Snakes

Ecology and Behavior

Richard A. Seigel
Department of Biological Sciences
Southeastern Louisiana University
Hammond, Louisiana

Joseph T. Collins
Museum of Natural History
The University of Kansas
Lawrence, Kansas

1993

xv + 414 pages

McGraw-Hill, Inc.

New York San Francisco Washington, D.C. Auckland Bogotá
Caracas Lisbon London Madrid Mexico City Milan
Montreal New Delhi San Juan Singapore
Sydney Tokyo Toronto

Chapter

8

Quantitative Genetics of Snake Populations

Edmund D. Brodie III

Theodore Garland, Jr.

Introduction

Quantitative genetics is a group of techniques used to study variation in continuously distributed traits (e.g., body size, shape, many behavioral and physiological measurements). In its strongest form, it can be used to isolate the relative importance of genetic and environmental factors to the expression of phenotypic variation (Mather and Jinks, 1982; Bulmer, 1985; Falconer, 1989). The integration of quantitative genetics with evolutionary theory has yielded explicit and testable hypotheses about phenomena from life-history evolution to sexual dimorphism and sexual selection (reviewed by Lande, 1988; Arnold, 1990, 1994). Explicit methodologies for measuring natural selection and for predicting the response of multiple traits to this selection have been developed (Lande, 1979; Lande and Arnold, 1983; Endler, 1986) and, in some cases, it now may be possible to reconstruct the patterns of selection necessary to account for phenotypic differences between populations and species (Arnold, 1981c, 1988a; Price et al., 1984; Price and Grant, 1985; Grant, 1986; Lofsvold, 1988).

Although many of the origins of quantitative genetics are due to evolutionary biologists (Fisher, 1918; Wright, 1921), most of the subsequent development and application of the techniques have been in applied animal and plant breeding. Some of the most familiar statistical concepts, including correlation, regression, and analysis of vari-

ance, arose as means of dealing with evolutionary problems of continuously varying traits (see Provine, 1971). Breeders of domestic stocks recognized that many of the characters of economic importance (e.g., milk yield in dairy cattle, carcass weight of hogs, oil content in maize) varied continuously, and adopted quantitative genetics as an analytical and predictive tool. Subsequent effort was concentrated on generating breeding and selection regimens that maximized the improvement of phenotypes for commercial value. The resultant research largely concerns domestic or laboratory populations and characters that may not have obvious ecological relevance in natural populations (e.g., defecation score in open field trials with mice, bristle number in *Drosophila*). Additionally, the statistical nature and jargon of this body of literature can be quite imposing to most biologists. It is not surprising, then, that few herpetologists have studied this literature and used quantitative genetic approaches in their own investigations.

The goal of this chapter is to introduce quantitative genetics to an audience that may not yet have considered what the technique can do for their research programs. Our approach will necessarily be simple, and more detailed treatments of the methods should be consulted before embarking on quantitative genetic analyses (Turner and Young, 1969; Ehrman and Parsons, 1981; Mather and Jinks, 1982; Becker, 1992; Bulmer, 1985; Falconer, 1989; Plomin et al., 1990; Arnold, 1994; Boake, 1994). We will provide an introduction to some of the basic concepts of quantitative genetics but concentrate on pointing out the types of problems that can benefit from a quantitative genetic approach. We will give special attention to specific problems and methodologies most often encountered when applying the approach to snake populations and will point out areas of research that are particularly suited to studies of snakes. Many snake ecologists will find that, with only minor modifications in sampling regimens, they can collect the kinds of data required for quantitative genetic analyses of the traits and species they currently study.

Why Study Variation or Quantitative Genetics—Who Cares?

The study of differences among individuals is a critical step toward understanding the processes that are responsible for the evolution of characters within and among populations. The most fundamental condition necessary for natural selection to occur is individual variation in a trait (Lewontin, 1970). Selection can be defined simply as a correlation between phenotype and reproductive success (Lewontin, 1970). If a trait does not differ among individuals, then it cannot be correlated to differences in individual reproductive success and therefore cannot be subject to selection. Therefore, studies attempting to determine whether or how selection is currently acting on a character must first consider whether the necessary substrate for selection, individual variation, is present (Arnold, 1981a; Lande and Arnold, 1983; Arnold and Bennett, 1984; Bennett, 1987; Garland, 1988; Boake, 1989; van Berkum et al., 1989; Brodie, 1993a).

Natural selection acts on phenotypes and does not necessarily result in evolution (Lande and Arnold, 1983; while some authors [Endler, 1986] define "natural selection" to include evolutionary change, we find it valuable to distinguish two separate processes, selection and response to selection). Quantitative genetics comes in when considering the evolutionary response of a trait to selection (Lande, 1979; Arnold, 1981c, 1983; Grant, 1986; Falconer, 1989). In order for selection to cause an evolutionary change, relatives must resemble each other. In other words, some of the phenotypic variation in a character must be heritable. For continuously distributed traits, it is the additive genetic variance (see below) that determines the resemblance between parents and their offspring and determines the response to selection. The equation

$$R = h^2 s$$

shows how the response to selection (R) is determined by the strength of selection (s) and the heritability (h^2) of a trait (Falconer, 1989). Heritability is merely the proportion of the total phenotypic variance that is additive genetic in origin. Heritability ranges between 0 and 1, so evolutionary response is always less than or equal to the strength of selection. A regression of mean offspring on mean parent values for a trait yields a line whose slope is equal to the heritability (explained below). If selection is measured as the difference between the means of the original population and the selected parents, and response is measured as the difference between the means of all potential offspring and the offspring of the selected parents, then it is easy to show graphically how greater heritability results in greater evolutionary response to a given intensity of selection (Fig. 8.1).

It should be clear, then, that measurable selection does not necessarily mean a character will change evolutionarily. Some, possibly all, of the variation acted upon by selection may be due to nonadditive genetic invariance environmental causes. Changes in such variation due to selection will not be transmitted to the next generation. On the other hand, measurable heritability almost ensures evolutionary change, because even in the absence of selection, the effects of stochastic processes such as genetic drift will be transmitted across generations (though the changes may be in terms of variances and covariances rather than means). Quantitative genetics strives to dis-

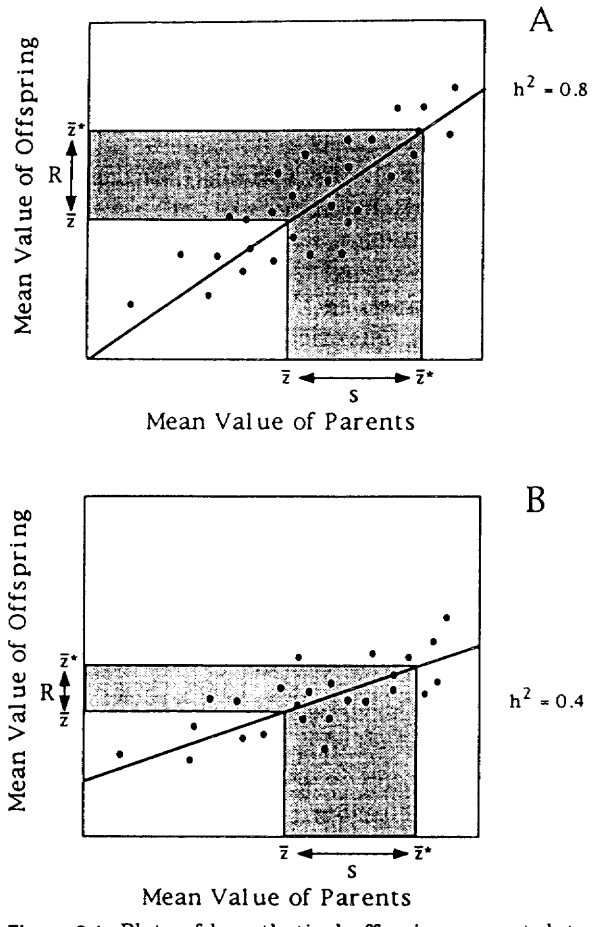

Figure 8.1 Plots of hypothetical offspring–parent data showing the effect of heritability on response to selection. Selection (s) is shown as the difference between the mean of the potential parents ($\bar{z}$) and the mean of the selected (actual) parents ($\bar{z}^*$). Evolutionary response (R) is shown as the difference between the mean of the offspring of the potential parents ($\bar{z}$) and the mean of the offspring of the selected parents ($\bar{z}^*$). The slope of the regression of offspring on parent values is equal to the narrow-sense heritability. Extrapolating from the intersection of the parental means with the heritability line to the offspring axis shows the trait mean in the next generation (shaded portion). The same strength of selection results in greater response when heritability is large (A) than when heritability is moderate (B).

cern the contributions of genetic and environmental factors to phenotypic variation, thus allowing predictions to be made regarding which traits can respond to selection, at what rate, and whether other traits will change as a result (because they are inherited together as indicated by genetic correlations [see below]).

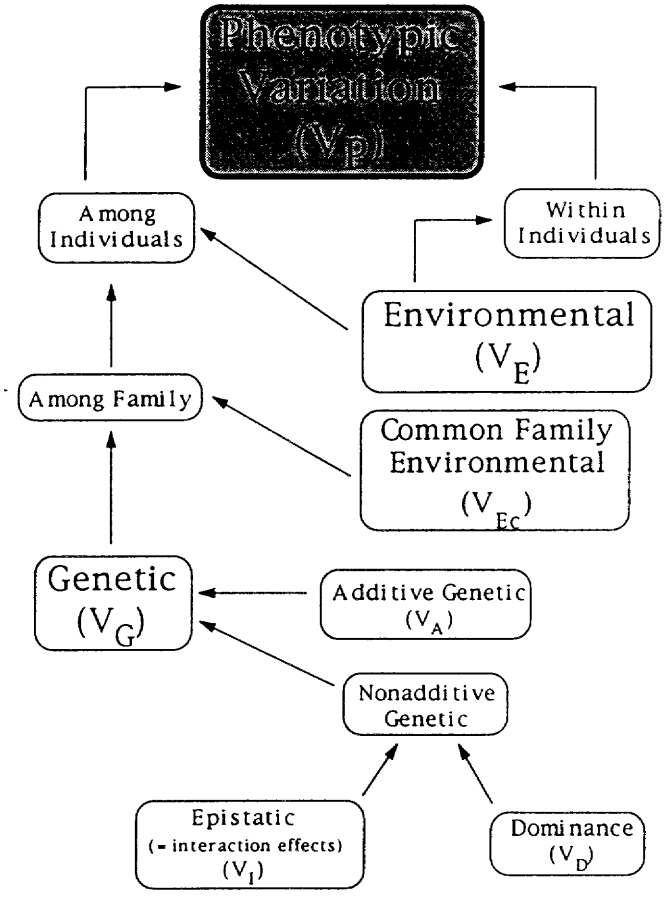

Figure 8.2 Path diagram showing components of phenotypic variation. Note that common-family environmental variance may include genetic and nongenetic maternal effects. See text for explanation of specific variance components.

Definitions

The basic goal of most quantitative genetic analyses is to separate the phenotypic variance of a trait into a number of additive elements (notation follows Falconer, 1989). Each of these *variance components* constitutes a portion of the total variance, and often itself can be further subdivided (Fig. 8.2). The calculation of variance components is often called *partitioning the variance* (the methods that are best suited to studies of snake populations will be discussed later). For instance, if one wanted to partition the variance in sprint speed in a population of snakes, the first level of analysis might be to determine how much variance is accounted for by differences between individual snakes (= *among individual component of variance*) versus variation

in speed within an individual (= *within individual component of variance*) (Fig. 8.2). The ratio of the variation between individuals to the total variation is the *repeatability* and provides a measure of how consistently a trait can be measured within an individual. Variation within a single individual (except ontogenetic variation) cannot have a genetic basis, so this component may be considered *environmental variance* (V_E) (Fig. 8.2).

It will generally be of interest to subdivide the variance among individuals further. Some of the difference in speed among individuals will also be the result of environmental differences (e.g., minor differences in the testing procedure experienced by different individuals, or possibly different environments experienced by individual snakes at critical periods in development). If the variance in speed is attributable to differences among families, much of this may be *genetic variance* (V_G), which is responsible for the inherited resemblance among these relatives. It is important to realize that not all differences among families are genetic in origin (Fig. 8.2). Family members share common nongenetic factors (e.g., same maternal environment in viviparous species, the same incubation temperature during embryonic development, a common physical condition of the mother) that may also account for resemblance. This component of variance is due to the *common family environment* (V_{Ec}) and includes both genetic and nongenetic maternal effects. These nongenetic bases of among-family variation can often be controlled experimentally or isolated by comparing different groups of relatives. The genetic variance for speed may result from a variety of gene actions. The component of variance due to additive effects of genes is the *additive genetic variance* (V_A), and will determine the degree of heritable resemblance between parents and offspring. Some alleles have phenotypic effects that are not strictly additive, which lead to the *dominance variance* (V_D). Still other alleles may be expressed as different phenotypes depending on the alleles that are present at other loci. These contribute to the *epistatic* (or *interaction*) *genetic variance* (V_I) (Fig. 8.2).

If we are interested in what proportion of the total variation in speed among all of the snakes is due to genetic factors, we may calculate a heritability. A *broad-sense heritability* (h_B^2) is simply the ratio of the genetic variance to the total phenotypic variance (Table 8.1). As mentioned above, it is only the proportion of the total variance that is due to additive genetic factors, the *narrow-sense heritability* (h_N^2), that determines the response to selection by quantitative characters (Table 8.1). The narrow-sense parameters will normally be of most interest. Depending on the groups of relatives available for comparison, it may not be possible to isolate either the additive genetic variance or the total genetic variance (Table 8.1). *Full-sib heritabilities*

TABLE 8.1 Variance Components of Different Parameters

Parameter	Variance components	Techniques
Broad-sense heritability h_B^2	$\frac{V_G}{V_P} = \frac{V_A + V_D + V_I}{V_P}$	
Narrow-sense heritability h_N^2	$\frac{V_A}{V_P}$	Offspring–parent regression,[a] half-sib comparison[b]
Full-sib heritability h_{FS}^2	$\frac{V_A + \frac{1}{2}V_D + \frac{1}{2}V_I + 2V_{Ec}}{V_P}$	Full-sib comparison

[a]Offspring–parent regression will also include common family environment (e.g., "maternal") effects, especially if the parent is the mother.
[b]Maternal half-sib comparisons may include common family environment effects, but paternal half-sibs can be used to eliminate this component of variance.

(h_{FS}^2), the estimates most commonly available for natural populations of vertebrates, include some of the dominance, epistatic, and common-family environmental variance (Table 8.1). Such estimates are often mistakenly called broad-sense heritabilities (Garland, 1994).

