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Thamnophis ordinoides

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Source: *Evolution*, Vol. 46, No. 5 (Oct., 1992), pp. 1284-1298

Published by: [Society for the Study of Evolution](#)

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CORRELATIONAL SELECTION FOR COLOR PATTERN AND ANTIPREDATOR BEHAVIOR IN THE GARTER SNAKE *THAMNOPHIS ORDINOIDES*

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Abstract.—Correlational selection favors combinations of traits and is a key element of many models of phenotypic and genetic evolution. Multiple regression techniques for measuring selection allow for the direct estimation of correlational selection gradients, yet few studies in natural populations have investigated this process. Color patterns and antipredator behaviors of snakes are thought to function interactively in predator escape and therefore may be subject to correlational selection. To investigate this hypothesis, I studied the survivorship of juvenile garter snakes, *Thamnophis ordinoides*, as a function of a suite of escape behaviors and color pattern. The only natural selection detected favored opposite combinations of stripedness of the color pattern and the tendency to perform during escape evasive behaviors called reversals. This selection presumably results from optical illusions created by moving patterns and their effects on visually foraging predators. Analysis of the bivariate selection surface shows that pure correlational selection can be thought of as a series of linear selection functions on one trait whose slopes depend on the value of the second trait. Alternatively, viewing the selection surface along its major axes reveals stabilizing and disruptive components of correlational selection. It is further shown that correlational selection alone can promote genetic variance and covariance within a generation. This phenomenon may be partially responsible for the extreme variation in color pattern and the genetic covariance between color pattern and behavior observed in natural populations of *T. ordinoides*.

Key words.—Antipredator behavior, color pattern, correlational selection, genetic covariance, natural selection, predation, Serpentes, *Thamnophis ordinoides*, variation.

Received October 9, 1991. Accepted February 22, 1992.

The view of natural selection as a topographic surface with highest fitness at the peaks has given us a valuable perspective for considering phenotypic evolution (Lande and Arnold, 1983; Phillips and Arnold, 1989). The mean of any trait is expected to evolve in the direction of the locally steepest uphill slope on such a multivariate topography (Lande, 1976, 1979; Wright, 1977). In the simplest case of only two characters, this surface is determined both by selection affecting the mean (“directional”) and the variance (“stabilizing/disruptive”) of each trait, as well as selection affecting the covariance between two traits (“correlational”) (Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987; Phillips and Arnold, 1989). It has been shown that bivariate views of selection surfaces can be misleading if only directional and stabilizing selection are considered (Phillips and Arnold, 1989). Therefore, to produce a full picture of the forces of natural selection on even a two trait phe-

notype, at least three forms of selection must be considered.

Multiple regression techniques can be employed to measure all three types of selection. The regression of relative fitness, w , on each trait, squared trait and cross product of two traits yields gradients that measure the forces of directional (β_i, β_j), stabilizing (γ_{ii}, γ_{jj}) and correlational (γ_{ij}) selection, respectively (Lande and Arnold, 1983). For two traits, z_i and z_j , measured as deviations from their respective means, the resulting regression equation is

$$w = \alpha + \beta_i z_i + \beta_j z_j + \frac{1}{2} \gamma_{ii} z_i^2 + \frac{1}{2} \gamma_{jj} z_j^2 + \gamma_{ij} z_i z_j + \epsilon$$

where α is the intercept and ϵ is an error term (see Lande and Arnold, 1983; Endler, 1986). These gradients measure the change in the distribution of a trait or trait combination due to selection acting directly on that character, independent of changes due to correlations with other traits that are included in the analysis (Lande and Arnold,

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1983; Mitchell-Olds and Shaw, 1987). The coefficients of selection obtained from such an analysis are directly related to quantitative genetic models of evolutionary change and can also be used to reconstruct selection surfaces (Lande and Arnold, 1983; Phillips and Arnold, 1989).

The ease with which this methodology can be applied to natural systems has resulted in an explosion of demonstrations of natural selection acting on a variety of traits and taxa (e.g., Grant, 1986; Kalisz, 1986; Schluter and Smith, 1986; Conner, 1988; Hews, 1990; Jayne and Bennett, 1990a; Smith, 1990; Weis and Gorman, 1990). However, most of these studies report estimates of only directional and sometimes stabilizing selection gradients. Attempts to detect correlational selection gradients are not often reported (but see Lande and Arnold, 1983; Moore, 1990; Mitchell-Olds and Bergelson, 1990; Johnston, 1991), and are rarely successful (Clark, 1989; Rauscher and Simms, 1989; Arnold, 1988; Jordan, 1991; but see Arnold and Bennett, 1988, for correlational performance gradients). This relative neglect of correlational selection is probably due to the large sample sizes necessary to estimate the additional correlational terms in quadratic regression equations, rather than a lack of interest in the phenomenon.

Correlational selection favors particular combinations of two traits expressed together in the same individual, but may not affect the distribution of either trait alone (Endler, 1986). Beyond its ecological interest, correlational selection is an important feature of a variety of theories of genetic and phenotypic evolution. It is the force by which traits become functionally integrated with one another and is thought to be an important mechanism in promoting genetic integration as well (Lande, 1980, 1984; Cheverud, 1982, 1984, 1988; Zeng, 1988; for the evolution of supergenes, see e.g., Charlesworth and Charlesworth, 1976; Turner, 1977). Many models for the maintenance of polymorphism via habitat selection implicitly invoke correlational selection that favors certain combinations of morphotype and habitat preference and thereby creates a genetic coupling between these traits (reviewed in Hedrick, 1986). Microevolu-

tionary theories explaining ecological specialization (Futuyma and Moreno, 1988), evolutionary novelties (Cheverud, 1982; Kingsolver, 1988; Emerson and Koehl, 1990), and interspecific patterns of covariance (Felsenstein, 1988; Zeng, 1988; Emerson and Arnold, 1989) also invoke selection for combinations of traits.

