

Divergence in male mating tactics between two populations of the soapberry bug: II. Genetic change and the evolution of a plastic reaction norm in a variable social environment

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Many social behaviors are conditional, but behavioral comparisons between populations do not normally distinguish genetic and environmental causation. As a result, the opportunity to test predictions about the evolution of strategic conditionality (genotype \times environment interaction) is lost. We apply these concepts in an examination of how interpopulation differences in mean and variance of sex ratio have led to genetic differences in the allocation of male effort to mate guarding versus nonguarding between genetically isolated populations of the soapberry bug in Oklahoma and Florida. We observed the mating behavior of males from the two populations at a series of experimental sex ratios, and modeled their mating decisions as first-order Markov chains of independent mating states. Likelihood ratio tests of these behavioral sequences showed that the populations differed significantly in their response to sex ratio, and that only males from the variable environment (Oklahoma) altered their behavior in response to differences in female availability among the treatments. The flexible strategy of this population may be adaptive and probably has evolved in response to sex ratio variability. *Key words:* alternative mating tactics, geographic variation, norm of reaction, phenotypic plasticity, sex ratio. [*Behav Ecol* 6:46–56 (1995)]

Comparisons among taxa are a fundamental tool for hypothesis testing in evolutionary biology (Endler, 1986). When comparing among taxa, a major problem involves distinguishing the extent to which differences in trait values result from independent evolution. Recent philosophical and statistical advances that have addressed this problem for interspecific comparisons (Harvey and Pagel, 1991) are valuable for relatively variable traits such as behavior, in which phenotypes are more difficult to quantify both in the present and historically. Nonetheless, such techniques cannot overcome limitations imposed by inaccuracies in our phylogenies, nor can they control for unobserved but potentially confounding historical variables that accumulate during the long times that separate many speciation events and the present.

One possible solution is to make comparisons that are more conservative phylogenetically, i.e., between populations within species (e.g., studies reviewed by Lott, 1991). Intraspecific comparisons may reduce uncontrolled phylogenetic differentiation, and they are increasingly employed in evolutionary studies (references below; Foster and Endler, in press). The relative similarity of populations within a species makes them ideal subjects for simultaneously assessing the environmental and population-genetic components of phenotypic variation. Here we develop this concept for the study of behavioral evolution.

Generally speaking, for few examples in nature can we confidently distinguish the fundamental sources of behavioral variation, either within or among populations. Behavioral distinctions among individuals may result from multiple sources: environmental differences, such as differences in the developmental environment or in the environmen-

tal conditions in which they are studied, genetic differences, and differences in the interaction of genotypes or populations with the environment (norms of reaction) manifested through developmental or facultative pathways. The two most common approaches used to account for behavioral variation do so only partially: studies of conditionality within populations generally ignore genetics (e.g., cases reviewed by Thornhill and Alcock, 1983; Lott, 1991), and studies of differences among populations or sibling species usually assume conditionality, or can assume only some genetic basis (for mating systems: Carroll, 1993; Dhont, 1987; Houde and Endler, 1990; Kodric-Brown, 1981; Koenig and Stacey, 1990; Lott, 1991; Mousseau and Collins, 1987; Reyer, 1980; Sherman, 1989; see Strong, 1973 for an early exception). Thus, while both approaches provide insight into the ecological determinants of behavior, neither distinguishes genetic and environmental sources of behavioral variation. This contrasts with studies of developmental and life history traits, in which genetic analyses of norms of reaction have commonly been used to explain phenotypic variation among populations (especially in plants: reviewed by Bradshaw, 1965; Schlichting, 1986; Sultan, 1987; in animals: Berven, 1982; Berven and Gill, 1983; Berven et al., 1979; Dingle et al., 1982; Hebert and Grewe, 1985; and Via, 1984, 1991). Reaction norms may be similarly used to study population-genetic and environmental contributions to behavioral variation.

