

Predator-Prey Relationships

*Perspectives and Approaches
from the Study of Lower Vertebrates*

Edited by

Martin E. Feder and George V. Lauder

10 Laboratory and Field Approaches to the Study of Adaptation

Stevan J. Arnold

1. Introduction

Adaptation and selection are central concepts in the study of predator-prey relationships. During predatory pursuit or struggle the adaptations of the predator are pitted against the adaptations of prey, allowing us to visualize the biological roles of behaviors, structures and physiological processes. Hypotheses about role or adaptive significance gained from the observation of predatory struggle can give ecologically sound motivation for studies of function (Chapter 2). The role of a structure or process can also be the focus of study, for we can ask whether variation in the structure affects variation in fitness: Does the horned lizard's armature really protect against predators? In principle we could ask whether lizards with intermediate armature leave the most progeny and whether average armature in the population coincides with an optimum amount of armor. These questions are equivalent, respectively, to asking whether stabilizing selection acts on armor and whether the population is perched on an adaptive peak. We could also ask whether selection has genetic consequences. Are differences in armature inherited? Answering these questions in practice is another matter, but the answers can be considered an analysis of adaptation. Clearly the answers do not tell us everything about adaptation that we would like to know. Questions about evolutionary history, for example, are unanswered. Nevertheless we would be able to tell whether a particular population is under selection, whether it is actively evolving and whether it is in a state of local adaptation. Other approaches to the study of adaptation and selection are reviewed by Endler (1985).

The University of Chicago Press
Chicago and London

1986

The goal of this paper is to discuss the practical aspects of a strategy for analyzing adaptations. The strategy focuses on measures of whole organism performance and uses natural variation in those measures to seek correlations with behavior, physiology, morphology, on the one hand, and correlations with fitness, on the other. By performance, I mean those standardized measures of organismal ability (e.g., sprint speed, running endurance, leaping ability) that are increasingly used by physiological ecologists and functional morphologists as integrative measures of a variety of underlying physiological processes and morphological structures (e.g., Bartholomew, 1958; Bennett, 1980; Drummond, 1983; Emerson, 1978; Feder and Arnold, 1982; Greenwald, 1974; Huey and Stevenson, 1979; Webb, 1984). Throughout this paper I will use "morphology" as a short-hand for such behavioral, physiological and morphological variables.

The particular approach discussed here was developed in collaboration with A. F. Bennett, while investigating crawling performance in newborn garter snakes. Initially, we simply planned to test for differences among litters in crawling performance. As we discussed logistics, we realized that if we counted vertebral numbers on each snake, we could seek correlations with performance and so determine whether natural selection on these skeletal features (already the focus of a field study) might be mediated by locomotion. Also, we realized that if we individually marked and released the snakes after scoring performance, we might be able to measure their fitnesses through recaptures and so estimate the selective value of performance. Furthermore, because data on families were available at each step, it might be possible to analyze the inheritance of morphology, performance and fitness, as well as their hereditary correlations. The steps in this plan are outlined in Table 1, together with the types of data analysis that are possible with success at each step. We were able to proceed only as far as step five with our garter snake project because demands on our time by other field projects prevented us from mounting an intensive recapture program. Nevertheless, the plan might succeed in its entirety with the right organism, under the right circumstances.

A critical feature of the species to be studied is whether cohorts of large size can be obtained and tested, because large samples are needed to conduct the multivariate statistical analysis of data. Thus it must be possible to obtain dozens or scores of gravid females or clutches in the field or to breed the organism in captivity. In the field phase of the program, it would help to use organisms that are conspicuous and

sedentary, so that recapture is feasible, and that are short-lived, so that lifetime fitness can be estimated. The virtue of the entire plan is that it integrates the laboratory study of performance with the field study of fitness. Total success could tell us, for example, whether and how strongly natural selection acts on various measures of performance. Partial success also reaps rewards. Thus if the field phase cannot be conducted, as in the garter snake case, one can nevertheless analyze the correlates of performance, as well as the inheritance of morphology and performance. The most critical step in the program is the choice of characters. In the ideal case, the character should play a key role in adaptation to a particular feature of the environment. Biomechanical analysis (e.g., Gans, 1974; Chapter 2), physiological (Chapter 6), ecological (e.g., Price et al., 1984a) or ethological studies (Curio, 1976; Chapter 6) might identify such plausibly adaptive traits. Likewise, rapid microevolution, as revealed by dramatic geographic variation within species, or a history of macroevolutionary change are also earmarks of worthy traits.

One can argue the opposite viewpoint, that selection studies should focus on traits of arbitrary adaptive value. Van Valen (1963), has suggested, for example, that traits should be chosen for study without reference to their adaptiveness so that we can gain a statistical picture of how strongly selection acts on the average character. In this view,

TABLE 1: A Scheme for Analyzing Adaptations in Natural Populations. "Morphology" is Short-hand for Behavioral, Physiological and Structural Traits

Research Step	Data Analysis
Laboratory Phase	
1. Obtain clutches or gravid females (or captive breeding)	Compute repeatability of performance, genetic variances and covariances of performance measures.
2. Gestation and birth in laboratory.	
3. Evaluate performance (two or three times).	
4. Score morphological traits.	Analyze morphological correlates of performance (performance gradients); genetic covariances between morphology and performance.
Field Phase	
5. Release individually-marked specimens in field.	Analyze correlations of morphology and performance with fitness (selection and fitness gradients); genetic variances and covariances of fitness components.
6. Score fitness with recapture program.	
7. Re-evaluate performance and morphology at each recapture	Compute repeatability and ontogeny of morphology and performance in the field.

human fingerprint ridges, waltzing in mice and attraction of moths to light are ranked equally as candidates for selection study with *Anolis* toe lamellae, rodent habitat choice and the evasion of bats by moths. I would prefer to study selection on the latter set of traits precisely because they are likely to be adaptive and because Peterson (1983), Wecker (1963) and Roeder (1963) have given us ecological perspectives for framing hypotheses and interpreting results using these characters. Fingerprints, waltzing and attraction to lights may be adaptive, but they might be simple epiphenomena whose significance will never be illuminated by measurements of selection. Choosing traits because they are plausibly adaptive biases the sample of selection studies, leaving Van Valen's query unanswered, but the sample will produce connections between disciplines.