If we expand our investigation from a single trait (e.g., speed) to multiple traits (e.g., speed and endurance), we must consider the association between these traits. The *phenotypic covariance* (COV_P) of two traits measures how closely associated they are among individuals. The *phenotypic correlation* (r_P) is merely a covariance standardized to range from −1 to 1. Quantitative genetic techniques allow us to treat covariances in the same way as variances. Throughout this chapter, comments about variances and heritabilities also hold true for covariances and genetic correlations between traits (unless otherwise noted). By partitioning the phenotypic covariance into genetic and environmental components, we can determine the degree to which certain traits are inherited together, or genetically coupled (Arnold, 1987). For comparison, genetic covariances (COV_G) are often standardized to vary between −1 and 1 and are then called *genetic correlations* (r_G). Genetic correlations among traits can arise from *pleiotropy* (where a single gene affects the expression of more than one trait) or from *linkage disequilibrium* (where traits are controlled by separate genes, but those genes tend to be inherited together, sometimes because of close physical association on a chromosome [termed *linkage*]). The full matrix of (usually additive) genetic variances and covariances for a set of traits is referred to as the *genetic variance–covariance matrix* or simply *G-matrix*.

Finally, it should be noted that phenotypic expression can vary among environments, even within an individual or among individuals sharing the same genotype. For example, it is well known that the

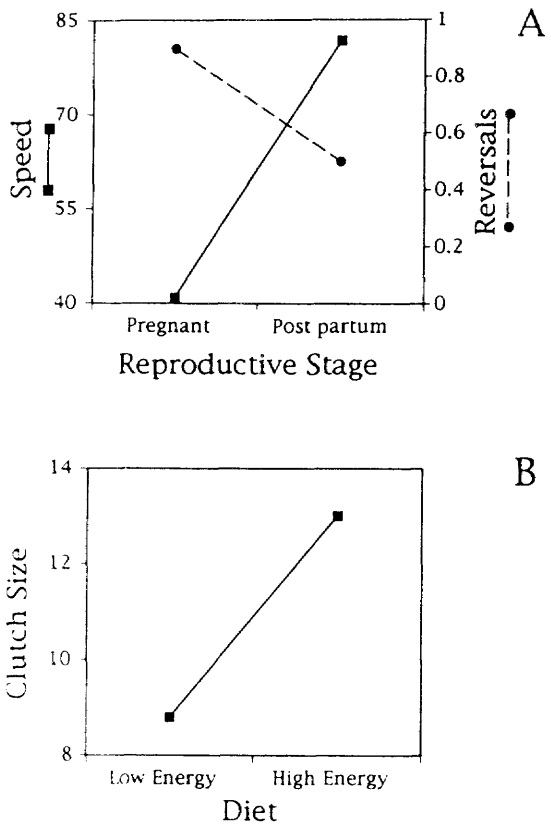

Figure 8.3 Reaction norms for phenotypes expressed in different environments. (*A*) Sprint speed and number of reversals during escape in *Thamnophis ordinoides* are shown as a function of reproductive condition (data from Brodie, 1989b). Females crawl slower and perform more reversals during pregnancy than after parturition. (*B*) Female *Thamnophis marcianus* have smaller clutch sizes when held on low-energy diets compared to high-energy diets during pregnancy (data from Ford and Seigel, 1989).

same snake crawls more slowly at 20 than at 30°C, during pregnancy compared to postparturition, or with a full stomach. The *norm of reaction* describes the phenotypic expression of a genotype across a range of possible environments (Schmalhausen, 1949; Levins, 1968; de Jong, 1990; Gomulkiewicz and Kirkpatrick, 1992) (Fig. 8.3). When the norm of reaction differs among genotypes (e.g., some snakes crawl faster at low temperatures whereas others crawl faster at high temperatures), this constitutes a *genotype-by-environment interaction,* or $G \times E$ (Via, 1984, 1987; Via and Lande, 1985; Falconer, 1989). Heritabilities and genetic correlations can also vary according to the

environment in which they are measured. Because heritabilities are expressed as ratios of genetic variance to total phenotypic variance, any environment that increases the phenotypic variation of a trait inflates the denominator of the heritability (Riska et al., 1989; Schwartz and Herzog, 1993). Thus, the heritability is decreased even though the genetic control (e.g., the V_A) of the trait is unchanged. Quantitative genetic parameters are therefore properties of the specific populations and environments for which they are estimated. Extrapolations of conclusions from laboratory to field or across environments are to be made with caution (Riska et al., 1989; Bull et al., 1982; Janzen, 1992; Schwartz and Herzog, 1993).

What Data Are Required?

The key prerequisite of a data set for performing quantitative genetic analyses is some knowledge of the relationships among individuals. Techniques are available to handle almost any set of relatives, even considering complicating factors such as inbreeding and unbalanced data (Bulmer, 1985; Shaw, 1987, 1991; Falconer, 1989; Becker, 1992). All of these methods are based on the average genetic relatedness, derived from simple Mendelian principles, among individuals with a particular familial relationship (e.g., full siblings, on average, share half their alleles in common; see Falconer, 1989, Chaps. 7 and 9). The sets of relatives most commonly available to biologists working with natural systems of vertebrates are sibling groups and sometimes mother–offspring groups. The specifics of comparing these groups will be discussed below.

Sampling errors in quantitative genetics are large, so very large samples are required to estimate parameters with much precision, or to show that they differ significantly from zero. It is not so much the total number of individuals as the number and size of families measured that determines the precision. The optimal design depends on what the true heritability or genetic correlation is for the population and so can rarely be calculated before doing a study. Falconer (1989, pp. 182–183) provides equations to determine the best design if the total number of individuals that can be measured is limited. Increases in the number of families generally improve precision more than do increases in the number of individuals measured per family. In practice, the sample size and family size for studies of natural populations of snakes will usually be determined by availability of subjects.

It is also important to consider just how precise an estimate need be for the purposes of a study. If the goal is simply to determine whether a character has significant additive genetic variance or whether two char-

acters are genetically correlated, a sample of 10–20 families may be sufficient (Arnold, 1981a, 1994; Brodie, 1989a). On the other hand, if one wishes to statistically compare parameters between populations or species, sample sizes in excess of 100 families in each group may be needed to gain the precision required to detect differences (Shaw, 1991). In a pessimistic pair of papers Klein and colleagues (Klein et al., 1973; Klein, 1974) suggested that 400 families of four offspring would have to be measured to demonstrate a significant heritability estimate of 0.20 ± 0.10. This outlook is overly gloomy for our purposes, because family sizes in snakes are usually greater than 4 (Arnold, 1994).

Efforts should be made to empirically reduce the common family environment shared by relatives, which can confound the estimated quantitative genetic parameters (Falconer, 1989). The postnatal common family environment can easily be eliminated in snakes by separating individuals at birth. However, siblings also share a common prenatal environment that is much harder to control. The condition of the female before and during pregnancy (Sinervo, 1990; Sinervo and Huey, 1990), thermoregulatory habits during gestation (Fox, 1948; Fox et al., 1961; Osgood, 1978; Arnold and Peterson, 1989), hydric and thermal features of nest sites (reviewed in Packard and Packard, 1988), and other unknown factors can all contribute to the resemblance among relatives through nongenetic effects. It may be possible to reduce prehatching common environments in oviparous species by splitting clutches as soon as they are laid (Tsuji et al., 1989). Statistical means of reducing maternal effects related to the condition of the female also may be used (explained below) but are not a substitute for experimental control.

In many cases, especially studies of behavior, it will be advantageous to measure the same trait repeatedly within individuals (Bennett, 1987; van Berkum et al., 1989; Huey et al., 1990). If there is measurement error in scoring a character, or if the character is not always expressed precisely the same by an individual (as is true for many behavioral, physiological, and performance traits), repeated measures will increase the accuracy of the estimated phenotypic variance (Arnold and Bennett, 1984; Lessels and Boag, 1987; Boake, 1989; Falconer, 1989). Differences in the trait value within an individual are attributable to the *special environmental variance* (V_{Es}), one-nth of which is contributed to the estimated phenotypic variance among individuals if n measurements are made:

$$V_P = V_G + V_E + V_{Es}/n.$$

The smaller the special environmental variance, the less advantage to performing multiple measurements. The optimal number of measurements depends on this component of variance and can be determined using a relationship given by Falconer (1989, p. 143). When two or more measurements are made, it is possible to calculate the repeatability, indicating how consistently a character can be measured in (or is expressed by) an individual, and then the average value of the character for an individual can be used in subsequent analyses. The heritability based on an average (or sum) of multiple measurements includes only a fraction ($1/n$) of V_{Es}, whereas the heritability (and repeatability) based on a single measure includes this whole component. Thus, if multiple measurements are used, heritabilities must be adjusted upwards to account for the reduced fraction of V_{Es} present in the denominator, or repeatabilities and heritabilities will not be of comparable scale (Brodie, 1989a, Brodie and Brodie, 1990). A table of scaling factors is provided by Becker (1992, Appendix 1) and the method is discussed in more detail by Arnold and Bennett (1984). Sometimes the highest of a series of measurements is analyzed, in an attempt to obtain measures of maximal performance abilities, free of motivational effects (see Garland, 1988; Tsuji et al., 1989; Garland and Losos, 1994).

Types of Characters Suitable for Quantitative Genetic Study

Quantitative genetics concerns itself with continuously varying characters. It is generally assumed that these characters are controlled by a large number of genes, each with small, additive effects on the phenotype (Mather and Jinks, 1982; Bulmer, 1985; Falconer, 1989). The term *quantitative* is used because individuals differ in degree (quantitatively) rather than type (qualitatively). Many of the traits of particular interest to students of evolution, ecology, and behavior exhibit this kind of variation (e.g., Boake, 1994).

The nature of quantitative inheritance (many genes, most of small effect) usually results in a phenotype that is normally distributed, at least when transformed to a suitable scale of measurement. Complex characters such as measures of performance (e.g., speed, endurance, prey-handling time), fitness components (viability, fecundity), and phenologies (date of emergence from hibernation, date of egg deposition) are especially appropriate for such analyses because they are probably comprised of many other characters and even more genes. Almost any continuously varying morphological (body size), behavioral (escape behavior, feeding preference) or physiological trait (maximal oxygen consumption) can also be examined with quantitative genetic techniques.

Traits that are controlled by one or a few genes of major effect are more appropriately studied using the techniques of populations genetics (Hartl and Clark, 1989). The presence of genes of major effect can be tested for by examining the phenotypic variances within families. If a few genes have large effects, then families with extreme phenotypes should be mostly homozygous for positive or negative alleles, whereas intermediate families should be heterozygous and therefore have higher variances (see Garland, 1988; Garland and Bennett, 1990, references therein; R. B. King, unpublished data).

Some characters are only expressible in whole-number units and so will have a necessarily discontinuous distribution. If many possible states exist, as in the number of ventral or subcaudal scales in snakes, phenotypic distributions may approach normality, and quantitative genetic theory is easily applied. Even characters with only a few discrete classes of expression (e.g., counts of head scales, number of dorsal scale rows) can be studied in a quantitative genetic context if a threshold model is assumed (Arnold, 1981b,c; Falconer, 1989; Dohm and Garland, 1993). For threshold traits, the underlying genetic and environmental variation is continuous but mapped onto fixed thresholds that determine the discrete phenotypes (Bull et al., 1982; Gianola, 1982). This interpretation of phenotypic variation allows quantitative genetic techniques to be used in the study of naturally discrete phenotypes, such as scale counts (Dohm and Garland, 1993) and color pattern elements (Beatson, 1976; Brodie, 1989a), and also of traits that can only be measured on a discrete scale, as in the case of many behaviors (Arnold, 1981b,c; Arnold and Bennett, 1984; Garland, 1988, 1994; Brodie, 1989a; Schwartz and Herzog, 1993). Additionally, discontinuous characters with only a few values may be combined into an index trait that is more continuously distributed, provided the index trait has some biological meaning (Arnold and Bennett, 1984; Garland, 1988; Brodie, 1989a, 1991, 1992, 1993b).

What Can Quantitative Genetics Do?

Most herpetologists will undoubtedly agree with the opinion of Dobzhansky (1973) that "nothing in biology makes sense except in the light of evolution." A variety of strategies is available to researchers attempting to shed this light. Traditionally, comparisons among taxa have been the most popular approach to studying phenotypic evolution in snakes and other reptiles (e.g., Seigel et al., 1987; Dunham et al., 1988). The comparative method treats taxonomic groups as "experimental" units and focuses on differences among these groups to describe patterns of evolution. This approach is historical and describes what has happened during the evolution of a particular clade. Recent advances in comparative techniques have improved the statistical rigor of this field (e.g., Harvey and Pagel, 1991; Martins and Garland, 1991; Lynch, 1991; Garland et al., 1991, 1992; Garland et al., 1993; Losos and Miles, 1994), leading to more powerful conclusions about the relative importance of selection and phylogenetic history in determining present-day patterns of phenotypic diversity.

An alternative approach is to study evolution at the level of the population. By investigating the pattern of variation and covariation in phenotype and fitness within a population, microevolutionary processes can be illuminated (Arnold, 1983, 1988b; Lande and Arnold, 1983; Grant, 1986). Quantitative genetics is one set of tools that can be used to study intrapopulational variation. This sort of microevolutionary approach was rarely employed in studies of reptiles until recently but can address a range of questions that should be of interest to many herpetologists. Aside from their obvious relevance to evolutionary ecology, results from quantitative genetic investigations may be important in systematics (Shaffer, 1986; Felsenstein, 1988; Lynch, 1989; Dohm and Garland, 1993) and conservation efforts (Dodd, Chap. 9, this volume), as well.

Nature versus nurture

The most obvious application of quantitative genetics is simply to determine the relative importance of genetic and nongenetic (environmental) factors in the expression of phenotypic variation (cf. Garland and Adolph, 1991, pp. 196–198). Besides revealing whether and how rapidly a trait will respond to selection (discussed above), this information is pertinent to a variety of other questions of interest to evolutionary ecologists.

Variation resulting from the environment is an important consideration for studies using cross-sectional data to attempt to detect selection. If phenotypic variance is regenerated each generation by the environment, selection may go undetected. Conversely, environmental changes may result in character differences across generations, even though no selection has occurred. Such scenarios seem especially important to consider in the study of certain behaviors that may be influenced by early experience. For example, feeding preferences and foraging behaviors may have high heritabilities at birth (Arnold, 1981a,c), but experience with certain prey during the first year may canalize feeding behavior in adults (see Fuchs and Burghardt, 1971; Arnold, 1977; Halloy and Burghardt, 1990). Differences in feeding behavior between generations or populations that might be interpreted as adaptive could actually be due to temporal or spatial changes in prey abundance.

