ities, or continuing contact with water. Females exposed to male courtship behaviors and insemination ovulate in *Taricha granulosa*, and plasma progesterone concentrations are highest in those females that possess oviducal ova (Moore et al., 1979). Plasma progesterone concentrations in females of *H. nigrescens* are low throughout the year except during the aquatic phase in March when females have some ova within the coelom and many ova in the oviducts and ovisacs after the completion of ovulation (Hasumi et al., 1993). In the present study, a surge of progesterone would be expected to occur 14–18 h after the injection of hCG if ovulation is dependent on progesterone, though the trigger for ovulation is unknown.

The present study suggests that globular products of secretions in the lumina of the ventral glands grow into colloidal secretions by the consecutive secretion from the epithelial cells. These colloids change again into globules after discharging outside the body. Secretory products in the lumina of the ventral glands had partially leaked outside the body 32 h after the injection. In several species of hynobiid salamanders, the male clasps or chases the female at the bottom of an aquarium during prestages of reproductive behavior (Hasumi, 1994; Sato, 1991). I suggested that these behaviors were responses of breeding males to a leakage of the secretions from the ventral glands of gravid females, rather than "courtship" (Hasumi, 1994). The present study reinforces this hypothesis.

The percentage of increase in body mass between group 0 h (12.5 g: just before entering a breeding pond) and group 50 h (18.3 g: just before oviposition in the pond) was 46.4%. Hasumi and Iwasawa (1990) showed the increase in percentage to be 31.2% at the transition between females before and after entering the pond. This lower value is due to the sample consisting of both postovulation and preoviposition females. The increase of 5.8 g in body mass was mostly the result of the absorption of water for the formation of egg sacs. In *H. nigrescens*, the mean mass of a pair of egg sacs just excised from the dilatable ovisacs is 5.37 g, including the egg mass of 12.1% (Hasumi et al., 1994). Thus, an increase in body mass not due to egg sac formation is also possible.

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# QUANTITATIVE GENETICS—WHAT IS IT GOOD FOR?

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ABSTRACT: A recent multi-author volume edited by Christine Boake, *Quantitative Genetic Studies of Behavioral Evolution*, offers a collection of conceptual and empirical works outlining the use of quantitative genetics in evolutionary research. Though the book is geared towards studies of behavior, many of the lessons and techniques pertain to any kind of trait. Contrary to some popular perceptions about quantitative genetics, the work presented in this book demonstrates the value and insight to be gained from a quantitative genetic approach to evolutionary biology. This theme is extended in this review with a discussion of exciting new directions in quantitative genetics and the prospects for this methodology in herpetological research.

*Key words:* Behavior; Evolution; Genetic correlation; Heritability; Maternal effects; Plasticity; Quantitative genetics

THE process of evolution is a deceptively simple combination of forces that acts within generations (i.e., selection, migration, drift) and a set of phenomena (i.e., genetics) that translates these forces into change across generations. There are many approaches to studying evolution, but a complete understanding must include both parts of the process. Quantitative genetics (QG) has become a popular approach to understanding evolution, in part because it provides a simple framework in which to combine knowledge of forces such as natural selection with an understanding of inheritance. This combination provides a powerful framework for predictions and/or descriptions of short term evolutionary change. The quantitative nature of models and empirical data that stem from QG thereby provides an appealing way to understand the relative importance of genetics and selection in driving evolution.

The focus of QG is on the phenotype, so that the traits of interest to ecologists, behaviorists, and natural historians can be directly examined with respect to inheritance. For many biologists, the shortcoming of most types of genetic investigation is that the variables observed (e.g., proteins, sequence variation) do not translate obviously into characters that matter in the real world. Conversely, virtually any trait that can be "seen" (and studied from an ecological perspective) can be subjected to QG analyses (Falconer, 1989). The compromise of QG is less direct information about the genetic bases of traits, but with the advantage of ecological relevance.

Most approaches and techniques experience a cycle of attitudes by the scientific public, and QG is no exception. The approach was popularized among evolutionary biologists by the so-called "Chicago School" (Grafen, 1988) in the early 1980's and enjoyed much excitement and easy acceptance for the better part of that decade. Key papers by Lande, Arnold, and Wade (Arnold and Wade, 1984*a*,*b*; Lande, 1979; Lande and Arnold, 1983) emphasized the importance of exploring the entire phenotype rather than individual traits, and they offered an explicit quantitative framework in which to study selection and evolutionary change. The initial appeal of QG has given way to a phase of disenchantment, wherein critics have focused more closely on the problems and pitfalls of the methodology, minimizing the advantages and insights to be gained.