Computational techniques for measuring selection are reviewed by Lande and Arnold (1983), Arnold and Wade (1984 a,b), and Endler (1985). The theory underlying computations for the particular strategy discussed here is outlined by Arnold (1983).

In the following sections I turn first to the laboratory phases in the plan and then to the field phase. In each section I focus on three sets of issues: 1) variation and selection, 2) ontogeny, and 3) inheritance. These are the classical Darwinian issues in the study of adaptation. They are also the major ingredients in equations for evolutionary change in continuously distributed, polygenic traits (e.g., Lande, 1979). Consequently, quantitative genetic theory can be used to integrate these issues and to model microevolution (e.g., Arnold, 1981a; Lande, 1979; Price et al., 1984b; Schluter, 1984). In this paper, however, I focus on the practical, logistical aspects of implementing the plan outlined in Table 1, rather than on relating it to a theoretical structure.

In each section I review recent progress in studies using fish, amphibians and reptiles with a focus on traits relevant to predator-prey interactions. In most instances only a few studies have been attempted. In other cases (e.g., longitudinal studies of performance) no studies have been attempted.

2. Laboratory Phase

2.1 Variation and Selection

Direct and indirect effects of selection. Correlations among characters will induce indirect effects of selection. Thus even if selection acts directly on only one character, correlated characters will

also be affected. Multivariate statistics can be used to separate the direct and indirect effects of selection (Lande and Arnold, 1983). The basic procedure is to measure the association between fitness (or performance) and one character while holding the effects of other characters statistically constant, using multiple regression analysis.

Of course, we cannot account for the effects of characters that are not included in the study. Thus if selection acts directly on an unmeasured character that is correlated with the characters in the study, we may misidentify the actual target of selection.

Garland's (1984) analysis of physiological correlates of running performance in black iguanas (*Ctenosaura similis*) illustrates the statistical technique of holding variables constant to measure direct effects on performance. Garland measured three aspects of locomotory performance (burst speed, endurance time and maximum running distance) in laboratory trials using a field collected sample of animals of varying size. Endurance, for example, was strongly correlated with size. After holding size (body mass) constant, Garland was able to account for nearly 90% of the residual variation in endurance with measures of leg muscle mass, maximum oxygen consumption, heart mass and enzyme (liver citrate synthase) activity. Individual differences in metabolism and metabolic enzyme activity accounted for 65% of the variation in maximum distance but none of the measurements accounted for variation in burst speed. Garland also used the hierarchical nature of his characters and accounted for 67% of the variation in oxygen consumption, for example, with enzymatic and organ mass variables.

Directional, stabilizing and correlational selection. Natural selection can act simultaneously on many aspects of the organism and in a variety of modes. Selection may directly affect the mean of a character (directional selection), the variance of a character (stabilizing or disruptive selection, depending on whether the variance decreases or increases), or the covariance between two characters (correlational selection). These modes of selection are not mutually exclusive alternatives. Selection might simultaneously shift the mean of one character while contracting its variance and also changing covariances with other characters.

The simultaneous and multifaceted effects of selection can be visualized as a selection surface. Selection on two characters is the easiest multiple character case to visualize. Imagine two axes, representing the two characters, and a vertical axis, representing relative fitness. A hill-shaped surface in this space would describe stabilizing selection on the two characters. The forces of directional

selection will vary depending on where the population mean is located in the character space. If the mean lies precisely on the top of the hill, there is no directional selection on either character. On the other hand, if the mean lies off the hilltop, there will be directional selection on both characters, in the steepest uphill direction. Other combinations of directional, stabilizing, disruptive and correlational selection can be represented by other surfaces (pits, saddles, elliptical ridges, etc.). When the object is to describe the effects of characters on performance we can summarize the results as a performance surface in which the vertical axis is relative performance, rather than fitness.

An example of a performance surface is shown in Fig. 1. The plot shows contours of burst speed in newborn garter snakes (*Thamnophis radix*) as a function of numbers of vertebrae in the body and tail (Arnold and Bennett, 1985). The laboratory testing procedure is

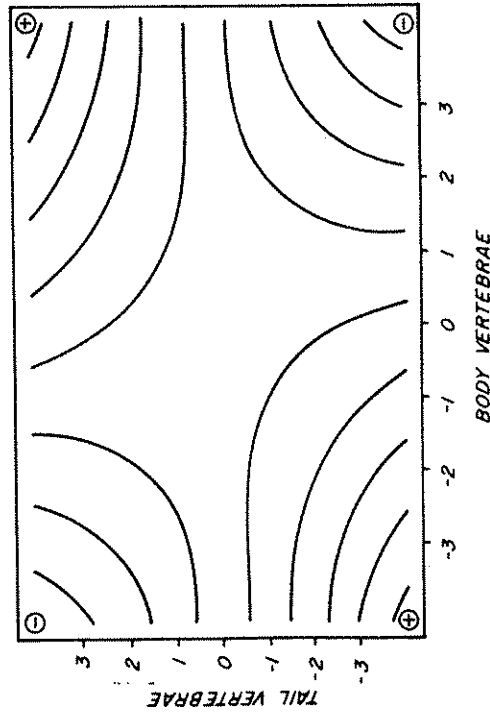


Fig. 1. Burst speed as a function of numbers of body and tail vertebrae in a sample ($n=100$) of newborn garter snakes (*Thamnophis radix*) tested under uniform conditions. Burst speed is shown as contour lines and increases towards the upper right-hand corner and towards the lower left-hand corner. The performance surface was drawn using coefficients from a multiple, curvilinear regression of burst speed on numbers of body vertebrae and tail vertebrae, squared number of body vertebrae, squared number of tail vertebrae and the product of body and tail vertebral numbers. The bivariate mean of the population is located at the center of the plot. Numbers of body and tail vertebrae are on a logarithmic scale in units of phenotypic standard deviation.

