

Carroll, S.P. + Corneli, P.S.

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The Evolution of Behavioral Norms of Reaction as a Problem in Ecological Genetics

Theory, Methods, and Data

SCOTT P. CARROLL

PATRICE SHOWERS CORNELI

Behavior, like other phenotypic traits, varies as a function of genes and environment. Variation occurs at all demographic levels, within individuals over time, between individuals, and between populations and species. Whether variation is important will depend on the behavior and its context. For example, whether a bird scratches its head by extending a leg above or below the adjacent wing may not have profound fitness consequences, although species differences in this character may shed light on phylogenetic relationships (e.g., Wallace 1963; Simmons 1964). In contrast, other behaviors, such as the instantaneous decision to migrate or not, may affect fitness directly by altering the schedule of fecundity or mortality (Dingle et al. 1982). Such strategic behaviors (Maynard Smith 1982), which often depend for their expression on the assessment of local cues (Moran 1992), are complicated and important evolutionary traits. The phenotypic variability that defines them, however, has hindered our ability to treat them with formal evolutionary-genetic analyses that are central to the complete understanding of any putative adaptation.

Much of the evolutionarily important variation observed in strategic behavior probably stems from differences among individuals due to genotype-environment interactions. To illustrate this in the most general terms, consider that behavioral distinctions among individuals may be based on (1) differences in the environmental conditions they experience, (2) differences in genetic elements that code for specific tactics or predispositions, or (3) differences in the genotype-environment interaction, manifested through developmental or facultative pathways, that is, "norms of reaction" (Schmalhausen 1949). Norms of reaction are functions that describe how a genotype is translated into a phenotype by the environment. They are becoming widely employed as a paradigm in evolutionary studies of physiological and life-history traits (e.g., Dingle 1992; reviewed by Stearns 1989),

but are not yet used widely in studies of behavioral traits (but see Thompson this volume). Because much of the variation that behaviorists observe within populations and species is likely the result of a complex combination of individual differences in genetic code and differences in environment, norms of reaction need to be explored as a method for understanding the sources and structure of behavioral variation.

In nature, behavioral variation occurs not just within populations, but among them as well. Comparative methods distinguish historical (e.g., phylogenetic) versus ecological contributions to phenotypes (e.g., Endler 1982), and geographic comparisons within species are useful in limiting phylogenetic variation, while taking advantage of environmental differences that may cause strategic divergence. For testing theoretical ideas about behavioral adaptation, this between-population approach (e.g., in birds: Reyer 1980, Dhont 1987, Koenig and Stacey 1990, Dunn and Robertson 1992; in fish: Kodric-Brown 1981, Mousseau and Collins 1987, Foster 1988, 1995; Houde and Endler 1990; in mammals: cf. Sherman 1989; in insects: Riechert 1986b, Carroll 1993; and most of the chapters in this volume) is similar to that taken in studies that examine conditional variation (norms of reaction) within a population as a function of resource variation (e.g., reviews of behavior by Thornhill and Alcock 1983, Lott 1991).

However, studies of geographic variation that do not also examine conditionality within populations may confound the sources of variation. Environmental differences between populations may cause behavioral differences even if the populations do not differ genetically. Or the population differences may have a genetic basis. Without making this distinction, population differences in behavior may be incorrectly assumed to have a genetic basis, while in fact neither the intra- nor interpopulation approach normally directly addresses genetic contributions to behavioral variation.

In figure 3-1, we illustrate the complexity implicit in interpreting the causes of geographic variation. To emphasize our point, we depict a one-dimensional domain with simple relationships between environmental and phenotypic values. Natural situations are typically more complex because environmental "gradients" are often nonlinear mosaics, multiple environmental factors interact, and complex phenotypes such as behavior may exhibit an array of potentially interchangeable and nonlinear (e.g., threshold) values, which may in turn influence the environmental conditions experienced.