A recent book edited by Christine Boake promises to rekindle excitement in the use of quantitative genetic approaches to the study of evolution:

*Quantitative Genetic Studies of Behavioral Evolution*. Edited by Christine R. B. Boake. 1994. University of Chicago Press, Chicago, Illinois. $24.95 paper.

The chapters presented in this volume cover a range of current conceptual issues in the field of microevolution of behavior, and they provide an introduction to some of the most important empirical work using a quantitative genetic approach to behavior. This volume should appeal to biologists of all stripes, whether they employ quantitative genetics or not. The book focuses on studies of the genetics of behavior, but its lessons are broad enough to offer insights into the general process of evolution of any category of phenotype, from morphology to life history. The book is roughly divided into two parts: the conceptual chapters (Ch. 2–6) represent a user-friendly introduction to some very complicated issues in evolution, while the taxonomic and phenotypic breadth of the empirical chapters (Ch. 7–13) are guaranteed to expand the knowledge base of most biologists.

Along with these two sections, Boake provides two chapters (Ch. 1, 14) that offer some cohesion to the collection of works presented in the book. In her introduction to the volume, Boake outlines some of the issues that the field of QG attempts to address, and she underscores the need for studies of the mechanisms and patterns of inheritance. As is true of the majority of the book, these comments are tailored to behavioral traits in particular, but they are relevant to virtually any trait of interest. The concluding chapter offers some cautionary notes about undertaking QG studies, from issues of sample size (they better be large!) to the cost–benefit relationship between the effort expended and the information gained. Some of the conceptual difficulties encountered in QG are mentioned (e.g., commonly violated assumptions of the models, limitations to the application of related theories), but as is expected in such a book, the negative dimensions are not overly indulged. Boake's discussions are an excellent starting point for assessing the feasibility and value of a QG approach to one's own system.

## THE CONCEPTUAL CHAPTERS

In many ways, the gem of the book is Stevan Arnold's chapter (Ch. 2) reviewing the basics of QG theory and methodology. A book of this type could live or die by the quality of a chapter that introduces the major concepts that are covered in subsequent chapters. The field of evolutionary QG has long awaited a succinct and simple overview of the major concepts in multivariate inheritance. Arnold's primer on QG fills this void by walking the thin line between simplicity and completeness. In just over 30 pages, he takes one through his "genetics without tears" approach to QG, from breeding value to maternal inheritance. The generous use of graphics to illustrate major concepts and the beginner's guide to matrix algebra offered as an appendix make the quantitative nature of QG accessible to even the most mathematically challenged among us.

Derek Roff's chapter (Ch. 3) explores the contrasts between optimality modeling and QG. The chapter delicately sidesteps what most biologists recognize as fervent antagonism between the two camps and concentrates on the complimentary aspects of the two approaches. In some ways, the differences reflect philosophies about how evolution works: optimality focuses on where a population should exist in phenotype space when fitness is maximized while QG examines the process by which the population gets there (or not) (e.g., Moore and Boake, 1994). As Roff points out, both aspects are important components of a complete view of evolution. Many critics of QG point out that equilibrium predictions of optimality and QG should be the same, but this is not necessarily the case. A recent paper by Gomulkiewicz (1997) outlined the unexceptional conditions under which the approaches yield different predictions.

The evolutionary causes and consequences of maternal effects are among the hottest topics in QG today, and the chapter by James Cheverud and Allen Moore (Ch. 4) provides an excellent introduction to the major concepts. The environment provided by parents and other relatives has long been known to affect the expression of some phenotypes in offspring. The models presented and reviewed in this chapter explore the evolutionary importance of such influences. The authors present in detail a model that treats maternal effects as a "performance" character (cf. Cheverud, 1984), wherein all the traits that might have an influence are lumped into a single trait called maternal performance. While this view of maternal effects masks the connection between specific parental (e.g., nest site selection, frequency and amount of provisioning to offspring) and offspring characters, the perspective is quite helpful in that it provides a mathematically simple model that explains the evolutionary importance of maternal effects. More complex multivariate models are also reviewed, and a "translation table" explaining the connection between variables in the simple model presented here and other multivariate models (e.g., Kirkpatrick and Lande, 1989) will assist readers in exploring the literature. The chapter concludes with an intriguing list of implications and directions for research that should stimulate any unfocused graduate student with an interest in this area.