described by Arnold and Bennett (1984). We were unable to detect statistically significant directional or stabilizing (disruptive) selection on either character. Our analysis did, however, reveal significant correlational selection and it is that selection coefficient that largely determines the surface portrayed in Fig. 1. In other words, the set of snakes showing the fastest burst speeds also had a higher correlation between body and tail vertebral numbers. Thus good performance was associated with the relative proportion of body and tail vertebral numbers rather than the absolute numbers in either region of the vertebral column. Swain and Lindsey (1984) staged encounters between sticklebacks (*Gasterosteus aculeatus*) and predatory sunfish (*Lepomis gibbosus*) and found directional selection for low vertebral counts. Such staged trials between predators and prey could be used to assess the stabilizing and correlational effects of selection on the attributes of both predators and prey.

2.2 Ontogeny

The repeatability and ontogeny of performance are critical issues that affect the prospects and techniques for analyzing both selection and inheritance. Repeatability is simply the consistency of individual performance. It is conveniently measured as correlation between trials, or (especially if there are more than two trials) as an intraclass correlation, estimated by analysis of variance (Falconer, 1981). In contrast to the random fluctuations in performance between trials close together in time, performance may also change progressively with age. Such individual histories can be described by ontogenetic trajectories or lines fitted to a plot of an individual's performance as a function of age, using linear or curvilinear regression (e.g., Cock, 1966).

Short-term fluctuation. Performance may vary from trial to trial without any pattern. Such fluctuations may reflect measurement error as well as intangible changes in physiology. Motivation, for example, is thought to be a leading cause of variation in performance among world-class athletes. Despite such random variation, there may be consistent differences among individuals. Thus lizards (*Sceloporus occiduensis*) maintained a consistent ranking in running performance in laboratory trials and relative performance, independent of body temperature (Bennett, 1980). Repeatability in garter snake (*Thamnophis radix*) locomotory performance, measured as the correlation between trials on successive days, ranged from $r=0.55$ ($n=139$) for endurance (total distance crawled) to $r=0.71$ ($n=39$) for burst speed (Arnold and

Bennett, 1985). Repeatability of antipredatory displays in these snakes fell in the same range (Arnold and Bennett, 1984).

Shaffer and Lauder (1985a,b) made repeated measurements of head movements and electromyographic responses during prey capture in ambystomatid salamanders. Seven aspects of head movement (e.g., cranial elevation, maximum gape) all showed significant individual differences, with an average repeatability of 0.37. Most of the eleven electromyographic variables showed significant individual variation (average repeatability = 0.31) and many showed significant differences between trials on different days. The good news from these studies is that conspecifics differ in prey catching movements. The sobering message is that movement repeatabilities may be in the low range.

Repeatability can be used as a criterion for deciding on testing protocols. If repeatability is so low that there are no significant differences among individuals, then there is no hope of detecting selection or analyzing inheritance. Improving the scoring protocol may require less effort and expense than boosting sample sizes in order to compensate for low repeatability. Another solution is to make multiple measurements on each individual and use the average or best score. Falconer (1981) discusses the gain from such multiple measurement; improvement is asymptotic with effort.

Long-term trajectories. Performance undoubtedly changes with age (and size) in many taxa and may reflect ontogenetic niche shifts, but the phenomenon has been little studied (Garland, 1985; Pough and Kamel, 1984; Werner and Gilliam, 1984). Pough (1977, 1978), for example, showed that juvenile naticine snakes had much less endurance capacity than adults. Because of such ontogenetic trends, it is crucial to control for age and size in studies of correlates of performance or in genetic analysis. One powerful approach is to make measurements of individuals of known age at regular intervals. Then individual trajectories can be used to describe performance. In the happy event that all trajectories are parallel, we would need only one measurement of each individual, so long as we knew its age. Individuals, however, are likely to vary in the slopes as well as the elevation of their trajectories. In this case one needs to follow individual performance histories.

2.3 Inheritance

Behavioral, physiological and morphological traits, as well as performance, are likely to be influenced by numerous genes. The body

of theory developed to analyze the inheritance of such polygenic traits is called quantitative genetics, which traces its ancestry to seminal papers by Weinberg (1909), Fisher (1918) and Wright (1921). In outline, the theory uses quantitative measures of resemblance among relatives in, say, performance to estimate two critical kinds of genetic parameters, additive genetic variances and covariances. These genetic parameters reflect the additive effects of genes that cause heritable resemblance between offspring and their parents. Consequently, these parameters enable us to predict traits in the next generation from selected parents in the preceding generation, and so they play a key role in equations for the evolution of polygenic traits. Falconer (1981) gives a lucid introduction to the discipline. Kempthorne (1957), Bulmer (1980), Mather and Jinks (1977), and Pollack et al. (1977) are good sources for information on special topics. Lande (1979, 1982) discusses applications to evolutionary problems.

The basic idea in applying quantitative genetics is to use replicated combinations of relatives (e.g., sets of parents and their offspring) to estimate genetic parameters. The mapping between phenotypic resemblance and the underlying genetic parameters has been worked out for most common kinds of relationships (e.g., Kempthorne, 1957).