An additional motive for treating tactical behaviors as norms of reaction is to develop a method of studying the evolution of behavioral flexibility. Behavioral flexibility provides a program for adapting to changes in the distributions of risks and op-

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portunities throughout each individual's lifetime, and is thus a phenotype of great potential evolutionary importance (*sensu* Slobodkin and Rapoport, 1974). Models by de Jong (1989) contrast the expected magnitude of phenotypic plasticity (the shape of the reaction norm) between populations that differ in the degree of environmental variation they experience, but to the best of our knowledge, such concepts have never been explicitly tested for animal behavior. At least three studies have relevant results, however. Lynch (1992) examined the effects of temperature on nest building behavior in mice, Riechert (1986) studied food availability and territoriality in spiders, and Dingle (1994) studied the effects of temperature on flight propensity in milkweed bugs. In each study, the responses of two or more populations were compared across two experimental environments. These environments were chosen to span a range of conditions that might provide cues for functional changes in behavior. Lynch (1992) and Dingle (1994) observed differentiation among populations in reaction norms, but Riechert (1986) did not.

Studies of this type have not been conducted for most social interactions. For male mating behavior, conditional responses may be predicted from the distributions of mates in space and time (e.g., Bradbury and Vehrencamp, 1977; Emlen and Oring, 1977; Parker, 1970; Rubenstein, 1980; Yamamura, 1986), and the effects of intrasexual and sperm competition (e.g., Parker, 1978; Yamamura, 1986). This approach has been used to predict how mating behavior should vary, both within populations (for insects, e.g., Alcock et al., 1977; Campanella and Wolf, 1974; Carroll, 1991; Clark, 1988; Hayashi, 1985; Johnson, 1982; McLain, 1980; Rubenstein, 1984; Sillén-Tullberg, 1981; Thornhill, 1981; Thornhill and Alcock, 1983; Waage, 1973) and between them (Carroll, 1993). The predictions are of two forms: what will the mating strategy be? and, if the strategy consists of alternative tactics, how will they be deployed as a function of environmental conditions?

To explore these ideas, we have compared the influence of sex ratio on male mating decisions between two populations of the soapberry bug (*Jadera haematoloma*; Insecta: Hemiptera: Rhopalidae) that differ in the mean and variance of adult sex ratio. In the United States, this primarily neotropical insect occurs mainly in two ecologically divergent and geographically disjunct populations, one in the south central/southwestern states, and the other in Florida (Carroll, 1988). In Oklahoma, near the northern edge of the species' range, differential juvenile and adult mortality often creates strongly male biased sex ratios, but in the Florida Keys, sex ratios are much closer to 1 : 1 (Carroll, 1988, 1991, 1993). Previous work has shown that males in these populations differ in their frequency of mate guarding, as predicted by models based on the differences in sex ratio (Carroll, 1993). Our goal in this study is to quantify the extent to which this between-population variation in mate guarding frequency is genetically based, and/or results from differential expressions of a species-wide conditional mating strategy, in which the probability of guarding depends on the prevailing mating opportunities. Using a "common garden" design in which we studied both populations under the same en-

vironmental conditions, we quantified norms of reaction for guarding and nonguarding in both populations across a range of experimental sex ratios. We found that the populations have differentiated genetically in their mating strategy, and that only males from the Oklahoma population, in which sex ratio is highly variable, altered their tactics in response to our sex ratio treatments.

METHODS

Sex ratios in nature

Aggregations of *J. haematoloma* were sampled at host plants in central and west-central Oklahoma in 1982–1987 (on western soapberry tree, *Sapindus saponaria* v. *drummondii*, and golden rain tree, *Koeleruteria paniculata*) and in the upper Florida Keys during 1985–1989 (on balloon vine, *Cardiospermum corindum*). Sites are described in detail by Carroll (1988). Aggregation sex ratios were measured by counting all adult males and females encountered on and under a host plant in a 20-min period. Only aggregations in which >50 adults were sampled are included in statistical analyses. More details about sampling and aggregation structure are given by Carroll (1991, 1993).

