeatabilities (R) and heritabilities (h^2) \pm standard error for all traits

		Tenmile (200, 29)	Alesa (122, 19)	McGribble (152, 29)	All (474, 77)
Stripe	R	—	—	—	—
	h^2	0.707 \pm 0.162	0.511 \pm 0.207	1.080 \pm 0.170	0.781 \pm 0.008
Distance	R	0.725 \pm 0.024	0.823 \pm 0.024	0.767 \pm 0.044	0.773 \pm 0.016
	h^2	0.798 \pm 0.164	0.575 \pm 0.212	0.387 \pm 0.169	0.593 \pm 0.103
Reversal	R	0.465 \pm 0.033	0.509 \pm 0.052	0.348 \pm 0.082	0.456 \pm 0.004
	h^2	0.245 \pm 0.122	0.225 \pm 0.110	0.783 \pm 0.184	0.366 \pm 0.007
Display	R	0.536 \pm 0.031	0.546 \pm 0.049	0.509 \pm 0.074	0.534 \pm 0.004
	h^2	0.161 \pm 0.112	0.630 \pm 0.216	0.513 \pm 0.178	0.377 \pm 0.007
Speed	R	0.528 \pm 0.032	0.840 \pm 0.021	0.766 \pm 0.041	0.728 \pm 0.003
	h^2	0.528 \pm 0.032	0.419 \pm 0.196	1.173 \pm 0.163	0.608 \pm 0.005

Estimates of repeatabilities are from intraclass correlations^{2,22} of four repeated measures for sprint speed and two repeated measures for other behaviours. The average of all three populations (weighted by the reciprocal of each population's sampling variance) is given under 'All'. The number of individuals and families, respectively, for each population is shown in parentheses. Specific components of colour pattern were scored and then combined into an index indicating 'stripedness'. Pattern components are mendelian characters (S. J. Arnold, unpublished data) and are combined to create a quantitative character more appropriate for quantitative genetic analyses. The index used is $\{(DS \times DC) + (LS \times LC) + 1\} / SPOT = STRIPE$, where DS and LS are the completeness of dorsal and lateral stripe on a 0–4 scale (0 = absent, 4 = present the entire length of the body), DC and LC are the contrast of dorsal and lateral stripe on a 0–3 scale and SPOT is the presence or absence of spots (1 = no spots, 2 = 1 row and 3 = 2 rows). Neonatal locomotor performance (sprint speed and endurance), defensive display²³ and the number of reversals in direction during flight¹⁶ were scored repeatedly at the same age (3–6 days old) for each individual¹⁶. Regression techniques were used to statistically remove the maternal effects associated with condition of the female for all behaviour scores²⁴. Residual behaviour scores from a regression on female mass and snout-vent length were used to calculate heritabilities and genetic covariances (Table 2). Additive genetic parameters were estimated by analyses of variance of covariance within and among presumed full-sib litters and therefore may include contributions from dominance deviations and the prenatal common environment².

TABLE 2 Genetic correlations between stripe and behaviour scores for each population

	Tenmile (29)	Distance	Reversal	Display	Speed
Stripe		–0.191	–0.751	0.150	0.280
		–0.173	–0.427**	0.106	0.219
Alesa (19)		0.384	–1.200	–0.180	0.635
		0.196	–0.499**	–0.060	0.291
McGribble (29)		0.491	–0.184	0.495	0.293
		0.187	–0.012	0.543*	0.303

The top row indicates covariance component estimate of the correlation based on full-sib data^{2,22}. Litter mean correlations are presented on the second row for purposes of significance testing^{4,25}. The number of litters for each population is shown in parentheses. Asterisks indicate the significance level of the litter mean correlation (** = $P < 0.01$; * = $P < 0.05$). See Table 1 for methods.

and antipredator display, but this correlation was due almost entirely to a single family and it was disregarded.

Sudden terminations of flight, such as the reversals scored here, can cause a predator to lose track of its quarry, allowing the prey a second chance to use crypsis as a defence^{16,17}. The correlations observed in the Tenmile and Alesa populations indicate that striped snakes flee directly whereas unstriped and spotted snakes exhibit a greater tendency for cryptic behaviour. This resembles the interspecific correlations between colour pattern and antipredator behaviour observed among all North American snakes¹⁴.

Genetic covariances result from pleiotropy (whereby genes affect multiple traits) or linkage disequilibrium (nonrandom association of alleles at different loci) or both. The data presented here cannot be used to distinguish between these causes, but the genetic covariances probably result from linkage disequilibrium rather than pleiotropy, because the coupling is between morphological and behavioural traits. In either case,

theory indicates that genetic covariances can be maintained by selection for particular combinations of traits¹⁸. The concordance between the correlations detected in this study and those observed across snake species indicates that selection favouring particular combinations of colour pattern and behaviour may be at least partially responsible for the maintenance of the genetic covariances reported here. Other phenomena that may contribute to the maintenance of genetic correlations include assortative mating, secondary contact of divergent populations, small effective population size and population subdivision¹⁹.

Selection favouring combinations of traits could also help to explain the extensive colour pattern polymorphism within populations of *Thamnophis ordinoides*. If the fitness of an individual with a particular colour pattern depends on its antipredator behaviour, then it may be that individuals with different combinations of colour pattern and antipredator behaviour have com-

parable fitnesses. A similar argument has been used to explain polymorphism in heterogeneous environments where different genotypes choose to occupy the microhabitat in which they are most fit. Under these conditions genetic polymorphisms within populations can be maintained with small genetic loads⁶.

The post-selection distribution of all characters will be a result not only of direct selection on those characters, but also of selection on genetically correlated characters. In this way, genetic covariances can constrain the rate²⁰ and even determine the direction²¹ of short-term evolutionary change. Thus, genetic correlations between morphology and behaviour imply a high degree of genetic integration of the entire phenotype, indicating that phenotypic evolution is more complex than even multivariate analyses of a single category of characters would indicate. □

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