Lorraine Heisler (Ch. 5) reviews some of the models that have incorporated QG into sexual selection theory. The bulk of these models concentrate on distinguishing the type of selection that is responsible for the evolution of female mating preferences—Fisherian runaway, good genes, the sexy son. Heisler points out the difficulties in empirically distinguishing between these alternatives based on the equilibrium predictions of the QG models. "Female preference functions" (i.e., the relationship between female preferences and the distribution of male phenotypes) are one key element of many of these models that remain virtually unstudied in natural systems.

The contrast between phenotypic and genetic approaches to studies of evolution is made plain in the chapter by Linda Partridge (Ch. 6). Drawing on examples from the *Drosophila* literature, Partridge illustrates how both approaches can be used to dissect direct and indirect selection and identify the actual targets of sexual selection. Costs of sexually selected traits and cryptic female mating preferences are also examined. The general considerations that should influence any researcher's decision to adopt either a genetic or nongenetic approach to a project are clearly outlined.

## THE EMPIRICAL CHAPTERS

Hugh Dingle (Ch. 7) reviews what is understood about the genetic bases of migratory behavior in a variety of taxa. Genetic variation has been detected in a wide array of specific behavioral elements, from the tendency to migrate to the preferred direction of migration. The necessity of a multivariate approach to evolutionary studies is underscored through Dingle's discussion of migration "syndromes". Adaptation to a migratory habit appears to involve a whole suite of correlated characters, including not only behavior but also morphology, physiology, and life history. Examples offered in this chapter illustrate some of the unexpected payoffs of a QG approach.

Conditional behavioral strategies (e.g., alternative male mating strategies) are a classic problem in behavioral ecology. Joseph Travis takes a genetic perspective on this phenomenon in his chapter (Ch. 8). The majority of the work reviewed is Travis' own research on size-dependent mating behavior in sailfin mollies. Size differences in male mollies are apparently controlled by a sex-linked locus of major effect, and so are not truly quantitative, but the general approach does yield the observation that behavior and size are genetically correlated, possibly through pleiotropic effects. Travis also offers a set of predictions about the evolution of behavior–morphology correlations and interpopulational differences in phenotype based on his genetic hypotheses.

Ary Hoffman (Ch. 9) reports on his studies of territoriality in natural populations of *Drosophila melanogaster.* Because of the logistics of the biological system, Hoffman was able to impose artificial selection on a number of lines of *Drosophila* to examine directly the genetic response to known levels of selection. This approach provides genetically divergent lines of high and low territoriality that enable Hoffman to investigate additional genetic hypotheses; territoriality in *Drosophila* does appear to have a strong genetic basis that is only slightly dependent on environment [little or no genotype-by-environment interaction (G × E)], and decreased longevity may be a trade-off of high levels of territoriality. Hoffman's research is a fine example of the complementarity of QG and optimality approaches to behavioral ecology.

Cannibalism is investigated by Lori Stevens (Ch. 10) in a model laboratory system, *Tribolium confusum.* Stevens presents an elegantly complete study of the inheritance of cannibalism in flour beetles, including not only evidence of genetic control, but also of dominance effects and loci of major effect for some behaviors. She is also able to dissect the importance of biotic and abiotic environmental factors in determining the expression of cannibalism. The ecological and evolutionary implications of cannibalism are discussed at great length. Of particular interest is the discussion of Wright's shifting balance theory as a mechanism that may maintain population differences in cannibalistic behavior.

The relevance of genetic studies is taken into the field in Ann Hedrick's studies of calling behavior in crickets (Ch. 11). Hedrick tackles the standard criticism of QG studies that laboratory measures of genetic variation are irrelevant because natural environmental variation will swamp out genetic effects. Individual differences among males in calling bout length were found to be highly repeatable and heritable in the laboratory. Experiments manipulating environmental factors did not affect these measures. Moreover, Hedrick reports results from field phonotaxis experiments that illustrate the ecological significance of individual differences in call characters.