Some kinds of relatives give better genetic information than others. If we measure performance in broods of a taxon with an unknown system of paternity, for example, we will not know whether all members of a brood are full-sibs or whether maternal half-sibs are present as well. We can test for differences among broods in performance (say, with an analysis of variance) and so make a rough test for heritable variation, but family resemblance might also be due to the environment that is common to families and to non-additive genetic effects.

Bennett's (1980) discovery of consistent individual differences in the running performance of *Sceloporus* lizards has encouraged the next stage in genetic analysis of reptiles, tests for significant variation among broods. Thus van Berkum and Tsuji (1985) have found significant family differences in burst speed in a population of *Sceloporus occidentalis*. Andrews and Pough (personal communication), likewise, found differences in locomotory performance among litters of the lizard *Chalcides ocellatus*.

Broods of full-sibs provide slightly better information. Because the relationship of littermates is known, we can place a bound on genetic variance or heritability. Heritability is simply a standardized genetic variance (the ratio of additive genetic variance to total phenotypic variance). Still, however, we can only place an upper bound on the

estimate because environmental and nongenetic effects are confounded with additive gene effects in producing similarity between full-sibs.

Studies of garter snake (*Thamnophis*) populations have revealed heritable variation in the prey recognition behavior, antipredatory displays and locomotory performance of newborn animals. All studies to date have analyzed variation within and among litters of full-sibs, so the heritability estimates are upper bounds. Ayres and Arnold (1983) review the substantial evidence that littermates are full-sibs and report heritability estimates in the range 0.31-0.54 for slug-eating scores in two populations of *T. elegans*. These same populations showed heritable variation in chemoreceptive (tongue-flicking) response to odors from slugs and a variety of other natural prey. Analysis of genetic covariances in chemoreception revealed genetic couplings between responses to taxonomically related prey but there were also some startling exceptions. Responses to slugs and leeches, for example, were genetically correlated (Arnold, 1981a,b).

Maternal effects probably did not inflate the heritability estimates in these garter snake studies. Burghardt (1971) failed to influence juvenile chemoreceptive responses to prey by manipulating maternal diet during gestation, and Arnold (1981c) did not detect maternal effects in crosses between populations. Furthermore, littermates were separated and individually housed shortly after birth, disrupting common family effects. This same postnatal protocol was followed in Arnold and Bennett's (1984) study of antipredator displays in newborn *T. radix*. This study reported a heritability of 0.37 for single trials (heritability = 0.45, 95% confidence limits = 0.19-0.97 for the average of two trials). Nevertheless, the possibility of environmental contributions to family resemblance can never be completely excluded with only full-sib data. The prospects for inflated heritability estimates are great for some characters, such as garter snake birth weight (heritability estimates for *T. elegans* are greater than one) and smaller for other traits, such as chemoreception scores. Despite their deficiencies, the full-sib studies are defensible as first generation attempts that suggest that very considerable levels of genetic variation exist in natural populations. The suggestion should now be tested with breeding designs that yield better genetic information.

The best estimates of genetic parameters are achieved by breeding designs that produce two or more levels of relationship. The easiest of these designs to implement is sets of mothers and their offspring. Heritability is estimated by calculating the slope of the statistical regression of offspring phenotype on mother's phenotype. Heritability

equals twice the regression slope. Equating twice the slope with heritability assumes that environmental effects do not contribute to the resemblance between parents and offspring. In addition, performance should be measured at the same age and under the same test conditions in both mothers and offspring. The most convenient test protocol, however, is to measure performance in mothers and offspring at the same time. With such data, the regression of offspring on mother's performance cannot be used to compute a heritability, unless performance is age-invariant, but they can be used to compute a genetic covariance or correlation between adult and juvenile performance.

The technique of estimating genetic variances and covariances with parent-offspring data can be illustrated with the example of vertebral number inheritance in garter snakes. Vertebral numbers in the body and tail are fixed before birth and remain constant in an individual through postnatal life (except for loss of tail tip, which is easily recognized). Because the two counts are age-invariant, the same traits can be conveniently scored in mothers and offspring at the same time, shortly after birth. The scores can be made by external counts of ventral and subcaudal scales, because of a one-to-one correspondence with body and tail vertebrae, respectively (Alexander and Gans, 1966; Voris, 1975). Heritabilities of the body and tail counts are 0.59 ± 0.19 standard error and 0.57 ± 0.18 standard error, respectively, based on regressions of about 500 offspring *T. elegans* on their 50 mothers in each of the two populations. The genetic correlation between body and tail vertebral counts can be estimated in two ways; by regressing offspring tail counts on mother's body vertebrae and by regressing offspring body counts on mother's tail vertebrae. Both estimates give the same surprising result: tail and body vertebral numbers are not genetically correlated. Even the phenotypic correlation is low ($r = 0.14$; $p < 0.02$).

Heritability can also be assessed using data on offspring and both of their parents. Greater statistical power and some gain in information is achieved by knowing the phenotypes of fathers as well as mothers. A greater slope for the offspring-mother regression compared to the offspring-father regression, for example, indicates maternal effects. Normally, however, captive breeding will be required to know paternity with confidence. If captive breeding can be done, other designs give more information than the offspring-parent regression approach. These designs also have the convenient feature that the phenotypes of parents are not measured.

The maternal full-sib/paternal half-sib design should be considered if captive breeding is feasible. The design entails breeding a small harem of females to each of several males. The rationale for the design is that difference among the offspring of the males will be due to additive gene effects if brood environments are controlled or randomized and if each male sires offspring from a comparable (large) sample of females. Under these conditions, genetic variance is equivalent to four times the among-sire component of variance (Falconer, 1981).