Environment may affect the estimation of quantitative genetic parameters themselves. An obvious example is the difference between heritabilities estimated in a controlled laboratory environment and those estimated in the field. Field conditions typically have more environmental variation influencing the phenotype, whereas the absolute amount of genetic variation is the same. Because heritabilities are expressed as a proportion of phenotypic variance, field heritabilities are expected to be lower than those estimated under laboratory conditions (Riska et al., 1989; Bull et al., 1982; Janzen, 1992; Schwartz and Herzog, 1993). The expected response to selection based on laboratory heritabilities may overestimate the rate of evolutionary change in nature. The same holds true for different environmental conditions in the field. If the heritability of sprint speed is higher at a snake's thermal optimum than at extreme temperatures, the evolutionary response of sprint speed to selection will depend on the temperature at which selection occurs. Selection at extreme temperatures may act on environmental variation, causing little or no evolutionary change in average speed at any temperature. Conversely, selection acting at preferred temperatures should result in relatively rapid evolution of average speed, even at extreme temperatures.

Traits experiencing stronger selection are generally expected to have lower heritabilities, because selection is usually thought to reduce genetic variation at equilibrium. However, many other factors such as gene flow, population structure, and sampling effects influence heritabilities, so this interpretation of the theory is somewhat controversial (Charlesworth, 1987; Price and Schluter, 1991; Boake, 1994). Comparing the heritabilities of traits may give some clues about the relative strength of selection they have experienced (Roff and Mousseau, 1987; Mousseau and Roff, 1987; Garland et al., 1990). This approach has been applied to locomotor performance in Garter Snakes to suggest if selection is stronger on organismal level performance (e.g., speed, endurance) than suborganismal components (i.e., physiological and morphological characters such as heart mass and enzyme activities). Behavior and performance generally had higher heritabilities in this study, suggesting that physiological attributes might experience stronger selection, possibly because each trait affects many types of organismal performance (Garland et al., 1990).

Genotype-by-environment interactions (G × E)

Environmental variation can have different effects on different genotypes. This genotype-by-environment interaction can be measured as the genetic correlation of a trait in two different environments. Any nonperfect correlation ($-1 < r < 1$) indicates some $G \times E$ (Via and Lande, 1985). Genotype-by-environment interaction is one form of genetic variation for plasticity of the phenotype. The evolution of traits in multiple or variable environments (i.e., phenotypic plasticity), such as maternal investment in offspring as a function of changing resource availability (e.g., Ford and Seigel, 1989), depends on $G \times E$.

The question "Is a jack-of-all-trades a master of none?" (Huey and Hertz, 1984), can also be addressed through investigations of $G \times E$ (de Jong, 1990; Gomulkiewicz and Kirkpatrick, 1992). A genotype that performs best in one environment may not perform well in another (e.g., sprint speed on different substrates or endurance at different temperatures). High levels of $G \times E$ would indicate that one genotype is not optimal under all conditions (Arnold, 1987; Gomulkiewicz and Kirkpatrick, 1992).

Constraints

The strength and nature of evolutionary constraints on adaptation can be illuminated through quantitative genetics. The most extreme evolutionary constraint is a lack of phenotypic or genetic variation. Selection cannot act on limb number in snakes because there is no variation for this trait. Even characters that show phenotypic variation cannot respond to selection unless nonzero heritability exists.

Developmental, physiological, and genetic integrations among suites of characters are thought to constrain evolutionary response (Alberch, 1980; Gould, 1980; Clark, 1987; but see Charlesworth et al., 1982; Zeng, 1988). Genetic correlations are one way to measure such integration (Reznick, 1985; Barker and Thomas, 1987; Clark, 1987; Arnold, 1981c, 1987, 1988a; Garland, 1988; Dohm and Garland, 1993; Boake, 1994). The evolutionary response of a trait is determined not only by selection acting directly on that trait, but also by selection acting on genetically correlated traits. The pattern of genetic correlations determines both the rate and direction of short-term evolutionary change and can even result in temporary, maladaptive states in some traits (Lande, 1979; Lande and Arnold, 1983; Arnold, 1981c, 1987, 1988a, 1990). The strength of constraint is reflected in the magnitude of the genetic correlations. Congenital feeding preferences in *Thamnophis elegans* exhibit a high degree of genetic integration (Arnold, 1981a,b,c), so preferences for some prey items are not free to evolve independently. Preference for potentially hazardous prey, leeches, is presumably maintained in a coastal population of *T. elegans* because it is genetically correlated with response to the main food item, slugs (Arnold, 1981a,b,c, 1992).

Coadaptation

Multiple characters sometimes function interactively to increase performance or fitness. Traits that have been jointly selected are said to be *coadapted* (Huey and Bennett, 1987; Garland et al., 1991). Selection for coadapted suites of traits should result in genetic integration, which can in turn be recognized as genetic correlations (Cheverud, 1982, 1984, 1988; Lande, 1980, 1984; Clark, 1987). The strength of genetic correlations maintained through functional interactions depends on aspects of the breeding system and the physical relationships among genes controlling the traits (i.e., pleiotropy, physical linkage) (Lande, 1980, 1984; Endler, 1986). However, weak selection alone is expected to maintain some genetic correlation among coadapted characters (Lande, 1984). This appears to be the case for a suite of antipredator traits in some populations of the Northwestern Garter Snake, *Thamnophis ordinoides,* where color pattern and escape behavior are genetically correlated (Brodie, 1989a, 1991, 1992, 1993b).

Nonadaptive forces can also result in genetic correlations, so demonstration of genetic integration alone does not prove coadaptation (Lande, 1980, 1984; Endler, 1986; Crespi, 1990). Selection on combinations of traits (correlational selection) can be directly measured using multiple-regression techniques (Lande and Arnold, 1983; described below). Demonstration of both genetic correlation and correlational selection in the same direction can be taken as evidence that suites of traits are coadapted. Both features have been shown for combinations of color pattern and antipredator behavior in *Thamnophis ordinoides* (Brodie, 1989a, 1991, 1992, 1993b).

Systematics

Systematists can also benefit from the study of genetic variances and covariances. Character weighting in phylogeny reconstruction is usually based on phenotypic variation, assuming that this reflects genetic variation (Archie, 1985). Heritabilities directly measure genetic variation and may be more appropriate weighting parameters. Some authors would assign higher weights to characters with high heritabilities because they better reflect phylogenetic relationships (Atchley, 1983; Shaffer, 1986; Mayr and Ashlock, 1991) and are presumably less correlated with fitness (Dohm and Garland, 1993). Others would weight characters by the inverse of the heritability, reasoning that high heritabilities indicate dimensions in which genetic drift or selection could lead to the most rapid evolutionary change (Schluter, 1984; Felsenstein, 1988; Lynch, 1989). In either case, it is clear that the genetic basis of phenotypic traits is an important consideration in phylogenetic reconstruction.

Phylogeny reconstruction generally is simplified by the use of independent characters. Inclusion of nonindependent traits can inflate the confidence in a particular phylogeny because it appears to be supported by too many characters (Shaffer, 1986). Genetic correlations can be used to identify suites of evolutionarily nonindependent traits (Shaffer, 1986; Dohm and Garland, 1993), so they may be handled in a more appropriate manner (cf. Wheeler, 1986). In practice, the necessary quantitative genetic information is available for very few taxa, underscoring the need for more efforts in this arena.

Measurement of selection

One of the most exciting spin-offs of the application of quantitative genetic theory to natural populations is the development of multiple regression techniques to measure selection. It should be stressed that these techniques are purely phenotypic and require no knowledge of the genetic basis of the characters in question, but do provide measures of selection that are directly related to quantitative genetic formulas for evolutionary change (see below). Traditional methods of detecting selection look at the total change in a trait after an episode of selection (the *selection differential,* Lande and Arnold, 1983; Endler, 1986). This measure confounds selection acting directly on the trait with the indirect effects of selection acting on phenotypically correlated traits (Lande and Arnold, 1983). By considering the pattern of phenotypic correlation among traits, multiple regression measures the strength of selection directly targeting a trait (the *selection gradient*), independent of other traits in the analysis (Lande and Arnold, 1983; Endler, 1986). Gradients measuring the strength of directional (acting to change the mean of a trait), stabilizing, or disruptive (acting to change the variance in a trait), and correlational (acting to change the covariance between two traits) selection can be calculated simply by including the appropriate higher order or interaction terms in a regression model (Lande and Arnold, 1983; Endler, 1986). The technique is potentially quite powerful, but is subject to the usual problems associated with regression analysis. In particular, the gradients estimated may include selection acting indirectly through correlated characters that are not included in the analysis, and strong correlations between traits (multicollinearity) may lead to problems of estimation by ordinary multiple regression (Lande and Arnold, 1983; Slinker and Glantz, 1985; Mitchell-Olds and Shaw, 1987; Crespi, 1990).

The greatest advantage of selection gradients is that they can be combined with estimates of the genetic variance–covariance matrix to predict evolutionary change across generations (Lande, 1979; Arnold, 1981c, 1988a; Lande and Arnold, 1983; Price et al., 1984; Price and

Grant, 1985; Lofsvold, 1988). Selection on one trait will result in evolutionary change in genetically correlated traits. To predict phenotypic change over multiple generations, one must consider both selection and the pattern of genetic covariances. The equation

$$\Delta\bar{z} = G\beta$$

(where $\Delta\bar{z}$ is a vector describing the change in the mean of traits $z_1,\ldots,z_n$, G is the genetic variance–covariance matrix, and ß is the vector of directional selection gradients) is the multivariate equivalent of the equation for response to selection by a single trait:

$$R = h^2 s.$$

If the amount of phenotypic divergence between two populations or taxa is known, we can use estimates of the G-matrix to calculate the cumulative selection necessary to account for the observed differences (Arnold, 1981c, 1988a). The reconstructed net selection gradients are the minimum amount of directional selection required to account for the phenotypic differences, assuming the most direct evolutionary trajectory. In reality, the populations may have followed more complex evolutionary paths during divergence. This method has been used to estimate the selection necessary to account for differences in vertebral number between inland and coastal populations of the Western Terrestrial Garter Snake, *Thamnophis elegans* (Arnold, 1988a,b; also for feeding preferences, Arnold, 1981c). The results suggest that nearly 50% of the divergence in number of tail vertebrae may be a correlated response to selection directly targeting the number of body vertebrate. Failure to consider genetic correlations among traits would have led to a gross overestimate of selection on tail vertebrae.

Both predictive and retrospective studies of multivariate selection assume that genetic variances and covariances remain relatively constant over the time frame in question (Lande, 1979; Lofsvold, 1986, 1988; Turelli, 1988; Barton and Turelli, 1989). Current theory is unable to make robust predictions about how long these parameters are expected to remain stable, so the problem has become an empirical one (Turelli, 1988). The few studies that have compared G-matrices among populations or species have produced ambiguous results (reviewed in Barton and Turelli, 1989; Wilkinson et al., 1990; Brodie, 1993b), suggesting unsurprisingly that the dynamics may vary depending on the traits and taxa being examined.

Quantitative Genetic Studies with Snakes

Several aspects of snake biology present distinct advantages for quantitative genetics, especially over other vertebrates. A variety of traits, some of special interest to herpetologists, can be examined using only a small subset of available quantitative genetic techniques. Natural populations of snakes are rarely ideal subjects for such studies, but no taxa really are. The limitations encountered with snakes usually have to do with their longevity, slow maturation, and uncertain paternity.

Why use snakes?

Subjects. Large numbers of related individuals can be obtained for many snake species. Gravid females can usually be collected early in the reproductive season, providing a researcher with two sets of relatives: sibling groups (usually assumed to be full siblings) and mother and offspring. These two sets can be used to partition different components of variance.

The large litter size of many snake species can be beneficial in several ways. Large families provide an opportunity to split litters among environmental treatments to address concepts empirically such as genotype-by-environment interactions and common family environment (including maternal) effects. Such studies have not yet been attempted with snakes. Also, the accuracy of the estimated heritabilities and genetic correlations increases as more individuals in each family are measured (Falconer, 1989). For species with very large clutches (e.g., some *Nerodia* with litters of 30–50) it may not be practical to measure all offspring, but rather to select the same number randomly from each family (Garland, 1988). Having a balanced number of individuals per family simplifies analyses and significance testing (see below).

Oviparous species present a unique opportunity to examine the importance of some specific nongenetic maternal effects. Prenatal conditions can be simply manipulated by varying parameters such as incubation temperature and hydric environment of eggs, factors known to affect postnatal phenotypes in other reptiles (Plummer and Snell, 1988; Burger, 1989, 1991). The effects of maternal condition and investment can be empirically altered by removing yolk from developing eggs as has been done in lizards (Sinervo, 1990; Sinervo and Huey, 1990).

Characters. Snakes are especially good subjects for quantitative genetic studies of behavior. Neonates are completely precocial and exhibit a variety of behaviors immediately following birth. Yolk reserves allow snakes to be tested repeatedly during the first few weeks of life, without the confounding environmental variation that accompanies feeding (or refusal to eat). The field of behavioral genetics in natural populations has already been greatly expanded by studies of

feeding preferences and antipredator behavior in snakes (Arnold, 1981a,b,c, 1992; Arnold and Bennett, 1984; Garland, 1988, 1994; Herzog and Burghardt, 1988; Brodie, 1989a, 1991, 1992, 1993a,b; Herzog et al., 1989, 1992; Schwartz, 1989; Schwartz and Herzog, 1993).

Scale counts and other meristic characters can be easily scored in snakes. These traits do not change with age, so mother–offspring comparisons can be used to calculate heritabilities and genetic correlations. Because of their importance in phylogenetic reconstruction, scale counts may be particularly valuable characters to study, providing a unique opportunity to combine quantitative genetics with systematics (Dohm and Garland, 1993). Color patterns also can be easily scored, and, in some species, are ontogenetically stable (Beatson, 1976; Brodie, 1989a, 1991, 1992, 1993b; King, 1987, 1992, unpublished data; J. Barron, unpublished data). The ecological importance of coloration and its functional integration with behavior (Jackson et al., 1976; Pough, 1976; Brodie, 1989a, 1992) make it an especially relevant trait to study.

Drawbacks. The most rigorous quantitative genetic analyses require complex breeding designs, often with males mated to multiple females. The difficulty of breeding large numbers (e.g., 20 males each mated to at least 3 females) of snakes in the laboratory may prohibit these kinds of studies. Even for taxa that can be bred reliably, maturity is usually not reached until 1–2 years of age, even in the laboratory. That means a minimum of 2–3 years from scoring an individual as a neonate until scoring its offspring (all individuals should be measured at the same age to control for ontogenetic effects; see below). Additionally, the possibility of sperm storage confounds attempts to mate females to multiple males. For most traits, this means analyses will be limited to sibling comparisons, so certain components of genetic variation can never be distinguished.

One of the main reasons to use snakes in quantitative genetics may also be considered a major drawback. While some species can be obtained in huge numbers, others are rarely encountered. This factor more than any other is likely to define which snakes are suitable subjects for quantitative genetics (see Parker and Plummer, 1987, for estimates of local population sizes of many species).