Some of these theoretical expectations may be useful in predicting specific situations where correlational selection is operating. For example, interspecific patterns of covariance between color pattern and behavior have been observed among North American species of snakes (Neill, 1963; Jackson et al., 1976). In general, striped patterns are associated with diurnal activity, use of open habitats, and flight as a primary defense. Broken, blotched, or banded patterns tend to correlate with secretive habits and habitat use, and cryptic or aggressive antipredator behavior. This coupling of color pattern and behavior is thought to reflect correlational selection favoring particular combinations of these traits because of their interaction during escape from predators (Klauber, 1931; Jackson et al., 1976). Motion is difficult to detect and speed difficult to judge in snakes with a longitudinally striped pattern. This effect becomes more pronounced when a snake has multiple narrow stripes. Conversely, banded, blotched, or spotted patterns provide fixed reference points for the eye, thereby enhancing the detection of movement (Brown, 1931a, 1931b; Klauber, 1931; Jackson et al., 1976). Thus, natural selection is expected to favor some combinations of color pattern and antipredator behavior over others.

A similar correlation between behavior and color pattern has been observed within populations of a single species of garter snake, *Thamnophis ordinoides*. This species exhibits extreme variation in color pattern (Nussbaum et al., 1983; Brodie, 1989a, 1991). Unmarked, spotted and varying degrees of striped individuals can be found within a single local population. In some populations, the level of stripedness of the color pattern is known to be negatively phenotypically and genetically correlated with an escape behavior called reversals (Brodie, 1989a, 1991). Reversals are stereotypical changes in direction during flight and are

an evasive maneuver thought to allow snakes to employ crypsis after initial detection by a predator (Pough, 1976; Brodie, 1989a, 1989b, 1991). In *T. ordinoides*, striped patterns are associated with direct flight and unmarked and broken patterns with evasive or cryptic behavior, similar to the correlation observed among species. Genetic covariances can arise from selection favoring combinations of traits (Lande, 1980, 1984; Cheverud, 1982, 1984, 1988), so it has been hypothesized that correlational selection is responsible for this association in *T. ordinoides* (Brodie, 1989a, 1991).

To determine whether correlational selection acts in a manner that might explain the observed genetic covariance, I conducted a longitudinal selection study in a natural population of *T. ordinoides*. Families of neonate snakes that were used to calculate the genetic variance-covariance matrix reported by Brodie (1989a, 1991) were marked and released into their natural population. Survivorship data based on recaptures of known individuals were used to calculate directional, stabilizing, and correlational selection differentials and gradients for a group of traits including stripedness and reversals. These parameters were then used to reconstruct the selection surface for this suite of antipredator characters. The measurement of selection in a population with a known genetic variance-covariance matrix facilitates comparisons of correlational selection with genetic correlations in a natural system.

MATERIALS AND METHODS

The subjects of this study were 646 neonate garter snakes born in the laboratory to 126 females taken from a natural population near Tenmile Creek, Lane County, Oregon (44°12'N, 124°00'W). Animals were obtained in three successive years: 162 individuals from 29 families in 1987, 237 individuals from 51 families in 1988, and 247 individuals from 46 families in 1989. These were a subset of the individuals used to estimate the genetic covariance matrix for color pattern and antipredator behavior in this population by Brodie (1989a, 1991). Details of captive maintenance can be found therein.

The study site was a clearing (approx-

mately 0.3 hectares), probably a former small sawmill site, adjacent to a large stream and located approximately 6 km inland from the Pacific coast. The clearing was bounded by a gravel road on one side and the stream on all other edges. Across the stream and across the road were old growth conifer stands. *Thamnophis ordinoides* concentrate in open areas, probably because of the abundance of suitable thermoregulation sites, and generally avoid entering water (Fitch, 1940; pers. obs.). This locality was chosen for recapture work because its physical features probably minimize emigration out of the population and because snakes were common enough to obtain a sufficiently large sample.

Measurement of Traits

Three antipredator behaviors were scored repeatedly on each individual during the six days immediately following birth. Sprint speed over a 0.5 m interval (=“speed”), the distance crawled until an antipredator display was performed (=“distance”), and the number of reversals of direction during flight (=“reversals”) were measured as described by Brodie (1989a, 1991, 1992). Garter snakes often bask a short distance from cover, and maximum speed over a 0.5 m interval may be important in escaping predators in these situations. *T. ordinoides* feed almost exclusively on slugs and earthworms (Fitch, 1941; pers. obs.) and often are found foraging in the middle of fields. Distance, a measure of behavioral tendency to sustain flight that probably also reflects stamina (Jayne and Bennett, 1990a), and reversals could take on an antipredator function under these circumstances. Each of these behaviors is highly repeatable (Brodie, 1989a, 1991, 1992). The average score of each behavior for a given individual was used for all analyses.

The overall stripedness of color pattern (=“stripe”) was scored for each individual (cf. Brodie, 1989a, 1991, 1992). This continuous index of stripedness has high values for individuals with three complete bright stripes, low values for individuals with no stripes but spots, and a value of zero for individuals with no markings.

The mass and snout-vent-length (SVL) of each neonate were also recorded for each

individual within 24 hours of birth. These measures of body size are highly correlated with speed and distance (Jayne and Bennett, 1990a) and were included as covariates in the selection analysis.

Mark-Recapture Methods

All neonates were marked with a unique identification code of clips on the ventral scales immediately following completion of behavior scoring. These marks persist for many years (at least seven, Jayne and Bennett, 1990a) and are not harmful to the snakes (Brown and Parker, 1976; Arnold, 1988). All individuals were released into the population within two weeks of birth.

Recapture work began in June, 1988, when the first cohort was nine months old, and was completed in September, 1990. Snakes were collected by hand both when active and from underneath cover objects. Collections were made on a total of 89 days over the three year period. All individuals recaptured at any time during the study ($N = 101$) were assigned an absolute fitness of one and those never recaptured ($N = 545$) were assigned an absolute fitness of zero. By the end of the study, the three cohorts were exposed to predation for different amounts of time (the 1989 cohort for one year, the 1988 cohort for two years, and the 1987 cohort for three years), but each was exposed to predation during the first year of life. If a snake was caught at any time during the three year study, it must have survived the first year. Scoring only individuals recaptured in the year following release would ignore information about first-year survivorship from snakes that were not recaptured until their second or third years. To use the most complete data on first-year survivorship, any snake known to have survived the first year was included in the selection analysis.