The decisions of how many sires to breed, the size of harems and how many littermates to score can be made using the criterion that the standard error of heritability should be minimized. Robertson (1959) found that in the absence of preliminary information about heritability and if approximately 1200 offspring can be scored, then a good general rule is to breed three or four females to each of 30-40 sires and score traits on about ten offspring in each full-sib family. An alternative plan should be pursued if nongenetic causes of resemblance among full-sibs are likely (pre- and postnatal maternal effects and common environment effects). In such cases the variation among half-sib families gives the most reliable information about heritability and genetic correlation. A good plan would be to score traits on 20-30 offspring from each of 40-60 sires, with each sire bred to multiple females (Roberston, 1959).

More complicated breeding designs should be considered if it is feasible artificially to fertilize ova, as in some amphibians and fish. The major gain from such design is that the magnitude of maternal effects can be estimated, as well as genetic parameters. One powerful design, for example, is to fertilize the ova of each female with the sperm from a series of males, while using the sperm from each male to fertilize the ova of several females. The rationale and details of such factorial designs are discussed by Cockerham (1963). Computations and interpretation are much simplified if the design is balanced and orthogonal. Special designs to elucidate maternal effects and their inheritance are detailed by Eisen (1967).

Recent work on the inheritance of flight performance in insects should encourage genetical studies of performance in vertebrates. Curtisinger and Laurie-Ahliberg (1981) characterized differences in flying performance among 21 lines of *Drosophila melanogaster* extracted from natural populations and differing only in chromosome 2. Heritability estimates ranged from 0.16 for wing stroke amplitude to 0.44 for inertial power. These are "broad sense" heritability estimates that include nonadditive genetic variance components.

3. Field Phase

3.1 Variation and Selection

Field measurement of fitness. Because selection is a statistical relationship between characters and fitness, accurate measurement of fitness is crucial. Ornithologists, following the pioneering studies of David Lack, have had the most success among vertebrate biologists in field measurement of fitness (e.g., McGregor et al., 1981; Noodwijk, 1982; Smith, 1985). Success has been achieved, for example, by banding entire breeding populations of passerines on small islands or forest tracts, constantly monitoring all nests during the breeding season and scoring laying and fledgling success. Intensive, long-term programs of this kind have yielded tallies of lifetime reproductive success for samples ranging in size from dozens to hundreds of individuals (reviewed in Clutton-Brock, 1985). The secretive habits of many fish, amphibians and reptiles frustrate measurement of fitness. Nevertheless, major components of fitness can be determined in many species, permitting measurement of particular types of selection as well as partial resolution of total selection. Thus clutch size can be determined in turtles by radiography (Gibbons and Greene, 1979), male mating success can be assessed by regularly counting clutches in the territories of male sculpins (Downhower and Brown, 1980) and frogs (e.g., Howard, 1981; Kluge, 1981) and survivorship can be established by intensive mark-recapture work (e.g., Fox, 1983; Tinkle, 1967). The current challenge is to adapt techniques developed for demographic studies, in which the focus was parameters of population growth, for use in studies of fitness and its components, in which the focus is on individual differences.

Longitudinal estimates of fitness generally provide better information than cross-sectional estimates (Lande and Arnold, 1983). In the ideal longitudinal approach, a cohort is followed from birth throughout life and the total fitness of every individual is scored. The approach is difficult because every animal must be individually recognizable and under constant surveillance, or at least monitored so closely that all progeny can be properly assigned to their parents. The advantages of the longitudinal approach are that inconsistencies of selection and the environment do not compromise the results, and selection on age-dependent traits can be measured. In the cross-sectional approach, the population is sampled at a single interval of time and the histories of individuals are not followed. Thus selection might be estimated, for example, by contrasting juvenile and adult

age-classes. The results, however, are predicated on the assumption that the current juvenile class closely resembles the juvenile cohort from which present day adults were derived (e.g., comparable environmental effects on phenotypes) and only age-invariant traits can be analyzed.

Morphological correlates of fitness. Longitudinal studies of selection have hardly ever been attempted with amphibians, fish and reptiles. In one of the few studies of this kind, Fox (1975) followed a marked cohort of about 250 juvenile lizards (*Uta stansburiana*) for about 8 months and measured mortality selection on age-invariant scale counts. Fox (1975, 1983) found statistically significant stabilizing selection (variance contraction) on several scale characters but was unable to resolve selection on several other counts. Ferguson and Fox (1984) also employed the longitudinal approach with *U. stansburiana* and detected significant directional selection on hatchling size.

In contrast, several cross-sectional studies of selection on reptile scale counts have been conducted, with the general result that variance often contracts from juvenile to adult cohorts (Beatson, 1976; Dunn, 1942; Hecht, 1952; Inger, 1943; Rand, 1954; but see Klauber, 1945).

Performance and fitness in the field. The adaptive value of performance is an almost completely unexplored issue. Even though most measures of performance seem plausibly adaptive, the goal of measuring selection on performance should not be viewed as merely an attempt to validate one's intuition. Different types of performance might be in conflict, for example. Selective conflicts could be revealed by measuring correlational selection.

One expedient approach to measuring selection on performance is to combine performance measurement with an ongoing demographic study that has already succeeded in scoring the fitness of individuals in the population (R. B. Huey, personal communication). Thus McGregor et al. (1981) juxtaposed individual measures of song repertoire size with ongoing studies of lifetime fitness in great tits (*Parus major*) and so were able to detect stabilizing selection on the behavioral trait. Trevor Price (personal communication) has shown that it is feasible to measure performance in the field, as well as its morphological correlates. By carefully following and observing marked finches (*Geospiza fortis*) in the Galapagos, Price was able to score their success as they foraged on a resource base consisting of only a few seed types. Price found significant correlations between bill dimensions and seed foraging performance.