Figure 3-1A shows the first empirical step: the observation of a difference in the mean phenotypic value of a trait between geographically distinct populations along an environmental gradient. Such an environmental axis could be a gradient in the physical environment, such as temperature variation with latitude, or a gradient in the social system of a species or in the community ecology of its habitat. Figure 3-1B-D show the predictions of three hypotheses that could explain the observation. Figure 3-1B depicts the hypothesis of genetic determination: the population difference will be maintained when the observations are made in the reciprocal environments. An analysis of variance (ANOVA) would show a significant population (genetic) effect, but nonsignificant environmental and population-by-environment interaction effects. Figure 3-1C depicts the hypothesis

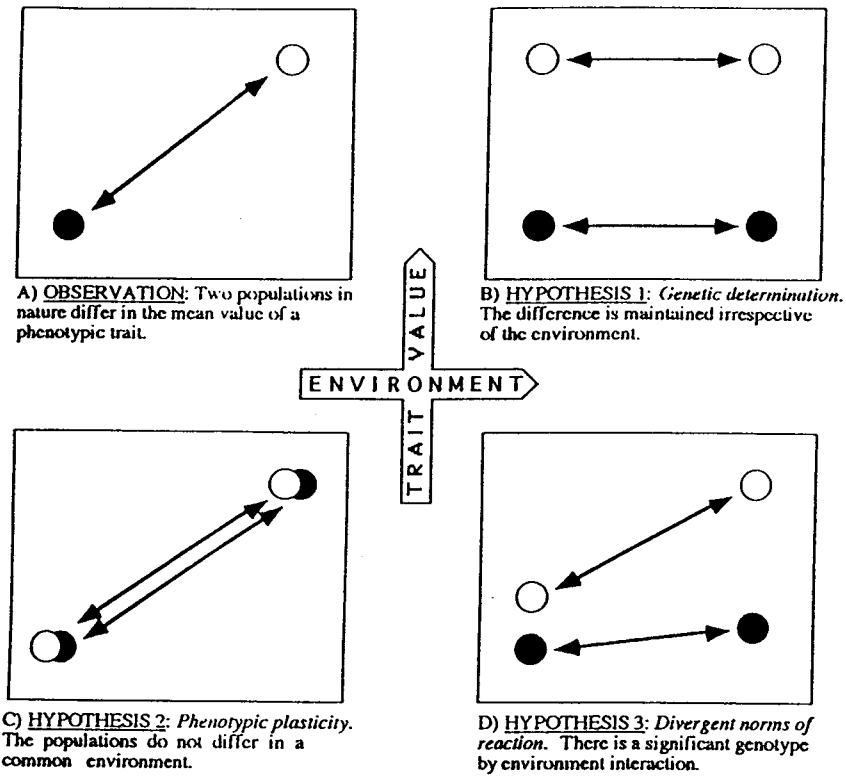


Figure 3-1 Alternative hypotheses for geographic variation in a phenotypic trait.

of species-wide phenotypic plasticity: members of the two populations show the same mean phenotypes when observed under identical conditions. In this case ANOVA would show a significant environment effect, but nonsignificant population and interaction effects. Figure 3-1C depicts the hypothesis of phenotypic plasticity: the populations do not differ in a common environment. In this case, ANOVA would show significant environment, population, and interaction terms. Note that in each case, the hypothesis is tested by observing each population at more than one point along the environmental gradient.

The norms of reaction depicted in figure 3-1 represent phenotypic mean responses. To the extent that these responses are genetically determined, the response of each population could be decomposed to show its constituent genotypic norms of reaction. Depending on intrapopulation heterogeneity, these could be tightly clustered about the mean responses or widely spread about the means. Gathering data at this level has the value of clarifying the nature and extent of differentiation both within and between populations. In addition, because plastic-

ity and genetic polymorphism are evolutionarily interdependent, as discussed below, more fully accounting for the sources of behavioral variation is a critical aspect of understanding the evolution of behavior in general.