Estimation of Selection

Measuring selection on body size was not a goal of this study (natural selection favoring increased body size has previously been demonstrated in garter snakes, Jayne and Bennett, 1990a). To reduce the dimensionality of the selection analysis (the full quadratic regression on four traits estimates 14 selection gradients, while the same anal-

ysis for six traits estimates 27 gradients) but still control for correlations between the behaviors and body size, size-adjusted behavior scores were used to calculate selection coefficients. Regressions of each behavior on mass and SVL were performed and were significant for speed and distance but not reversals. Residuals scores from these regressions were uncorrelated with body size and were substituted for the original speed and distance scores in subsequent analyses (Jayne and Bennett, 1990a).

Relative rather than absolute fitness is used to calculate selection coefficients so it was necessary to convert the values of absolute fitness assigned to each individual. Relative fitness of each individual was calculated by dividing its absolute fitness by the average absolute fitness in the population. In a mark-recapture study where absolute fitness is equal to one if recaptured and zero if never recaptured, the average absolute fitness is equal to the proportion recaptured. In this study, 15.6% of the marked population was recaptured so relative fitness was equal to 6.4 for the recaptured snakes and 0 for those never recaptured.

A selection differential measures the total change in a trait due to the sum of direct and indirect selection and is equivalent to the covariance between a trait and relative fitness (Lande and Arnold, 1983). Directional selection differentials were calculated as the difference between the mean of a trait for all released individuals and the mean for those recaptured. If no directional selection occurs, stabilizing selection differentials can be approximated by the difference between the variance of each trait before and after selection, and correlational selection differentials as the difference between the covariances of each pair of traits (after Lande and Arnold, 1983; Eq. 13b). Because no directional selection was detected on any traits in this study (see below), stabilizing and correlational selection differentials were calculated as changes in variance and covariances, respectively. Each differential was then standardized to unit variance by dividing by the standard deviation of the character, the variance of the character (for stabilizing selection differentials), or the product of the standard deviations of two

TABLE 1. Phenotypic means, variances, correlations and covariances before selection in the Tenmile population. Pearson product-moment correlations are shown above the diagonal, covariances are shown below. Means (\bar{x}) and variances (s^2) are shown at bottom. Asterisks indicate Bonferroni adjusted (for 15 estimated parameters) significance levels of the phenotypic correlations.

	Mass	SVL	Speed (m/s)	Distance (cm)	Stripe	Reversals
Mass	—	0.813**	0.345**	0.152**	0.046	0.117*
SVL	2.99	—	0.526**	0.270**	0.064	0.010
Speed	0.01	0.34	—	0.416**	0.085	0.040
Distance	11.45	679.59	5.65	—	0.050	-0.026
Stripe	0.18	8.14	0.06	132.84	—	-0.178**
Reversals	0.07	0.19	0.00	-10.01	-3.48	—
\bar{x}	1.85	141.86	0.270	333.51	13.13	1.944
s^2	0.11	121.98	0.003	49,346.54	130.92	2.862

* $P < 0.05$, ** $P < 0.01$.

characters (for correlational selection differentials). Significance levels of differentials were assessed with nonparametric Spearman-rank correlations of relative fitness with the trait, its square, or the cross-product of two traits (Lande and Arnold, 1983).

Directional selection gradients were estimated from a multiple regression of relative fitness on all four traits. The stabilizing and correlational selection gradients were then estimated from a separate multiple regression including all four traits, the squares of each trait and the cross-products of all six pairwise-combinations of traits. Separate regressions are required to estimate the linear and quadratic coefficients because these terms will be correlated if data are not multivariate normal. Nonnormality will cause estimates of the linear coefficients to depend on whether or not quadratic terms are included in the equation (Lande and Arnold, 1983; Manly, 1985; Endler, 1986; Phillips and Arnold, 1989). The means of all traits were set equal to zero before analysis (Lande and Arnold, 1983). A delete-one jackknife procedure was used to estimate the standard errors of and test the significance of all selection gradients (Mitchell-Olds and Shaw, 1987). All the gradients were standardized to unit variance after analysis to reduce rounding errors and facilitate comparisons (Lande and Arnold, 1983; Endler, 1986).

Because the distributions of some independent variables were nonnormal and the residuals from the linear regression analysis were not well behaved, logistic regression was performed to further test the relation-

ships between the characters and survival (McCullagh and Nelder, 1984; Weisberg, 1985). Maximum likelihood estimation was used to fit the logit function of relative fitness to the four characters and their quadratic forms using PROC CATMOD in PC-SAS version 6.03 (SAS Institute Inc., 1988). Significance levels of each selection coefficient from this logistic regression were used to further test the significance of the selection gradients from the linear regression. Analysis of deviance (McCullagh and Nelder, 1984; Weisberg, 1985; Williams et al., 1990) was conducted to compare the contribution of linear, stabilizing, and correlational terms to the fit of the logistic regression model.

Because of the number of coefficients tested, significance levels were adjusted using a sequential Bonferroni technique (Rice, 1989). Adjustments were made for 14 tests to control the Type-I error rate within each type of parameter (differentials and gradients). Significance was accepted at the tablewise 0.05 level. Because of the conservatism of the Bonferroni adjustment, single-test significance levels less than 0.05 are also reported. All analyses were performed using PC-SAS release 6.03 (SAS Institute Inc., 1988).