In the lone chapter concerning reptiles (Ch. 12), Theodore Garland presents his multivariate approach to understanding the inheritance of locomotor physiology and behavior in garter snakes, *Thamnophis sirtalis.* Garland compares a variety of behavioral, morphological, and physiological characters in an attempt to identify correlated suites of traits and the genetic potential for response to selection. The rationale that traits experiencing stronger selection should have lower heritability (because selection exhausts genetic variation) is used to predict which characters are most important to selection. While intriguing, the theoretical difficulties of the approach (Charlesworth, 1987; Mousseau and Roff, 1987; Price and Schluter, 1991) make this indirect method of identifying targets of selection suggestive at best. Contrary to the predictions, few of the physiological and morphological measures correlated with organismal measures of performance, and speed and endurance were strongly positively correlated.

Carol Lynch's chapter (Ch. 13) presents some of the best work to date on correlated suites of traits. Her studies of laboratory and natural populations of the house mouse (*Mus domesticus*) reveal adaptations to cold environments that include an integrated set of physiological (brown adipose tissue), behavioral (nest building), and morphological (body size) characters. Lynch capitalizes on the laboratory nature of her system to explore the genetic bases and integration among these traits through controlled breeding and selection line experiments. Predictions generated by the genetic results are then investigated in field populations of *Mus,* and a latitudinal cline in cold-adaptedness is revealed. Finally, a paradoxically low value of a physiological trait in northern populations is explained through the observed negative genetic correlation (i.e., trade-off) with body size.

### QUANTITATIVE GENETICS—WHY BOTHER?

As is apparent from the work reviewed in Boake's book, QG studies are tedious and resource consuming. Why, then, bother with a research approach that requires meticulous husbandry and breeding, huge numbers of individuals, and a few leaps of faith on assumptions underlying statistical analyses?

Adaptive evolution is a process that begins with variation—for selection to act, there must be differences among individuals (Lewontin, 1970). The factors that control individual variation (i.e., genetics and environment) are the agents that translate selection into change across generations. Quantitative genetics as an approach examines the relative importance of causal components of variation (both genetic and environmental), which leads to an understanding of how evolution proceeds. Many of the chapters in Boake's book emphasize the fact that selection only results in evolution if the characters in question are heritable. The greater the heritability, the stronger the effect of selection. Environmental variation also affects evolutionary trajectories, whether by masking genetic variation or by influencing translation of genetic variation into phenotypes (e.g., plasticity, genotype-by-environment interaction). In the case of maternal effects, environmental variation may even have an underlying genetic component (see the chapter by Cheverud and Moore). Knowledge of the sources and patterns of phenotypic variation and covariation is essential to understanding the evolution of any traits or taxa.

Alternative approaches to studying evolution are available, but they do not address the same parts of the process. Comparative studies, popular since Darwin and rejuvenated by recent statistical advances, offer insight into the history of evolution and the patterns produced by it (Brooks and McClennan, 1991; Harvey and Pagel, 1991). Optimality and game theory approaches dissect the details of natural selection, but they do not consider the process by which change is transmitted across generations (chapter by Cheverud and Moore; Gomulkiewicz, 1997; Moore and Boake, 1994). Quantitative genetics is essentially a statistical tool kit designed to examine sources of variation and covariation; it is a powerful technique for studying evolutionary process within populations (Boake, 1994; Falconer, 1989), but QG becomes most valuable as a methodology for tackling specific biological questions. Many of the classical problems in behavior (Boake, 1994), systematics (Dohm and Garland, 1993; Felsenstein, 1988; Leroi et al., 1994; Shaffer, 1986), life history (chapters by Dingle and Roff; Mousseau and Dingle, 1991; Reznick, 1985), and even conservation (Cheverud et al., 1994; Janzen, 1994) can be fruitfully addressed from a QG perspective. A number of such specific applications are reviewed in Boake's book and elsewhere (Brodie and Garland, 1993). The herpetological literature has produced two of the best examples of the benefits of applying QG to specific biological problems or systems.