In this chapter, we discuss some of the reasons strategic behavioral traits, and especially behavioral plasticity, are important and unusual evolutionary traits. We present the merits of studying geographic variation in behavioral norms of reaction and review some salient literature on the evolutionary genetics of population differentiation in behavior and phenotypic plasticity. Then, using an example from our work with soapberry bugs, we present an analysis of geographic variation in the plasticity of the male mating strategy and its underlying genetic variation. We find that this intraspecific comparison presents a special opportunity for considering the effects of both environmental and genetic differences.

Behavioral Plasticity and Genetic Variation

Behavioral traits are even more complex than many physiological and life-history components of fitness (e.g., Price and Schluter 1991) because they may often be more flexible (i.e., exhibit reversible change) and more frequently revised (i.e., altered after assessment). The flexibility and responsiveness of behavior are among the traits of greatest functional importance in all of evolution because they provide a program for "adapting" to environmental changes throughout each individual's lifetime (Thoday 1953, Slobodkin and Rapoport 1974). Two general views have been developed to describe the evolutionary importance of behavioral flexibility. First, such within-generation plastic responses may promote homeostasis and thereby "buffer" the genetic effects of natural selection (Wright 1931, Sultan 1987). Alternatively, adaptive behavioral flexibility may increase the variety of habitats to which a genotype has access, ultimately enhancing a population's potential for evolutionary change (Morgan 1896, Waddington 1953, Wcislo 1989, West-Eberhard 1989). These ideas are developed below.

The power of natural selection to shape populations depends in part on three aspects of genotype-environment interaction that determine the relative fitness of individuals under diverse conditions: the capacity for adaptive plasticity inherent within genotypes, the pattern of diversity among genotypic norms of reaction within populations, and the distribution of environmental variability (Levins 1968, Sultan 1987, 1993). As a result, plasticity and genetic polymorphism will interact in evolutionary time. For example, both phenotypic plasticity (de Jong 1989) and genetic polymorphism may be maintained by spatial variation in selection (Levene 1953, Maynard Smith and Hoekstra 1980, Via and Lande 1985), while plasticity, evolved in response to spatial or especially to temporal variation (Moran 1992), may act to reduce the intensity of diversifying selection (sensu Wright 1931, Levins 1963, Slobodkin and Rapoport 1974). In other words, once an organism is sufficiently plastic, it will not experience spatial variation in selection at the level experienced by less plastic counterparts. On the other hand, in a population of plastic individuals, disparate genotypes may converge on a common adaptive phenotype, effectively shielding genetic variation. Moreover, even when

genotypes differ in their responses to environment, these differences may sum to equal fitnesses across environments, again shielding them from natural selection (Haldane 1946, Via 1987, Gillespie and Turelli 1989, Barton and Turelli 1989). These hypotheses are important because the potential for evolutionary change in a population depends in part on its genetic variation (Fisher 1958).

The inherent complexity of genotype-environment interactions indicates the importance of studying genetic and environmental variation in tandem. A foundation for such an approach comes from the work of quantitative geneticists, who in recognizing the importance of environmental variation in determining phenotypic values, work to control the environmental conditions in which they conduct their studies (e.g., Falconer 1981). Until recently, the converse could not be said of ecologists, and behavioral and other variation is still most often related to environmental variation with scant consideration for genetic variation, especially at the empirical level. One useful technique is the "common garden experiment," developed by botanists, in which study subjects from disparate environments are observed in the same setting to test for genetic differences. This approach has been used to show genetically based population differentiation in the social behavior of amphipods (Strong 1973), spiders (Uetz and Cangialosi 1986), and fish (Magurran 1986, Magurran and Seghers 1990).

The common garden technique may be readily extended to permit the measurement of norms of reaction by observing populations across a range of reciprocal environmental conditions. At least four studies have used this approach to study population divergence in strategic behavior. Lynch (1992) studied the effects of temperature on nest-building behavior in mice, Riechert (1986a) examined food availability and territoriality in spiders, Dingle (1994) studied the effects of temperature on flight propensity in milkweed bugs, and Carroll and Corneli (1995) examined the effects of sex ratio on male mate-guarding decisions in the soapberry bug. All but Riechert (1986a) observed differentiation among populations in reaction norms; Riechert (1993, this volume) provides evidence that gene flow among her study populations has retarded divergence.