Male mating behavior and sex ratio manipulations

Similarities in the breeding environments of the Oklahoma and Florida Keys populations (Carroll, 1988) made it possible to provide each group with suitable captive conditions in a greenhouse (University of Utah, Department of Biology). The grandparents of the bugs used in this experiment were collected from Boiling Springs State Park in Woodward County, Oklahoma, and Plantation Key, Monroe County, Florida. More than 200 individuals were collected from each site. They were held in captivity, where they reproduced feeding on the seeds of their native host plants. We paired F_1 adults in a half-sib mating design (Falconer, 1981). Experimental (F_2) individuals were taken from these parents as newly molted (virgin) adults, and given individually-identifying numbers on the dorsum, as in field studies (Carroll, 1993). Members of each F_2 family were distributed uniformly through the sex ratio treatment replicates (by population; below) to minimize genetic differences among treatments. Quantitative genetic analyses are presented elsewhere (Carroll and Corneli, in press).

Arenas were clear plastic storage boxes 33 × 24 × 11 cm high. They were coated on the interior rim with Fluon AD-1, floored with a large sheet of filter paper, and covered with clear plastic lids that had mesh-covered ventilation portals 7.5 cm in diameter. The Fluon prevented the bugs from walking out when the lids were removed for observations. Twenty-four adults, initially virgin, were placed in each arena, in groups consisting of 8 males and 16 females, 12 males and 12 females, 16 males and 8 females, and 18 males and 6 females. We chose these four sex ratios because they span much of the natural range of sex ratios observed for the species. The two populations were treated separately; they were not mixed in the arenas. We simultaneously replicated each sex ratio treatment

Table 1
Matrix of mating state transition probabilities

	Second behavioral state		
	1	2	3
First behavioral state			
1	p_{11}	p_{12}	p_{13}
2	p_{21}	p_{22}	p_{23}
3	p_{31}	p_{32}	p_{33}

four times per population. Light and temperature conditions simulated those typical of reproduction in the field (13.5 L : 10.5 D, Daylight fluorescent tubes; 30°C average in daytime, 26° average at night). The pan floors were marked with red lines in a grid at 5-cm intervals to facilitate censusing. Unlimited food from the appropriate native host plant and water (in cotton-stoppered 2 dram vials) were provided. To avoid disturbing the insects, box lids were carefully removed during observations, and red light was used for night observations. Bugs did not attempt to fly from the pans. Individuals that died during the study (<2%) were replaced with sexually mature virgins of the same sex and population, and when possible, the same family.

The mating status (copulating or single) of all individuals, was recorded at 3-h intervals, eight times each day, for 8 days. Three hours was the minimum logistically feasible sampling interval; though a small minority of matings lasts less than 3 h (Carroll, 1991, 1993), this interval is sufficient to detect the majority of transitions. Also recorded at these times were instantaneous observations of movement, mounts by males on other single males, on single females and on mating pairs, and female resistance to copulation (shaking and running by single females, shaking and kicking by mated females).

The most common point at which individual pairings terminate is shortly after oviposition (Carroll, 1988, 1991). As a result, any differences in the interval between ovipositions by females, either among sex ratios or between populations, could strongly affect mating patterns. In the present study, we recorded ovipositions either by observing them directly, or from changes in egg load (on a 0–4 scale of increasing abdominal expansion) between consecutive samples taken at 3-h intervals.

For all descriptive statistics, means are presented ± 1 standard deviation.

A statistical model for the sequence of mating behaviors

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, each a stochastic process in which the probability that an event occurs depends only on the immediately preceding event. For a male making allocation decisions, the present mating state should depend, in part, on the previous one. The probabilities of transitions from one behavioral state to another should differ among males employing different mating strategies. A guarding male should be more likely to stay with the same female from one observation

to the next than should a male who devotes more effort to searching. The latter male should switch from one female to another relatively more often. Possible differences between males in the amount of time allocated to mate guarding and promiscuous mate searching should be revealed by comparing the results of fits of the mating data to suitable probabilistic models.