Techniques used in studies of snakes

Animal and plant breeders have developed methods to analyze resemblance between virtually every set of relatives imaginable, from parents and offspring to siblings to various degrees of cousins. Crosses between populations (cf. Garland and Adolph, 1991) may be performed to test for nonadditive genetic variance and maternal effects

(Arnold, 1981b). Another strategy is to artificially impose selection and measure the response, but this method requires replicated selection lines and many generations (Falconer, 1989; Boake, 1994). Such approaches usually are impractical for studies of snake populations. In fact, either full-sib or mother–offspring comparisons account for almost all studies done to date on snakes.

Full-sib comparisons. Comparison of the resemblance between litter mates is the most widely applicable means of partitioning variances. It requires only clutches of siblings that have been scored for a trait. Because all siblings will be the same age, measurements can be made in a relatively short amount of time, and even ontogenetically variable traits can be studied. Full-sib relationships within a litter (i.e., single paternity) generally must be assumed, but even if some litters have multiple paternity, this method will yield conservative estimates (see below).

The resemblance between siblings can be measured as the *intraclass correlation, t,* or the ratio of the variance between groups (σ_B^2) to the total variance ($\sigma_B^2 + \sigma_W^2$, where σ_W^2 is the variance within groups):

$$t = \sigma_B^2/(\sigma_B^2 + \sigma_W^2).$$

What the intraclass correlation describes depends upon the average level of relatedness between members of the group (Falconer, 1989) (Table 8.1). Full-sibs, on average, share half of the additive genetic variance, and a quarter of the dominance variance. Half-sibs, on average, share only a quarter of the additive genetic variance and none of the dominance variance. To calculate a heritability, one must simply multiply the intraclass correlation from half-sib data by a factor of 4, from full-sib data by a factor of 2. The full-sib heritability will then include a fraction (½) of the dominance variance, and all interpretations of this parameter should recognize that it does not represent the pure additive genetic variance (Falconer, 1989; Garland, 1994; Arnold, 1994) (Table 8.1). Reviews of studies in a variety of taxa show very little difference between full-sib heritabilities and narrow-sense heritabilities (Roff and Mousseau, 1987; Mousseau and Roff, 1987), but the contribution of dominance effects is likely to vary depending on the trait in question (Dohm and Garland, 1993).

For full-sib data, the simplest method to derive the between- and within-family components of variance is through a one-way analysis of variance (ANOVA) with family as the main effect. The mean squares from the resulting ANOVA table can be used to calculate the necessary variance components. The error mean square is the within-family variance and the family mean square is a sum of the between-

family component of variance and some function of the within-family component of variance. The exact methods depend on whether family sizes are balanced (i.e., same number of siblings in each family), and are outlined in detail in other texts (Becker, 1992; Lessels and Boag, 1987; Falconer, 1989). The technique for partitioning the variance among half-sibs is similar, but requires a slightly more complex ANOVA design (Becker, 1992; Falconer, 1989).

A useful approximation to the genetic correlation between two traits is the correlation between family (= litter) means (Arnold, 1981b; Via, 1984; Garland, 1988; Brodie, 1989a; Garland and Bennett, 1990; Garland et al., 1990) (Fig. 8.4). The numerator of the expression for a genetic correlation is the covariance among families (COV_a). The covariance of family means (COV_m) also includes a fraction of the covariance within families (COV_w):

$$COV_m = COV_a + (1/n_o)COV_w,$$

where n_o is the average number of offspring per family corrected for differences in family size (Arnold, 1981b; Via, 1984). Thus, the family-mean correlation includes a fraction of the within-family covariance, but this factor becomes diminishingly small as family size increases.

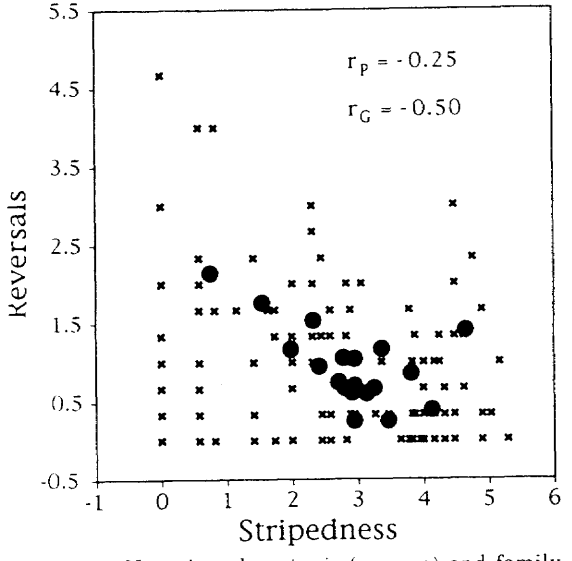

Figure 8.4 Negative phenotypic (crosses) and family-mean (dots) correlations between reversals and stripedness (square-root transformed) in *T. ordinoides* (Alsea population, see Brodie, 1989a). Note that the genetic correlation (r_G) approximated by the litter-mean correlation is greater in magnitude than the phenotypic correlation (r_P).

For large families, litter-mean correlations may be reasonable alternative estimates of genetic correlations (Fig. 8.4). An additional advantage of this estimate is that significance testing is clear-cut even for unbalanced designs, because it is a standard product–moment correlation (Via, 1984).

Multiple paternity has been detected whenever examined in snakes (*Thamnophis sirtalis,* Gibson and Falls, 1975; Schwartz et al., 1989; *Nerodia sipedon,* Barry et al., 1992; *Vipera berus,* Stille et al., 1986; Madsen et al., 1992; *Lampropeltis getula,* Zweifel and Dessauer, 1983). This phenomenon acts to reduce the average relatedness of litter mates below one-half (if all litter mates had a different father, they would all be half-sibs and the average relatedness would be ¼). Ideally, the average relatedness within litters could be calculated based on paternity analysis (cf. Schwartz et al., 1989), but this usually will not be possible. In the absence of such information, a full-sib assumption renders quantitative genetic parameters underestimates (the intraclass correlation is multiplied by 2 for full-sibs and 4 for half-sibs; partial multiple paternity would be somewhere intermediate). Full-sib parameters are also assumed to include some dominance variance; the actual contribution of this confounding factor to the estimate becomes less important as multiple paternity increases.

Mother–offspring comparisons. A somewhat more powerful method of partitioning variances is to compare the resemblance between mother and offspring. This is done by regressing the average value of the trait in the offspring on the mother's value (Bulmer, 1985; Falconer, 1989; Becker, 1992). The slope of the regression line equals one-half of the additive genetic variance (Fig. 8.5). This estimate is not confounded by nonadditive genetic variance components, but does not include maternal effects. Genetic covariances can be obtained similarly by comparing one trait in the offspring with another in the parents.

The use of the parent–offspring regression technique is limited to traits that do not change with age or to traits measured at the same age and environment in both generations. Characters that change ontogenetically (and, in fact, some that do not) may have different genetic control at different ages (Arnold, 1990). In such circumstances, a parent–offspring heritability would really describe the genetic covariance between the trait at two ages (which may be considered two different traits), rather than the genetic variance of the trait at a particular age (Falconer 1989; Arnold, 1990).

Population crosses. Crossing individuals from two divergent populations can reveal several components of variance that may not be distinguishable in analyses of either population alone (Falconer, 1989). If phenotypes of the F_1 hybrids are not intermediate between those of

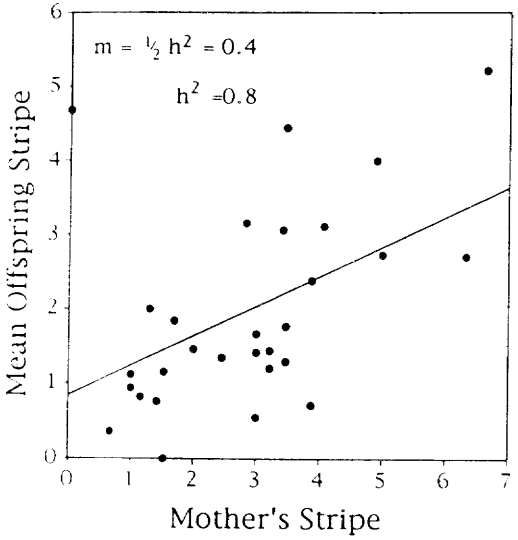

Figure 8.5 Offspring–mother plots for stripedness (square-root transformed) in *Thamnophis ordinoides* (McGribble population, see Brodie, 1989a). The slope of the regression of mean stripedness of offspring on the stripedness of their mother is, in the absence of maternal effects, equal to one-half the narrow-sense heritability (the estimate of heritability reported here is lower than the full-sib heritability reported by Brodie [1989a] for the same data and may indicate some contribution of dominance variance to the full-sib heritability).

the parent populations, dominance or maternal effects would be suspected. If F_1 progeny from reciprocal crosses more closely resemble their maternal phenotype, then maternal effects are likely to be important determinants.

Although this method requires laboratory breeding, relatively few crosses are required to get useful results. One study of *T. elegans* has employed this technique (Arnold, 1981b), and it stands as the only direct investigation of dominance or maternal effects on any trait in snakes (see below).

Common family environment. Estimates of quantitative genetic parameters from either full-sib or mother–offspring comparisons will be confounded by common family environment, including maternal effects (Table 8.1, Fig. 8.2). The importance of splitting families as soon as possible was discussed above, and, especially with oviparous species, several methods of empirically reducing or investigating the effects of common family environments can be employed.

In spite of these efforts, it will be impossible to reduce some prenatal maternal effects empirically. Statistical methods may be useful in

further eliminating this source of confounding environmental variance. Many nongenetic maternal effects are likely to be mediated through the condition of the female during energy allocation of the ova and gestation. Statistical covariation with measures of female condition (female mass, mass-to-length ratios, etc.) can be eliminated by regressing the trait in question on such measures (cf. Garland, 1988, 1994; Tsuji et al., 1989; Brodie, 1989a, 1991, 1993b; Garland and Bennett, 1990; Garland et al., 1990; Brodie and Brodie, 1990; Dohm and Garland, 1993). Residuals from this regression will reflect variation in the trait independent of female condition. These residuals may then be substituted for the original trait in the usual analyses. This technique will eliminate nongenetic maternal effects that are associated with these condition measures, but will also eliminate genetic covariances between female condition and the trait in question. This conservative approach has been used previously, especially in studies of locomotor performance (Garland 1988, 1994; Brodie 1989a, 1991, 1993b; Garland and Bennett, 1990; Garland et al., 1990; Brodie and Brodie, 1990). No empirical validation of the technique has yet been attempted, but would be extremely valuable.

Statistical considerations. In addition to the ANOVA and regression methods outlined above, maximum likelihood estimation (MLE) may be used to calculate quantitative genetic parameters, using any set of relatives (e.g., Shaw, 1987, 1991). MLE has several advantages over standard techniques, including better handling of unbalanced family sizes, the ability to use data from multiple sets of relatives, and more direct significance testing, but is somewhat difficult to implement in practice (but see Garland, 1988; Garland and Bennett, 1990; Dohm and Garland, 1993 for some successes). The computer resources needed to analyze even modest data sets with MLE have prevented many researchers from utilizing the technique. But, as computational facilities improve and algorithms for MLE are refined, this promises to become a more practical tool for quantitative genetic analyses.

Significance testing of heritabilities and genetic correlations can be problematic. The expected distributions for quantitative genetic parameters are poorly understood, and unbalanced family sizes further complicate matters. In the past, most researchers have calculated standard errors for their estimates and used *t*-tests for approximate significance testing. The popularization of computer-intensive resampling testing procedures allows more rigorous tests to be performed (Efron and Tibshirani, 1991; Crowley, 1992). Jackknifing has been demonstrated to be effective for many types of data distributions (Sokal and Rohlf, 1981; Arveson and Schmitz, 1970; Knapp et al., 1989; Mitchell-Olds and Bergelson, 1990). This method creates a *t*-distributed set of parameter estimates by resampling the original

data without replacement. The standard errors from this distribution can be used to test a variety of hypotheses by means of a *t*-test (Knapp et al., 1989). Bootstrapping resamples the data with replacement, creating a distribution of the parameter based on each data set. Parameter estimates can then be tested against this expected distribution for the probability of obtaining such an estimate by chance (Efron and Tibshirani, 1991). Randomization tests are another nonparametric method of significance testing (Sokal and Rohlf, 1981; Mitchell-Olds, 1987; Jayne and Bennett, 1990b) and may be applied to quantitative genetic data.

What has been done with snakes

As compared with other wild vertebrates, snakes have been the subject of a relatively large number of quantitative genetic analyses (reviews in Arnold, 1981c, 1983; Ehrman and Parsons, 1981; Mousseau and Roff, 1987; Weir et al., 1988; Plomin et al., 1990; Boake, 1994; Garland, 1994). A few species of lizards have been studied (reviews in Bennett and Huey, 1990; Garland and Losos, 1994). Very few quantitative genetic studies of chelonians (Bull et al., 1982; Janzen, 1992, 1993), and apparently none of crocodilians have been attempted, although their large clutches, relative ease of incubation and husbandry (e.g., in commercial crocodile farms), and conservation status would seem to make them good models.

Scale counts. Some of the earliest studies of quantitative variation among related individuals in nonhuman vertebrates involved scale counts of snakes (Dunn, 1915, 1942; Inger, 1943; Endler, 1986); however, these early studies were concerned with demonstrating natural selection and did not attempt to estimate heritabilities. Snake scale counts are obvious targets for quantitative genetic analyses, because (1) they are easy to score on both living and preserved specimens; (2) they do not change ontogenetically, thus allowing immediate offspring–parent comparisons; and (3) they show quasicontinuous variation (Arnold, 1988a; Dohm and Garland, 1993).

Numbers of ventral and subcaudal scutes, the scale counts studied most commonly, show a 1-to-1 correspondence with numbers of body and tail vertebrae, respectively (references in Arnold, 1988a; Dohm and Garland, 1993). The first quantitative genetic study of any trait in snakes estimated a full-sib heritability of 0.75 for ventral scales in *Nerodia sipedon* (Beatson, 1976). Using offspring-on-dam regressions, narrow-sense heritabilities of 0.65–0.79 for ventrals and 0.46–0.64 for subcaudals were estimated in *Thamnophis elegans* (Arnold, 1988a). Corresponding values of 0.3 and 0.4, respectively, were calculated for

T. sirtalis (Dohm and Garland, 1993) using both conventional and restricted maximum likelihood (Shaw, 1987, 1991). Schwartz (1989) reports full-sib heritabilities of 0.6–0.7 and 0.8 for ventrals and subcaudals, respectively, in a Michigan and a Wisconsin population of *T. sirtalis*. Numbers of ventrals and subcaudals showed a significant positive additive genetic correlation in each of these populations: 0.3 in *T. elegans* (Arnold, 1988a), 0.7 in California *T. sirtalis* (Dohm and Garland, 1993), and full-sib correlations of 0.5–1.0 in Michigan and Wisconsin *T. sirtalis* (Schwartz, 1989).