These studies, as well as other recent genetic studies (summarized in table 3-1), offer some preliminary answers to questions about the genetics of behavioral traits strongly tied to fitness. Most basically, behavioral variation among populations often has some genetic basis. Behavioral variation among individuals within populations has a genetic basis as well, with instances of both Mendelian and quantitative control documented (Orr and Coyne 1992). In addition, some behavior patterns are tightly correlated with other traits and may form genetically based, coadapted complexes with morphological values (e.g., male mating morphs within populations of swordtails, *Xiphophorus nigrensis* [Ryan et al. 1992], and of sponge-dwelling isopods [Shuster 1989]), life-history values (e.g., differences in age of first reproduction in differentially migratory morphs between populations of milkweed bugs, *Oncopeltus fasciatus* [Dingle 1994]), and behavioral values (e.g., mating success [Hoffmann and Cacoyianni 1989]).

Taken together, these results show that genetic differences among individuals can be important in behavioral differentiation both within and among populations.

Table 3-1 Examples of the use of quantitative genetics as a tool for studying the biology of behaviors related to fitness.

Behavior	Reference
Intraspecific crosses	
Foraging	Arnold 1981, Schemmel 1980, Hedrick and Riechert 1989
Migration	Berthold and Querner 1980
Predator avoidance	Riechert and Hedrick 1990
Courtship	Krebs 1990
Territorial and agonistic behavior	Riechert 1986a, Riechert and Maynard Smith 1989
Parent-offspring regression	
Migratory behavior	Caldwell and Hegmann 1969
Host preference	Fox 1993
Half-sib designs	
Migratory behavior	Dingle 1988, Fairbairn and Roff 1990
Dispersal	Greenwood et al. 1979, Mikasa 1990
Agonistic behavior	Riddell and Swain 1991
Antipredator behavior	Brodie 1989, Breed and Rogers 1991
Male mating strategy	This chapter
Full-sib designs	
Host preference	Via 1986, Fox 1993
Among-colony comparisons (honeybees)	
Behavioral ontogeny	Page et al. 1992
Artificial selection	
Migratory behavior	Palmer and Dingle 1989
Agonistic behavior	Ruzzante and Doyle 1991
Male mating strategy	Cade 1981
Territorial and mating success	Hoffmann and Cacoyianni 1989

Most of these studies have not formally considered behaviors as norms of reaction, but several have investigated the genetics of behavioral differences between populations.

An example of how this genetic perspective can be extended to comparisons of behavioral reaction norms is the subject of the next section.

Geographic Variation in Behavioral Plasticity in the Soapberry Bug: Environmental, Population, and Additive Genetic Effects

We are comparing the form and flexibility of male mating tactics (mate guarding versus nonguarding) among populations of soapberry bugs from two types of environments: those that exhibit spatial and temporal stability in male/female ratios (southern Florida), and those that exhibit exceedingly variable male/female ratios (Oklahoma). Our focus is to test whether (1) behavioral differences between populations have a genetic basis, (2) males from the more variable environment show a more plastic mating strategy than do those from the more constant environment, and (3) the populations differ in the amount of additive genetic variation underlying the behavioral reaction norms.

The soapberry bug, *Jadera haematoloma* (Insecta: Hemiptera: Rhopalidae), is a mainly neotropical seed predator. It follows the distribution of one of its host plants, the western soapberry tree, *Sapindus saponaria* v. *drummondii* northward into the temperate south-central United States, and the distribution of another, the balloon vine, *Cardiospermum corindum*, into subtropical Florida. Thus it forms two ecologically divergent and geographically disjunct metapopulations in the United States. We have studied aggregations at host plants in central and west-central Oklahoma and in the upper Florida Keys for several years. Bugs from the two regions are essentially identical in appearance and are interfertile, but several lines of evidence suggest that there is probably little gene flow between them (Carroll and Boyd 1992). As a result, they may evolve differentially in response to regional differences in selection (see Thompson this volume for further discussion).