At a given time a male was either single or mating. The data were contracted to a three-state sequence: if a male was single, he was in state 3. Once he began mating he entered state 1, where he remained until he either stopped mating, when his state reverted to 3, or he switched to another female. Upon so switching he was in state 2, where he remained until he either stopped mating (state 3) or switched mates again (back to state 1). States 1 and 2 were essentially identical mating states, distinguished only for the purpose of evaluating guarding and switching behavior. If X_n = the state of a male at time n , then the sequence, $\{X = X_1, \dots, X_n, \dots\}$ retains all information about the frequencies with which a male stays with a female, switches to a new mate, and does not mate at all.

If p_{ij} is the probability that the male is in mating state j given that his last state was i , then the matrix of transition probabilities is shown in Table 1, where some of the transitions represent the same event. Thus p_{11} and p_{22} both represent the probability that the male continues mating with the same female at time n as at time $n - 1$. Likewise p_{12} and p_{21} are both the probability that the male will switch mates from one observation to the next, and both p_{13} and p_{23} are the probability that the male, who had been mating at the last observation, is now single. By construction, the transition $3 \rightarrow 2$ cannot occur and so $p_{32} = 0$. Also since $\sum_j p_{ij} = 1$, ($i, j = 1, 2, 3$) there are only three independent parameters.

Letting $\alpha = p_{11} = p_{22}$, $\beta = p_{12} = p_{21}$, and $\gamma = p_{31}$, the transition probability matrix for the proposed Markov chain describing a sequence of male mating behaviors has the general form shown in Table 2.

A male allocating more effort to mate guarding should have a larger α than a male investing more in searching for additional females. β should be relatively larger for the searching male than for the mate-guarding male, and if some searches last longer than 3 h, then γ , the probability of finding a mate, also should be larger. The probabilities of losing a mate ($1 - \alpha - \beta$), finding a mate (γ), and not mating for two successive intervals ($1 - \gamma$), should vary for all males in response to female availability. Comparison of these parameters, among various groups of males, formed the basis for the analysis.

If male soapberry bugs in a population adjust their mating behavior in accordance with the availability of females, then we would expect to find that different Markov chains are associated with different sex ratios. The null hypothesis (H_0) is that the transition probabilities do not differ among the four ratios. The null model has three independent parameters, α_0 , β_0 and δ_0 [where $\delta_0 = (1 - \alpha_0 - \beta_0)$], and the alternative model is described by 12 independent parameters, α_k , β_k , and δ_k ($k = 1, 2, 3, 4$), since the assumption is that up to four Markov chains best model the data. Rejection of the null suggests a plastic response to the availability of females.

Likewise, for the null hypothesis that, at a given ratio, Oklahoma and Florida males do not differ with regard to mate guarding tactics, the model has three parameters. The alternative hypothesis, that the two populations differ, assumes that two Markov chains (six parameters) best describe the mating data, and rejection of the null model suggests divergent mating strategies.

Likelihood ratio test (LRT) statistics, designated $-2 \ln \lambda$, were used to test these two hypotheses, as well as the assumption that a first-order Markov chain describes the data better than a model in which successive states are independent (0-order Markov chain). The p values for tests were determined by comparing the LRT statistic ($-2 \ln \lambda$) to tabled χ^2 values. Subsets of the parameters were tested for differences among sex ratios and between the two populations using likelihood ratio statistics, and linear models were constructed to describe the relationship between certain parameters and the sex ratio. A summary of the statistical methods is in the appendices.

For the model, the behavioral sequences of the individual males within a mating arena were not considered to be independent samples because their mating behaviors must have been correlated. This was because a mating female was unavailable to other males, thus altering the effective mating M:F ratio from the true ratio as each successive male found a mate, and thereby reducing the probability that the remaining unmated males would find a mate. This lack of independence and the resulting statistical bias should have been especially pronounced in arenas where the M:F ratio was 18:6. Therefore the model treated each mating arena as a replicate so that for each population there were four independent replicates for each of the four ratios.

RESULTS

Sex ratios in nature

Adult sex ratios in Oklahoma ranged from 0.62–4.71 males per female ($\bar{X} \pm 1 \text{ SD} = 2.64 \pm 0.99$, $N = 28$ aggregations), but were restricted to about 1:1 in Florida (range = 0.56–1.67, $\bar{X} = 1.09 \pm 0.26$ males/female, $N = 19$ aggregations). Oklahoma sex ratios were significantly greater than those in Florida ($Z_U = 4.19$, $p < .0001$, Mann-Whitney U test). Sex ratio values for 19 of the 28 aggregations in Oklahoma differed significantly from 1:1 ($p < .05$; χ^2 goodness-of-fit tests), while none did in Florida.

