
Quantitative Genetic Studies of Behavioral Evolution

Edited by Christine R. B. Boake

x + 390 pages

The University of Chicago Press *Chicago and London*

Christine R. B. Boake is an associate professor in the Department of Zoology and in the Programs in Ecology and Ethology at the University of Tennessee, Knoxville.

For my parents

The University of Chicago Press, Chicago 60637
The University of Chicago Press, Ltd., London
© 1994 by The University of Chicago
All rights reserved. Published 1994
Printed in the United States of America

03 02 01 00 99 98 97 96 95 94 1 2 3 4 5
ISBN: 0-226-06215-5 (cloth)
0-226-06216-3 (paper)

Library of Congress Cataloging-in-Publication Data

Quantitative genetic studies of behavioral evolution /
Christine R. B. Boake, editor.

p. cm.

Includes bibliographical references and index.

1. Behavior genetics. 2. Behavior evolution.
 3. Quantitative genetics. I. Boake, Christine R. B.
- QH457.Q36 1994
591.5'1—dc20

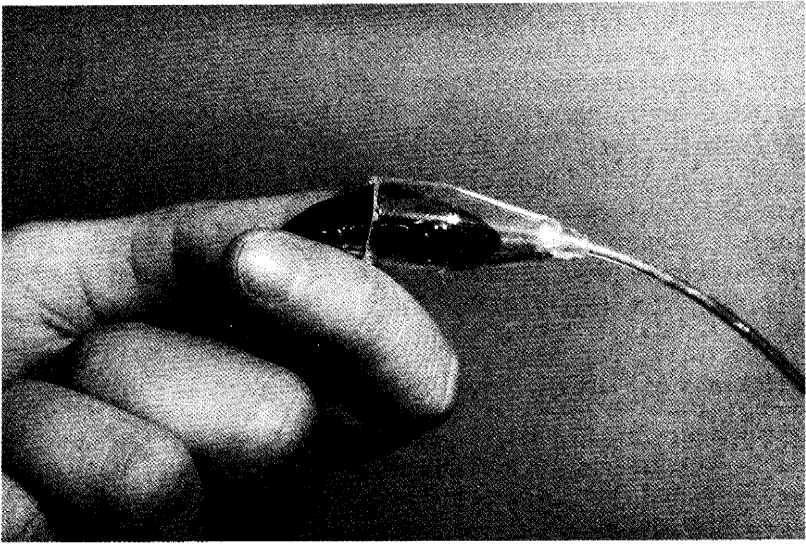
93-33824
CIP

∞ The paper used in this publication meets the minimum requirements of the American National Standard for Information Sciences—Permanence of Paper for Printed Library Materials, ANSI Z39.48-1984.

12

Quantitative Genetics of Locomotor Behavior and Physiology in a Garter Snake

Theodore Garland, Jr.



Black racer (*Coluber constrictor*) wearing a plastic mask for determination of maximal oxygen consumption and energetic cost of locomotion (Walton, Jayne, and Bennett 1990; photograph courtesy of B. C. Jayne). A similar mask, but smaller, was used in the present study for measuring newborn garter snakes.

In this chapter I demonstrate the use of quantitative genetic analyses for studying the evolution of certain behavioral traits related to locomotor capacities and underlying elements of morphology, physiology, and biochemistry. I studied the common garter snake (*Thamnophis sirtalis*), one member of a genus that has served as an increasingly common model in studies of individual

variation and its genetic bases. The strengths of this study include (1) its use of a natural population, (2) its focus on behavioral and whole-animal performance traits thought to be of considerable ecological and selective importance (e.g., antipredator display, maximal crawling speed, endurance), and (3) its inclusion of measures of other traits at lower levels of biological organization (e.g., heart size, blood hemoglobin level, tissue enzyme activities) that may have mechanistic links with traits at the whole-animal level, but are of less direct selective importance.

Quantitative genetic theory offers some (not always straightforward) predictions concerning how heritable traits of differing selective importance ought to be. In addition, existing knowledge of mechanisms from exercise physiology allows the formulation of some a priori predictions as to which traits are likely to show genetic couplings. These couplings may be estimated as genetic correlations and tested for statistical significance. Genetic correlations are important because they can significantly constrain (or facilitate) the course of multivariate evolution, depending on the form of natural selection (Arnold 1981c, 1987a, 1988, 1992b; Arnold, chap 2; Falconer 1989; Chaverud and Moore, chap. 4; Roff, chap. 3). The importance of studying multiple traits when attempting to identify possible constraints has been emphasized by Pease and Bull (1988; see also Lynch, chap. 13).

Relevance of Exercise Physiology for Behavioral Evolution

Many behaviors involve locomotion (which is itself a behavior). Capacities for locomotion may therefore place constraints on behavioral repertoires or on the frequency or intensity with which elements of repertoires can be employed (e.g., Halliday 1987; Hertz, Huey, and Garland 1988; Walton 1988; Pough 1989; Garland, Hankins, and Huey 1990; Garland and Losos 1994). Whether such constraints actually occur in any particular situation depends on the physical intensity of the behavior (e.g., rate of ATP use by particular muscles) in relation to the capacity of the relevant muscles to produce ATP aerobically and/or anaerobically, and potentially on a variety of other psychological, physical, physiological, and biochemical factors (Brooks and Fahey 1984; Astrand and Rodahl 1986; Garland 1993). The important point here is simply that many behaviors depends on locomotion.

Whenever behavior involves locomotion, we can expect correlated evolution of behavior and relevant locomotor capacities

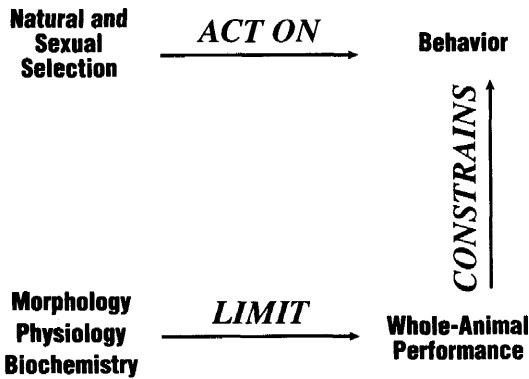


Fig. 12.1 Conceptual relationships of morphological, performance, and behavioral traits in relation to natural selection (original concept by Arnold [1983a], modifications by Garland, Bennett, and Daniels [1990]; Garland and Carter [1994]; Garland and Losos [1994]). Many other arrows might be added to such a diagram, and their significance can be addressed empirically through the use of path analysis (Arnold 1983a; Garland and Losos 1994). Natural selection is seen as acting most directly on behavior, rather than on organismal performance capacities. Thus, behavior may act as a buffer between selection and performance, with morphological, physiological, and biochemical traits being even further removed from the direct effects of selection (Garland, Bennett, and Daniels 1990). Whether lower-level traits, such as morphology, ever have direct effects on fitness is a difficult conceptual and empirical issue (Garland and Losos 1994).

(cf. Lynch, chap. 13, on thermoregulatory behavior in mice). "Coadaptation" (sensu Huey and Bennett 1987) refers to correlated evolution (sensu Martins and Garland 1991) that is caused by correlated selection pressures. Given that we expect behavior and appropriate locomotor capacities to be under correlational selection (e.g., Brodie 1992), then coadaptation per se of behavior and locomotor capacities would be expected (cf. fig. 12.1). We would also expect coadaptation of the various morphological, physiological, and biochemical characteristics that determine locomotor capacities (but see Garland and Huey 1987). Complementary to ideas about correlated evolution are the concepts of constraints and "trade-offs" (Maynard Smith et al. 1985; Pease and Bull 1988; Arnold 1992b; Roff, chap. 3). Given the physical properties of the materials with which organisms are constructed and the finiteness of their environments, we can expect both internal (e.g., physiological, biomechanical, genetic) and external (e.g., behavioral, ecological) constraints on the ways in which multiple phenotypic traits

can coadapt. Formulating more specific predictions about correlated evolution can be quite difficult, and many complementary approaches are possible (e.g., see Garland and Carter 1994; Garland and Losos 1994). Here, I focus on the utility of applying quantitative genetic approaches to predictions about the correlated evolution of locomotor performance capacities and associated elements of behavior and physiology (cf. Dohm and Garland 1993).

Defining Performance as Opposed to Behavior

I define *behavior* as anything an animal does (or, in some cases, fails to do), and *physiological capacity* as the ability of an animal to perform a particular act under forced conditions (i.e., with maximum motivation). For example, endurance capacity may be defined operationally as the length of time an animal can run on a treadmill before fatigue, with fatigue being defined as failure to maintain the work rate due to preceding work (Simonson and Weiser 1976). Measuring endurance capacity in such a way may be difficult if one cannot clearly determine when fatigue occurs. Motivation can be a very problematic confounding factor (Bolles 1975). How, for example, can one be sure that an animal is actually performing to its physiological limits? In humans it is well known that differences in motivation can lead to large differences in performance (e.g., the better the competition, the better the maximum performance). But in many wild animals, including fishes (references in Garland and Adolph 1991), amphibians (e.g., Moore and Gatten 1989), lizards (e.g., Garland 1984; Huey et al. 1984; Garland and Losos 1994), and small mammals (Djawdan 1993), fatigue is relatively easy to identify and sometimes occurs shortly prior to complete exhaustion (e.g., loss of righting response in lizards: Huey et al. 1984). Supplementary physiological measurements (such as blood lactate levels) may be used to help gauge whether animals have performed to their physiological limits (Arnold and Bennett 1984; Djawdan 1993; discussion in Garland and Losos 1994).