RESULTS

Phenotypic means, variances, correlations and covariances for each trait and combination of traits before selection are reported in Table 1. Except for correlations of SVL with mass and speed, which were removed before further analysis (see Materials and Methods), none of the correla-

TABLE 2. Standardized directional selection differentials (s') and gradients (β') and stabilizing selection differentials (C') and gradients (γ'_{ij}) for all traits. All differentials and gradients are standardized to unit variance. None of the parameters are significant at $P < 0.05$.

	s'	β'	C'	γ'_{ij}
Stripe	0.122	0.102 \pm 0.092	0.027	-0.034 \pm 0.131
Reversals	0.294	0.008 \pm 0.096	0.030	0.017 \pm 0.083
Speed	0.126	0.119 \pm 0.092	-0.019	-0.055 \pm 0.042
Distance	-0.016	-0.059 \pm 0.089	-0.016	-0.122 \pm 0.049

tions among characters was greater than 0.5. Additionally, condition numbers and variance inflation factors indicated that collinearity was not a problem for the 14 independent variables used in the regression analyses (Weisberg, 1985).

No significant change in the mean or variance of any trait was detected after selection (Table 2). Similarly, no directional or stabilizing selection gradients were significant for any trait (Table 2).

The covariance between stripedness and reversals became more negative after selection, though the change was not significant after the Bonferroni adjustment of significance levels (Table 3). The only significant correlational selection gradient indicated selection favoring the most opposite combinations of stripe and reversal scores (Table 3, Fig. 1). In the logistic regression, this gradient was the only one of the 14 gradients with a single-test significance level $P < 0.05$. Adjustment for the number of parameters tested, however, elevated the significance level to $P = 0.15$.

Addition of the correlational selection gradients significantly improved the fit of the logistic regression compared to models with linear or linear and stabilizing terms (Table 4). A model with correlational terms alone was not significantly improved by the addition of linear or linear and stabilizing terms (Table 4). The same results were obtained using only stripe and reversals and

their quadratics in the logistic regression models.

DISCUSSION

Correlational Selection

None of the traits examined in this study affected survival when considered by themselves. Only the combination of stripe and reversals was correlated with survivorship through the first year. The correlation between these characters was more negative after selection and the gradient analysis showed that this was probably due to selection acting directly on the combination of stripe and reversals. Selection on unmeasured characters that might be correlated with these traits could confound this interpretation (Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987), but the inclusion of other antipredator behaviors in the analysis should minimize this problem.

The correlational selection on the combination of stripe and reversals favored opposite combinations of these traits (Fig. 1). Individuals with high values of one trait coupled with low values of the other trait had the highest probability of survival. Snakes with high or low values of both traits were the least likely to survive. Because no directional or stabilizing selection acted on either trait alone, the bivariate selection surface for this pair of traits can be pictured as a saddle with corners at opposite combi-

TABLE 3. Standardized correlational selection gradients and differentials. All gradients (γ'_{ij} , shown above the diagonal) and differentials (C'_{ij} , shown below the diagonal) are standardized to unit variance.

	Stripe	Reversals	Speed	Distance
Stripe	—	-0.268 \pm 0.097**	-0.018 \pm 0.096	-0.092 \pm 0.102
Reversals	-0.099*	—	0.230 \pm 0.097	-0.166 \pm 0.113
Speed	-0.027	0.069	—	0.128 \pm 0.093
Distance	-0.023	-0.001	0.014	—

Significance of each estimate is indicated by asterisks. * = single-test significance $P < 0.011$; ** = $P < 0.028$, single-test significance from logistic regression $P < 0.011$.

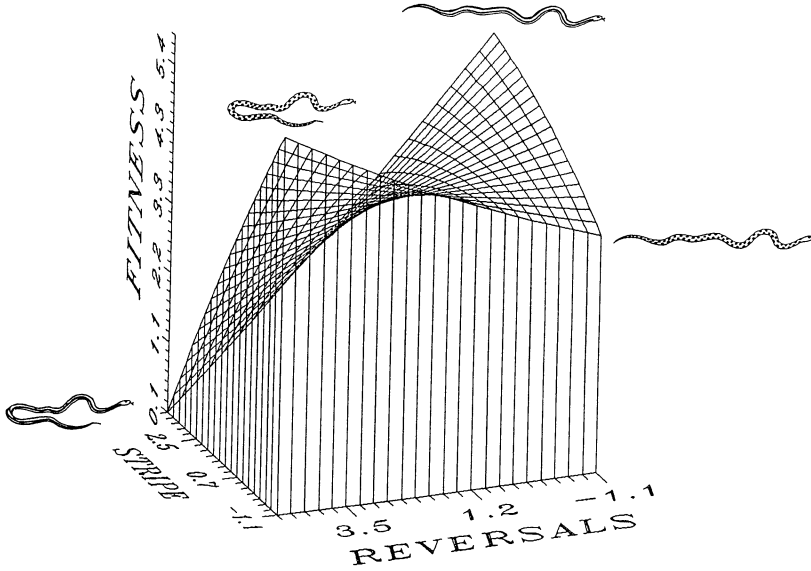


FIG. 1. Three-dimensional view of the saddle-shaped bivariate selection surface on stripe and reversals. High values of fitness correspond to low values of one trait and high values of the other. Each trait is shown on a standardized scale (mean of zero, unit variance) and the surface is drawn according to all of the standardized selection gradients [fitness = 4.2 + (0.008 × reversals) + (0.102 × stripe) + (0.017 × reversals²) - (0.034 × stripe²) - (0.268 × reversals × stripe)].

nations of stripe and reversal rising to the highest values of fitness (Fig. 1).

Viewing the surface directly from the axis of one of the traits, say stripe, shows why no directional or stabilizing selection was detected. If the correlational selection function is evaluated for different values of reversals, the surface can be envisioned as a series of different linear selection functions on stripe (Fig. 2). This can be shown algebraically by considering the regression equation for correlational selection alone.

$$w = \alpha + \gamma_{ij}z_i z_j + \epsilon$$

and then setting one of the traits, z_i , equal to a constant, k , that depends on the value of that trait. The resultant equation is a straight line:

$$w = \alpha + k\gamma_{ij}z_j + \epsilon.$$

This fitness function describes linear directional selection on the trait, z_j , but the magnitude and slope depend on the value of a second trait, $z_i = k$. In the case of stripe, directional selection is positive for low values of reversals and negative for high values of reversals (Fig. 2). At intermediate values of reversals, there is no selection on stripe (Fig. 2). This can be shown algebraically by considering both traits on a standardized scale with a mean of zero. At the mean value of trait z_i , $k = 0$ and the fitness function becomes

$$w = \alpha + \epsilon$$

a flat line of constant fitness for all values

TABLE 4. Analysis of deviance comparing competing logistic regression models. Deviance refers to the reduction in deviance resulting from inclusion of additional terms in the regression model. Significant deviance indicates an improvement in the fit of the model.