The principal mating decision that adult male soapberry bugs can make is whether to guard mates after insemination or depart and search for additional matings (sensu Parker 1978). Sperm transfer is completed in 10 min or less, but males often remain in copula with females after inseminating them. In the field, pairs of marked individuals have been observed to remain together for as long as 11 days, with the female laying several clutches of eggs while the male attends (Carroll 1991).

Males in the two regions may have evolved differences in mating behavior at three levels. First, differences between bug populations in the relative costs and benefits of mate guarding versus nonguarding could select for differences in male propensity to exhibit either tactic (the mean of the reaction norm). Second, any differences in the variability of mating opportunities could select for differences in behavioral plasticity (the slope of the reaction norm). Third, any differences specifically in the spatial variability of mating opportunities could also result in the maintenance of different levels of genetic variation for the male behavioral reaction norm.

As indicated above, the regional difference with the greatest potential impact on the male mating system is in the mean and variability of sex ratio in large reproductive aggregations around the host plants. In Oklahoma, sex ratios have ranged from 0.62 to 4.71 males per female (mean = 2.60 ± 1.02 SD, $n = 33$ aggregations); in contrast, they are restricted much more closely to 1:1 in Florida (range = 0.56–1.67, mean = 1.07 ± 0.29 males/female, $n = 21$ aggregations). Sex ratio is also significantly more variable in Oklahoma (variance = 1.27) than in Florida (variance = 0.08; $F(1, 54) = 17.0$, $p < .0001$; Carroll and Corneli 1995). Thus, the populations differ in both the magnitude and variability of female availability as mates. This pattern may cause the populations to differ in the form and intensity of sexual selection on male mating behavior as well as other characters (Carroll and Salamon 1995). The primary sex ratio is 1:1 in both populations, but greater female than male mortality occurs during most phases of the life cycle in Oklahoma, apparently in association with environmental and developmental stresses related to ephemeral breeding opportunities in a highly variable climate (Carroll 1988, 1991).

The difference in mean sex ratio is reflected in the costs of mate searching in

the two populations. In field experiments, the search time required for a male to find a mate was about three times greater in an Oklahoma aggregation (sex ratio 3:1) than in a Florida aggregation (sex ratio 1:1). Consistent with predictions based on this difference, brief (unguarded or minimally guarded) pairings were almost twice as common in Florida as in Oklahoma (Carroll 1993). This behavioral observation is of the type depicted in figure 3-1A. The regional difference in sex ratio variation also suggested that males from Oklahoma, but not Florida, might show the capacity to alter their tactical allocation as a function of the sex ratio experienced.

To test this hypothesis, we observed males from both populations in greenhouse arenas over a range of four experimental sex ratios (a "common garden" design; male:female 1:2, 1:1, 2:1, and 3:1). The results showed that the strategic differences between the populations have a genetic basis and that the population from the more variable sex ratio environment (Oklahoma) appears to be more plastic behaviorally (details below; Carroll and Corneli 1995).

Further, we incorporated a half-sib breeding design into this experiment to investigate how the plasticity of the phenotype interacts with its genetic variation at the population level (fig. 3-2, Falconer 1981). This gave us our third basic result: the Oklahoma population appears to have significant additive genetic variation for the male strategy, whereas the Florida population does not. These findings are also detailed below. Because of our small number of sire families, we followed the suggestion of Via (1986) to avoid relying on estimates of variance components and instead limited our treatment to analyses of the interaction between sire family and sex ratio within each population.