Other scale counts, especially head scales, are less variable and have been studied as threshold characters. Dohm and Garland (1993), again using maximum likelihood analyses of full-sib plus mother data, showed a significant narrow-sense heritability for the number of temporal scales in *Thamnophis sirtalis*. Three other head-scale counts (supralabials, infralabials, and postoculars) and two derived characters involving the position of the umbilical scar were not significantly heritable. Schwartz (1989) reported full-sib heritabilities for preoculars, postoculars, supralabials, infralabials, and pretemporals (all analyzed as threshold characters), but did not test significance. Dohm and Garland (1993) also found that some of the genetic correlations between body and head scales were significant. Thus, the meristic characters they studied do not represent eight evolutionarily independent traits. Arnold (1988a, personal communication) is continuing a large-scale study of the evolutionary stability of the genetic variance–covariance matrix in *Thamnophis* and *Nerodia,* using both full-sib and parent–offspring analyses.

Color patterns. Brodie (1989a, 1991, 1993b) showed significant full-sib heritabilities for a composite index of color pattern termed "stripedness" that describes the overall linearity of color pattern in *Thamnophis ordinoides*. This index trait was analyzed after preliminary analysis detected high levels of genetic correlation among individual pattern components including presence and contrast of dorsal and lateral stripes and spot rows. All four populations of *T. ordinoides* studied to date have full-sib heritabilities in the range 0.5–1.0 (Brodie, 1989a, 1991, 1993b).

The number of dorsal and lateral blotches, size of lateral blotches, and the extent of ventral pigmentation are all significantly heritable in Northern Water Snakes (*Nerodia sipedon*) (Beatson, 1976; R. B. King, personal communication; J. Barron, personal communication). Both full-sib and mother–offspring comparisons reveal moderate to high heritabilities (0.3–1.0) and positive genetic correlations (0.24–0.82) among most of the pattern components measured (R. B. King, unpublished data). Genes with major effects also appear to influence

some color pattern components of *N. sipedon* from Lake Erie (R. B. King, unpublished data).

Antipredator behavior. In the fall of 1981, S. J. Arnold and A. F. Bennett began studying locomotor performance of Garter Snakes. Their initial protocol was to chase newborn snakes around a rectangular track and record the time to cover the initial 1.0 m ("burst speed"), the time to cover from 1.0 to 2.5 m ("mid-distance speed"), and the total distance and time crawled until the snake stopped locomoting (Arnold and Bennett, 1988). They discovered that snakes typically adopted some type of "antipredator display" when they stopped crawling. Based on measures of whole-body lactic acid concentrations, snakes seemed to have reached their anaerobic capacities when they assumed antipredator displays, although this may not be true for other species (see Jayne and Bennett, 1990b, p. 1223; Brodie, 1991, 1992, 1993a,b). Arnold and Bennett (1984) argued that the antipredator display could be scored on a quasicontinuous scale of 0–6 and hence analyzed by standard quantitative genetic techniques. The behavioral score of an individual *Thamnophis radix* was repeatable across trial days (and even across different testing temperatures), and showed full-sib heritabilities of 0.37 for a single trial and 0.45 for the average of two trials. This was the first study of heritability of antipredator behavior in any terrestrial vertebrate.

Antipredator displays of *Thamnophis sirtalis* crawling to exhaustion on a motorized treadmill were studied by Garland (1988). He used an expanded scoring scale (0–9.9) to reflect the exhibition of more offensive behavioral components, such as striking and biting, in this species. The displays of *T. sirtalis* under these conditions were also repeatable across trial days, and also showed a full-sib heritability of about 0.4.

Brodie (1989a,b, 1991, 1992, 1993a,b) has studied antipredator behavior in several populations of *Thamnophis ordinoides*. When chased around a circular track, this species performed stereotyped changes in direction called "reversals." The number of reversals during a trial was taken as a measure of evasiveness during flight and is thought to be important in causing predators to lose sight of the prey. Four different populations of *T. ordinoides* showed significant full-sib heritabilities (0.33–0.65) for reversals, and in two populations reversals were negatively genetically correlated with stripedness (Brodie, 1989a, 1991, 1993b). Antipredator display (cf. Arnold and Bennett, 1984) was also scored in three populations and showed significant but low full-sib heritability (phenotypic variation in the display was much less in *T. ordinoides* than in *T. radix* or *T. sirtalis*; Brodie, 1989a).

Antipredator responses of snakes (numbers of strikes) to moving and nonmoving stimuli (a human index finger) have been studied by

Schwartz and colleagues (Schwartz, 1989; Herzog and Schwartz, 1990; Schwartz and Herzog, 1993; references therein). Schwartz and Herzog (1993) showed significant full-sib heritabilities for *T. sirtalis* (Michigan and Wisconsin), *T. butleri,* and *T. melanogaster*. While not formally employing quantitative genetic methods, several other studies have detected significant family differences in antipredator behavior and rate of habituation to threat stimuli (Herzog and Burghardt, 1988; Herzog et al., 1989, 1992). Litter differences among neonates appear to be stable for at least one year (Herzog and Burghardt, 1988).

Schwartz (1989) measured aggregative tendencies as the nearest-neighbor distance of a snake with any of its litter mates when placed into a 1-m-diameter arena. No population differences were found between animals from Michigan and Wisconsin, but a significant full-sib heritability of 0.26 was estimated for the Michigan population.

Locomotor performance and physiology. Motivated by the recent emphasis in physiological ecology and functional morphology on direct measurement of whole-animal performance abilities (reviews in Bennett and Huey, 1990; Garland and Losos, 1993), several workers have examined the genetics of locomotor abilities in snakes, in all cases using full-sib data. California *T. sirtalis* showed significant full-sib heritabilities for sprint speed over 0.5 m on a photocell-timed racetrack (0.58) and for treadmill endurance at 0.4 km/h (0.70) (in both cases, size-corrected values were analyzed) (Garland, 1988). Contrary to expectations based on exercise physiology, the two performances showed a positive phenotypic (0.36) and genetic (0.59) correlation. Using the same techniques (although analyzing mean rather than best performances) and the same population, Jayne and Bennett (1990a) also reported a positive phenotypic correlation between speed and endurance, as well as similar heritability estimates. Four separate populations of *T. ordinoides* from Oregon exhibited significant heritabilities for both speed over 0.5 m and distance crawled in a circular track, as well as positive phenotypic and genetic correlations (Brodie, 1989a, 1991, 1993b). Garland (1988, 1993) discusses the possible biological basis for the surprising lack of a genetic trade-off between speed and stamina (see also Garland and Losos, 1994).

Locomotor performance was used as a bioassay of resistance to tetrodotoxin in *Thamnophis sirtalis* by Brodie and Brodie (1990, 1991). A full-sib heritability of 0.72 for resistance (measured as a relative reduction in sprint speed after injection with tetrodotoxin) was detected in a population of *T. sirtalis* that feeds on the toxic Roughskin Newt, *Taricha granulosa* (Brodie and Brodie, 1990). This study was the first to establish the ability of predators to respond evo-

lutionarily to defensive adaptations of prey, providing empirical support for the arms-race view of predator–prey coevolution.

Garland and Bennett (1990) reported significant full-sib heritabilities for maximal oxygen consumption (0.89), blood hemoglobin content (0.63), and relative heart (ventricle) mass (0.41). Treadmill endurance (from Garland, 1988) showed a significant positive phenotypic (0.18) but not a genetic correlation with maximal oxygen consumption. In turn, maximal oxygen consumption was significantly positively correlated with ventricle mass both phenotypically (0.27) and genetically (0.64), presumably reflecting the effect of heart size on cardiac output and hence oxygen delivery. In general, low full-sib heritabilities were found for enzyme activities measured as maximal in vitro catalytic rates of citrate synthase (a key aerobic enzyme) and pyruvate kinase (an anaerobic enzyme) in liver, ventricle, and skeletal muscle samples from these same *Thamnophis sirtalis* (Garland et al., 1990).

Schwartz (1989) has shown significant full-sib heritability of 0.6–0.8 for resistance to cold temperatures (critical thermal minimum) in *T. sirtalis.*

Feeding behavior. Garter Snakes show individual and geographic variation in responses to prey odors, in their propensity to eat pieces of slugs in the laboratory, and in their diet in nature (Burghardt, 1970, 1975; Arnold, 1977, 1981a,b,c, 1992; references therein). In a path-breaking series of papers that included the first estimates of behavioral heritabilities for any natural population of vertebrates, Arnold (1977, 1981a,b,c, 1992; Ayres and Arnold, 1983) has studied the quantitative genetics of these behaviors. Slug-eating by naive, newborn snakes was bimodally distributed within each of several populations of *Thamnophis elegans,* although coastal and inland populations showed significant differences in the frequencies of slug eaters (Arnold, 1977, 1981b,c, 1992). Full-sib heritabilities for slug eating were about 0.3–0.5, and probably not different, in two populations (Arnold, 1981a,c; Ayres and Arnold, 1983). Litter differences in response to slug, fish, anuran, and salamander odors were also detected in each of three populations of *T. elegans* and *T. sirtalis* (Arnold, 1992). In a one-of-a-kind study for snake quantitative genetics, Arnold (1981b) crossed populations and demonstrated general intermediacy of slug-eating scores in the F_1, but with some directional dominance for slug-refusing (see also Ayres and Arnold, 1983), and no indication of maternal effects.

Chemoreception responses of *T. elegans* to 10 different prey odors on cotton-tipped swabs were continuously distributed, and most showed significant full-sib heritabilities (Arnold, 1981a,c). Estimated genetic correlations between leech and slug chemoreceptive scores, when compared with differences in population means, suggest that selection may have acted antagonistically on these two behaviors during population divergence (Arnold, 1981a,c). Arnold (1981a) provided what appear to be the first geographic comparisons of quantitative genetic parameters in wild vertebrates, concluding that "estimates of genetic correlation appear roughly comparable" (see also Brodie, 1991, 1993b, for comparisons of *G*-matrices between two populations of *T. ordinoides*). Schwartz (1989) has also demonstrated significant geographic variation and full-sib heritability of responses to water and to minnow and worm extracts in *T. sirtalis.*

Integrative studies. Quantitative genetic analyses are useful for understanding the correlated evolution of traits at multiple levels of biological organization (Arnold, 1983, 1987; Mousseau and Roff, 1987; Roff and Mousseau, 1987; Garland, 1988, 1994; Garland and Losos, 1994; Brodie, 1991, 1992, 1993b). Thus, several studies have measured more than one type of trait and investigated their relationships through genetic correlations.

Several studies have examined the interaction of scale counts with other characters, especially locomotor performance. Numbers of body and tail vertebrae have an interactive phenotypic effect on burst speed over 1.0 m in *Thamnophis radix* (Arnold and Bennett, 1984, 1988), but genetic correlations were not estimated. Similarly, numbers of ventrals and subcaudals have an interactive, and ventrals a direct (negative), effect on 0.5 m burst speed in *T. sirtalis* (Garland, 1988; Dohm and Garland, 1993, unpublished data). Additionally, significant bivariate correlations were also found between scale counts and antipredator display and treadmill endurance (Dohm and Garland, unpublished data). One possible explanation for the different results of these studies is the larger sample size employed (240 vs. 100 individuals) and the inclusion of head-scale counts in the analyses by Dohm and Garland (unpublished data). Genetic correlations (as weighted family-mean correlations) were also estimated by Dohm and Garland (unpublished data) for *T. sirtalis.* These were always greater in magnitude than the phenotypic correlations (e.g., −0.21 vs. −0.15 for the correlation between ventrals and burst speed), and several were significant. Both the phenotypic and genetic correlations may reflect functional linkages (cf. Garland, 1988; Garland and Bennett, 1990). Positive genetic correlations between ventral scales and dorsal and lateral blotches also were found in *Nerodia sipedon* (Beatson, 1976). The genetic correlations between scale counts and traits such as performance and color pattern mean that selection acting on the latter would also result in correlated morphological responses. This finding adds credence to the idea that at least some of the interpopulation and interspecific variation in scale

counts seen among snakes (references in Arnold, 1988a; Dohm and Garland, 1993) has functional and hence adaptive significance.

Garland and coworkers have estimated heritabilities for traits ranging from behavioral to biochemical in the same individual *T. sirtalis* (Garland, 1988, 1994; Garland and Bennett, 1990; Garland et al., 1990; Dohm and Garland, 1993), and Jayne and Bennett (1989, 1990a,b) have further studied allometry of and selection on performance in this population. These studies were made possible by S. J. Arnold's long-term field studies with both *T. sirtalis* and *T. elegans* in northern California. A brief summary of results is as follows. First, measures of locomotor performance are heritable and sometimes subject to natural selection. Second, contrary to some theoretical expectations, measures of organismal-level traits, which should be closer to fitness, have higher heritabilities than do lower-level traits. Third, phenotypic and genetic correlations between traits can in some cases be predicted based on physiological or biomechanical knowledge but in other cases cannot.

Additional multivariate analyses are possible. A principal-component (PC) analysis of the phenotypic correlation matrix for all 13 characters (presented in Garland et al., 1990) reflects the weak correlation structure. The first PC accounts for only 16% of the variance, and 10 PC's (of 13 total) are required to account for 90% of the variance. Thus, the 13 traits measured show little evidence of functional "integration" (Cheverud, 1982, 1984; Cheverud et al., 1989, references therein) at the phenotypic level. PC3 (12% of variance) shows relatively strong loadings for antipredator display, speed, and endurance (see also Jayne and Bennett, 1990a,b; Garland, 1988, 1994). A principal-component analysis of the correlations of weighted litter means (presented in Garland et al., 1990) also reflects the weak correlation structure at the genetic level. The first PC accounts for only 17% of the variance, and 9 PCs are required to account for 90% of the variance. PC1 shows relatively strong loadings for antipredator display, speed, and endurance.

Brodie (1989a,b, 1991, 1992, 1993a,b) has undertaken a series of studies of antipredator behavior in relation to color pattern and locomotor performance in *Thamnophis ordinoides*. Antipredator display, speed, distance crawled, the number of reversals during the distance test, and the color pattern index "stripedness" all show significant full-sib heritabilities in at least two to four populations. Significant negative phenotypic and genetic correlations exist between stripedness and reversals in two populations but not in two others (Brodie, 1989a, 1991, 1993b). Mark–recapture work showed significant selection for the combination of stripedness and reversals in the Tenmile population, suggesting that genetic correlations may result from natural selection (Brodie, 1992). Comparisons of the genetic variance–covariance matrices of two of the populations show no significant differences (Brodie, 1991, 1993b).