Developmental plasticity is an obvious

feature of many pond breeding amphibians. The genetic and environmental factors influencing developmental rate have been well studied in a range of species (e.g., Berven, 1987; Newman, 1988, 1989; Pfennig et al., 1991). A QG approach has revealed that there is genetic variation for time to metamorphosis and developmental rates (Blouin, 1992; Emerson et al., 1988; Travis et al., 1987). Moreover, genetic variation has been detected for plasticity of larval period (i.e., genotypes respond differently to environmental variation)—a key requisite for adaptation to ephemeral environments (Newman, 1994). Other studies have investigated the possibility that differences in timing and rate of development might cause changes in adult morphology (i.e., heterochrony) through genetic correlations between morphology and larval life history traits (Blouin, 1992; Emerson et al., 1988). The incorporation of QG has provided a better understanding of both the mechanisms responsible for and the possible consequences of plasticity in larval life history.

Quantitative genetics has also shed new light on old problems. The maintenance of polymorphism, especially in color pattern, has long been the focus of evolutionary biologists. One of the classic case studies is the variation in banding pattern of water snakes (*Nerodia sipedon*) in and around Lake Erie. Earlier work suggested that different frequencies of pattern morphs in island and mainland populations were maintained by differences in selection balanced by migration (Beatson, 1976; Camin and Ehrlich, 1958; Camin et al., 1954), but no quantitative predictions about the magnitude of selection or migration necessary to maintain this variation were possible. Recent studies by Rich King have examined this hypothesis in detail (King, 1987, 1992, 1993*a*,*b*; King and Lawson, 1995). By incorporating QG and related techniques into the investigation, King was able to make and test quantitative predictions about the microevolutionary forces causing population differentiation (King and Lawson, 1995). Empirical results suggest that differential selection and gene flow are indeed important forces, but they also point to the importance of stochastic processes (e.g., drift, founder effect) in generating the observed polymorphism in color pattern. This work has emerged as one of the most complete examinations of microevolution in any taxon.

## Hot Directions in QG

Many scientists seem to view QG as a dead arena for research—most of the exciting advances were offered up in the 1980's, and current research is simply building the base of empirical knowledge. Moreover, QG is often viewed as a laboratory science, with limited application to natural systems. In fact, the production of novel QG theory is far outpacing our empirical knowledge, and a number of the chapters in Boake's book demonstrate the utility and applicability of QG to the "real world". The development of new analytical techniques promises to extend QG into new topics from parental care to ontogeny. While some of these "hot directions" are of interest mostly to quantitative geneticists, many will no doubt lead to new ways of looking at old problems throughout biology.

Maternal effects are influences of the mother (or any relative) on her offspring's (or other relative's) phenotype that are not a result of the direct inheritance of genetic information—they might take the form of provisioning an egg, selecting a nest site, or direct parental care such as feeding. Recent theoretical advances (reviewed in the chapter by Cheverud and Moore) point out that these environmental effects might have underlying genetic bases, and thereby drive evolutionary change. Genes that control a trait for parental care in the parent influence different aspects of the offspring's phenotype, but are themselves inherited by the offspring. Thus, while care is an environmental influence on the offspring, variation in care can reflect genetic differences among parents that can be passed on (along with other genes) to the offspring. This cross-generational effect sets up the possibility of some very non-intuitive evolutionary dynamics, from generational delays in the response to selection to maladaptive evolution (see chapter by

Cheverud and Moore; Kirkpatrick and Lande, 1989). Furthermore, maternal effects may themselves be adaptations to fluctuating environments—the environment experienced by a mother during egg provisioning or deposition may influence her offspring's phenotype directly, allowing for more fine scale tracking of the environment than can be accounted for by changes in gene frequency. These possibilities have only begun to be investigated empirically (e.g., Mousseau, 1991; Mousseau and Dingle, 1990, 1991).

Developmental trajectories and ontogeny are of concern to students of morphology and behavior alike. One common approach is to view ontogeny as a series of states expressed at different points in time, yet many theories are founded on assumptions about the actual shape of the growth curve or developmental trajectory. Statistical machinery for evaluating growth and development as curves is now available by viewing these characters as "infinite-dimensional" traits, or functions relating the values of one character (e.g., body size) to an environmental variable such as time (Gomulkiewicz and Kirkpatrick, 1992). This approach has an intuitive appeal, in that development can be understood as the continuous character it is, rather than a collection of (usually) arbitrarily chosen discrete points along a developmental pathway (e.g., Cheverud and Leamy, 1985). Investigations of the QG of infinite-dimensional characters will directly address the problem of developmental constraint and the role of genetic variation for ontogenetic trajectories in evolution. The "infinite-dimensional" view of phenotypes can be adapted to other kinds of characters the expression of which varies with environmental variables (Gomulkiewicz and Kirkpatrick, 1992). Any norm-of-reaction (e.g., sprint speed as a function of body temperature) or behavioral plasticity (e.g., calling frequency as a function of group size) could be modeled as an "infinite-dimensional" trait by relating the trait to a continuous environmental variable, generating a function or multivariate surface.