Territory size may usefully be considered a type of performance, a variable interposed between morphology and fitness. Treating territory size in this way, we can measure: 1) effects of morphology on territory

size, 2) effects of territory size on fitness and 3) effects of morphology on fitness not mediated via territory size. If, on the other hand, we treat territory size as just another character (e.g., Price, 1984), we may exclude the possibility that selection acts on a character via its effects on territoriality.

3.2 Ontogeny

Performance and fitness trajectories. Two important issues in field studies are individual consistency and ontogenetic trajectory. Both issues could be approached by measuring performance, for example, at each sighting or recapture. A similar approach can be applied to fitness components, such as annual fertility or clutch size, with a repeating feature. Houck et al. (1985) illustrate measurement of repeatability of a fitness component, namely mating success, in laboratory trials.

3.3 Inheritance

Fitness genetics. The inheritance of lifetime fitness and its components in natural populations of fish, amphibians and reptiles is a virtually unexplored field. The studies conducted so far have primarily focused on tests for genetic differences between populations in growth rate and on qualitative tests for genetic variation within population rather than on parameter estimation (Berven, 1982; Reznick, 1982; Stearns, 1983; Travis, 1983). Recent progress using other taxonomic groups is reviewed by Dingle and Hegmann (1982).

A major unresolved issue is the question of whether there are tradeoffs between fitness components that would be revealed by negative genetic correlations. Genetic variance for total lifetime fitness should be nonexistent in equilibrium populations (Fisher, 1958). Nevertheless, any or all components of fitness might have non-zero genetic variances (Lande, 1982). The result is not surprising, if we remember that the variance of a sum is composed of both the variances of its parts and the covariances between the parts. If some of the genetic covariances between fitness components are negative, they could cancel the contributions from fitness component variance (which must be non-negative), and so yield zero genetic variance for total fitness.

Falconer (1981) has described a pleiotropic evolutionary process that produces negative genetic covariances between fitness components. Genes with only positive effects on either or both of two fitness components will eventually be fixed in the population. In contrast, a

gene with a positive effect on one fitness component and a negative effect on the other component may be held at intermediate frequencies. Genes of this type, with antagonistic pleiotropic effects, will be the major source of genetic covariance between fitness components and that covariance will tend to be negative. The prediction of such negative covariances has been confirmed by some studies (e.g., Rose and Charlesworth, 1981) but tests are still rare. An outstanding challenge is to test the prediction of negative genetic covariances for fitness components measured in nature.

A major practical problem confronting genetical studies of fitness is that at least one full generation of surveillance is required. Unlike the scoring of age-invariant traits, such as scale counts, which can be done immediately after birth, scoring total fitness requires following individuals for a lifetime. Furthermore, because fitness and its components are often sensitive to maternal and other environmental effects, sophisticated multi-generation breeding and cross-fostering designs are highly desirable. Thus the genetical study of fitness, especially a field study, is a major undertaking and most practical with short-lived organisms. Some recent progress in laboratory studies is summarized in Dingle and Hegmann (1982).

Genetic covariance between performance and fitness components. A study that succeeds in measuring major components of fitness can provide a test for genetic coupling between performance and fitness components, if the data are family-structured. Such genetic covariances reflect pleiotropic gene action (i.e., segregating genes that affect both performance and fitness) and linkage disequilibrium (i.e., non-random associations of alleles affecting performance with alleles at other loci that affect fitness) and provide genetic evidence for a relationship between performance and fitness. Likewise, genetic covariances between morphology and fitness components are important evolutionary parameters. A study that provides estimates of total fitness might permit computation of genetic covariances between performance (or morphology) and total fitness, but we expect these covariances to be zero in a population at genetic equilibrium (Crow and Nagylaki, 1976).

4. Summary

Because behaviorists, morphologists, systematists and physiological ecologists usually study different kinds of traits, we miss many important connections between our fields. A natural way to build bridges is to include different sets of traits in one study (e.g., combine

meristic and morphometric traits with whole animal measurement of performance or with behavioral reactions to prey). Do meristics and morphometrics affect locomotory performance, for example? Inheritance and selection on these same traits can be studied using the tools of quantitative genetics and ecology. Are the traits used by systematists heritable? Is performance under directional and/or stabilizing selection in nature? By combining studies of inheritance and selection, we can determine whether selection has genetic consequences. It helps to have an organism that readily delivers young or breeds in the lab, that can be individually marked and recaptured and that permits large sample sizes for both laboratory and field operations (e.g., naticine snakes, ambystomatid salamanders). Against the promise of finding new connections between fields, one must weigh the logistic difficulties of large-scale breeding and mark/recapture work and the possibility that both genetic and selection effects will be weak and, so, hard to detect.

Acknowledgments

I am grateful to A. F. Bennett, J. A. Cheverud, S. Emerson, M. E. Feder, T. Garland Jr., R. B. Huey, H. B. Shaffer, J. S. Tsuji and F. H. van Berkum for discussion and comments on the manuscript. The preparation of the manuscript was supported by N.S.F. grant BSR 81-11489 and by U.S. Public Health grant 1-K04-HD00392-01.