Physiological capacities so measured fall within the general term *organismal performance*. In two papers that seem to have crystallized the thoughts of many, Huey and Stevenson (1979) and Arnold (1983a) argued that measures of organismal performance are crucial links between morphology, physiology, or biochemistry, on the one hand, and ecological importance—or fitness—on the other (see also Price and Schluter 1991). In particular, Arnold

(1983a) argued that selection acts directly on performance capacities rather than on lower-level traits such as morphology or physiology. Garland and Losos (1994) have argued further that Arnold's morphology \rightarrow performance \rightarrow fitness paradigm should be modified to include behavior, as shown in figure 12.1. In this expanded scheme, behavior is seen as a potential "filter" between selection and performance capacities (Garland, Bennett, and Daniels 1990; Garland and Carter 1994).

Defining and eliciting maximal physiological performance from wild animals tested in the laboratory is possible for many species (but see discussion in Garland and Losos 1994). Determining whether animals in nature commonly or rarely behave in ways that tax their maximal physiological capacities is a separate problem. Unfortunately, few quantitative empirical studies have been designed explicitly to address this fundamental question (Halliday 1987; Hertz, Huey, and Garland 1988; Walton 1988; Pough 1989; Garland, Hankins, and Huey 1990; Garland 1993; references therein).

Genetic Correlations, Evolutionary Constraints, and Complementary Predictions

Quantitative genetic analyses can be used to address questions concerning the correlated evolution of behavior and physiology. This approach is complementary to studies of individual (e.g., Garland 1984; Bennett 1987; Bennett, Garland, and Else 1989; Garland, Hankins, and Huey 1990), interpopulation (Arnold 1981b,c, 1988; Garland and Adolph 1991), and interspecific (Brooks and McClelland 1991; Harvey and Pagel 1991; Martins and Garland 1991; Garland et al. 1993) variation and covariation, as well as to experimental manipulation of physiological capacities or hormonal levels to assess their effects on behavior (e.g., references in Wingfield et al. 1990; Garland and Adolph 1991; Crews 1992; Garland and Losos 1994).

Understanding the genetic basis of natural variation allows one to draw inferences about the past history of selection acting on a population and to make specific predictions about the likely future results of hypothetical patterns of natural selection (cf. Lynch, chap. 13). Current genetic "architecture" (sensu Broadhurst and Jinks 1974; Mather and Jinks 1982) is both the result of past selection and the determinant of future responses to selection. For example, a high heritability suggests that a trait has not

been subject to strong selection in the past and would respond to future selection. Conversely, a low heritability suggests that a trait may have been subject to strong past selection (although many other possibilities exist: see Discussion; Garland, Bennett, and Daniels 1990; Price and Schluter 1991) and would respond only slowly to future selection. Genetic correlations may result from past selection pressures (Cheverud 1984b, 1988b; Brodie 1992, 1993) and also may indicate whether genetic response to future selection will be impeded or facilitated by the prevailing polygenic architecture. When estimates of multivariate phenotypic differences among related taxa are available, the genetic covariance matrix can be used to reconstruct the net forces of selection necessary to have produced these differences, although this requires the genetic parameters to have remained constant during divergence (e.g., Arnold 1981a,c, 1988, 1990, 1992b; Arnold, chap. 2; Lande 1988; Turelli 1988a,b; Brodie 1993).

We can also use knowledge of behavioral and physiological mechanisms to generate predictions about genetic correlations, and vice versa (cf. Henderson 1989; Garland and Carter 1994). In particular, speed and endurance might be expected to show a "trade-off" because of the way muscles are constructed and the way they function (discussion in Garland 1988). This hypothetical trade-off should be evidenced as a negative genetic correlation. Moreover, two different behavior patterns, one of which requires speed and the other endurance for execution, should also show a negative genetic correlation and hence a trade-off. Thus, individuals good at one behavior would necessarily be less good at the other. Under this scenario, positive selection for one behavior pattern would result in a negative correlated response in the other.

Rationale for Studying Garter Snakes

Garter snakes (genus *Thamnophis*) are New World natricine snakes, closely related to the New World water snakes (*Nerodia*) (Lawson 1985; A. de Queiroz and R. Lawson, pers. comm.). They represent a relatively recent radiation within the family Colubridae, and just over twenty species are currently recognized. Many species of garter snakes can be locally abundant and, in many populations, relatively large numbers of gravid females can be captured. This fact has been exploited by a number of workers who study individual variation in neonates and/or the genetic basis of phenotypic traits (e.g., Herzog and Bailey 1987; Herzog and

Burghardt 1988; Herzog, Bowers, and Burghardt 1989b; Schwartz and Herzog 1993; review in Brodie and Garland 1993).

Thamnophis sirtalis is an excellent study organism because of (1) its broad geographic distribution, (2) the wealth of background information and ongoing ecological studies on this and related species (e.g., Arnold 1981a,b,c; Arnold, pers. comm.; Kephart 1982; Kephart and Arnold 1982; references therein), and (3) the ease with which quantitative locomotor and behavioral data can be collected. The common garter snake is an ecological generalist with the broadest geographic range of any North American reptile. Geographic variation in scale counts and color patterns (on which the taxonomy is based; Ruthven 1908) is extensive, and has been used to designate eleven subspecies (Fitch 1965; Fitch and Maslin 1961; Christman 1980; Stebbins 1985; see also Arnold 1988). Electrophoretic studies reveal extensive protein variation, both within and among populations of *T. sirtalis* and among the species of *Thamnophis* (Dowling et al. 1983; Lawson 1985; Dessauer, Cadle, and Lawson 1987; Schwartz 1989; Schwartz, McCracken, and Burghardt 1989; A. de Queiroz and R. Lawson, pers. comm.). The morphologically based subspecific designations do not necessarily correspond to electrophoretic patterns (R. Lawson, pers. comm.) nor to quantitative analyses of coloration, scalation, or internal anatomy (Benton 1980). Geographic variation in behavioral traits has also been demonstrated in *T. sirtalis* (Burghardt 1970; Herzog and Schwartz 1990; Arnold 1992a; see also Drummond and Burghardt 1983; Arnold 1981a,b,c on *T. elegans*). Recently, Schwartz (1989; Schwartz, pers. comm.) has demonstrated differences in scale counts, chemical prey preferences, aggregation and antipredator behaviors, critical thermal minimum, and protein polymorphisms between two populations from Wisconsin and Michigan.

This chapter focuses on antipredator displays, a behavior that is easily quantified and heritable (Arnold and Bennett 1984; Garland 1988; Brodie 1992, 1993). Antipredator displays can be scored at the end of endurance trials, and afford the opportunity to study variation in a behavioral character as it relates to underlying variation in performance capabilities, physiology, morphology, and biochemistry. Antipredator behaviors may also evolve in concert with appropriate color patterns (Brodie 1989b, 1992, 1993; discussion regarding *T. sirtalis* in Fitch 1965), and color pattern variation seems often to be related to crypsis in snakes (King 1987; Greene 1988).

METHODS FOR THIS STUDY

Animal Collection and Husbandry

During the summer of 1984, Steve Arnold and I collected gravid garter snakes at his study sites near Eagle Lake, California. These were returned to Al Bennett's laboratory at the University of California at Irvine and housed individually under standardized conditions (further details are presented in Garland 1988; Garland, Bennett, and Daniels 1990; Garland and Bennett 1990; Dohm and Garland 1993). Newborn snakes were housed individually and tested over a period of several weeks. Because we were measuring several traits on each of many individuals, logistics precluded us from measuring all individuals at the same age (see below).

Measurement of Behavior, Performance, and Physiology

Measurement protocols can be found elsewhere (Garland 1988; Garland and Bennett 1990; Garland, Bennett, and Daniels 1990) and will not be repeated in detail here. Snakes were tested for maximal sprint crawling speed on two consecutive days, then for treadmill endurance at 0.4 km/h on two consecutive days, and finally for maximal oxygen consumption on two consecutive days ($\dot{V}O_2\text{max}$) while snakes wore a lightweight transparent mask and crawled on the treadmill (Garland and Bennett 1990). Antipredator displays (Arnold and Bennett 1984) were scored on a scale of 0–9.9 (Garland 1988) after snakes were exhausted at the end of endurance trials; higher scores indicate more offensive or aggressive behavior (e.g., striking and biting). Thus, each of the four whole-animal traits was scored twice to assess repeatability. All measurements were made at 30° C, near the mean body temperature for *T. sirtalis* when active in the field (see Garland 1988; Jayne and Bennett 1990b; Schiefflen and de Queiroz 1991; references therein). Snakes were then sacrificed for measurement of ventricle and liver masses, blood hemoglobin content, aerobic and anaerobic enzyme activities (Garland, Bennett, and Daniels 1990), and ultimately scale counts (Dohm and Garland 1993).

Multiple Regressions to Reduce Maternal Effects

Estimates of heritabilities and genetic correlations based on partitioning variance and covariance among versus within families of full sibs can be inflated by maternal effects (Falconer 1989; Arnold,

chap. 2; Cheverud and Moore, chap. 4), as well as by nonadditive genetic effects (see Brodie and Garland 1993, table 8.1). Multiple regression techniques can be used to partly remove these effects (Garland 1988; Brodie 1989b, 1992, 1993; Garland and Bennett 1990; Garland, Bennett, and Daniels 1990). More specifically, Garland (1988) suggested that in reptiles, which have indeterminate growth, many maternal effects may be mediated through maternal size and/or condition. For example, larger dams tend to give birth to larger offspring. Variation in dam size may be partly genetically based, but much of it will be due to variation in age and/or past nutritional history. To the extent that variation in dam size is due to nongenetic effects (e.g., age, nutrition) and affects offspring characteristics, estimates of genetic variances and covariances based on full-sib analysis of variance (or offspring-on-dam regression) will be inflated. On the other hand, if the variation in dam size is genetically based, and if this variation is genetically correlated with the offspring trait of interest, then removing phenotypic correlations between the offspring trait and dam size will probably remove some of the genetic variance, thus leading to *underestimation* of heritabilities (Tsuji et al. 1989; Brodie and Garland 1993).