Adult sex ratios were also significantly more variable in Oklahoma (variance in Oklahoma = 1.24, variance in Florida = 0.07, $F_{(1,17)} = 17.7$, $p < .0001$).

Comparisons of oviposition intervals among sex ratio treatments

The average interval between ovipositions, pooling all arenas by state, was 19.2 ± 10.0 h for Florida females ($N = 957$ ovipositions), and 21.6 ± 12.3 h for Oklahoma females ($N = 1019$ ovipositions) ($Z = 4.30$, $p < .0001$, Mann-Whitney U test). Mean values ($\pm \text{SE}$) for the four replicates at each sex ratio are shown in Figure 1. Oviposition intervals differed significantly among replicates of Florida bugs at sex ratios of 1:1 and 3:1 (χ^2 approximate

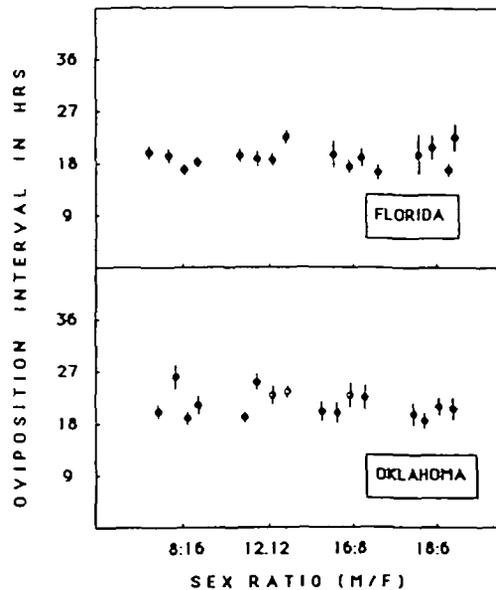


Figure 1
Mean ($\pm \text{SE}$) oviposition intervals by sex ratio replicate for Florida and Oklahoma females. To facilitate comparison, the results are presented on the same scale and in the same order by replicate as in Figure 4.

of Kruskal-Wallis test = 20.86, $df = 3$, $p < .0001$, and 9.47, $df = 3$, $p < .03$, respectively) and among replicates of Oklahoma bugs at sex ratios of 1:1 (χ^2 approximate of Kruskal-Wallis test = 18.4, $df = 3$, $p = .0005$). However, no clear pattern associates sex ratio and oviposition interval. The relative uniformity of oviposition intervals under all experimental conditions suggests that oviposition interval is largely independent of sex ratio.

The effects of sex ratio on male mating decisions and options

Proportion of time spent mating

Males spent most of their time mating when there was no shortage of females (M:F ratios of 1:2 and 1:1), but were more likely to be found unmated at higher ratios ($p < .001$, Table 3). Mating frequency of Oklahoma and Florida males was essentially identical ($p > .10$).

Independence versus first-order Markov chain

The transition probability matrices (Table 4) suggest a lack of independence between the present state and the previous state (the probability values on the diagonal are highest). In particular, a male that is mating in one period has a high probability of remaining with the same female until the next period. LRT statistics are very large ($\chi^2 > 900$, $df = 1$, $p < .0001$ for both populations at all four

Table 2
Elements of the Markov chain

	Second behavioral state		
	1	2	3
First behavioral state			
1	α	β	$(1-\alpha-\beta)$
2	β	α	$(1-\alpha-\beta)$
3	γ	0	$(1-\gamma)$

Table 3
Proportion of observations in which males were mating

Ratio	Oklahoma	Florida
8:16	0.82	0.81
12:12	0.82	0.79
16:8	0.47	0.46
18:6	0.29	0.31

Mean proportions from data pooled over replicates. Males are far less likely ($p < .001$) to be found mating at male biased sex ratios than at even or male based ratios. There is no evidence from these data that mating frequencies differ between Oklahoma and Florida ($p > .10$).

sex ratios) and indicate that the Markov chain model better describes the data than does a model that assumes independence of the successive states.