Plasticity can also be examined under discrete environments or conditions, and, while the topic of much empirical work, is still a controversial issue (Via et al., 1995). Many issues in behavior are questions of plasticity, and it is surprising that none of the chapters in Boake's book address this approach. Genotype-by-environment interactions and genetic correlations between the same trait expressed in different environments (e.g., size at metamorphosis in the presence or absence of a particular predator) can be used to investigate evolutionary constraints to adaptation in multiple environments (the "jack-of-all-trades is a master of none" paradigm) (Gomulkiewicz and Kirkpatrick, 1992). One of the most heated debates in evolutionary genetics today concerns the genetic basis of plasticity—whether genetic variation exists for plasticity per se, or whether genetic variation in each environment explains the observed variation in reaction norms (reviewed in Via et al., 1995).

One of the criticisms of QG is that it treats genetics as a "black box"—it relies on statistics to infer underlying causal components of variation from phenotype and relatedness. Examining the genes, or more accurately, the additive effects of genes, that influence quantitative traits has remained an elusive dream of quantitative geneticists. With the advent of increasingly powerful molecular techniques, the ability to examine the molecular basis of polygenes ("quantitative trait loci" or "QTLs") is growing and is likely to have a significant impact on future studies of evolutionary quantitative genetics (Cheverud and Routman, 1993, 1995; Mitchell-Olds, 1995; Routman and Cheverud, 1994). Through the combination of known pedigrees and genetic mapping, correlations between particular regions of the genome and quantitative traits can be identified. Once QTLs are located, quantitative geneticists will have a more fundamental understanding of the genetic phenomena underlying trait variation. These empirical data are crucial for evaluating hypotheses about the frequency of genes of major effect, the stability of the **G** matrix, the ubiquity of pleiotropy, the basis of genotype-by-environment interactions, and the role of epistasis. Such advances will enable QG and complementary studies of selection (e.g., Brodie et al., 1995) to tackle some of the major questions in evolutionary biology from the genetic basis of speciation to the importance of macromutation in adaptation.

## HERPETOLOGICAL RESEARCH AND QG

Herpetologists will recognize that most amphibian and reptilian systems do not make ideal subjects for QG studies (see chapters by Arnold and Boake; also Brodie and Garland, 1993). Difficulties with controlled breeding, space and facilities needed for husbandry, and the longevity/age to maturity of most species present tremendous obstacles to the implementation of a QG research program. The sample sizes required for good estimates of genetic parameters (from 30–200 families, depending on the question and breeding system) are prohibitive for many laboratories and species. In wild caught families, questions of parentage (i.e., multiple paternity within a litter) complicate statistical analyses. But the picture is not all dark—herpetological research has made some major contributions to the field of QG, especially through applications to natural populations. The trail blazing empirical studies of evolutionary QG in the wild were conducted by Arnold in the early 1980's on garter snakes (Arnold, 1981*a*,*b*, 1988; Ayres and Arnold, 1983).

Not least among the advantages of herpetological systems is the wealth of interesting biological problems—any technique is only as exciting as the problem to which it is applied. Herpetology has contributed greatly to our understanding of ecology, functional morphology, development, endocrinology, behavior—practically all biological disciplines. Investigations of the sources of individual variation in any of these dimensions would expand an understanding of the evolutionary processes that are responsible for the phenomena observed.

Surprisingly, there are even logistical advantages to some herpetological systems. A few species can be obtained in large numbers (e.g., *Thamnophis*, *Hyla*, *Scaphiopus*). Large clutch/litter sizes of many species reduce the standard errors of estimated QG parameters while providing an opportunity for split-family experiment manipulations of environmental sources of variation (e.g., Arnold and Peterson, 1989; Osgood, 1978; Sinervo, 1990; Sinervo and Huey, 1990). External fertilization in anurans allows certainty of paternity and even the opportunity to produce artificial crosses. In most species of reptiles and amphibians, egg development is external, so developmental environment and even investment by parents can be directly manipulated (e.g., Sinervo, 1990; Sinervo and Huey, 1990).