Many of the traits we have studied (e.g., endurance, metabolic rate, heart size) correlate strongly with body size (e.g., Garland 1988; Garland and Bennett 1990; Jayne and Bennett 1990a; review in Garland and Losos 1994; see also Travis, chap. 8). In turn, offspring size is correlated with dam size ($r = .34-.46$; Garland 1988, table 2). Moreover, estimates of heritabilities based on raw trait values exceeded unity for speed and endurance (Garland 1988), clearly indicating inflation. Therefore, I used multiple regression to control statistically for variation due to offspring mass and snout-vent length, maternal mass and snout-vent length, and litter size. For some variables, I also used the amount of mass lost between birth and testing as an independent variable (Garland, Bennett, and Daniels 1990). Residuals from multiple regression equations were used in all quantitative genetic analyses. Heritabilities calculated for residuals never exceeded unity.

Another factor inflating among-family variance components was age at testing. For logistical reasons, not all offspring could be tested at the same age. Thus, for example, endurance and anti-predator display were measured when snakes were 6–56 days of age (Garland 1988). In addition (see Discussion in Garland 1988; Garland and Bennett 1990), offspring were not fed. Thus, both ontogenetic and starvation effects would contribute to among-family

variance. We therefore used age and age squared at time of testing as additional independent variables. Fasting for such periods of time is not an unusual situation for snakes in nature. Finally, for the enzyme activities, we also used assay batch (coded as a series of dummy variables) as an independent variable.

RESULTS

Repeatabilities

Day-to-day repeatability was highly significant ($P < .0001$) for each of the four whole-animal traits. Pearson product-moment correlations between trials were .674 for antipredator display, .802 for speed, .696 for treadmill endurance, .882 for whole-animal $\dot{V}O_2\text{max}$, and .796 for $\dot{V}O_2\text{max/g}$ body mass (Garland 1988; Garland and Bennett 1990). Corresponding intraclass correlation coefficients were virtually identical, although $\dot{V}O_2\text{max}$ showed a slight (about 3%) decrease from day 1 to day 2. In general, these repeatabilities set an upper limit to heritabilities (Boake 1989b; Brodie and Garland 1993; Falconer 1989).

Statistical Control for Maternal Effects

Table 12.1 shows the significant independent variables for the four whole-animal traits. The greatest amount of variance explained was for the physiological trait $\dot{V}O_2\text{max}$, due primarily to its strong correlation with body mass. Interestingly, about 5% of the variance in antipredator display is explained by litter size, with individuals from larger litters tending to exhibit somewhat more aggressive or offensive displays. The biological significance of this correlation is obscure. Residual values for the four organismal traits were approximately normally distributed (e.g., Garland 1988, fig. 1).

Heritabilities

Table 12.2 presents heritabilities based on twice the among-family components of variance (Garland 1988; Garland and Bennett 1990; Garland, Bennett, and Daniels 1990). Somewhat surprisingly, the three organismal performance traits (speed, endurance, $\dot{V}O_2\text{max}$) show high heritabilities. The biochemical traits show the lowest heritabilities, and the "morphological" traits (hemoglobin, ven-

Table 12.1 Significant predictors of organismal characters

Character (multiple r^2)	Body Mass	Snout- Vent Length	Dam Mass	Dam Length	Litter Size	Age and Age ²
Antipredator display (4.8%)					+4.8	
Sprint speed (32.5%)		+17.1	-1.0	+1.3		13.1
Endurance (35.7%)	+23.8	+1.9			+4.1	7.8
$\dot{V}O_2\text{max}$ (71.1%)	+42.7					23.9

Note: Based on stepwise multiple regression analyses ($P < .05$). Values are partial r^2 (percentage), preceded by sign of partial regression coefficient. Partial r^2 due to age and age² have been summed for simplicity.

Table 12.2 Estimated heritabilities based on analysis of variance of presumed full-sib families

Character (# families, # individuals)	h^2 and 95% Confidence Interval
Behavior	
Antipredator display (46, 249)	0.19 < 0.41 < 0.71
Organismal performance	
Maximal crawling speed (46, 249)	0.33 < 0.58 < 0.88
Treadmill endurance (46, 249)	0.44 < 0.70 < 1.00
$\dot{V}O_2$ max (45, 245)	0.62 < 0.89 < 1.19
Mean = 0.72	
Morphology	
Hemoglobin (45, 244)	0.38 < 0.63 < 0.94
Ventricle mass (45, 244)	0.19 < 0.41 < 0.70
Liver mass (45, 245)	0.36 < 0.61 < 0.91
Mean = 0.55	
Biochemistry	
Liver citrate synthase (45, 242)	0.02 < 0.21 < 0.50
Liver pyruvate kinase (45, 242)	0.32 < 0.58 < 0.90
Ventricle citrate synthase (45, 241)	-0.14 < 0.01 < 0.26
Ventricle pyruvate kinase (45, 242)	0.05 < 0.26 < 0.56
Muscle citrate synthase (45, 244)	-0.08 < 0.09 < 0.34
Muscle pyruvate kinase (45, 242)	0.01 < 0.19 < 0.46
Mean = 0.22	

Source: Garland 1988; Garland and Bennett 1990; Garland, Bennett, and Daniels 1990.

Note: Residuals from multiple regression equations were used (see text and Table 12.1) 95% confidence intervals are from Bulmer's (1980, 84) algorithm.

tricle mass, liver mass) show intermediate heritabilities, similar to that for antipredator behavior ($h^2 = 0.41$). Analysis of variance indicates that the mean heritabilities of these three categories of traits differ significantly (Garland, Bennett, and Daniels 1990).

Tests for Major Genes

A crude test for the presence of genes with large effect involves comparing the variability of families that, on average, have high or low versus intermediate scores (references and discussions in Garland 1988; Garland and Bennett 1990). Briefly, if "major genes" are present, then families with extreme phenotypes will be fixed for one or the other allele at the major gene locus, and consequently

will show less variability than do intermediate families, which will represent a mixture of genotypes. For the four whole-animal traits, Levene's tests (Conover, Johnson, and Johnson 1981; in this application, an analysis of variance based on absolute deviations of each individual's value from its family mean) indicate that families do differ in variability, but quadratic regressions indicate that intermediate families are actually *less* variable.

Phenotypic and Genetic Correlations

Phenotypic correlations were generally low. Figure 12.2 and table 12.3 show phenotypic correlations between antipredator display and each of the other three whole-animal traits. Antipredator display is weakly positively correlated with both speed and endurance, but not with $\dot{V}O_2\text{max}$. Importantly, none of the lower-level traits (e.g., blood hemoglobin content, enzyme activities) are significant predictors of variation in antipredator display, in either bivariate correlations or a multiple regression (Garland, Bennett, and Daniels 1990). Unexpectedly, the residuals for speed and endurance are positively correlated, both phenotypically and genetically (Garland 1988). As expected, endurance and $\dot{V}O_2\text{max}$ are positively correlated. Also as expected, $\dot{V}O_2\text{max}$ is positively correlated with ventricle (heart) mass ($r = .27$; Garland, Bennett, and Daniels 1990). In multiple regression analyses, only 3–4% of the variation in speed and endurance could be explained by lower-level traits (Garland and Bennett 1990; Garland, Bennett, and Daniels, 1990). This r^2 is much lower than in some species of lizards (Garland 1984; reviews in Garland and Bennett 1990; Garland and Losos 1994). The unexplained variation in (repeatable) measures of speed and endurance may be due to correlations with variation in other morphological and physiological characters, such as scale counts or tail length (Arnold and Bennett 1988; Jayne and Bennett 1989; Dohm and Garland 1993), and/or behavioral factors, such as motivation.

DISCUSSION

Why Are Organismal Traits So Heritable?

A phenotypic trait cannot respond to either direct or correlated natural selection, nor will it undergo genetic drift, unless its narrow-sense heritability is greater than zero. Selection tends to

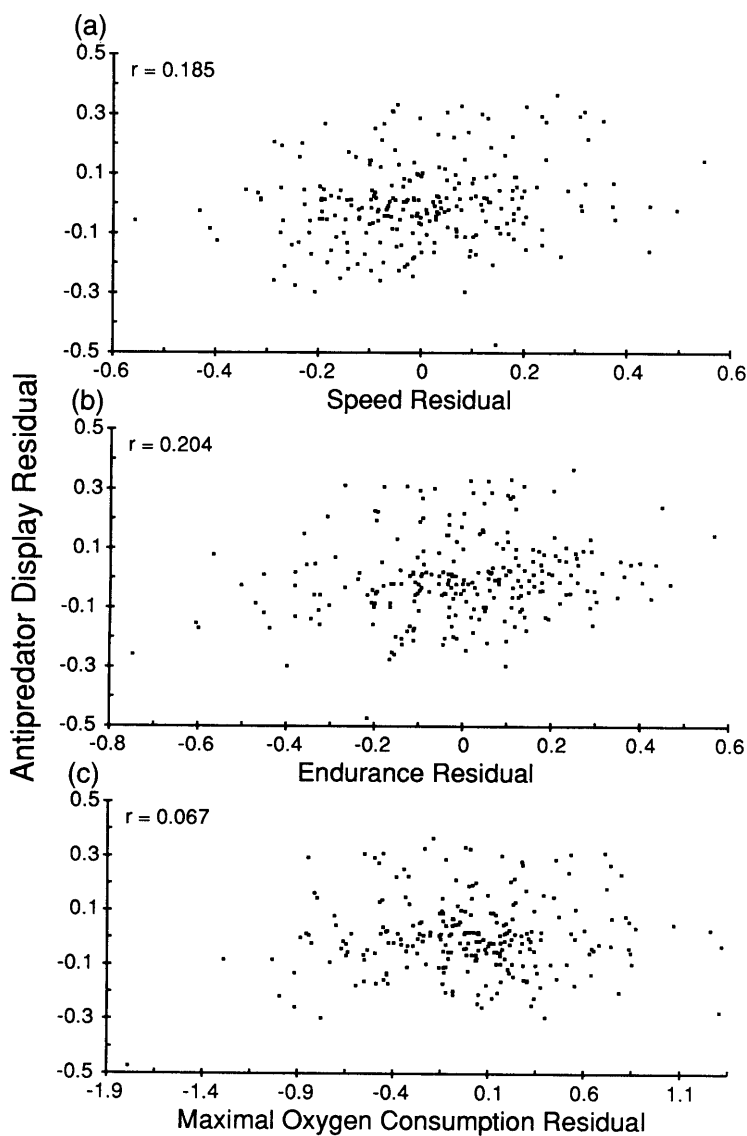


Fig. 12.2 Phenotypic correlations between antipredator display and the three whole-organism performance traits: (a) speed, (b) endurance, and (c) $\dot{V}O_2$ max.