Models compared	Deviance	df	P <
Linear vs. linear and stabilizing	1.18	4	NS
Linear vs. linear and correlational	12.71	6	0.05
Correlational vs. linear and correlational	4.41	4	NS
Correlational vs. all terms	6.80	8	NS
Linear and stabilizing vs. all terms	13.53	6	0.05

of the trait, z_j . Thus, most values of stripe may take any of the range of fitness values depending on the corresponding value of reversals. Though this example describes the fitness of stripe as a function of reversals, the same relationships will be true for any pair of traits experiencing only correlational selection.

Another way to consider how correlational selection affects the bivariate phenotype of stripe and reversals is to rotate the selective surface so that it is viewed from its major axes (Phillips and Arnold, 1989). For a surface of pure correlational selection without stabilizing or directional components, one major axis corresponds to the sum of the two traits ($z_i + z_j$) and the other to the differences between the two traits ($z_i - z_j$). Graphically, this is equivalent to rotating the surface in Figure 1 so that it is viewed diagonally from one of its corners. The view along one axis shows the form of selection on the other. This procedure reveals that selection acting on the sum of stripe and reversals is stabilizing, being non-linear with an intermediate optimum (Fig. 3). The difference between stripe and reversals experiences disruptive selection (Fig. 3). Any pure correlational selection surface will be saddle-shaped (Phillips and Arnold, 1989), so one major axis will always be under stabilizing selection while the other experiences disruptive selection. The methods for applying this analysis to surfaces complicated by stabilizing selection affecting individual traits are discussed by Phillips and Arnold (1989) and have been used to examine multivariate selection on herbivore resistance by Simms (1990).

Natural Selection on Antipredator Traits

Although multivariate analyses of selection can reveal the form of selection affecting traits and trait combinations, they do not explain the mechanisms of that selection (Endler, 1986; Wade and Kalisz, 1990). In most cases, this requires direct experimentation (Wade and Kalisz, 1990), but sometimes knowledge of the functional properties of the characters in question and the natural history of the organisms involved can shed light on the proximal causes of selection. The ability to accurately per-

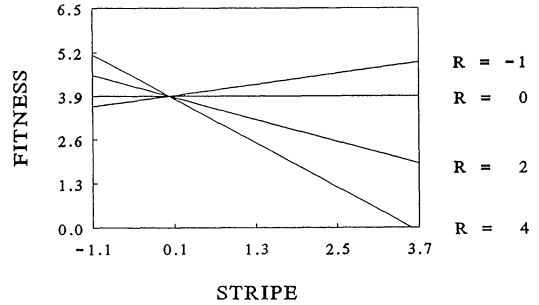


FIG. 2. The fitness of stripe as a function of different values of reversals (R). Except for the mean, any value of stripe may take on a range of fitness values depending on the corresponding value of reversals. Stripe is expressed on a standardized scale (mean of zero, unit variance) and the standardized correlational selection gradient is evaluated at different values of reversals (R) to produce a series of linear selection functions (see text for details).

ceive motion and velocity of an object depends upon the color pattern of that object and its surrounding field (Brown, 1931a, 1931b). Striped snakes appear to be stationary when crawling slowly and generally seem to be moving more slowly than they actually are (Klauber, 1931; Jackson et al., 1976). Such an optical illusion has obvious advantages in predator escape and implies that flight may be more effective in striped than in spotted snakes. Selection mediated by visual predators would then favor alternative antipredator behaviors in snakes with heterogeneous patterns. This prediction precisely fits the pattern of correlational selection observed in the Tenmile population of *T. ordinoides*, where the snakes with the highest probability of survival perform uninterrupted flight if striped but flee evasively if spotted or unstriped.

Because this adaptive scenario involves an optical illusion associated with moving color patterns, it could result only from visually foraging predators. At the Tenmile locality, the primary visual predators are birds, especially Steller's jays (*Cyanocitta stelleri*), robins (*Turdus migratorius*) and crows (*Corvus brachyrhynchos*). The only bird that I observed taking juvenile snakes from this population was a Steller's jay, but I have seen crows take garter snakes elsewhere along the Oregon coast, and robins are known to feed on juvenile garter snakes at other localities (Jayne and Bennett,