References

- Alexander, A. A., and C. Gans. 1966. The pattern of dermal-vertebral correlation in snakes and amphisbaenians. *Zool. Mededeelingen* 41: 171-190.
- Arnold, S. J. 1981a. The microevolution of feeding behavior. In *Foraging behavior: ecological, ethological and psychological approaches*, ed. A. Kamil and T. Sargent, pp. 409-453. New York: Garland STPM Press.
- Arnold, S. J. 1981b. 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. 1981c. Behavioral variation in natural populations. II. The inheritance of feeding response in crosses between geographic

- races of the garter snake, *Thamnophis elegans*. *Evolution* 35: 510-515.
- Arnold, S. J. 1983. Morphology, performance and fitness. *Am. Zool.* 23: 347-361.
- 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. 1985. Behavioural variation in natural populations. V. Morphological correlates of locomotory performance in the garter snake *Thamnophis radix*. Manuscript.
- Arnold, S. J., and M. J. Wade. 1984a. On the measurement of natural and sexual selection: theory. *Evolution* 38: 709-719.
- Arnold, S. J., and M. J. Wade. 1984b. On the measurement of natural and sexual selection: applications. *Evolution* 38: 720-734.
- 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.
- Bartholomew, G. A. 1958. The role of physiology in the distribution of terrestrial vertebrates. In *Zoogeography*, ed. C. L. Hubbs, pp. 81-95. Washington, D. C.: Amer. Assoc. Adv. Sci.
- Beatson, R. R. 1976. Environmental and genetical correlates of disruptive coloration in the water snake, *Natrix s. sipedon*. *Evolution* 30: 241-252.
- Bennett, A. F. 1980. The thermal dependence of lizard behaviour. *Anim. Behav.* 28: 752-762.
- Berven, K. A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. I. An experimental analysis of life history traits. *Evolution* 36: 962-983.
- Bulmer, M. G. 1980. *The mathematical theory of quantitative genetics*. Oxford: Clarendon Press.
- Burghardt, G. M. 1971. Chemical-cue preferences of newborn snakes: influence of prenatal maternal experience. *Science* 171: 921-923.
- Clutton-Brock, T. H., ed. 1985. *Reproductive Success*. Chicago: Univ. of Chicago Press.
- Cock, A. G. 1966. Genetical aspects of metrical growth and form in animals. *Quart. Rev. Biol.* 41: 131-190.
- Cockerham, C. C. 1963. Estimation of genetic variances. In *Statistical genetics and plant breeding*, ed. W. D. Hanson and H. F. Robinson, pp. 53-94. National Academy of Science: National Research Council Publ. No. 982.

- Crow, J. F., and T. Nagylaki. 1976. The rate of change of a character correlated with fitness. *Am. Nat.* 110: 207-213.
- Curio, E. 1976. *The ethology of predation*. New York: Springer-Verlag.
- Curtis, J. W., and C. C. Laurie-Ahberg. 1981. Genetic variability of flight metabolism in *Drosophila melanogaster*. I. Characterization of power output during tethered flight. *Genetics* 98: 549-564.
- Dingle, H. and J. P. Hegmann. 1982. *Evolution and genetics of life histories*. New York: Springer-Verlag.
- Downhower, J. F. and L. Brown. 1980. Mate preferences of female mottled sculpins, *Cottus bairdi*. *Anim. Behav.* 28: 728-734.
- Drummond, H. 1983. Aquatic foraging in garter snakes: a comparison of specialists and generalists. *Behaviour* 86: 1-30.
- Dunn, E. R. 1942. Survival value of varietal characters in snakes. *Am. Nat.* 76: 104-109.
- Eisen, E. J. 1967. Mating designs for estimating direct and maternal genetic variances and maternal covariances. *Can. J. Genet. Cytol.* 9: 13-22.
- Emerson, S. 1978. Allometry and jumping in frogs: helping the twain to meet. *Evolution* 32: 551-564.
- Endler, J. 1985. *Natural selection in the wild*. Princeton: Princeton Univ. Press.
- Falconer, D. S. 1981. *Introduction to quantitative genetics*, 2d ed. London: Longman.
- Feder, M. E., and S. J. Arnold. 1982. Anaerobic metabolism and behavior during predatory encounters between snakes (*Thamnophis elegans*) and salamanders (*Plethodon jordani*). *Oecologia* 53: 93-97.
- Ferguson, E. W., and S. F. Fox. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution* 38: 342-349.
- Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. *Trans. Roy. Soc. Edinb.* 52: 399-433.
- Fisher, R. A. 1958. *The genetical theory of natural selection*, 2d ed. New York: Dover.
- Fox, S. F. 1975. Natural selection on morphological phenotypes of the lizard *Uta stansburiana*. *Evolution* 29: 95-107.
- Fox, S. F. 1983. Fitness, home-range quality, and aggression in *Uta stansburiana*. In *Lizard ecology*, ed. R. B. Huey, E. Pianka, and T. Schoener, pp. 149-168. Cambridge: Harvard Univ. Press.

- Gans, C. 1974. *Biomechanics, an approach to vertebrate biology*. Philadelphia: Lippincott.
- Garland, T., Jr. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. *Am. J. Physiol.* 247: R806-R815.
- Garland, T. Jr. 1985. Ontogenetic and individual variation in size, shape, and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool.*, in press.
- Gibbons, J. W., and J. L. Greene. 1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. *Herpetologica* 35: 86-89.
- Greenwald, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia* 1974: 141-148.
- Hecht, M. K. 1952. Natural selection in the lizard genus *Aristelliger*. *Evolution* 6: 112-124.
- Houck, L. D., S. J. Arnold, and R. A. Thisted. 1985. A statistical study of mate choice: sexual selection in a plethodontid salamander (*Desmognathus ochrophaeus*). *Evolution* 39: 370-386.
- Howard, R. D. 1981. Male age size distribution and male mating success in bullfrogs. In *Natural selection and social behavior*, ed. R. D. Alexander and D. W. Tinkle, pp. 61-77. New York: Chiron Press.
- Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19: 357-366.
- Inger, R. F. 1943. Further notes on differential selection of variant juvenile snakes. *Am. Nat.* 77: 87-90.
- Kempthorne, O. 1957. *An introduction to genetic statistics*. New York: John Wiley.
- Klauber, L. M. 1945. Herpetological correlations. I. Correlations in homogeneous populations. *Bull. Zool. Soc. San Diego* 21: 5-101.
- Kluge, A. G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. *Misc. Publ. Mus. Zool. Univ. Mich.* 160: 1-170.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33: 402-416.
- Lande, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* 62: 607-615.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210-1226.