Table 12.3 Phenotypic, genetic, and environmental correlations between traits measured at the whole-animal level

	Correlation	Sprint Speed	Treadmill Endurance	$\dot{V}O_2\text{max}$
Antipredator display	Phenotypic	0.185*	0.204*	0.067
	Genetic	0.407	0.240	-0.056
	Environmental	-0.029	0.171	0.390
Sprint speed	Phenotypic		0.359*	-0.012
	Genetic		0.585*	-0.159
	Environmental		-0.006	0.470
Treadmill endurance	Phenotypic			0.166*
	Genetic			0.098
	Environmental			0.546

Note: Phenotypic, genetic (maximum likelihood: Shaw 1987; Garland 1988; Garland and Bennett 1990), and environmental (maximum likelihood) correlations (from top to bottom within each trait) are based on residuals from multiple regression equations (see text and table 12.1).

* $P < .05$ by two-tailed test; sample sizes are given in table 12.2.

eliminate additive genetic variation through fixation of favored alleles, while mutation tends to add genetic variation each generation. A mutation-selection balance may therefore be reached such that the heritability of a trait reflects, in part, the relative strength of past selection and mutation. Thus, traits that have been subject to particularly strong selection may be expected to show low heritabilities (recent reviews in Rose, Service, and Hutchinson 1987; Lande 1988; Turelli 1988a; references in Arnold 1990; Garland, Bennett, and Daniels 1990; but see Price and Schluter 1991). Empirical support for this idea comes from the observation that life history traits generally show lower heritabilities than do morphometric, physiological, or behavioral traits (Mousseau and Roff 1987; Roff and Mousseau 1987; Willis, Coyne, and Kirkpatrick 1991; Partridge, chap. 6; references in Garland, Bennett, and Daniels 1990; Price and Schluter 1991).

Measures of whole-animal performance abilities, such as locomotor speed and endurance, are also thought to be subject to relatively strong selection (Huey and Stevenson 1979; Arnold 1983a; Pough 1989; Jayne and Bennett 1990b; Garland and Carter 1994; Garland and Losos 1994). Thus, we might expect them to show relatively low heritabilities, as compared with lower-level traits. In addition, measures of organismal performance are composite traits,

determined by multiple underlying traits, and thus are subject to additional sources of environmental variance (as argued by Price and Schluter [1991] for life history traits). Because environmental variance occurs in the denominators of the formulae for heritability, this alone could lead to relatively low values. Contrary to these expectations, however, my three measures of locomotor performance and antipredator display all showed relatively *high* heritabilities (table 12.2). I will briefly consider several possible explanations for this finding (see Garland, Bennett, and Daniels [1990]).

First, as composite characters (cf. Riska 1989; Price and Schluter 1991), measures of organismal performance will incorporate mutational input of genetic variance at loci affecting all lower-level characters that affect performance. This alone could lead to more equilibrium genetic variance in organismal performance than in lower-level traits. Second, narrow-sense heritabilities will be overestimated if nonadditive genetic effects and/or maternal effects are present (see below). However, such overestimation would not necessarily explain why performance traits should show higher heritabilities than do the enzyme activities. Third, the population we studied might not be at genetic equilibrium, possibly due to relatively recent disturbance by such human activities as cattle ranging and logging (Garland, Bennett, and Daniels 1990; Brodie 1992, 1993). Fourth, locomotor performance might show a trade-off with some other components of fitness, such as growth rate or litter size (cf. Rose, Service, and Hutchinson 1987; Price and Schluter 1991; Partridge, chap. 6; Roff, chap. 3). However, Jayne and Bennett's (1990b) data indicate *positive* correlations between locomotor performance and survival. Unfortunately, we have no data on other fitness components (such as litter size or growth rates) for the newborn snakes we studied. Fifth, perhaps a nonheritable trait, such as nutritional status, affects both locomotor performance and fitness in nature (cf. Price, Kirkpatrick, and Arnold 1988).

Finally, perhaps selection on locomotor performance simply is not as strong as conventional wisdom might dictate. Jayne and Bennett (1990b) report significant positive directional selection acting on both speed and endurance for yearling snakes but *not* for newborns during their first few months of life. Selection intensities were similar to those reported by other workers in a variety of contexts, but it is not clear what level of genetic variance would be expected to obtain. Brodie (1992) also showed no significant selection acting on speed or on distance crawling capacity in *Thamnophis ordinoides* during their first year.

Several factors might account for relatively weak selection on the locomotor performance of young snakes. First, as suggested in figure 12.1, behavior may act as a "filter" between selection and performance (Garland, Bennett, and Daniels 1990; Garland and Carter 1994; Garland and Losos 1994). Selection acts on what an animal actually does, not on what it can or could do. If, for example, all individuals in a population employed stationary antipredator displays, then variation in locomotor performance might be irrelevant. Second, the effectiveness of a behavior involving locomotion may be strongly context dependent, influenced by the substrate, temperature, recent feeding, and type and experience of predator or prey involved (cf. Garland and Arnold 1983; Arnold and Bennett 1984; Ford and Shuttlesworth 1986; Herzog and Burghardt 1988; Brodie 1989a, 1991, 1992; Herzog, Bowers, and Burghardt 1989b). Third, variation in context also might lead to lower repeatability for field locomotor performance and behavior than is apparent in laboratory studies (Boake 1989b). For example, variation in temperature can cause variation in locomotor performance or behavior through direct biochemical (Q_{10}) effects on muscle and nerve function (e.g., Bennett, Garland, and Else 1989; Bennett 1990; references in Huey and Stevenson 1979; Garland and Losos 1994). Also, several species of garter snakes and lizards are known to alter their defensive behavior at low temperatures, after recent feeding, or when gravid (Arnold and Bennett 1984; Herzog and Bailey 1987; Seigel, Huggins, and Ford 1987; Brodie 1989a; Schiefflen and de Queiroz 1991). Lower field repeatability would have the effect of lowering the selection intensity on a trait; it is as if the selective agent cannot precisely define the phenotype (Boake 1989b; Arnold 1990; Brodie 1991, chap. 1; Brodie 1992). Fourth, perhaps individual variation in laboratory measures of locomotor performance (on a smooth racetrack or treadmill) simply does not reflect the variation or covariation that would occur under natural conditions; laboratory and field performance may not be tightly correlated either phenotypically or genetically (cf. Arnold and Bennett's [1984] descriptions of antipredator displays in the field versus the laboratory). For example, since low temperature reduces sprint speed and may cause more aggressive antipredator displays (see Arnold and Bennett 1984; Schiefflen and de Queiroz 1991), the effective correlation between these two traits in the field—where temperatures of active snakes show considerable variation—might be negative in contrast to the positive correlation observed at a constant temperature of 30° C (see fig. 12.2). Fifth, as suggested by Jayne and Bennett's

(1990b) results, selection on locomotor performance may act primarily on older snakes, whereas our heritability estimates were for neonates; the genetic correlation between locomotor capacities at birth and at older ages is entirely unknown. Genetic correlations between elements of locomotor performance measured at different ages are certainly likely to be less than unity, such that selection acting at one age may have little effect on genetic variances of the corresponding behavior at other ages (Arnold 1990). Finally, perhaps selection acts more strongly on absolute than on relative performance (cf. Huey and Bennett 1987, 1105; Bennett 1991, 2); all of our analyses have been on residual scores, correcting for variation related to size and age (this computation of residuals was necessary to remove artifactual sources of variation). Resolving the foregoing possibilities will be a challenge for behavioral and physiological ecologists.

Why Don't Speed and Endurance Show a Trade-off?

Although I have argued that knowledge of behavioral or physiological mechanisms may allow predictions of genetic correlations, the one example in the present study—the trade-off between speed and endurance hypothesized on physiological grounds (Garland 1988)—is refuted by empirical evidence (see table 12.3; see also Jayne and Bennett 1990a). Brodie (1993) also reported significant positive phenotypic and genetic correlations (both between .3 and .5) between sprint speed and distance crawling capacity (treadmill endurance was not measured) in both of two populations of *T. ordinoides*.