Mating decisions and options

Sex ratio affected the transition probabilities for both populations (Table 4), suggesting that mating strategies may differ among the groups of males subjected to different sex ratios. Likelihood ratio statistics show that the mating patterns of the males are not independent of sex ratio (Oklahoma, LRT statistic = 277.9, $p < .005$; Florida, LRT statistic = 327.7, $p < .005$).

The two populations differed in mating patterns at M:F ratios of 8:16 and 12:12, but not at ratios of 16:8 and 18:6 (Table 5). With females in excess, mating Oklahoma males were less likely to remain with the same female, and more likely to switch females or to begin mating in the next pe-

Table 4
Transition probability matrices for the Markov chains describing mating behavior sequences for males from Oklahoma and Florida populations of soapberry bugs

	Oklahoma			Florida			
	1	2	3	1	2	3	
M:F 8:16							
1	0.77	0.16	0.07	1	0.90	0.06	0.03
2	0.16	0.77	0.07	2	0.06	0.90	0.03
3	0.30	0.00	0.70	3	0.14	0.00	0.86
M:F 12:12							
1	0.91	0.04	0.05	1	0.91	0.06	0.04
2	0.04	0.91	0.05	2	0.06	0.91	0.04
3	0.24	0.00	0.76	3	0.17	0.00	0.83
M:F 16:8							
1	0.90	0.01	0.08	1	0.92	0.01	0.07
2	0.01	0.90	0.08	2	0.01	0.92	0.07
3	0.08	0.00	0.92	3	0.06	0.00	0.94
M:F 18:6							
1	0.89	0.01	0.10	1	0.92	0.01	0.07
2	0.01	0.89	0.10	2	0.01	0.92	0.07
3	0.05	0.00	0.95	3	0.03	0.00	0.97

Row labels designate the "present" mating state and column labels the next state.

States 1 and 2 are mating states and state 3 is a nonmating state.

riod. At higher sex ratios, Oklahoma males more closely resemble Florida males, but at 12:12, single Oklahoma males were still more likely to mate in the next period.

Increasing male bias in sex ratio reduced the options that a male had for some behaviors, but not for others. At higher sex ratios, far fewer females were available at any given time, and accordingly, the probability that a single male would be mating in the next interval (γ) declined and varied significantly among the four ratios in both populations (LRT statistics for Oklahoma and Florida = 301.0 and 148.3, respectively; $p < .005$ in each case). Among the linear models tested, binomial logit models (Appendix B), with γ as a function of ratio, provided the best fit for both populations. A plot of the fitted values from the linear model (Figure 2) indicates that single Florida males were less likely to subsequently mate at ratios of 8:16 and 12:12 than single Oklahoma males. There was no difference between Oklahoma and Florida values of γ when females were scarce (for ratios of 16:8 and 18:6, $p > .10$).

In contrast, the behavior of mating males largely controls their subsequent states, independent of sex ratio. For both populations, some or all of the multinomial probabilities that a mated male will be with the same female in the next period (α), will switch females (β), or will stop mating ($\delta = 1 - \alpha - \beta$) differed significantly among the ratios (LRT statistics for Oklahoma and Florida = 386.7 and 179.4, respectively, with $p < .005$ in each case). Multinomial logit models of the parameters as a function of ratio provided a better fit than the null model of no relationship. Fitted values (Figure 3) show that the probability of guarding did not change as a function of ratio (Appendix B) among Florida males as it did for Oklahoma males. The probability that a mating male switches mates declined (Figure 3) and the probability of losing a mate increased as a linear function of ratio for both populations (Appendix B). Oklahoma males differed from Florida males with respect to these parameters only in the presence of excess females (for a sex ratio of 8:16, $p < .005$, for all other ratios $p > .10$).