Schwartz (1989) studied scale counts, antipredator responses, thermal tolerance, responses to prey extracts, and aggregative tendencies in two populations of *Thamnophis sirtalis*. Interestingly, he reports several significant full-sib correlations between different types of traits, e.g., ventrals with CTMin, antipredator response with tongue-flick response to minnow extract. The biological significance of such correlations is unclear, and some may be inflated by uncontrolled maternal effects.

Studies of selection in the wild. As discussed above, studies of inheritance comprise one-half of the equation for describing microevolution; studies of natural (or sexual) selection, drift, and gene flow form the other half. The combination of quantitative genetics with selection estimation enables ecologists to predict (at least micro-) evolutionary change (Lande and Arnold, 1983). To date, virtually no study has been able to measure anything near true fitness (e.g., lifetime reproductive success) of individual snakes in nature (but see Madsen and Shine, 1993). Rather, cross-sectional comparisons (Lande and Arnold, 1983; Endler, 1986) of juveniles and adults have been used to infer selection (Dunn, 1942; Inger, 1943; Beatson, 1976; King, 1987, 1992), or survivorship or growth rate has been correlated with some phenotypic trait(s).

Lake Erie Water Snakes (*Nerodia sipedon insularum*) have received continued study by herpetologists and evolutionary biologists (Camin et al., 1954; Camin and Ehrlich, 1958; Ehrlich and Camin, 1960). Most recently, King (1992, personal communication) has found "support for the hypothesis that unbanded morphs are favoured by natural selection in island populations" (King, 1992, p. 115).

Natural selection in a Kansas population of Northern Water Snakes favored increases in both dorsal and lateral blotches (Beatson, 1976). Genetic correlations with ventral scutes, which experienced stabilizing selection, apparently retarded the evolutionary increase of the number of dorsal and lateral blotches.

In a longitudinal study, Arnold (1988a) found some correlations between the combination of ventral and caudal scutes and growth rate in *Thamnophis elegans*. He further employed estimates of the *G*-matrix for scale counts to estimate the strength of selection that would have been necessary to account for phenotypic differences in scale counts between inland and coastal populations of *T. elegans* (Arnold, 1988a). His results suggest that both body and tail vertebrae experienced direct positive selection, but that nearly half of the divergence in tail vertebrae was due to a correlated response to selection acting directly on the number of body vertebrae.

Jayne and Bennett (1990b) scored three kinds of locomotor performance on several hundred *T. sirtalis,* marked the animals by scale-clipping, then released them back into nature. Of 275 cohort snakes tested within eight days of birth in 1985, 79 were recaptured in subsequent years; only birth snout–vent length was a statistically significant (positive) predictor of their probability of survival from 1985 to 1986. However, separate tests of yearling and older snakes did show significant predictive value for both speed and distance crawled (with effects of body sized removed by computing residuals), but apparently not for residual endurance.

Brodie (1992) documented significant correlational selection on stripedness and the tendency to reverse direction in the Tenmile population of *Thamnophis ordinoides.* The direction of this correlated selection is the same as the genetic correlation between these two traits, suggesting that previous selection may have shaped the genetic architecture.

Correlating phenotypic and genetic correlations. As stressed elsewhere in this chapter, studies of heritabilities and genetic correlations can be crucial to microevolutionary analyses (see also Arnold, 1981c, 1983, 1987, 1988a, 1990; Grant, 1986; Garland et al., 1990; Garland, 1994; Brodie, 1992; Boake, 1994). Since phenotypic correlations are much easier to estimate than genetic correlations, it would expedite evolutionary analyses if we could use the former to approximate the latter. Cheverud (1988) reviewed the available data and concluded that phenotypic correlations were generally similar to genetic correlations and "may be substituted for their genetic counterparts in models of phenotypic evolution" (p. 966). However, problems with the data and the statistical analyses prompted Willis et al. (1991) to disagree with this assertion. What do the available data for snakes indicate?

For the behavioral and physiological traits measured in *Thamnophis sirtalis* (Garland, 1988, 1994; Garland and Bennett, 1990; Garland et al., 1990) phenotypic correlations are similar to genetic correlations, but their relationship is not exceptionally tight (Fig. 8.6; $r = 0.76$, $n = 76$). Moreover, the phenotypic correlations tend to underestimate genetic correlations; the reduced major axis (RMA) slope is 1.23 (Fig. 8.6). A statistical comparison of phenotypic and genetic correlations estimated from the same data is problematical (estimates are nonindependent), but for a general comparison of their relative magnitude, consider the plot in Fig. 8.6. While the bulk of the genetic correlations are of similar sign and greater magnitude than the corresponding phenotypic correlations (as evidenced by the positive RMA slope), some values (18 of 76 or 24%; all those in the upper left and lower right quadrants of Fig. 8.6) are of different sign.

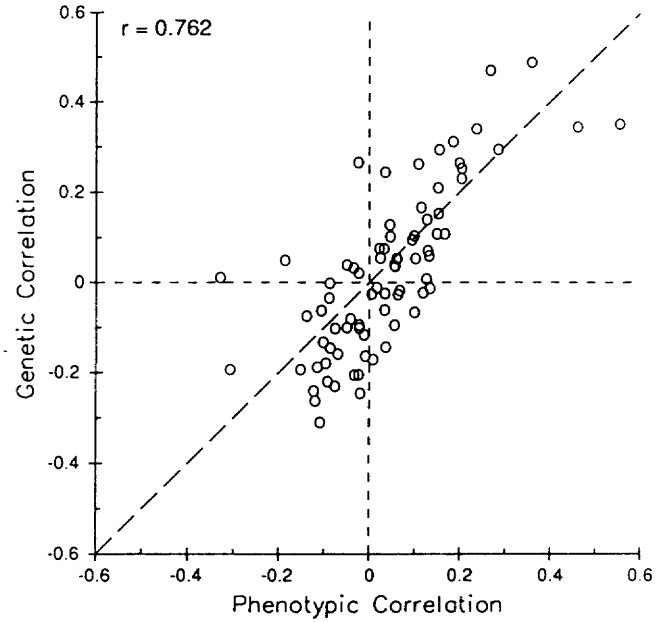

Figure 8.6 Relationship between phenotypic and genetic (estimated as correlations of weighted litter means) correlations (n = 78) for behavioral and physiological traits in *Thamnophis sirtalis* (from Garland, 1988; Garland and Bennett, 1990; Garland et al., 1990). Points falling on the dashed line at a 45° angle correspond perfectly in both sign and magnitude. For correlations falling in the positive–positive and negative–negative quadrants, the genetic correlations tend to be stronger.

For the eight scale characters measured in *Thamnophis sirtalis,* phenotypic and additive genetic correlations (estimated by maximum likelihood) show a considerably weaker relationship ($r = 0.40$, $n = 28$), and the underestimation of genetic by phenotypic correlations is even more extreme (RMA slope = 3.79; data from Dohm and Garland, 1993).

The phenotypic and genetic correlations for stripedness, reversals, speed, and distance crawled in two populations of *Thamnophis ordinoides* reported by Brodie (1991, 1993b) also show rather strong correlations ($n = 6$, $r = 0.97$ for the Tenmile population and $r = 0.87$ for the CCQ population). Again, genetic correlations tend to be greater (RMA slope = 1.24 and 1.58, respectively).

Arnold (1981a) presents phenotypic and genetic (weighted-litter-mean) correlations for tongue-flick scores in response to 10 prey odors and two controls for both of two populations of *T. elegans* (his Tables 1 and 2). The correlations between these two estimates ($n = 66$ correlations for each) are 0.62 and 0.70 for coastal and inland populations, respectively. In both cases, phenotypic correlations greatly underesti-

mate genetic correlations; reduced major axis slopes are 2.24 and 2.45, respectively.

In general then, the data from studies of snakes suggest that phenotypic correlations underestimate genetic correlations, and the correlation between the two is positive (0.4–0.97), but not always strong. Some of the discrepancies may be related to small sample sizes (Cheverud [1988] found genetic and phenotypic correlations tend to be more similar when effective sample sizes are large), but real differences in the two parameters cannot be ruled out. The use of phenotypic correlations when genetic estimates are unavailable will likely lead to flawed conclusions about phenotypic evolution (see Willis et al., 1991).

Summary and Future Research

Quantitative genetics and related techniques can be profitable tools for studying a variety of problems in snake ecology. Understanding the sources and patterns of variation at different levels is integral to any study of evolutionary processes. The specific problems that can be addressed with quantitative genetics are virtually limitless (see above for some examples) and the techniques are relatively simple. The necessary requisites for a quantitative genetic analysis amount to little more than individuals of known relationship, large samples, and some basic statistics.

Although snakes have been the subjects of a large proportion of previous quantitative genetic studies of vertebrates, there has actually been very little work in this area. Two perspectives may guide future quantitative genetics studies of snake populations: (1) what can this approach tell us about snake ecology and evolution; and (2) what general problems can be particularly well addressed using snakes?

Examples of problems in snake biology that can benefit from quantitative genetics may be found in this chapter and throughout this volume. Mating systems, thermoregulatory ecology, endocrinology, and habitat preferences are all unstudied from a quantitative genetic perspective (see Duvall, Schuett, and Arnold, Chap. 5; Ford and Burghardt, Chap. 4; Peterson, Gibson, and Dorcas, Chap. 7; and Reinert, Chap. 6, all this volume). Perhaps the most important direction is to study different taxa. With the exception of two studies on *Nerodia,* all quantitative genetic studies to date have been conducted on *Thamnophis* (and even these two genera are closely related; Table 8.2). Other taxa are common enough to obtain the large samples needed for quantitative genetics (see Parker and Plummer, 1987, for population estimates) and some may even be bred in captivity. It is time such taxa are examined.

TABLE 8.2 Quantitative Genetic Studies of Snake Populations

Traits	Species	Locality	Number of families[a]	Parameters	Method[b]	Study
Scale counts						
Ventrals	*N. sipedon*	Kansas	14	h^2_{FS}	1	Beatson (1976)
Ventrals, subcaudals	*T. elegans*	California	100	h^2_N	2	Arnold (1986)
		Inland, coastal California	84–159	h^2_N, r_G	2	Arnold (1988a)
	T. sirtalis	Wisconsin	≤5	h^2_{FS}, r_G	1	Schwartz (1989)
		Michigan	≤23	h^2_{FS}, r_G	1	Schwartz (1989)
Ventrals, subcaudals, head scales	*T. sirtalis*	California	47	h^2_N, h^2_{FS}, r_G	1,2,3,4	Dohm and Garland (1993)
Head scales	*T. sirtalis*	Wisconsin and Michigan	28	h^2_{FS}	1	Schwartz (1989)
Color pattern						
Number of blotches	*N. sipedon*	Kansas	14	h^2_{FS}, r_G	1,2	Beatson (1976)
		Indiana	58	h^2_N	2	J. Barron (unpublished data)
Number and size of blotches	*N. sipedon*	Lake Erie, Michigan	38	h^2_{FS}, h^2_N, r_G	1,2	R. B. King (unpublished data)
Stripedness	*T. ordinoides*	Oregon	19–126	h^2_{FS}	1	Brodie (1989a, 1991, 1993b)
Antipredator behavior						
Display	*T. radix*	Illinois	15	h^2_{FS}	1	Arnold and Bennett (1984)
	T. sirtalis	California	46	h^2_{FS}	1,3,4	Garland (1988)
Display, reversals	*T. ordinoides*	Oregon	19–77	h^2_{FS}, r_G	1,4	Brodie (1989a)
Reversals	*T. ordinoides*	Oregon	77, 126	h^2_{FS}	1	Brodie (1991, 1993b)
Number of strikes	*T. butleri*	Michigan	7	h^2_{FS}	1	Schwartz and Herzog (1993)
	T. melanogaster	Jalisco, Mexico	9	h^2_{FS}	1	Schwartz and Herzog (1993)
	T. sirtalis	Wisconsin	5–20	h^2_{FS}	1	Schwartz and Herzog (1993)
		Michigan	3–27	h^2_{FS}	1	Schwartz and Herzog (1993)

(Continued)

TABLE 8.2 Quantitative Genetic Studies of Snake Populations (Continued)

Traits	Species	Locality	Number of families[a]	Parameters	Method[b]	Study
Number of strikes	*T. sirtalis*	Wisconsin	≤5	h^2_{FS}	1	Schwartz (1989)
(various stimuli)		Michigan	≤23	h^2_{FS}	1	Schwartz (1989)
Aggregative tendency	*T. sirtalis*	Wisconsin	≤5	h^2_{FS}	1	Schwartz (1989)
		Michigan	≤23	h^2_{FS}	1	Schwartz (1989)
Locomotor performance						
Speed, endurance	*T. sirtalis*	California	46	h^2_{FS}, r_G	1,3,4	Garland (1988)
		California	34	h^2_{FS}	1	Jayne and Bennett (1990a)
Speed, distance	*T. ordinoides*	Oregon	19–126	h^2_{FS}, r_G	1,4	Brodie (1989a, 1991, 1993b)
Physiology						
Cold resistance	*T. sirtalis*	Wisconsin	≤5	h^2_{FS}	1	Schwartz (1989)
		Michigan	≤23	h^2_{FS}	1	Schwartz (1989)
Tetrodotoxin resistance	*T. sirtalis*	Oregon	23	h^2_{FS}	1	Brodie and Brodie (1990)
Enzyme activities	*T. sirtalis*	California	45	h^2_{FS}, r_G	1,4	Garland et al. (1990)
Maximum oxygen consumption, blood hemoglobin, relative heart and liver mass	*T. sirtalis*	California	45	h^2_{FS}, r_G	1,3,4	Garland and Bennett (1990); Garland et al. (1990)
Feeding behavior						
Slug-eating tendency	*T. elegans*	Inland, coastal California	56, 68	h^2_{FS}	1	Arnold (1981c); Ayres and Arnold (1983)
			8–68	Dominance, maternal effects	5	Arnold (1981b)
Feeding preferences	*T. elegans*	Inland, coastal California	10,19	h^2_{FS}, r_G	1,4	Arnold (1981a,c)
(tongue-flick score)	*T. sirtalis*	Wisconsin	≤5	h^2_{FS}	1	Schwartz (1989)
		Michigan	≤23	h^2_{FS}	1	Schwartz (1989)
Integrative studies						
Scale counts, color pattern	*N. sipedon*	Kansas	...	h^2_{FS}, r_G, selection	1,2,6	Beatson (1976)
Scale counts, locomotor performance	*T. elegans*, *T. radix*	California, Illinois	...	h^2_N, r_G, selection	2,7	Arnold (1988a); Arnold and Bennett (1988)
Antipredator behavior, color pattern, locomotor performance	*T. ordinoides*	Oregon	...	h^2_{FS}, r_G, selection	1,4,7	Brodie (1989a, 1991, 1992, 1993a,b)
Scale counts, antipredator behavior, locomotor performance, physiology	*T. sirtalis*	California	...	h^2_N, h^2_{FS}, r_G, selection	1,2,3,4,7	Garland (1988); Garland and Bennett (1990); Garland et al. (1990); Jayne and Bennett (1990a,b); Garland (1993); Dohm and Garland (1993)
Scale counts, antipredator behavior, physiology, feeding behavior	*T. sirtalis*	Wisconsin, Michigan	...	h^2_{FS}, r_G	1	Schwartz (1989)

[a]Number of families differs according to the population and specific trait in some studies.
[b]1 = full-sib ANOVA; 2 = mother–offspring regression; 3 = maximum likelihood estimation; 4 = family mean correlation; 5 = population crosses; 6 = intensity of selection; 7 = selection gradient.