One line of evidence I cited (Garland 1988) as suggesting a necessary trade-off was the fact that world-class sprinters and marathoners are different individuals with different physiques and muscle fiber types. But perhaps this example is misleading. World-class athletes are a highly selected subsample of the human population (cf. Wallace 1991). If we consider a random sample of humans, it may be that speed and endurance are actually *positively* correlated—that is certainly what I remember from physical education classes! Perhaps it is only when we consider the subset of the very best athletes that there is a negative correlation between speed and endurance. This argument is illustrated graphically in figure 12.3, and is reminiscent of the antagonistic pleiotropy model for the evolution of negative genetic correlations between major components of fitness (e.g., Rose, Service, and Hutchinson 1987;

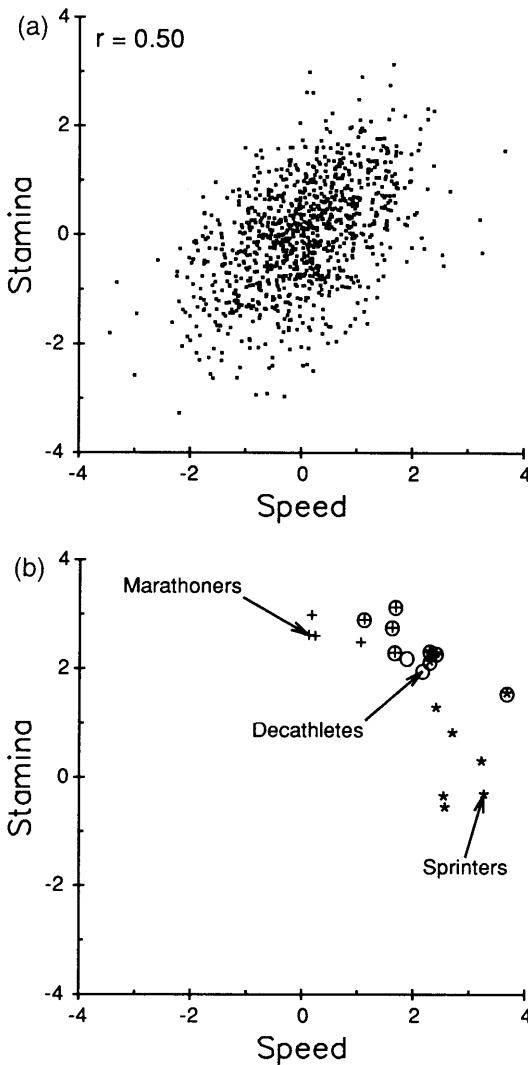


Fig. 12.3 (a) One thousand data points drawn randomly from a bivariate normal distribution with a correlation of $+ .50$, means of zero, and standard deviations of unity. (b) Most extreme 1% ($N = 10$) of points in terms of speed (asterisks), endurance (plus signs), or their sum (circles). Selection based on these criteria is not always mutually exclusive; thus, the total N is less than 30. Within this highly selected subpopulation, analogous to that represented by world-class athletes (cf. Wallace 1991), speed and endurance actually show a negative correlation, suggesting a trade-off.

Cheverud 1988b; Falconer 1989); a different but related argument is presented by Wallace (1991).

The idea that trade-offs appear only in extreme subsamples may apply to many biological examples. For instance, it has been suggested that mathematical and musical ability are positively correlated in the human population as a whole, but are uncorrelated in geniuses (J. F. Crow, pers. comm.). Similarly, Hiraizumi (1961) found negative genetic correlations between rate of development and female fertility only in lines of *Drosophila melanogaster* exhibiting relatively high values of both traits. On the other hand, a comparison of two closely related lizard species showed a physiologically based trade-off between capacities for speed and endurance (Huey et al. 1984), whereas comparisons of multiple species of lizards (T. Garland, unpublished data) and of mammals (Garland, Geiser, and Baudinette 1988) spanning broad phylogenetic ranges do not show such a trade-off.

Phenotypic and Genetic Correlations: Constraint or Facilitation?

The fact that some phenotypic correlations are significant (Garland 1988; Garland and Bennett 1990; Garland, Bennett, and Daniels 1990) means that some correlated selection (Arnold, chap. 2; Brodie 1992) probably occurs in nature. The fact that some genetic correlations are also significant means that some correlated responses to selection will occur as well (Arnold, chap. 2; Brodie 1993). Thus, the traits I have studied are not entirely free to evolve independently.

Antipredator display shows no significant genetic correlations with the other measured traits, and only two significant phenotypic correlations (see table 12.3, fig. 12.2; Garland, Bennett, and Daniels 1990). This is surprising because different extremes of this behavior might be expected to depend on different aspects of physiological performance abilities (cf. Arnold and Bennett 1984; Garland 1988, 1993; Bennett 1991; Garland and Losos 1994). One might expect "correlational selection" to favor particular combinations of antipredator behavior and locomotor performance capacities (Garland 1988), and these combinations may change with age and size (Brodie 1991, chap. 1), leading to coadaptation (cf. Huey and Bennett 1987) as well as to the evolution of appropriate genetic correlations. In fact, Brodie (1989b, 1993) has detected correlational selection for combinations of antipredator behavior and color pattern.

Apparently, the observed genetic correlations do not place important "constraints" on the joint evolution of the traits I have studied. In fact, the positive genetic correlation between speed and treadmill endurance may actually *facilitate* adaptive evolution, given that positive directional selection may occur on both (Jayne and Bennett 1990b). If both speed and endurance are generally under positive selection, then perhaps the positive genetic correlation between them is partly the result of past selection pressures (cf. Cheverud 1984b, 1988b; Brodie 1992, 1993). Although comparative data for other snakes are scarce (see references in Garland 1988; Garland and Losos 1994), garter snakes appear to be neither exceptionally fast nor enduring; they have not (yet?) evolved to phenotypic extremes at which physiological trade-offs may become ineluctable (see end of previous section).

The significant genetic correlations agree with intuitive reasoning in one case (positive between $\dot{V}O_2$ max and heart size: Garland, Bennett, and Daniels 1990) but not in the other (negative between speed and endurance: Garland 1988) (see also Dohm and Garland 1993 for examples involving scale counts). The existence of unexpected genetic correlations may suggest underlying mechanisms different from those that had previously been imagined (cf. Arnold 1981a, 505–6; Arnold 1981c; Garland 1988, 345; Garland and Carter 1994).

The constancy of genetic correlations over evolutionary time should depend in part on their origin. Genetic correlations due to linkage disequilibrium, for example, should dissipate rather quickly (Lande 1980a, 1988; Falconer 1989). Those due to fundamental biochemical, physiological, or biochemical interactions or constraints should last longer (cf. Maynard Smith et al. 1985; Clark 1987, 935; Roff, chap. 3; Arnold, 1992a). Brodie (1993) reported no significant differences in the genetic variance-covariance matrices for two populations of *Thamnophis ordinoides*, based on speed, distance crawling capacity, tendency to reverse crawling direction, and color pattern (see Brodie and Garland 1993 for other examples with snakes).

Limitations of Full-Sib Heritabilities and Genetic Correlations

This study is based on information only from sets of full sibs because we do not know paternity and hence cannot identify half sibs. Although mothers were available, all of the measured traits change ontogenetically such that any measurements of the dams would be affected by age (unknown for our dams), body size, and uncertain

ontogenetic repeatability (Garland 1985; Herzog and Burghardt 1988; van Berkum et al. 1989; Arnold 1990; Jayne and Bennett 1990a; Brodie 1991, chap. 1; Shaffer, Austin, and Huey 1991). Thus, newborn offspring-on-dam regressions would be unreliable. Captive breeding programs are possible (Arnold 1981b) but are difficult for several reasons: garter snakes may store sperm, they do not breed as reliably in the laboratory as do *Mus* or *Drosophila*, and they take 2–4 years to reach sexual maturity. The foregoing constraints may apply to many natural populations; therefore, sets of full sibs may be the only relatives from which information will be available. In this section I review the reasons that estimates of genetic parameters based only on full-sib data may differ from estimates based on measures of other relatives (Arnold, chap 2).

Full-sib data alone do not allow estimation of either narrow-sense or what is conventionally defined as "broad-sense" heritability (Arnold, chap. 2; Brodie and Garland 1993). Instead, twice the among-family component of variance estimates additive genetic variance plus half of the dominance variance plus half of the epistatic variance plus twice the common family environmental effects (including maternal effects) (Falconer 1989; Cheverud and Moore, chap. 4). Estimates of genetic correlations from full-sib data are also potentially inflated by influences of dominance, epistasis, and environmental factors (Falconer 1989).

Unfortunately, we do not have a good idea of how large the non-additive genetic effects might be for traits we studied in garter snakes, nor do we know whether they might differ in magnitude among traits (see also Schwartz and Herzog 1993; Dohm and Garland 1993). Thus, we have no reasonable way to correct for the potential upward biases their presence might introduce into estimates of (narrow-sense) heritabilities and genetic correlations. On the other hand, two recent reviews suggest that full-sib heritability estimates often are not much larger than narrow-sense heritabilities (Roff and Mousseau 1987; Mousseau and Roff 1987; but see Dohm and Garland 1993 on scale counts in the present snakes).

We were able to reduce the influence of potential common family environmental effects via husbandry: specifically, newborns were separated and housed in separate containers on the day of birth, so the problem was eliminated from that point on. For both logistical reasons and to minimize age variation, testing of individuals was done in blocks of six families. Although this may have allowed more common family environmental effects to creep in, we do not consider this a likely possibility, and age was used as an in-

dependent variable when computing residuals. In general, any environmental effect experienced uniquely by all members of a single family is of concern, because it will tend to make them deviate from the overall population mean (Boake, chap. 14). As our heritability estimates are based on the among-family component of variance, they may be inflated by common family environmental effects.

In our study, as in several others of garter snakes, these common maternal environments ended on the day of birth. Additionally, all dams experienced a common set of controlled laboratory conditions for about one month prior to giving birth. These two procedures will not, of course, remove possible effects of dam age and size, although the latter might reduce variation in dam condition and hence its effects. Our use of residuals controlled statistically for the effects of dam size, condition, age, and litter size. In all cases, heritabilities estimated for residual traits were lower than those estimated for raw traits, suggesting that we were at least partly successful. On the other hand, this may also have removed some genetic variance from the traits of interest (Tsuji et al. 1989; Brodie and Garland 1993).