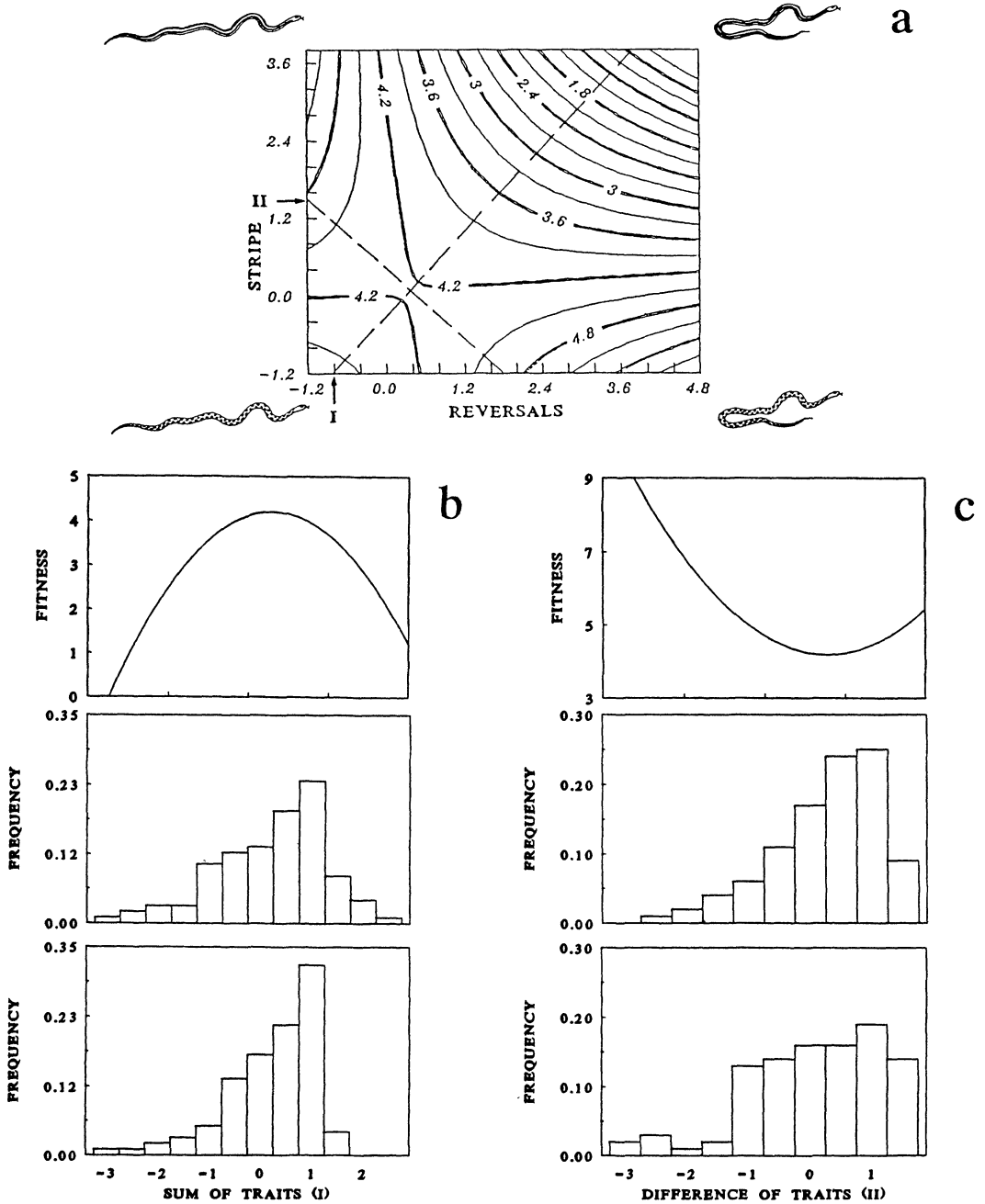


FIG. 3. The correlational selection surface viewed along its major axes. The contour view of the selection surface (a) shows the position of the major axes on the original surface (see Fig. 1). Each contour in (a) indicates a line of equal fitness with relative peaks at the upper left and lower right corners, and relative valleys at the lower left and upper right corners. On a pure correlational selection surface, the major axes correspond to the sum of traits (I) and the difference of traits (II). These views show that stabilizing selection is operating on the sum of traits axis (b), while the difference of traits axis experiences disruptive selection (c). Distributions of the sum of traits (b) and the difference of traits (c) before (upper histograms) and after selection (lower histograms) are shown below their respective selection functions. The surface shown in (a) and in Figure 1 incorporates the nonsignificant directional and stabilizing gradients, so the major axes are slightly rotated and are calculated according to Phillips and Arnold (1989) [difference of traits = $(-0.394 \times \text{stripe}) - (0.919 \times \text{reversals})$; sum of traits = $(-0.919 \times \text{stripe}) + (0.394 \times \text{reversals})$].

1990a). While red-tail hawks (*Buteo jamaicensis*) have also been observed taking adult snakes from this population, they are probably not common predators on juveniles because of their size. Other potential predators at Tenmile include coyotes (*Canis latrans*), raccoons (*Procyon lotor*), minks (*Mustela vison*) and shrews (*Sorex* sp.), all primarily nocturnal foragers that are unlikely to rely heavily on vision for prey capture. Thus, circumstantial evidence suggests the selection acting on combinations of stripe and reversals is a result of avian predation and the optical properties of moving color patterns.

This study examined the covariance between a major component of fitness, juvenile survival, and a suite of antipredator traits. Because of this narrow measure of fitness, conclusions about the selective advantages of these traits refer only to their impact on juvenile survivorship. Predation is probably most intense on snakes during the first few years of life. Juvenile garter snakes are much smaller than adults and therefore have a wider range of possible predators. Birds such as robins and jays may take juvenile snakes but are incapable of handling larger individuals (Brodie, unpubl. data). Likewise, some small mammals including shrews may eat neonate and yearling snakes but in turn are eaten by larger members of another garter snake species (*T. sirtalis*) (Brodie, unpubl. data). Predation during the first year of life would then be expected to account for much of the selection affecting the evolution of antipredator mechanisms in garter snakes.

It is plausible that the relative importance of certain defensive behaviors changes with age and condition of the individuals (Brodie, 1989b, 1991, 1992). If juvenile snakes are unable to attain a speed sufficient to escape most predators, then speed will not affect survivorship at this age. However, as individuals grow and their locomotor abilities increase (Jayne and Bennett, 1990b), speed may become an important antipredator mechanism. This hypothesis is supported by the results of a selection study by Jayne and Bennett (1990a), who found that locomotor performance was not correlated with survivorship through the first year, but was important in yearling and adult snakes.

This could explain the apparent lack of selection on speed and distance in neonate *T. ordinoides*, and suggests that alternative modes of predator escape, such as the combined effects of stripe and reversals, are especially important for the survival of neonates.