Ontogeny has been virtually unstudied from a quantitative genetic perspective in any taxon (Cheverud et al., 1983; Atchley, 1984; Riska et al., 1984; Price and Grant, 1985; Arnold, 1990). Techniques and theoretical frameworks for applying quantitative genetics to an ontogenetic dimension are rapidly becoming available (see references in Kirkpatrick et al., 1990a,b). Antipredator behavior of snakes is a model system to begin this avenue of research. A large body of literature on the genetics of neonate behavior already exists, as well as studies of the phenotypic development of behavior, and predictions about the dynamics of the *G*-matrix for behaviors and color patterns have been offered (Brodie, 1993a).

Maternal effects on phenotype are also largely unknown. Again, theory is outpacing empirical investigation. Oviparous reptiles are ideal subjects for studies of maternal effects, but only recently have studies of this kind been performed (Sinervo, 1990; Sinervo and Huey, 1990; for viviparous taxa, see Osgood, 1978; Arnold and Peterson, 1989; Ford and Seigel, 1989). Eggs allow manipulation of investment (i.e., yolk), temperature, and other prenatal environmental components, and many species of snakes have large clutch sizes that allow for families to be split among several treatments. Empirical tests of the efficacy of statistical reduction of maternal effects through regression would be especially valuable.

The approach of studying genotype-by-environment interactions is especially well suited to ectotherms, so many of whose traits depend on microenvironment (e.g., behavior and physiology as a function of temperature). A quantitative genetic approach promises to increase our understanding not only of snake ecology, but also of the evolution of reaction norms and phenotypic plasticity in general (de Jong, 1990; Gomulkiewicz and Kirkpatrick, 1992). Again, split-family designs could be incorporated to test for environmental affects, while providing partial genetic controls.

Finally, some of the greatest advances may come from the integration of macro- and microevolutionary approaches. Comparative studies may provide clues to interesting systems to study at the population level and vice versa (Brodie's [1989a, 1991, 1992, 1993a,b] study of the integration of color pattern and antipredator behavior was motivated by the species comparisons of Jackson et al. [1976]). Investigations of microevolutionary processes may help to explain patterns of diversity among taxa (Price et al., 1984; Emerson and Arnold, 1989; Garland and Losos, 1994). Even hypotheses of genetic drift and selection as differentiating forces among populations or taxa can now be tested through quantitative genetic studies of multiple groups (Lofsvold, 1988).

Acknowledgments

We thank Brent Charland, Harry Greene, Fred Janzen, and an anonymous reviewer for comments on earlier versions of the manuscript. S. J. Arnold, J. Barron, R. B. King, and J. Schwartz graciously provided unpublished data and/or manuscripts. Supported in part by N.S.F. grant BSR-9157268 to T.G. and a Miller Fellowhsip to EDB III.

Literature Cited

Alberch, P., 1980, Ontogenesis and morphological diversification, *Amer. Zool.*, 20:653–667.

Archie, J. W., 1985, Methods for coding variable morphological features for numerical taxonomic analysis, *Syst. Zool.*, 34:326–345.

Arnold, S. J., 1977, Polymorphism and geographic variation in the feeding behavior of the garter snake *Thamnophis elegans, Science*, 197:676–678.

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, in A. Kamil and T. Sargent, eds., *Foraging Behavior: Ecological, Ethological and Psychological Approaches*, Garland, New York, pp. 409–453.

Arnold, S. J., 1983, Morphology, performance and fitness, *Amer. Zool.*, 23:347–361.

Arnold, S. J., 1986, Laboratory and field approaches to the study of adaptation, in M. E. Feder and G. V. Lauder, eds., *Predator–Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates*, Univ. Chicago Press, Chicago, pp 157–179.

Arnold, S. J., 1987, Genetic correlation and the evolution of physiology, in M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey, eds., *New Directions in Ecological Physiology*, Cambridge Univ. Press, Cambridge, pp. 189–215.

Arnold, S. J., 1988a, Quantitative genetics and selection in natural populations: Microevolution of vertebral numbers in the garter snake *Thamnophis elegans*, in B. S. Weir, E. J. Eisen, M. J. Goodman, and G. Namkoong, eds., *Proceedings of the Second International Conference on Quantitative Genetics*, Sinauer, Sunderland, Massachusetts, pp. 619–636.

Arnold, S. J., 1988b, Behavior, energy and fitness, *Amer. Zool.*, 28:815–827.

Arnold, S. J., 1990, Inheritance and the evolution of behavioral ontogenies, 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, pp. 167–189.

Arnold, S. J., 1992, 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., 1994, Multivariate inheritance and evolution: A review of concepts, in C. R. Boake, ed., *Quantitative Genetic Analyses of the Evolution of Behavior*, Univ. Chicago Press, Chicago, in press.

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.

Arnold, S. J., and C. R. Peterson, 1989, A test for temperature effects on the ontogeny of shape in the garter snake *Thamnophis sirtalis, Physiol. Zool.*, 62:1316–1333.
Arveson, J. N., and T. H. Schmitz, 1970, Robust procedures for variance component problems using the jackknife, *Biometrics*, 26:677–686.
Atchley, W. R., 1983, Some genetic aspects of morphometric variation, in J. Felsenstein, ed., *Numerical Taxonomy*, NATO ASI Series, Vol. G1, Springer, Berlin, pp. 346–363.
Atchley, W. R., 1984, Ontogeny, timing of development, and genetic variance-covariance structure, *Amer. Nat.*, 123:519–540.
Ayres, F. A., and S. J. Arnold, 1983, Behavioural variation in natural populations, IV. Mendelian models and heritability of a feeding response in the garter snake, *Thamnophis elegans, Heredity*, 51:405–413.
Barker, J. S. F., and R. H. Thomas, 1987, A quantitative genetic perspective on adaptive evolution, in V. Loeschcke, ed., *Genetic Constraints on Adaptive Evolution*, Springer, Berlin, pp. 3–23.
Barry, F. E., P. J. Weatherhead, and D. E. Phillipp, 1992, Multiple paternity in a wild population of northern water snakes, *Nerodia sipedon, Behav. Ecol. Sociobiol.*, 30:193–199.
Barton, N. H., and M. Turelli, 1989, Evolutionary quantitative genetics: How little do we know? *Ann. Rev. Genet.*, 23:337–370.
Beatson, R. R., 1976, Environmental and genetical correlates of disruptive coloration in the water snake, *Natrix s. sipedon, Evolution*, 30:241–252.
Becker, W. A., 1992, *Manual of Quantitative Genetics*, Academic Enterprises, Pullman, Washington.
Bennett, A. F., 1987, Inter-individual variability: An underutilized resource, in M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey, eds., *New Directions in Ecological Physiology*, Cambridge Univ. Press, Cambridge, pp. 147–169.
Bennett, A. F., and R. B. Huey, 1990, Studying the evolution of physiological performance, *Oxford Surv. Evol. Biol.*, 7:251–284.
Boake, C. R. B., 1989, Repeatability: its role in evolutionary studies of mating behavior, *Evol. Ecol.*, 3:173–182.
Boake, C. R. B., 1994, *Quantitative Genetic Analyses of the Evolution of Behavior*, Univ. Chicago Press, Chicago, in press.
Brodie, E. D., III, 1989a, Genetic correlations between morphology and antipredator behaviour in natural populations of the garter snake *Thamnophis ordinoides, Nature*, 342:542–543.
Brodie, E. D., III, 1989b, Behavioral modification as a means of reducing the cost of reproduction, *Amer. Nat.*, 134:225–238.
Brodie, E. D., III, 1991, Functional and genetic integration of color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*, Doctoral Dissertation, Univ. Chicago.
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, 1993a, Consistency of individulal differences in antipredator behaviour and colur patterns in the garter snake *Thamnophis ordinoides, Anim. Behav.*, in press.
Brodie, E. D., III, 1993b, Homogeneity of the genetic variance-covariance matrix for antipredator traits in two natural populations of the garter snake *Thamnophis ordinoides, Evolution*, in press.
Brodie, E. D., III, and E. D. Brodie, Jr., 1990, Tetrodotoxin resistance in garter snakes: An evolutionary response of predators to dangerous prey, *Evolution*, 44:651–659.
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.
Bull, J. J., R. C. Vogt, and M. G. Bulmer, 1982, Heritability of sex ratio in turtles with environmental sex determination, *Evolution*, 36:333–341.
Bulmer, M. G., 1985, *The Mathematical Theory of Quantitative Genetics*, Clarendon, Oxford.

Burger, J., 1989, Incubation has long-term effects on behaviour of young pine snakes (*Pituophis melanoleucus*), *Behav. Ecol. Sociobiol.*, 24:201–207.
Burger, J., 1991, Effects of incubation temperature on behavior of hatchling pine snakes: Implications for reptilian distribution, *Behav. Ecol. Sociobiol.*, 28:297–303.
Burghardt, G. M., 1970, Intraspecific geographical variation in chemical food cue preferences of newborn garter snakes (*Thamnophis sirtalis*), *Behaviour*, 36:246–257.
Burghardt, G. M., 1975, Chemical preference polymorphism in newborn garter snakes *Thamnophis sirtalis, Behaviour*, 52:202–225.
Camin, J., and P. Ehrlich, 1958, Natural selection in water snakes (*Natrix sipedon* L.) on islands in Lake Erie, *Evolution*, 12:504–511.
Camin, J., C. Triplehorn, and H. Walter, 1954, Some indications of survival value in the type 'A' pattern of the island water snakes in Lake Erie, *Nat. Hist. Misc.*, 131:1–3.
Charlesworth, B., 1987, The heritability of fitness, in J. W. Bradley and M. B. Andersson, eds., *Sexual Selection: Testing the Alternatives*, Wiley, Chichester, pp. 21–40.
Charlesworth, B., R. Lande, and M. Slatkin, 1982, A neo-Darwinian commentary on macroevolution, *Evolution*, 36:474–498.
Cheverud, J. M., 1982, Phenotypic, genetic, and environmental morphological integration in the cranium, *Evolution*, 36:499–516.
Cheverud, J. M., 1984, Quantitative genetics and developmental constraints on evolution by selection, *J. Theoret. Biol.*, 110:155–171.
Cheverud, J. M., 1988, A comparison of genetic and phenotypic correlations, *Evolution*, 42:958–968.
Cheverud, J. M., J. J. Rutledge, and W. R. Atchley, 1983, Quantitative genetics of development: Genetic correlations among age-specific trait values and the evolution of ontogeny, *Evolution*, 37:895–905.
Cheverud, J. M., G. P. Wagner, and M. M. Dow, 1989, Methods for the comparative analysis of variation patterns, *Syst. Zool.*, 38:201–213.
Clark, A. G., 1987, Genetic correlations: The quantitative genetics of evolutionary constraints, in V. Loeschcke, ed., *Genetic Constraints on Adaptive Evolution*, Springer, Berlin, pp. 25–45.
Crespi, B. J., 1990, Measuring the effect of natural selection of phenotypic interaction systems, *Amer. Nat.*, 135:32–47.
Crowley, P. H., 1992, Resampling methods for computation-intensive data analysis in ecology and evolution, *Annu. Rev. Ecol. Syst.*, 23:405–447.
de Jong, G., 1990, Quantitative genetics of reaction norms, *J. Evol. Biol.*, 3:447–468.
Dobzhansky, Th., 1973, Nothing in biology makes sense except in the light of evolution, *Amer. Biol. Teach.*, March 1973, pp. 125–129.
Dohm, M. R., and T. Garland, Jr., 1993, Quantitative genetics of scale counts in the garter snake *Thamnophis sirtalis, Copeia*, in press.
Dunham, A. E., D. B. Miles, and D. N. Reznick, 1988, Life history patterns in squamate reptiles, in C. Gans and R. B. Huey, eds., *Biology of the Reptilia, Ecology B: Defense and Life History*, Vol. 16, Alan R. Liss, New York, pp. 441–522.
Dunn, E. R., 1915, The variations of a brood of watersnakes, *Proc. Biol. Soc. Washington*, 28:61–68.
Dunn, E. R., 1942, Survival value of varietal characters in snakes, *Amer. Nat.*, 76:104–109.
Efron, B., and R. Tibshirani, 1991, Statistical data analysis in the computer age, *Science*, 253:390–395.
Ehrlich, P., and J. Camin, 1960, Natural selection in Middle Island water snakes (*Natrix sipedon* L.), *Evolution*, 14:136.
Ehrman, L., and P. A. Parsons, 1981, *Behavior Genetics and Evolution*, McGraw-Hill, New York.
Emerson, S. B., and S. J. Arnold, 1989, Intra- and interspecific relationships between morphology, performance, and fitness, in D. B. Wake and G. Roth, eds., *Complex Organismal Functions: Integration and Evolution in Vertebrates*, Wiley, Chichester, pp. 295–314.
Endler, J. A., 1986, *Natural Selection in the Wild*, Princeton Univ. Press., Princeton, New Jersey.