Heritability estimates for organisms raised in the laboratory should tend to be higher than for those raised in nature (Riska, Prout, and Turelli 1989; Willis, Coyne, and Kirkpatrick 1991). This potential problem is reduced in the present study because newborn snakes were studied. Moreover, they experienced more than half of their development inside dams raised under field conditions. In any case, no simple correction procedure is possible. The technique described by Riska, Prout, and Turelli (1989; see also Schwartz and Herzog 1993) for estimating "field heritabilities" with offspring-on-parent regressions was not possible in the present study because offspring were not raised to their parent's age prior to measurement.

A final possible confounding factor is multiple paternity. Under multiple paternity, some individuals within a litter are half sibs rather than full sibs, and the among-family component of variance should be multiplied by a factor greater than two (Falconer 1989). Schwartz, McCracken, and Burghardt (1989) demonstrated multiple paternity in over half of the litters from two midwestern populations of *Thamnophis sirtalis*, and calculated that treating all families as if they were composed of full sibs would lead to underestimating heritabilities by a factor of 1.35. Thus, our values will have underestimated heritabilities if multiple paternity was present.

Although we do not know exactly how the various factors listed in this section may have biased our estimates of genetic parameters, such estimates represent an important first step toward understanding the inheritance of behavior in natural populations (cf. Arnold 1981a,b,c, 1988; Arnold, chap. 2).

Suggestions for Future Research

Although garter snakes have long generation times, they are often easy to capture in large numbers and can be maintained relatively easily in captivity. Thus, future studies may be able to use other breeding designs to estimate true narrow-sense heritabilities and genetic correlations. Estimation of these parameters would go a long way toward answering many of the questions raised above. One could also use breeding designs or population crosses (e.g., Arnold 1981b,c) to test for the presence of directional dominance (cf. Lynch, chap. 13). Traits that have been subject to directional selection are predicted to show directional dominance in the favored direction (Broadhurst and Jinks 1974; Mather and Jinks 1982); thus, we might predict that both speed and endurance will show dominance for higher performance. Directional dominance for antipredator display could suggest whether past selection had favored either offensive (aggressive) or defensive behavior. On the other hand, ambidirectional dominance would suggest that past selection had been stabilizing (cf. Rose, Service, and Hutchinson 1987; Travis 1989b).

For predicting the course of microevolution in nature, estimates of genetic parameters for animals raised in the field are necessary. Field heritabilities are expected to be lower than for laboratory-reared animals because environmental sources of variance should be much greater in nature (Riska, Prout, and Turelli 1989; Schwartz and Herzog 1993).

Compared with garter snakes, few organisms offer such rich opportunities for integrative studies of multivariate phenotypic evolution (but see Lynch, chap. 13). Their antipredator displays, open-field behavior (e.g., Herzog and Burghardt 1986), color patterns, and scale counts are particularly noteworthy because all may interact through the common pathway of locomotor abilities (Arnold and Bennett 1984, 1988; Garland 1988). Thus, recent work by Brodie (1989a,b, 1992, 1993) focuses on the functional and genetic integration of antipredator behavior and color pattern in *Thamnophis ordinoides*. Arnold (pers. comm.) is investigating the constancy of

genetic variance-covariance matrices for scale counts in natricine snakes. Finally, Dohm and Garland (1993) have measured scale counts in the same individuals studied herein, thus allowing extension of our present comparisons to morphological traits of a very different type. Further comparisons of correlated selection and genetic correlations for different types of traits—such as foraging or antipredator behavior in relation to speed and stamina—would be of particular interest (Arnold 1988; Brodie 1992, 1993).

The relatively long life span of garter snakes means that information on the ontogenetic consistency of individual differences at the phenotypic level—and of parameters in the genetic variance-covariance matrix—is crucial for a complete understanding of multivariate evolution (e.g., Arnold 1981a, 1990). The available data for reptiles indicate that repeatabilities of behavioral and locomotor traits may be statistically significant for relatively long portions of the life span (e.g., 1 year), but that they are generally much lower than day-to-day repeatabilities (Arnold and Bennett 1984, 1988; van Berkum et al. 1989; Jayne and Bennett 1990a; Brodie 1991, chap. 1). Limited results of Jayne and Bennett (1990a) suggest that heritabilities of locomotor performance may decrease with age. Herzog and Burghardt (1988) show that family differences in antipredator responses can be consistent for at least 1 year in captivity, but do not provide heritability estimates. Again, garter snakes would be good models for such studies, because they exhibit many traits that change ontogenetically and some that do not (e.g., scale counts: Arnold 1988; Dohm and Garland 1993).

Finally, we need information concerning how often and under what conditions animals actually use their maximal abilities. Similarly, we need to determine the response of free-living animals to natural predators. How often is speed an important determinant of escape success? Is maximal speed ever used in foraging? Do the answers to these questions depend on the type of predator or prey involved? Answering such questions is not easy, because many animals—including garter snakes—are difficult to observe in nature and because the events of interest are relatively rare, thus requiring long and continuous periods of direct observation. Nonetheless, direct observations of individual animals (yielding "quantitative ethograms") could allow us to get much closer to understanding how, exactly, selection in nature occurs (cf. Pough 1989; Garland and Losos 1994). Integrating information on selection and its agents with knowledge of inheritance under natural conditions is an obtainable goal for some organisms.

SUMMARY

Morphological, physiological, and biochemical traits determine organismal capacities for locomotion, which in turn set ultimate limits within which normal behavior must be accomplished. This hierarchy suggests that behavioral traits or measures of whole-animal "performance" capacities (e.g., maximal speed, endurance) will be of more direct ecological and selective importance than are lower-level morphological or physiological traits (e.g., heart size, enzyme activities). In turn, quantitative genetic theory predicts that, in populations at genetic equilibrium, traits of greater selective importance should exhibit lower heritabilities. Heritabilities are important because they determine how rapidly (if at all) traits can respond to natural (or artificial) selection. A. F. Bennett, C. B. Daniels, and I have therefore compared heritabilities of thirteen traits representing different levels of biological organization by studying offspring born to wild-caught, gravid *Thamnophis sirtalis*.

Quantitative measures of the four whole-animal traits (antipredator display, sprint speed, treadmill endurance, maximal oxygen consumption) were highly repeatable on a day-to-day basis. Prior to genetic analyses, we computed residuals from multiple regression equations in an attempt to statistically remove variation related to body size, dam size, litter size, and age (as well as assay batch for enzyme activities). This treatment is presumed to have reduced the magnitude of maternal effects mediated through dam size and/or condition, but may also have removed some genetic variation. Contrary to theoretical expectations, the organismal performance traits (speed, endurance, $\dot{V}O_2\text{max}$) generally showed higher broad-sense heritabilities ($h^2 = 0.58\text{--}0.89$) than did morphological, physiological, or biochemical characters ($h^2 = 0.01\text{--}0.63$), with antipredator display showing an intermediate heritability of 0.41. Phenotypic correlations among traits were generally low, and antipredator display was not significantly correlated with any lower-level trait. However, a few morphological and biochemical traits did correlate significantly with the three measures of organismal performance. Significant genetic correlations existed between speed and endurance (+.59—a surprising result), between $\dot{V}O_2\text{max}$ and relative ventricle mass (+.64), and between liver and ventricle pyruvate kinase activities (−.55). Because antipredator display does not appear to be genetically correlated with any other measured trait, it should be relatively free to evolve independently.

ACKNOWLEDGMENTS

I thank C.R.B. Boake and A. V. Hedrick for the invitation to participate in the symposium that spawned this book. Much of this research was done in collaboration with A. F. Bennett and C. B. Daniels, with assistance from S. J. Arnold, who provided initial motivation and encouragement for this work, as well as study animals from his field sites. C.R.B. Boake, E. D. Brodie III, M. R. Dohm, R. E. Jung, J. M. Schwartz, and an anonymous reviewer provided helpful comments on the chapter, and E. D. Brodie III kindly provided a copy of his unpublished Ph.D. dissertation. Bruce C. Jayne graciously supplied the snake photograph. Financial support was provided first by NSF Grant DEB-8214656 to T. G. and A. F. Bennett, then by other NSF grants to A.F.B., and most recently by NSF Grants BSR-9006083 and BSR-9157268 to T. G., as well as by the University of Wisconsin Graduate School.

Literature Cited

- Arnold, S. J. 1981a. Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans*. *Evolution* 35:489-509.
- Arnold, S. J. 1981b. Behavioral variation in natural populations. II. The inheritance of a feeding response in crosses between geographic races of the garter snake, *Thamnophis elegans*. *Evolution* 35:510-515.
- Arnold, S. J. 1981c. The microevolution of feeding behavior. Pages 409-453 in A. Kamil and T. Sargent, eds. *Foraging behavior: ecological, ethological and psychological approaches*. Garland Press, New York.
- Arnold, S. J. 1983. Morphology, performance and fitness. *Am. Zool.* 23:347-361.
- Arnold, S. J. 1987. Genetic correlation and the evolution of physiology. Pages 189-215 in M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey, eds. *New directions in ecological physiology*. Cambridge Univ. Press, Cambridge, U.K.
- Arnold, S. J. 1988. Quantitative genetics and selection in natural populations: Microevolution of vertebral numbers in the garter snake *Thamnophis elegans*. Pages 619-636 in B. S. Weir, E. J. Eisen, M. J. Goodman, and G. Namkoong, eds. *Proceedings of the second international conference on quantitative genetics*. Sinauer Associates, Sunderland, Mass. 724 pp.
- Arnold, S. J. 1990. Inheritance and the evolution of behavioral ontogenies. Pages 167-189 in M. E. Hahn, J. K. Hewitt, N. D. Henderson, and R. H. Benno, eds. *Developmental behavior genetics: neural, biometrical, and evolutionary approaches*. Oxford Univ. Press, New York.
- Arnold, S. J. 1992a. Constraints on phenotypic evolution. *Am. Nat.* 140(Supplement):S85-S107.
- Arnold, S. J. 1992b. Behavioural variation in natural populations. VI. Prey responses by two species of garter snakes in three regions of sympatry. *Anim. Behav.* 44:705-719.
- Arnold, S. J., and A. F. Bennett. 1984. Behavioural variation in natural populations. III. Antipredator displays in the garter snake *Thamnophis radix*. *Anim. Behav.* 32:1108-1118.