The mark-recapture method of assessing selection has several drawbacks. First, failure to recapture an individual does not necessarily indicate death. Migration out of the population, inactivity during the periods of collection, or vagaries of sampling would also result in nonrecapture. As long as these phenomena are random with respect to the traits examined, the results of the mark-recapture study are unaffected. Each of these effects is probably random, but migration tendency could conceivably be correlated with stamina (distance). Repeated collections throughout the three year study failed to turn up a single marked individual in any of the nearby (one to two km away) clearings or on the opposite side of the stream from the study site, so migration probably had no effect on the mark-recapture results. A second problem with this technique is that nonrecaptured individuals could have died at any time during the study. If traits change significantly during this period, selection might have acted on any of a range of trait values. An ontogenetic study of this population indicates slight increases in stripe and decreases of reversals during the first two years, but this age effect disappears when size differences are considered. More importantly, individual differences remain constant over this period so that snakes retain their relative rankings on a scale of stripedness or reversals (Brodie, 1991, 1992). Neonatal scores are therefore good predictors of individual trait values throughout the first two years. Selection gradients based on neonate traits may be slightly shifted in scale but should be accurate representations of the shape of the selection surface (Brodie, 1991, 1992). A third problem arises if surviving individuals were not recaptured by the end of the study. This problem of censored data (e.g., Adams, et al., 1988) could lead to biased predictions of the relationship between survival at different ages and antipredator traits. For this reason, this study considers only first-year

survivorship and does not attempt to draw conclusions about age-dependent selection on antipredator traits.

Visually oriented recapture of individuals also might be expected to bias the sample of recaptured individuals (Endler, 1986). In practice, field collection of snakes is often aurally based (snakes are heard moving through grass) but also relies on visual detection by the researcher. To the extent that human collection of snakes is affected by the same optical illusions that are proposed to account for the correlational selection for color pattern and reversals, the recaptured sample of snakes should resemble that taken by visual predators. This event would bias the sample against detecting correlational selection (and other forms of selection due to visual predation) and might cause the strength of selection gradients to be underestimated.

Genetic Implications of Correlational Selection

Theory predicts that correlational selection should have major effects on the genetic variance-covariance structure of a population (Lande, 1980, 1984; Cheverud, 1982, 1984, 1988). Selection that favors certain combinations of traits can promote genetic correlation between them by creating linkage disequilibrium (Lande, 1984) or by favoring pleiotropic mutations (Lande, 1980). Genetic variation in each of the traits selected to be correlated can also be maintained through such a process. Precisely how correlational selection affects genetic variances and covariances can be demonstrated graphically with different views of the selection surface.

Rotating the correlational selection surface to its major axes revealed two new traits corresponding to the sum and difference of the original traits (see above, Fig. 3). The sum of traits axis corresponds to a line of a positive covariance, whereas the difference of traits axis represents a negative covariance. In the example of stripe and reversals in *T. ordinoides*, the sum of the traits experienced stabilizing selection while the difference between them was subject to disruptive selection (Fig. 3). Within a generation, stabilizing selection reduces variation in a trait, while disruptive selec-

tion maintains or even increases variation (Mather, 1955; Thoday, 1972). Thus, selection on *T. ordinoides* favors a reduction in the positive covariance between stripe and reversals but an increase in the analogous negative covariance.

The predicted result of this selection on the phenotypic distribution of stripe and reversals is little variation along the sum of traits axis but a wide spread along the difference of traits axis. Overlaying the true phenotypic distribution of the population on a contour plot of the selection surface illustrates exactly this pattern (Fig. 4). The stabilizing selection function experienced by the sum of traits was asymmetrical about the mean of the bivariate phenotypic distribution, with little variation in fitness between the smallest values and the mean (Fig. 3b). Virtually all of the phenotypic variation along this axis was found in that region. No individuals existed with high values for the sum of stripe and reversals (Figs. 3b and 4). Conversely, the full range of possible values were observed along the axis corresponding to negative covariance between the traits. The resultant bivariate distribution shows a moderate negative correlation and high variance along each of the univariate trait axes (Fig. 4). By acting to contract variation on one major axis but expand it on the other (Fig. 3), correlational selection can increase the magnitude of the covariance between two traits while simultaneously promoting variation for each trait alone.

This graphical model explains only the effects of correlational selection on phenotypic variances and covariances within a generation. A genetic response to selection is required for these processes to be translated into genetic variation and correlations. This response, of course, depends on the amount of additive genetic variation present for each of the traits and their genetic covariance. The change in genetic variances and covariances within a generation is described by the equation

$$\Delta \mathbf{G} = \mathbf{G}(\boldsymbol{\gamma} - \beta \beta^T) \mathbf{G}$$

[Phillips and Arnold, 1989, Eq. 2; after Lande (1980) and Lande and Arnold (1983)], where \mathbf{G} is the genetic variance-covariance matrix and β^T is the transposed vector of