The nature of the data (sequences of states observed at discrete time intervals) and of the hypotheses suggested modeling the sequences of mating behavior as first-order Markov chains. These are stochastic processes in which the probability of an event occurring depends only on the immediately preceding event. For a male making tactical decisions, the present mating state should depend, in part, on the previously sampled one. For example, a guarding male should be more likely to stay with the same female from one observation to the next than a male who devotes more effort to searching. The latter male should switch from one female to another relatively more often. The probabilities of transitions from one behavioral state to another should differ among males and populations employing different mating strategies. By fitting the mating data to suitable probabilistic models and comparing the results of the fits, the differences should be revealed in log-likelihood ratio tests (LRT) of maximum likelihood estimators (MLEs) (Carroll and Corneli 1995). The null hypothesis is that the transition probabilities do not differ among the four sex ratios. We used first-order chains rather than more complex models because the mating state just before the current one is probably much more likely to have a significant effect on the current one than are more removed mating states.

The main results are shown in figure 3-3. Guarding behavior changed significantly as a linear function of sex ratio in the Oklahoma population (LRT = 66.8, $df = 1$, $p < .001$), but not in the Florida population (LRT = 1.6, $df = 1$, $p > .10$; Carroll and Corneli 1995). To examine additive genetic variation, we used a nes-

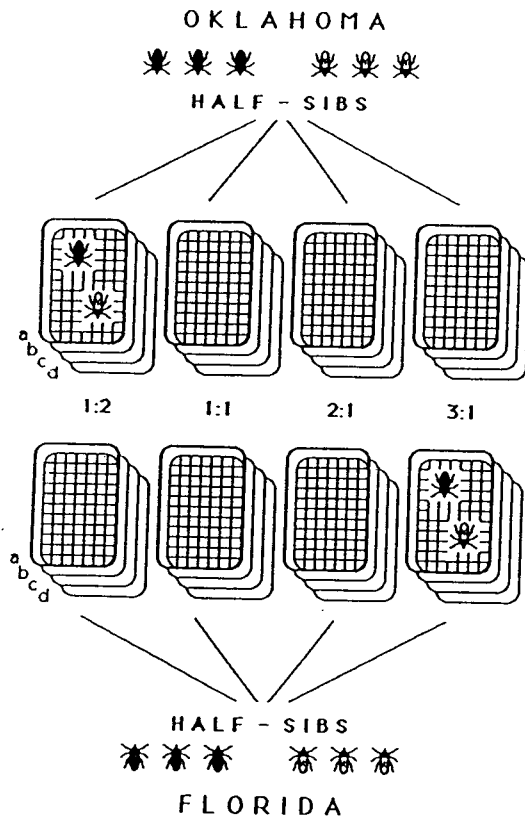


Figure 3-2 Stylized depiction of the experimental design. The grandparents of the bugs used in this experiment were collected from Boiling Springs State Park in Woodward County, Oklahoma, USA, and Plantation Key in Monroe County, Florida, USA. They were held in captivity in identical rearing cages at similar densities, where they reproduced feeding on the seeds of their native host plants. First-generation adults were paired in a half-sib mating design, with seven sires for Oklahoma and eight for Florida, each mated to three or four different females. Their offspring were similarly reared in full sib-groups. Experimental (second-generation) individuals were taken from these parents as newly molted (naive virgin) adults, measured, and given an individually identifying number on the dorsum. Members of each full-and-half-sib family were distributed nearly uniformly through the sex ratio treatment replicates. Arenas were plastic boxes 33 × 24 × 11 cm high. Twenty-four virgin adults were placed in each arena, in groups consisting of 8 males + 16 females, 12 males + 12 females, 16 males + 8 females, and 18 males + 6 females. Each sex ratio treatment was simultaneously replicated four times per population. Light and temperature conditions simulated those typical of reproduction in the field, and food and water were provided ad libitum. The mating status (copulating or single) of all individuals, was recorded at 3-h intervals, eight times each day, for 8 days.