The duration of copulatory guarding varied with sex ratio only in Oklahoma, where in each of the four replicates at a 1:2 female-biased sex ratio, durations averaged about 50% of those at the other three sex ratios [Figure 4; χ^2 approximate of Kruskal-Wallis test of values pooled among replicates = 85.446, $df = 3$, $p < .0001$]. The mean copulation durations of Oklahoma males, averaged among four replicates, at sex ratios of 1:2, 1:1, 2:1, and 3:1, were 12.45 ± 18.8 h ($N = 352$), 28.91 ± 40.98 h ($N = 233$), 27.79 ± 28.95 h ($N = 185$), and 26.04 ± 27.39 h ($N = 141$), respectively. Sex ratio significantly affected copulation duration. Mean copulation durations of Florida bugs were much more constant among the sex ratio treatments: 26.91 ± 38.01 h ($N = 163$), 30.84 ± 39.90 h ($N = 196$), 30.76 ± 35.61 h ($N = 158$), and 31.41 ± 39.77 h ($N = 119$), respectively (χ^2 approximate of Kruskal-Wallis test = 6.31, $df = 3$, $p = .1$).

Homogeneity among replicates

The tests above assume that the four replicates of each ratio are governed by the same probability model. Under this assumption, the same Markov

chain describes the behavioral sequence for each replicate of a ratio. In fact, significant differences do exist: for Oklahoma bugs, replicates differ ($p < .05$) within the ratios 8 : 16 and 12 : 12, and 16 : 8, and for Florida bugs, replicates differ at the ratios 8 : 16 and 12 : 12 (Table 6). However, these LRT values are so much smaller than those used to compare the various sex ratios, that sex ratio clearly is a substantial component of overall variability and a primary factor in determining the mating behavior of males from both populations.

DISCUSSION

Importance of the results

We found evidence of population divergence in the male mating strategy. High female availability induced males from the socially variable population to shift their effort away from mate guarding; males from the socially stable population showed no such flexibility. This difference cannot be explained as the simple result of genetic divergence in a canalized behavior, nor as the result of environmentally induced expressions of behaviors available to all male soapberry bugs. Rather, it is the reaction norm that has evolved, resulting in an inherited differential response that depends on the conditions a male experiences. More than just "controlling" for phylogenetic effects, the "common garden, norm of reaction" approach permits the simultaneous evaluation of genetic differentiation and phenotypic conditionality that may or may not be independent from genetic differentiation.

Our discovery of a genetic difference in the flexibility of a social behavior strategy is a novel result. It shows that the behavioral capacity for dealing with the problems and opportunities created by demographic variation can differ between populations, with potentially important evolutionary consequences (discussed below). The magnitude of the differences observed at a given sex ratio is not especially large, but it is important from the perspective of studying behavioral flexibility as an evolved trait.

Interpretation of the data

For both populations, the mating state of a male soapberry bug was not a sequence of random events (Tables 4 and 5). Rather, the likelihood that he would be in a particular mating state in the near future depended on his present mating state, making certain mating sequences much more characteristic than others. In particular, regardless of sex ratio, males from either population would most likely continue to mate with the same female within the subsequent 3 h. The mean mating durations suggest that males frequently guarded females through at least one oviposition.

Nonetheless, different behavioral norms of reaction have evolved in males of the two populations. While males from each population spent the same proportion of time mating at a given ratio (Table 3), the Markov chains describing the behavioral sequences of the two populations were significantly different when females were not limiting (Tables 4 and 6). When single females were common, Oklahoma males were less likely to guard than were

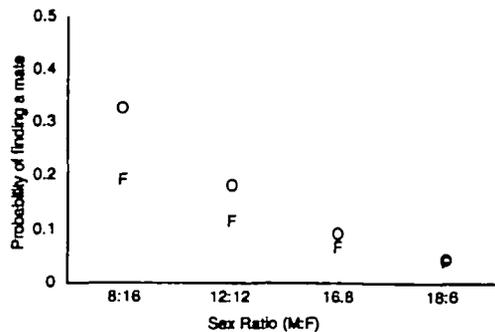


Figure 2
Binomial-logit-regression estimates of the probability that a single male will be mating in the next observation period (γ) as a function of sex ratio (O = Oklahoma, F = Florida)