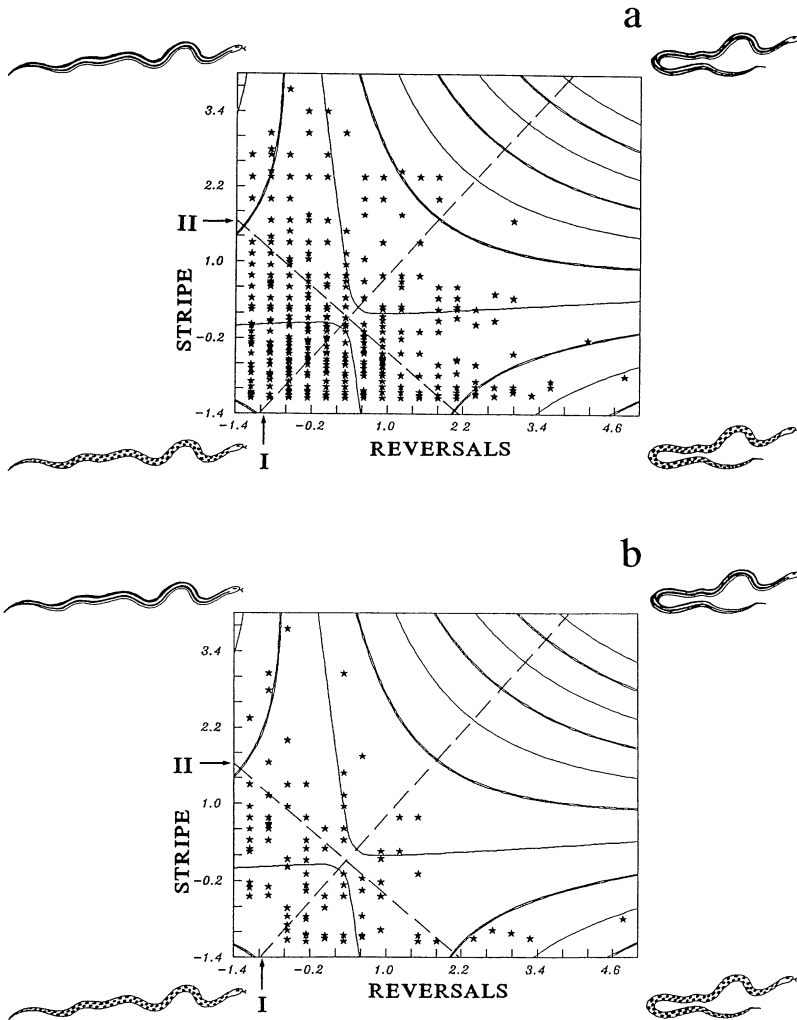


FIG. 4. Contour view of the selection surface with the phenotypic distributions before and after selection. Each contour indicates a line of equal fitness with relative peaks at the upper left and lower right corners, and relative valleys at the lower left and upper right corners. The diagonal dashed lines (I, II) denote the major axes of the selection surface as in Figure 3. Before selection, less variation is observed along the sum of traits axis than along the difference of traits axis (a), as expected from the forms of selection acting on each (see Fig. 3). This effect is even more pronounced in the recaptured portion of the population (b). Both traits are expressed on a standardized scale (mean of zero, unit variance). Three hundred and twenty four points are hidden in (a), 14 in (b).

directional selection gradients. If no directional selection occurs, then this reduces to

$$\Delta G = G\gamma G.$$

If no traits experience stabilizing or disruptive selection, then the diagonal elements of the γ -matrix are zero. Therefore, for two traits experiencing only correlational selection, the changes in the genetic variances, G_{ii} and G_{jj} , are

$$\Delta G_{ii} = 2G_{ii}G_{ij}\gamma_{ij}$$

and

$$\Delta G_{jj} = 2G_{jj}G_{ij}\gamma_{ij}.$$

The change in the genetic covariance between the traits, G_{ij} , is

$$\Delta G_{ij} = \gamma_{ij}(G_{ij}^2 + G_{ii}G_{jj}).$$

Substituting the signs of each parameter into

these equations shows the direction of change of the genetic variances and covariances within a generation. There can be a genetic response to selection only if G_{ii} and G_{jj} are greater than zero, so the sign of each is assumed to always be positive. When the genetic covariance (G_{ij}) is of the same sign as the correlational selection gradient (γ_{ij}), both ΔG_{ii} and ΔG_{jj} are positive and the genetic covariance increases in magnitude. However, if the correlational selection gradient and the genetic covariance are of opposite sign, the change of both additive genetic variances is negative and the magnitude of the genetic covariance is reduced. Thus, correlational selection will promote genetic variation as long as it does not oppose the sign of an existing genetic correlation.

In the Tenmile population of *T. ordinoides*, correlational selection for and the genetic correlation between stripe and reversals are both negative (Brodie, 1989a, 1991). Correlational selection may, therefore, promote both the large amounts of additive genetic variation found for each of these traits and the genetic coupling between them (Brodie, 1989a, 1991). The dynamics of the genetic variance-covariance matrix across generations are controversial and depend on a variety of assumptions about the distribution and magnitude of allelic effects (reviewed by Turelli, 1988). It is not yet clear whether correlational selection is a plausible mechanism for long-term maintenance of genetic variance and covariance.

Furthermore, a saddle-point on a selection surface is not expected to be stable over evolutionary time if fitnesses remain constant (Wright, 1977; Lande, 1976). Under the view of phenotypic evolution as a hill climbing process, the population mean is predicted to evolve in the direction of the steepest uphill slope. If correlational selection remains constant, the bivariate mean of the population should eventually evolve up one or the other peak. For the population to be maintained near the saddle, selection must change in such a way as to force the population back to this region whenever it moves up one of the peaks. Frequency-dependent selection favoring rare combinations of pattern and behavior could create

such a force (e.g., Greenwood, 1984; Endler, 1988). As the population mean evolves up one peak, this combination would become less fit and selection would force the population in the opposite direction. The selection surface, in this case, would appear to rock back and forth about the saddle as the population moved away. This sort of temporally changing selection might explain why the bivariate mean of the Tenmile population resides near the saddle of the surface.

By decomposing the correlational selection surface into its stabilizing and disruptive components, it is clear how such a process can promote genetic correlation between traits and genetic variation in individual traits. It appears that selection for combinations of traits, possibly in conjunction with frequency-dependent selection, is an important factor in maintaining genetic variation in color pattern and antipredator behavior in the Tenmile population of *T. ordinoides*. Correlational selection is also likely to be responsible for creating the observed genetic correlation between these traits, though other possible causes such as pleiotropic effects of new mutations or properties of the breeding system, have not been ruled out (Lande, 1980, 1984). Because of the statistical difficulties of detecting this form of selection, data are not available to evaluate its general importance as a promoter of genetic variation and correlations among traits in natural populations. This avenue of research promises to shed light on a variety of intra- and interspecific patterns of variation and covariation (Cheverud, 1982, 1984; Felsenstein, 1988; Kingsolver, 1988; Zeng, 1988; Emerson and Arnold, 1989).

ACKNOWLEDGMENTS

Advice from S. Arnold, J. Arnold, G. Arnqvist, R. Lande, P. Phillips and two anonymous reviewers significantly improved the presentation of these ideas. J. Gladstone, F. Janzen, and N. Reagan assisted in the field. D. and M. Brodie provided facilities throughout this study. T. Mitchell-Olds provided his Free-Stat program to perform jackknife tests of regression coefficients. Financial support was provided by Sigma Xi, The Hinds Fund of the

University of Chicago, the Theodore Roosevelt Fund of the American Museum of Natural History, and NSF Dissertation Improvement Grant BSR-8714955.

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