Falconer, D. S., 1989, *Introduction to Quantitative Genetics*, 3rd ed., Longman, London.
Felsenstein, J., 1988, Phylogenies and quantitative characters, *Annu. Rev. Ecol. Syst.*, 19:445–471.
Fisher, R. A., 1918, The correlations between relatives on the supposition of Mendelian inheritance, *Trans. R. Soc. Edinb.*, 52:399–433.
Ford, N. B., and R. A. Seigel, 1989, Phenotypic plasticity in reproductive traits: Evidence from a viviparous snake, *Ecology*, 70:1768–1774.
Fox, W., 1948, Effect of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus*, *Copeia*, 1948:252–262.
Fox, W., C. Gordon, and M. H. Fox, 1961, Morphological effects of low temperatures during the embryonic development of the garter snake *Thamnophis elegans*, *Zoologica*, 46:57–71.
Fuchs, J. L., and G. M. Burghardt, 1971, Effects of early feeding experience on the response of garter snakes to food chemicals, *Learn. Motiv.*, 2:271–279
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., 1994, Quantitative genetics of locomotor behavior and physiology in a garter snake, in C. R. B. Boake, ed., *Quantitative Genetic Analyses of the Evolution of Behavior*, Univ. Chicago Press, Chicago, in press.
Garland, T., Jr., and S. C. Adolph, 1991, Physiological differentiation of vertebrate populations, *Annu. Rev. Ecol. Syst.*, 22:193–228.
Garland, T., Jr., and A. F. Bennett, 1990, Quantitative genetics of maximal oxygen consumption in a garter snake, *Amer. J. Physiol.*, 259 (*Regulatory Integrative Comp. Physiol.*, 28):R986–R992.
Garland, T., Jr., and J. B. Losos, 1994, Ecological morphology of locomotor performance in squamate reptiles, in P. C. Wainwright and S. M. Reilly, eds., *Ecological Morphology: Integrative Organismal Biology*, Univ. Chicago Press, Chicago, in press.
Garland, T., Jr., A. F. Bennett, and C. B. Daniels, 1990, Heritability of locomotor performance and its correlates in a natural population, *Experientia*, 46:530–533.
Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones, 1993, Phylogenetic analysis of covariance by computer simulation, *Syst. Biol.*, in press.
Garland, T. Jr., R. B. Huey, and A. F. Bennett, 1991, Phylogeny and coadaptation of thermal physiology in lizards: A reanalysis, *Evolution*, 45:1969–1975.
Garland, T. Jr., P. H. Harvey, and A. R. Ives, 1992, Procedures for the analysis of comparative data using phylogenetically independent contrasts, *Syst. Biol.*, 41:18–32.
Gianola, D., 1982, Theory and analysis of threshold characters, *J. Anim. Sci.*, 54:1079–1096.
Gibson, A. R., and J. B. Falls, 1975, Evidence for multiple insemination in the common garter snake, *Thamnophis sirtalis*, *Can. J. Zool.*, 53:1362–1368.
Gomulkiewicz, R., and M. Kirkpatrick, 1992, Quantitative genetics and the evolution of reaction norms, *Evolution*, 46:390–411.
Gould, S. J., 1980, Is a new and general theory of evolution emerging? *Paleobiology*, 6:119–130
Grant, P. R., 1986, *Ecology and Evolution of Darwin's Finches*, Princeton Univ. Press, Princeton, New Jersey.
Halloy, M., and G. M. Burghardt, 1990, Ontogeny of fish capture and ingestion in four species of garter snakes (*Thamnophis*), *Behaviour*, 112:299–317.
Hartl, D. L., and A. G. Clark, 1989, *Principles of Population Genetics*, Sinauer, Sunderland, Massachusetts.
Harvey, P. H., and M. D. Pagel, 1991, *The Comparative Method in Evolutionary Biology*, Oxford Univ. Press, Oxford.
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. Schwartz, 1990, Geographical variation in the antipredator behaviour of neonate garter snakes, *Thamnophis sirtalis*, *Anim. Behav.*, 40:597–598.
Herzog, H. A., Jr., B. B. Bowers, and G. M. Burghardt, 1989, 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, 1992, Development of antipredator response of snakes: V. Species differences in ontogenetic trajectories, *Develop. Psycholbiol.*, 25:199–211.
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 P. E. Hertz, 1984, Is a jack-of-all-temperatures a master of none? *Evolution*, 38:441–444.
Huey, R. B., A. E. Dunham, K. L. Overall, and R. A. Newman, 1990, Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*, *Physiol. Zool.*, 63:845–872.
Inger, R. F., 1943, Further notes on differential selection of variant juvenile snakes, *Amer. Nat.*, 77:87–90.
Jackson, J. F., W. Ingram, III, and H. W. Campbell, 1976, The dorsal pigmentation pattern of snakes as an antipredator strategy: A multivariate approach, *Amer. Nat.*, 110:1020–1053.
Janzen, F. J., 1992, Heritable variation for sex ratio under environmental sex determination in the common snapping turtle (*Chelydra serpentina*), *Genetics*, 131:155–161.
Janzen, F. J., 1993, An experimental analysis of natural selection on body size of hatchling turtles, *Ecology*, in press.
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. Exper. 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.
King, R. B., 1987, Color pattern polymorphism in the Lake Erie water snake, *Nerodia sipedon insularum*, *Evolution*, 41:241–255.
King, R. B., 1992, Lake Erie water snakes revisited: Morph- and age-specific variation in relative crypsis, *Evol. Ecol.*, 6:115–124.
Kirpatrick, M., D. Lofsvold, and M. Bulmer, 1990a, Analysis of the inheritance of growth trajectories and other complex quantitative characters, *J. Math. Biol.*, 27:429–450.
Kirpatrick, M., D. Lofsvold, and M. Bulmer, 1990b, Analysis of the inheritance, selection and evolution of growth trajectories, *Genetics*, 124:979–993.
Klein, T. W., 1974, Heritability and genetic correlation: Statistical power, population comparisons, and sample size, *Behav. Genet.*, 4:171–189.
Klein, T. W., J. C. DeFries, and C. T. Finkbeiner, 1973, Heritability and genetic correlation: standard errors of estimates and sample size, *Behav. Genet.*, 3:355–364.
Knapp, S. J., W. C. Bridges, Jr., and M.-H. Yang, 1989, Nonparametric confidence interval estimators for heritability and expected selection response, *Genetics*, 121:891–898.
Lande, R., 1979, Quantitative genetic analysis of multivariate evolution, applied to brain: Body size allometry, *Evolution*, 33:402–426.
Lande, R., 1980, The genetic covariance between characters maintained by pleiotropic mutations, *Genetics*, 94:203–215.
Lande, R., 1984, The genetic correlation between characters maintained by selection, linkage and inbreeding, *Genet. Res.*, 44:309–320.
Lande, R., 1988, Quantitative genetics and evolutionary theory, in B. Weir, E. Eisen, M. Goodman, and G. Namkoong, eds., *Proceedings of the Second International Conference on Quantitative Genetics*, Sinauer, Sunderland, Massachusetts, pp. 71–84.
Lande, R., and S. J. Arnold, 1983, The measurement of selection on correlated characters, *Evolution*, 37:1210–1226.
Lessels, C. M., and P. T. Boag, 1987, Unrepeatable repeatabilities: A common mistake, *Auk*, 104:116–121.

Levins, R., 1968, *Evolution in Changing Environments,* Princeton Univ. Press., Princeton, New Jersey.
Lewontin, R. C., 1970, The units of selection, *Ann. Rev. Ecol. Syst.,* 1:1–18.
Lofsvold, D., 1986, Quantitative genetics of morphological differentiation in *Peromyscus,* I. Tests of the homogeneity of genetic covariance structure among species and subspecies, *Evolution,* 40:559–573.
Lofsvold, D., 1988, Quantitative genetics of morphological differentiation in *Peromyscus,* II. Analysis of selection and drift, *Evolution,* 42:54–67.
Losos, J. B., and D. B. Miles, 1994, Adaptation, constraint, and the comparative method: Phylogenetic issues and methods, in P. C. Wainwright and S. M. Reilly, eds., *Ecological Morphology: Integrative Organismal Biology,* Univ. Chicago Press, Chicago, in press.
Lynch, M., 1989, Phylogenetic hypotheses under the assumption of neutral quantitative-genetic variation, *Evolution,* 43:1–17.
Lynch, M., 1991, Methods for the analysis of comparative data in evolutionary biology, *Evolution,* 45:1065–1080.
Madsen, T., and R. Shine, 1993, Determinants of reproductive success in female adders, *Vipera berus, Oecologia (Berlin),* in press.
Madsen, T., Shine, R., Loman., J., and Hakansson, T., 1992, Why do female adders copulate so frequently? *Nature,* 335:440–441.
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.
Mayr, E., and P. D. Ashlock, 1991, *Principles of Systematic Zoology,* McGraw-Hill, New York.
Mitchell-Olds, T., 1987, Analysis of local variation in plant size, *Ecology,* 68:82–87.
Mitchell-Olds, T., and J. Bergelson, 1990, Statistical genetics of an annual plant, *Impatiens capensis.* I. Genetic basis of quantitative variation, *Genetics,* 124:407–415.
Mitchell-Olds, T., and R. G. Shaw, 1987, Regression analysis of natural selection: Statistical inference and biological interpretation, *Evolution,* 41:1149–1161.
Mousseau, T. A., and D. A. Roff, 1987, Natural selection and the heritability of fitness components, *Heredity,* 59:181–187.
Osgood, D. W., 1978, Effect of temperature on the development of meristic characters in *Natrix fasciata, Copeia,* 1978:33–37.
Packard, G. C., and M. J. Packard, 1988, The physiological ecology of reptilian eggs and embryos, in C. Gans and R. B. Huey, eds., *Biology of the Reptilia, Ecology B: Defense and Life History,* Vol. 16, Alan R. Liss, New York, pp. 523–605.
Parker, W. S., and M. V. Plummer, 1987, Population ecology, in R. A. Seigel, J. T. Collins, S. S. Novak, eds., *Snakes: Ecology and Evolutionary Biology,* McGraw-Hill, New York, pp. 253–301.
Plomin, R., J. C. DeFries, and G. E. McClearn, 1990, *Behavioral Genetics: A Primer,* W. H. Freeman, New York.
Plummer, M. V., and H. L. Snell, 1988, Nest site selection and water relations of eggs in the snake, *Opheodrys aestivus, Copeia,* 1988:58–63.
Pough, F. H., 1976, Multiple cryptic effects of cross-banded and ringed patterns of snakes, *Copeia,* 1976:834–836.
Price, T. D., and P. R. Grant, 1985, The evolution of ontogeny in Darwin's finches: A quantitative genetic approach, *Amer. Nat.,* 125:169–188.
Price, T. D., and D. Schluter, 1991, On the low heritability of life-history traits, *Evolution,* 45:853–861.
Price, T. D., P. R. Grant, H. L. Gibbs, and P. T. Boag, 1984, Recurrent patterns of natural selection in a population of Darwin's finches, *Nature,* 309:787–789.
Provine, W. B., 1971, *The Origins of Theoretical Population Genetics,* Univ. Chicago Press, Chicago.
Reznick, D., 1985, Costs of reproduction: An evaluation of the empirical evidence, *Oikos,* 44:257–267.

Riska, B., W. R. Atchley, and J. J. Rutledge, 1984, A genetic analysis of targeted growth in mice, *Genetics,* 107:79–101.
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.
Schluter, D., 1984, Morphological and phylogenetic relations among Darwin's finches, *Evolution,* 38:921–930.
Schmalhausen, I. I., 1949, *The Factors of Evolution,* Blakiston, Philadelphia.
Schwartz, J. M., 1989, Multiple paternity and offspring variability in wild populations of the garter snake *Thamnophis sirtalis* (Colubridae), Doctoral Dissertation, Univ. 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.
Seigel, R. A., J. T. Collins, and S. S. Novak, 1987, *Snakes: Ecology and Evolutionary Biology,* McGraw-Hill, New York.
Shaffer, B., 1986, Utility of quantitative genetic parameters in character weighting, *Syst. Zool.,* 35:124–134.
Shaw, R. G., 1987, Maximum likelihood approaches applied to quantitative genetics of natural populations, *Evolution,* 41:812–826.
Shaw, R. G., 1991, The comparison of quantitative genetic parameters between populations, *Evolution,* 45:143–151.
Sinervo, B., 1990, The evolution of maternal investment in lizards: An experimental and comparative analysis of egg size and its effect on offspring performance, *Evolution,* 44:279–294.
Sinervo, B., and R. B. Huey, 1990, Allometric engineering: An experimental test of the causes of interpopulational differences in performance, *Science,* 248:1106–1109.
Slinker, B. K., and S. A. Glantz, 1985, Multiple regression for physiological data analysis: The problem of multicollinearity, *Amer. J. Physiol.,* 249 (*Regulatory Integrative Comp. Physiol.,* 18):R1–R12.
Sokal, R. R., and F. J. Rohlf, 1981, *Biometry,* W. H. Freeman, New York.
Stille, B., T. Madsen, and M. Niklasson, 1986, Multiple paternity in the adder, *Vipera berus, Oikos,* 47:173–175.
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, *Evol. Ecol.,* 3:240–252.
Turelli, M., 1988, Phenotypic evolution, constant covariances, and the maintenance of additive variance, *Evolution,* 42:1342–1347.
Turner, H. N., and S. Y. Young, 1969, *Quantitative Genetics in Sheep Breeding,* Macmillan, Melbourne, Australia.
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.
Via, S., 1984, The quantitative genetics of polyphagy in an insect herbivore, II. Genetic correlations in larval performance within and among host plants, *Evolution,* 38:896–905.
Via, S., 1987, Genetic constraints on the evolution of phenotypic plasticity, in V. Loeschcke, ed., *Genetic Constraints on Adaptive Evolution,* Springer, Berlin, pp. 46–71.
Via, S., and R. Lande, 1985, Genotype-environment interaction and the evolution of phenotypic plasticity, *Evolution,* 39:505–522.
Weir, B., E. Eisen, M. Goodman, and G. Namkoong, 1988, *Proceedings of the Second International Conference on Quantitative Genetics,* Sinauer, Sunderland, Massachusetts.

Wheeler, Q. D., 1986, Character weighting and cladistic analysis, *Syst. Zool.*, 35:102–109.
Wilkinson, G. S., K. Fowler, and L. D. Partridge, 1990, Resistance of genetic correlation structure to directional selection in *Drosophila melanogaster*, *Evolution*, 44:1990–2003.
Willis, J. H., J. A. Coyne, and K. Kirkpatrick, 1991, Can one predict the evolution of quantitative characters without genetics? *Evolution*, 45:441–444.
Wright, S., 1921, Systems of mating, *Genetics*, 6:111–173.
Zeng, Z.-B., 1988, Long-term correlated response, interpopulation covariation and interspecific allometry, *Evolution*, 42:363–374.
Zweifel, R. G., and H. C. Dessauer, 1983, Multiple insemination demonstrated experimentally in the kingsnake (*Lampropeltis getulus*), *Experientia*, 39:317–319.

Library of Congress Cataloging-in-Publication Data

Snakes—ecology and behavior / [edited by] Richard A. Seigel, Joseph T. Collins
p. cm.
Includes bibliographical references and index.
ISBN 0-07-056056-0
1. Snakes—Ecology. 2. Snakes—Behavior. I. Seigel, Richard A. II. Collins, Joseph T.
QL666.06S65 1993
597.96'0451—dc20 93-18568
CIP

1 2 3 4 5 6 7 8 9 0 DOC/DOC 9 9 8 7 6 5 4 3

ISBN 0-07-056056-0

The editing supervisor for this book was Frank Kotowski, Jr. and the production supervisor was Donald F. Schmidt. It was set in Century Schoolbook by McGraw-Hill's Professional Book Group composition unit.

Printed and bound by R. R. Donnelley & Sons Company.