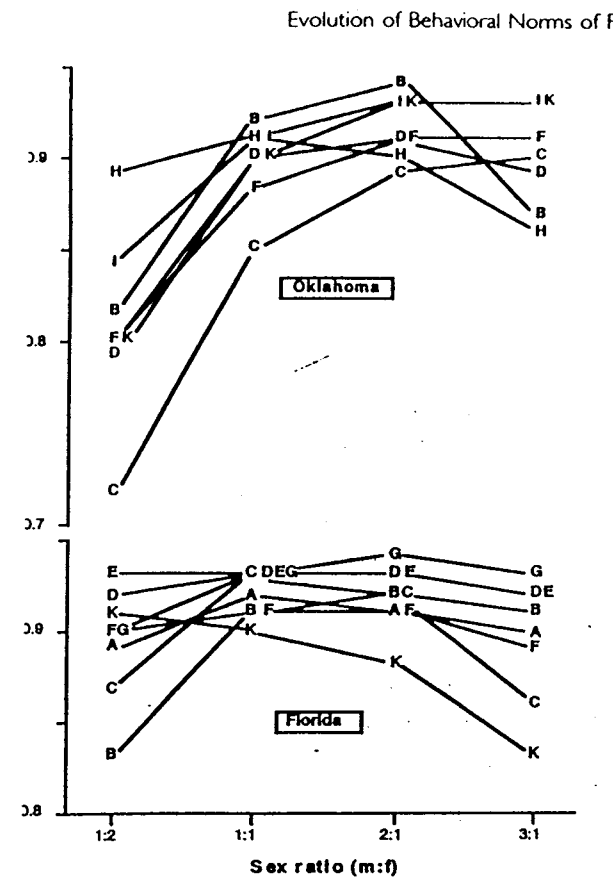


Figure 3-3 Mean probabilities of guarding a female from one observation period to the next (3-h observation interval) for each of seven half-sib families (Oklahoma, above), or eight half-sib families (Florida, below), measured at four sex ratios. Letters designate each family within a population.

ted design and a binomial model in which we fit a slope to each family's norm of reaction across sex ratio treatments (comparable to an ANCOVA). The interaction between family and ratio was significant for Oklahoma (LRT = 15.5, $df = 6$, $p < .025$), indicating that slopes differ among families as a result of additive genetic variation. The results of the "ANCOVA" model analysis also suggest that slopes are significantly different from zero ($p < .05$) for each family except B and H.

In contrast, Florida families did not differ in guarding behavior (LRT = 7.5, $df = 7$, $p > .10$) when all families were considered simultaneously (fig. 3-3). Likewise, examination of the individual slope parameters and their standard errors for each family separately showed no change in mating behavior as a linear function of sex ratio, with the possible exception of family B ($p < .05$).

Interpretation of the Results and General Conclusions

Without the results of our common garden, norm of reaction experiment, one could readily argue that the phenotypic differences in soapberry bug mate-guarding originally observed between populations in nature by Carroll (1993) reflect an evolved, unconditional difference in mating strategy. One biologist could equally well argue that what was observed is part of the range of behavior available to all male soapberry bugs depending on the environmental conditions. Both analyses would be incomplete and potentially misleading. The populations have differentiated in both senses; it is the reaction norm that has differentiated, resulting in an inherited differential response that depends on the conditions a male experiences.

More broadly, we have found variation across environmental conditions, between populations, and perhaps as a function of additive genetic variation as well. Phenotypic variation at all of these levels results from a combination of behavioral plasticity and evolutionary response to diversifying selection. Behavioral plasticity is predicted to evolve chiefly in response to temporal variation in environmental conditions (Moran 1992), but to the extent that individuals may encounter variable conditions by moving, spatial variation may play an important role as well. Both kinds of variation are experienced by male soapberry bugs during their adult lifetimes (Carroll 1988, 1993, unpublished data).