- Mather, K., and J. L. Jinks. 1977. *Introduction to biometrical genetics*. London: Chapman and Hall.
- McGregor, P. K., J. R. Krebs, and C. M. Perrins. 1981. Song repertoires and lifetime reproductive success in the great tit (*Parus major*). *Am. Nat.* 118: 149-159.
- Noodwijk, A. J. van. 1982. Genetic variation in life history traits in natural populations of birds. In *Evolution and the genetics of populations*, ed. S. D. Jayakar and L. Zonta, pp. 141-152. *Aui. Ass. Genet. Ital.*, Vol. 29 (Suppl).
- Peterson, J. A. 1983. The evolution of the subdigital pad of *Anolis*. 2. Comparisons among iguanid genera related to the anolines and a view from outside the radiation. *J. Herpetol.* 17: 371-397.
- Pollack, E., O. Kempthorne, and T. B. Bailey, Jr. 1977. *Proc. Internat. Conf. on Quantitative Genetics*. Ames, Iowa: Iowa State Univ. Press.
- Pough, F. H. 1977. Ontogenetic change in blood transport capacity and endurance in garter snakes (*Thamnophis sirtalis*). *J. Comp. Physiol.* 116: 337-345.
- Pough, F. H. 1978. Ontogenetic changes in endurance in water snakes (*Natrix sipedon*): physiological correlates and ecological consequences. *Copeia* 1978: 69-75.
- Pough, F. H., and S. Kamel. 1984. Post-metamorphic change in activity metabolism of anurans in relation to life history. *Oecologia* 65: 138-144.
- Price, T. D. 1984. Sexual selection on body size, territory and plumage variables in a population of Darwin's finches. *Evolution* 38: 327-341.
- Price, T. D., P. R. Grant, and P. T. Boag. 1984a. Genetic changes in the morphological differentiation of Darwin's ground finches. In *Population biology and evolution*, ed. K. Woehrmann and V. Loeschke, pp. 49-66. Berlin: Springer-Verlag.
- Price, T. D., P. R. Grant, H. L. Gibbs, and P. T. Boag. 1984b. Recurrent patterns of natural selection in a population of Darwin's finches. *Nature* 309: 787-789.
- Rand, A. S. 1954. Variation and predator pressure in an island and mainland population of lizards. *Copeia* 4: 260-262.
- Reznick, D. 1982. The impact of predation on life history evolution in Trinidadian guppies: Genetic basis of observed life history patterns. *Evolution* 36: 1236-1250.
- Robertson, A. 1959. Experimental design in the evaluation of genetic parameters. *Biometrics* 15: 219-226.

- Roeder, K. D. 1963. *Nerve cells and insect behavior*. Cambridge: Harvard Univ. Press.
- Rose, M. R., and B. Charlesworth. 1981. Genetics of life-history in *Drosophila melanogaster*. I. Sib-analysis of adult females. *Genetics* 97: 173-186.
- Schluter, D. 1984. Morphological and phylogenetic relations among the Darwin's finches. *Evolution* 38: 921-930.
- Shaffer, H. B., and G. V. Lauder. 1985a. Aquatic prey capture in ambystomatid salamanders: patterns of variation in muscle activity. *J. Morph.* 183: 273-284.
- Shaffer, H. B., and G. V. Lauder. 1985b. Patterns of variation in aquatic ambystomatid salamanders: kinematics of the feeding mechanism. *Evolution* 39: 83-92.
- Smith, J. N. M. 1985. Determinants of lifetime reproductive success in the song sparrow. In *Reproductive success*, ed. T. Clutton-Brock. Chicago: Univ. of Chicago Press.
- Stearns, S. C. 1983. The genetic basis of differences in life-history traits among six populations of mosquitofish (*Gambusia affinis*) that shared ancestors in 1905. *Evolution* 37: 618-627.
- Swain, D. P., and C. C. Lindsey. 1984. Selective predation for vertebral number of young sticklebacks, *Gasterosteus aculeatus*. *Can. J. Fish. Aquat. Sci.* 41: 1231-1233.
- Tinkle, D. W. 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Publ. Mus. Zool. Univ. Mich.* 132: 1-182.
- Travis, J. 1983. Variation in development patterns of larval anurans in temporary ponds. I. Persistent variation within a *Hyla gratiosa* population. *Evolution* 37: 496-512.
- Van Berkum, F. H. and J. S. Tsuji. 1985. Among-family differences in sprint speed of hatching *Sceloporus occidentalis*. Manuscript.
- Van Valen, L. 1963. Selection in natural populations: Human fingerprints. *Nature* 200: 1237-1238.
- Voris, H. K. 1975. Dermal scale-vertebra relationships in sea snakes (Hydrophidae) *Copeia* 1975: 746-755.
- Webb, P. W. 1984. Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* 24: 107-120.
- Wecker, S. C. 1963. The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdi*. *Ecol. Monogr.* 33: 307-325.
- Weinberg, W. 1909. Über Vererbungsgesetze beim Menschen. II. Spezieller Teil. Allgemeine Lösung des Problems der Wirkung

- der Panmixie bei ein factor Vermischung und alternativer Vererbung. *Z. für Induk. Abstamm. Vererbungslehre* 2: 276-330.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15: 393-425.
- Wright, S. 1921. Systems of mating. *Genetics* 6: 111-178.