There is still great potential for significant advances in ecology and evolution through the use of QG. The understanding of the genetic bases of most traits is minimal and yet their implications for an understanding of evolution is great. Boake's book, supplemented with a basic understanding of statistics and a few well chosen references on QG (e.g., Falconer, 1989; Weir et al., 1988) can go a long way toward stimulating important and exciting research. Interested researchers will find Boake's book to contain advice and caution about implementing QG in their own research programs, as well as a fount of biological problems waiting to be addressed.

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# ADDITIONAL COMMENTS ON THE ORIGIN OF THE WEST INDIAN HERPETOFAUNA

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In his response to our recent essay (Crother and Guyer, 1996), Hedges (1996*a*) took issue with each of our major points. Because biogeography represents the ultimate puzzle in biology, it is not surprising that such polar positions could be taken by scientists examining the same data. Our major point was that the sampling regime used by Hedges and his colleagues to assess the roles of vicariance and dispersal in the Caribbean was biased and, therefore, incapable of arbitrating between these two explanations. As an aid to readers interested in sorting our differing views, we add the following observations associated with specific points raised by Hedges.

Hedges (1996*a*) complained that we missed significant literature dealing with molecular evolution of Caribbean taxa. In our defense, we note that virtually all of

the references, listed by Hedges as missing from our paper, are present in the citations associated with our text.

Hedges argued that our statistical treatment of a clearly identified pool of immunological data was unnecessary because the appropriate data are the most recently derived sister-taxa that can be found for pairs of sites. This observation by Hedges crystallizes our differing views and, we think, illuminates flaws in methods and logic used by Hedges et al. (1992) and repeated by Hedges (e.g., 1996*b*). The sampling universe now described by Hedges does not reflect pairs of taxa that appeared in Hedges et al. (1992), especially for mainland–island comparisons. Because phylogenies clearly identifying sister taxa for Caribbean taxa are not available, one could not expect to design a sampling protocol for the pool now described. We argue that the sampling pool that we outlined appropriately mimics the one implied by Hedges et al. (1992:Table 1) and, therefore, that immunological distances besides the ones listed by those authors must be considered. The observation that a fossilized anole is known from the Caribbean [Rieppel (1980); upper Eocene (40–36 ma), but may be as young as 30–17 ma (Grimaldi, 1995)] that is older than the divergence events selected by Hedges et al. (1992; 16.8 ma; Table 2) to describe the origination of that lineage within the Greater Antilles provides further support for our contention that immunological data associated with older divergence events must be considered. Hedges and his colleagues admitted that the fossil evidence was problematic but failed to recognize its impact on their sampling universe.

Hedges (1996*a*) claimed that no consistent pattern exists among published phylogenies of Caribbean taxa. Additionally, he asserted that our attempt to extract such a pattern merely reflected the inclusion of currently unpublished data on xenodontine snakes (Crother, 1989). Because the quality of data used to create some published phylogenies has been questioned (e.g., Hass, 1991; Page and Lydeard, 1994), we attempted to include only studies that were at least minimally defensible. Again, we clearly identified the pool from which we sampled, used a currently recognized analytical tool (Brooks and McLennan, 1991) to describe an overall pattern, and provided a crude test of the significance of that pattern. The same pattern is recovered from our sample of phylogenies when the study by Crother (1989) is eliminated. This pattern is demonstrably nonrandom, illustrating how easily one's eyes can cause one to conclude, falsely, that phylogenetic trees lack pattern (see also Simberloff, 1989).

Because dispersal between a pair of sites can occur in either direction and at any time, the method championed by Hedges cannot be used to arbitrate between islands containing taxa originating exclusively by overwater dispersal [or nearly so, according to Hedges (1996*b*)] from islands containing taxa originating via vicariance followed by occasional dispersal to and from those islands. We do not believe that Hedges or his collaborators have addressed this point adequately nor do we believe that they can, given the well known problems with determining directionality for dispersal events and determining history from two-taxon statements (Rosen, 1978).

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