- Arnold, S. J., and A. F. Bennett. 1988. Behavioral variation in natural populations. V. Morphological correlates of locomotion in the garter snake *Thamnophis radix*. Biol. J. Linn. Soc. 34:175-190.
- Astrand, P. O., and K. Rodahl. 1986. Textbook of work physiology. 3rd ed. McGraw-Hill, New York. 756 pp.
- Bennett, A. F. 1987. Inter-individual variability: an underutilized resource. Pages 147-169 in M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey, eds. New directions in ecological physiology. Cambridge Univ. Press, Cambridge, U.K.
- Bennett, A. F. 1990. The thermal dependence of locomotor capacity. Am. J. Physiol. 259 (Regulatory, Integrative Comp. Physiol. 28):R253-R258.
- Bennett, A. F. 1991. The evolution of activity capacity. J. Exp. Biol. 160:1-23.
- Bennett, A. F., T. Garland, Jr., and P. L. Else. 1989. Individual correlation of morphology, muscle mechanics and locomotion in a salamander. Am. J. Physiol. 256 (Regulatory, Integrative Comp. Physiol. 25):R1200-R1208.
- Benton, M. J. 1980. Geographic variation in the garter snakes (*Thamnophis sirtalis*) of the north-central United States, a multivariate study. Zool. J. Linn. Soc. 68:307-323.
- Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behavior. Evol. Ecol. 3:173-182.
- Bolles, R. C. 1975. Theory of motivation. 2nd. ed. Harper and Row, New York. 568 pp.
- Broadhurst, P. L., and J. L. Jinks. 1974. What genetical architecture can tell us about the natural selection of behavioral traits. Pages 43-63 in J. H. F. van Abeelen, ed. The genetics of behaviour. North-Holland Publ. Co., Amsterdam. 450 pp.
- Brodie, E. D., III. 1989a. Behavioral modification as a means of reducing the cost of reproduction. Am. Nat. 134:225-238.
- Brodie, E. D., III. 1989b. Genetic correlations between morphology and antipredator behaviour in natural populations of the garter snake *Thamnophis ordionoides*. Nature 342:542-543.
- Brodie, E. D., III. 1991. Functional and genetic integration of color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. Unpubl. Ph.D. Dissertation, Univ. of Chicago. 123 pp.

- Brodie, E. D., III. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution* 46:1284-1298.
- Brodie, E. D., III. 1993. Homogeneity of the genetic variance-covariance matrix for antipredator traits in two natural populations of the garter snake *Thamnophis ordinoides*. *Evolution* 44:844-854.
- Brodie, E. D., III, and E. D. Brodie, Jr. 1991. Evolutionary response of predators to dangerous prey: reduction of toxicity of newts and resistance of garter snakes in island populations. *Evolution* 45:221-224.
- Brodie, E. D., III, and T. Garland, Jr. 1993. Quantitative genetics of snake populations. Pages 315-362 in *Snakes: ecology and behavior*. R. A. Seigel and J. T. Collins, eds. McGraw Hill, New York.
- Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, ecology, and behavior. A research program in comparative biology. Univ. Chicago Press, Chicago. 434 pp.
- Brooks, G. A., and T. D. Fahey. 1984. Exercise physiology: human bioenergetics and its applications. John Wiley and Sons, New York.
- Bulmer, M. G. 1980. The mathematical theory of quantitative genetics. Clarendon Press, Oxford. pp. 256.
- Burghardt, G. M. 1970. Intraspecific geographical variation in chemical food cue preferences of newborn garter snakes (*Thamnophis sirtalis*). *Behaviour* 36:246-257.
- Cheverud, J. M. 1984. Quantitative genetics and developmental constraints on evolution by selection. *J. Theoret. Biol.* 110:155-171.
- Cheverud, J. M. 1988. The evolution of genetic correlation and developmental constraint. Pages 94-101 in D. de Jong, ed. *Population genetics and evolution*. Springer-Verlag, Berlin.
- Christman, S. P. 1980. Patterns of geographic variation in Florida snakes. *Bull. Florida State Mus. Biol. Sci.* 25:157-256.
- Clark, A. G. 1987. Senescence and the genetic-correlation hang-up. *Am. Nat.* 129:943-940.
- Conover, W. J., M. E. Johnson, and M. M. Johnson. 1981. A comparative study of tests for homogeneity of variances, with

applications to the outer continental shelf bidding data.
Technometrics 23:351-361.

- Crews, D. 1992. Behavioural endocrinology and reproduction: an evolutionary perspective. *Oxford Reviews of Reproductive Biology* 14:303-370. S. R. Milligan, ed. Oxford Univ. Press, Oxford. 374 pp.
- de Queiroz, A., and R. Lawson. In review. Phylogenetic relationships of the garter snakes based on DNA sequence and allozyme variation: a pluralistic approach to resolving conflict between trees. *Biol. J. Linn. Soc.*
- Dessauer, H. C., J. E. Cadle, and R. Lawson. 1987. Patterns of snake evolution suggested by their proteins. *Fieldiana Zoology* 34:1-34.
- Djawdan, M. 1993. Locomotor performance of bipedal and quadrupedal heteromyid rodents. *Funct. Ecol.* 7:195-202.
- Dohm, M. R., and T. Garland, Jr. 1993. Quantitative genetics of scale counts in the garter snake *Thamnophis sirtalis*. *Copeia* 1993:987-1002.
- Dowling, H. G., R. Highton, G. C. Maha, and L. R. Maxon. 1983. Biochemical evaluation of colubrid snake phylogeny. *J. Zool., Lond.* 201:309-329.
- Drummond, H., and G. M. Burghardt. 1983. Geographic variation in the foraging behavior of the garter snake, *Thamnophis elegans*. *Behav. Ecol. Sociobiol.* 12:43-48.
- Falconer, D. S. 1989. Introduction to quantitative genetics. 3rd. ed. Longman, London.
- Fitch, H. S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. *Univ. Kans. Mus. Nat. Hist. Publ.* 15:493-564.
- Fitch, H. S., and T. P. Maslin. 1961. Occurrence of the garter snake, *Thamnophis sirtalis*, in the Great Plains and Rocky Mountains. *Univ. Kans. Mus. Nat. Hist. Publ.* 13:289-308.
- Ford, N. B., and G. A. Shuttlesworth. 1986. Effects of variation in food intake on locomotory performance of juvenile garter snakes. *Copeia* 1986:999-1001.
- Garland, T., Jr. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. *Am. J. Physiol.* 247 (Regulatory, Integrative Comp. Physiol. 16):R806-R815.

- Garland, T., Jr. 1985. Ontogenetic and individual variation in size, shape, and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool., Lond. (A)* 207:425-439.
- Garland, T., Jr. 1988. Genetic basis of activity metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake *Thamnophis sirtalis*. *Evolution* 42:335-350.
- Garland, T., Jr. 1993. Locomotor performance and activity metabolism of *Cnemidophorus tigris* in relation to natural behaviors. Pages 163-210 in J. W. Wright and L. J. Vitt, eds. *Biology of whiptail lizards (Genus Cnemidophorus)*. Oklahoma Museum of Natural History, Norman. xiv + 417 pp.
- Garland, T., Jr., and S. C. Adolph. 1991. Physiological differentiation of vertebrate populations. *Annu. Rev. Ecol. Syst.* 22:193-228.
- Garland, T., Jr., and S. J. Arnold. 1983. Effects of a full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). *Copeia* 1983:1092-1096.
- Garland, T., Jr., and A. F. Bennett. 1990. Quantitative genetics of maximal oxygen consumption in a garter snake. *Am. J. Physiol.* 259 (Regulatory Integrative Comp. Physiol. 28):R986-992.
- Garland, T., Jr., and P. A. Carter. 1994. Evolutionary physiology. *Annu. Rev. Physiol.* 56:579-621.
- Garland, T., Jr., and R. B. Huey. 1987. Testing symmorphosis: does structure match functional requirements? *Evolution* 41:1404-1409.
- Garland, T., Jr., and J. B. Losos. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pages 240-302 in P. C. Wainwright and S. M. Reilly, eds. *Ecological morphology: integrative organismal biology*. Univ. Chicago Press, Chicago.
- Garland, T., Jr., A. F. Bennett, and C. B. Daniels. 1990a. Heritability of locomotor performance and its correlates in a natural population. *Experientia* 46:530-533.
- Garland, T., Jr., F. Geiser, and R. V. Baudinette. 1988. Comparative locomotor performance of marsupial and placental mammals. *J. Zool., Lond.* 215:505-522.
- Garland, T., Jr., E. Hankins, and R. B. Huey. 1990b. Locomotor capacity and social dominance in male lizards. *Funct. Ecol.* 4:243-250.

- Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* 42:265-292.
- Greene, H. W. 1988. Antipredator mechanisms in reptiles. Pages 1-152 in C. Gans and R. B. Huey, eds. *Biology of the Reptilia*. Vol. 16, Ecology B, Defense and Life Histories. Alan R. Liss, N.Y. 659 pp.
- Halliday, T. R. 1987. Physiological constraints on sexual selection. Pages 247-264 in J. W. Bradbury and M. B. Andersson, eds. *Sexual selection: testing the alternatives*. John Wiley & Sons, New York. 308 pp.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford Univ. Press, Oxford. 239 pp.
- Henderson, N. D. 1989. Interpreting studies that compare high- and low-selected lines on new characters. *Behavior Genetics* 19:473-502.
- Herzog, H. A., Jr. 1990. Experimental modification of defensive behaviors in garter snakes (*Thamnophis sirtalis*). *J. Comp. Psychol.* 104:334-339.
- Herzog, H. A., Jr., and B. D. Bailey. 1987. Development of antipredator responses in snakes: II. Effects of recent feeding on defensive behaviors of juvenile garter snakes (*Thamnophis sirtalis*). *J. Comp. Psych.* 101:387-389.
- Herzog, H. A., Jr., and G. M. Burghardt. 1986. Development of antipredator responses in snakes: I. Defensive and open-field behaviors in newborns and adults of three species of garter snakes (*Thamnophis melanogaster*, *T. sirtalis*, *T. butleri*). *J. Comp. Psych.* 100:372-379.
- Herzog, H. A., Jr., and G. M. Burghardt. 1988. Development of antipredator responses in snakes. III. Stability of individual and litter differences over the first year of life. *Ethology* 77:250-258.
- Herzog, H. A., Jr., and J. M. Schwartz. 1990. Geographic variation in the anti-predator behavior of neonate garter snakes, *Thamnophis sirtalis*. *Anim. Behav.* 40:597-598.
- Herzog, H. A., Jr., B. B. Bowers, and G. M. Burghardt. 1989a. Stimulus control of antipredator behavior in newborn and juvenile garter snakes (*Thamnophis*). *J. Comp. Psych.* 103:233-242.

- Herzog, H. A., Jr., B. B. Bowers, and G. M. Burghardt. 1989b. Development of antipredator responses in snakes. IV. Interspecific and intraspecific differences in habituation of defensive behavior. *Developmental Psychobiology* 22:489-508.
- Hertz, P. E., R. B. Huey, and T. Garland, Jr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are ectotherms Olympians or Boy Scouts? *Am. Zool.* 28:927-938.
- Hiraizumi, Y. 1961. Negative genetic correlation between rate of development and female fertility in *Drosophila melanogaster*. *Genetics* 46:615-624.
- Huey, R. B., and A. F. Bennett. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098-1115.
- Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19:357-366.
- Huey, R. B., A. F. Bennett, H. B. John-Alder, and K. A. Nagy. 1984. Locomotor capacity and foraging behavior of Kalahari lacertid lizards. *Anim. Behav.* 32:41-50.
- Jayne, B. C., and A. F. Bennett. 1989. The effect of tail morphology on locomotor performance of snakes: a comparison of experimental and correlative methods. *J. Exp. Zool.* 252:126-133.
- Jayne, B. C., and A. F. Bennett. 1990a. Scaling of speed and endurance in garter snakes: a comparison of cross-sectional and longitudinal allometries. *J. Zool., Lond.* 220:257-277.
- Jayne, B. C., and A. F. Bennett. 1990b. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204-1229.
- Kephart, D. G. 1982. Microgeographic variation in the diets of garter snakes. *Oecologia* 52:287-291.
- Kephart, D. G., and S. J. Arnold. 1982. Garter snake diets in a fluctuating environment: a seven-year study. *Ecology* 63:1232-1236.
- King, R. B. 1987. Color pattern polymorphism in the Lake Erie water snake, *Nerodia sipedon insularum*. *Evolution* 41:241-255.
- Lande, R., 1980. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* 94:203-215.

- Lande, R. 1988. Quantitative genetics and evolutionary theory. Pages 71-84 in B. S. Weir, E. J. Eisen, M. J. Goodman, and G. Namkoong, eds. Proceedings of the second international conference on quantitative genetics. Sinauer Associates, Sunderland, Massachusetts. 724 pp.
- Lawson, R. 1985. Molecular studies of thamnophine snakes. Unpublished Ph.D. thesis. Louisiana State Univ. 182 pp.
- Martins, E. P., and T. Garland, Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* 45:534-557.
- Mather, K., and J. L. Jinks. 1982. Biometrical genetics: the study of continuous variation. 3rd ed. Chapman and Hall, London. 396 pp.
- Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert. 1985. Developmental constraints and evolution. *Quart. Rev. Biol.* 60:265-287.
- Moore, F. R., and R. E. Gatten, Jr. 1989. Locomotor performance of hydrated, dehydrated, and osmotically stressed anuran amphibians. *Herpetologica* 45:101-110.
- Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. *Heredity* 59:181-197.
- Pease, C. M., and J. J. Bull. 1988. A critique for measuring life history trade-offs. *J. Evol. Biol.* 1:293-303.
- Pough, F. H. 1989. Organismal performance and Darwinian fitness: Approaches and interpretations. *Physiol. Zool.* 62:199-236.
- Price, T., and D. Schluter. 1991. On the low heritability of life-history traits. *Evolution* 45:853-861.
- Price, T. D., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and evolution of breeding data in birds. *Science* 240:789-799.
- Richardson, C. S., M. R. Dohm, and T. Garland, Jr. 1994. Metabolism and thermoregulation in crosses between wild and randombred laboratory house mice (*Mus domesticus*). *Physiol. Zool.* 67:944-975.
- Riska, B. 1989. Composite traits, selection response, and evolution. *Evolution* 43:1172-1191.

- Riska, B., T. Prout, and M. Turelli. 1989. Laboratory estimates of heritabilities and genetic correlations in nature. *Genetics* 123:865-871.
- Roff, D. A., and T. A. Mousseau. 1987. Quantitative genetics and fitness: lessons from *Drosophila*. *Heredity* 58:103-118.
- Rose, M. R., P. M. Service, and E. W. Hutchinson. 1987. Three approaches to trade-offs in life-history evolution. Pages 91-105 in V. Loeschcke, ed. *Genetic constraints on adaptive evolution*. Springer-Verlag, Berlin. 188 pp.
- Ruthven, A. G. 1908. Variations and genetic relationships of the garter-snakes. *Smithsonian Inst. U. S. Nat. Mus. Bulletin* 61.
- Schiefflen, C. D., and A. de Queiroz. 1991. Temperature and defense in the common garter snake: warm snakes are more aggressive than cold snakes. *Herpetologica* 47:230-237.
- Schwartz, J. M. 1989. Multiple paternity and offspring variability in wild populations of the garter snake *Thamnophis sirtalis* (Colubridae). Unpubl. Ph.D. Dissertation, Univ. of Tennessee, Knoxville.
- Schwartz, J. M., and H. A. Herzog, Jr. 1993. Estimates of heritability of antipredator behavior in three garter snake species (*Thamnophis butleri*, *T. melanogaster*, and *T. sirtalis*) in nature. *Behav. Genetics*. In press.
- Schwartz, J. M., G. F. McCracken, and G. M. Burghardt. 1989. Multiple paternity in wild populations of the garter snake, *Thamnophis sirtalis*. *Behav. Ecol. Sociobiol.* 25:269-273.
- Secor, S. M., B. C. Jayne, and A. F. Bennett. 1992. Locomotor performance and energetic cost of sidewinding by the snake *Crotalus cerastes*. *J. Exp. Biol.* 163:1-14.
- Seigel, R. A., M. M. Huggins, and N. B. Ford. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia* 73:481-485.
- Shaffer, H. B., G. C. Austin, and R. B. Huey. 1991. The consequences of metamorphosis on salamander (*Ambystoma*) locomotor performance. *Physiol. Zool.* 64:212-231.
- Shaw, R. G. 1987. Maximum likelihood approaches applied to quantitative genetics of natural populations. *Evolution* 41:812-826.

- Simonson, E., and P. C. Weiser, eds. 1976. Psychological aspects and physiological correlates of work and fatigue. Springfield, Ill., Charles C. Thomas Publ.
- Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. 2nd ed. Boston, Houghton Mifflin.
- Travis, J. 1989. The role of optimizing selection in natural populations. *Annu. Rev. Ecol. Syst.* 20:279-296.
- Tsuji, J. S., R. B. Huey, F. H. van Berkum, T. Garland, Jr., and R. G. Shaw. 1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. *Funct. Ecol.* 3:240-252.
- Turelli, M. 1988a. Population genetic models for polygenic variation and evolution. Pages 601-618 in B. S. Weir, E. J. Eisen, M. J. Goodman, and G. Namkoong, eds. Proceedings of the second international conference on quantitative genetics. Sinauer Associates, Sunderland, Mass. 724 pp.
- Turelli, M. 1988b. Phenotypic evolution, constant covariances, and the maintenance of additive variance. *Evolution* 42:1342-1347.
- van Berkum, F. H., R. B. Huey, J. S. Tsuji, and T. Garland, Jr. 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird & Girard). *Funct. Ecol.* 3:97-105.
- Wallace, B. 1991. The manly art of self-defense: on the neutrality of fitness components. *Quart. Rev. Biol.* 66:455-465.
- Walton, B. M. 1988. Relationships among metabolic, locomotor, and field measures of organismal performance in the Fowler's toad (*Bufo woodhousei fowleri*). *Physiol. Zool.* 61:107-118.
- Walton, M., B. C. Jayne, and A. F. Bennett. 1990. The energetic cost of limbless locomotion. *Science* 249:524-527.
- Willis, J. H., J. A. Coyne, and M. Kirkpatrick. 1991. Can one predict the evolution of quantitative characters without genetics? *Evolution* 45:441-444.
- Wingfield, J. C., R. E. Hegner, A. M. Dufty, Jr., and G. F. Ball. 1990. The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* 136:829-846.