It is interesting to consider how these findings relate to the general and often conflicting notions about the interaction of plasticity and genetic variation. In the Oklahoma population, relatively great behavioral plasticity and genetic diversity co-occur. This indicates that in the more variable environment, genetic differences among individuals in behavioral predisposition exist in spite of plasticity that potentially shields genetically different bugs from differential reproductive success. In addition, two of the seven Oklahoma half-sib families were not plastic, and one of the eight Florida families was. Thus the genetic predispositions for behavioral plasticity and nonplasticity appear to exist currently in both populations. Exploring such questions further will require larger sample sizes for each population to give greater statistical power for analyzing genetic and environmental components of variance, as well as data from more populations in diverse environments to test the generality of our results.

The co-occurrence of plasticity and genetic variation in the male mating strategy of the Oklahoma population also relates to theories addressing "evolutionary potential" in populations. Genetic variation is required for evolutionary change, and the rate of evolutionary response to selection is directly proportional to the amount of additive genetic variation present (Fisher 1958). In addition, West-Eberhard (1989), independently developing a premise originally put forth by Morgan (1896), suggested that relatively plastic organisms are more likely to encounter novel conditions that could increase the diversity of genotype by environment interaction manifested and thus increase the diversity of potential evolutionary trajectories. Because of the special power of behavioral plasticity to influence the selective environments experienced by other phenotypic traits, this argument

should be especially relevant for behavioral plasticity as compared to plasticity in other fitness-related traits.

To the extent that both strategic plasticity and genetic variation for the behavioral strategy are greater in Oklahoma, that population's potential for evolutionary change may be greater than that of the more tropical, environmentally static Florida population. Oklahoma bugs, which inhabit an unstable environment at the northern edge of the species range, are probably derived from more tropical ancestors. Their local adaptations to environmental variability, including behavioral plasticity, may serve to accelerate their rate of evolutionary divergence from tropical antecedents beyond that which would be predicted from measurements of mean selection intensity and genetic variation alone.

Our study does not test whether individuals in each population exhibit optimal or evolutionarily stable tactics within and across sex ratios. Nor do our results distinguish the genetic basis of the population difference. Our focus was simply to ask whether there is plasticity and whether this allows the individual to do well in its own environment. In this sense we have taken a sufficiency rather than an optimality approach. This approach has permitted us to ask evolutionary questions about complicated fitness-associated traits that are difficult to model, and it has revealed a fascinating tactical complex within the species.

Dobzhansky (1951) argued that norms of reaction, rather than specific traits, are the targets of selection, a perspective that has continued to be explored into the present (Via et al. 1995). He was making a plea for incorporating more of the complexity of nature into scientific study, a perspective that clearly applies to behavior hypothesized to be adaptively flexible. All the current model approaches to behavioral evolution—evolutionarily stable strategies, optimality, quantitative genetics, norms of reaction—are simplistic caricatures of the true complexity of natural systems. Yet, because they are complementary and can be combined, as shown here and in our related work (Carroll 1993, Carroll and Corneli 1995), progress can be made in analyzing the evolution of strategic conditionality.

Behavioral strategies may be viewed as tool kits that organisms use to solve problems and to take advantage of the opportunities they encounter. Because the form and frequency of problems and opportunities differ among environments, geographic comparisons are valuable for testing hypotheses about the selective basis of strategic variation. When possible, it is also important to test whether population differences in behavior result from genetic diversification or from phenotypic plasticity. Only by doing so can a researcher know whether the phenomena under study are different expressions of the same strategy or different strategies altogether; whether a biologist uses adaptation as a "null hypothesis" or has specifically demonstrated adaptive differentiation, it will be valuable to know the manner in which the pattern results from environment and/or genetics. Distinguishing these sources of variation is basic to understanding both the structure of adaptation within and among populations and the processes by which new behavioral phenotypes evolve. To ignore this issue is to remain at the crossroads in the battle between those who champion the power of selection in phenotypic evolution and those who argue for the importance of "phylogenetic constraints." By

instead comparing strategies as norms of reaction, in reciprocal environments, it may be possible to move beyond this superficial dichotomization of "adaptation versus constraints" and study instead the adaptive process within a genetic lineage.

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