Florida males, and nonmating Oklahoma males were also more likely to begin mating within 3 h. Extreme natural differences between the populations in female availability and its predictability are the probable selective agents behind the evolutionary divergence in strategies. While the LRT statistics comparing Markov chain models among replicates were large enough to indicate significant differences for some of the ratios (Table 6), they were so much smaller than those used to compare the various sex ratios (LRT statistics = 277.9 and 327.7 for Oklahoma and Florida, respectively) that sex ratio is clearly indicated as a primary experimental factor in determining the mating sequences of males from both populations. Male soapberry bugs in each population may use different cues to make their mating decisions, or perhaps more likely they interpret similar cues differently.

Whereas the mating behavior of males from Oklahoma was characterized by versatility, Florida males showed no predilection to change guarding behavior in response to changing sex ratio. In the Florida populations, guarding seemed to be the tactic of choice regardless of female availability. It is true that mating sequences differed significantly among the four sex ratios, but guarding behavior did not change as a result of sex ratio nor did males become promiscuous in response to female abundance as did Oklahoma males (Figure 3). Florida males from groups with access to numerous females (8 : 16) did not differ in any regard from males in groups with an even (12 : 12) ratio. Only the probability of finding a mate (γ) changed, declining as a function of ratio (Figure 2). It is the change in this parameter, therefore, that evidently is responsible for the differences in mating sequences among the ratios. There is no evidence that in Florida promiscuity is a strategy for exploiting an abundance of females. Thus Florida males may opt ei-

Table 5

LRT statistics comparing experimental results to the null hypothesis that Oklahoma and Florida males do not differ in mating tactics

Ratio	$-2 \ln \gamma$	p
8 : 16	128.7	$< .005$
12 : 12	13.9	$.025 < p < .05$
16 : 8	6.2	$> .10$
18 : 6	11.0	.05

p values are based on the upper percentage points of the Bonferroni χ^2 statistics (Kres, 1983) for testing four hypotheses simultaneously.

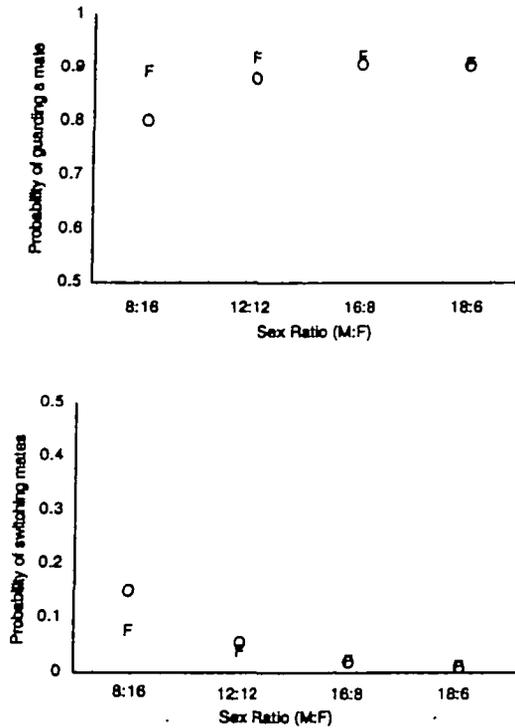


Figure 3
Multinomial-logit-regression estimates of the probability that a male guards his mate through the next observation (α), and the probability that a male switches mates (β), both as functions of sex ratio (O = Oklahoma, F = Florida).

ther to mate (and guard) or not to mate at all. The significant differences in mating sequence, apparently due to the declining probability of finding a mate, may result from simple numerical constraints imposed by the scarcity of females. Though this study was not designed to test this hypothesis, we believe that scarcity is the most parsimonious explanation for the declining probability of finding a mate. The scarcity of females may have constrained males of both populations to behave identically when ratios were male-biased, whereas the difference in behavioral plasticity explains why the Oklahoma and Florida bugs differed at sex ratios of 1 : 2 and 1 : 1.

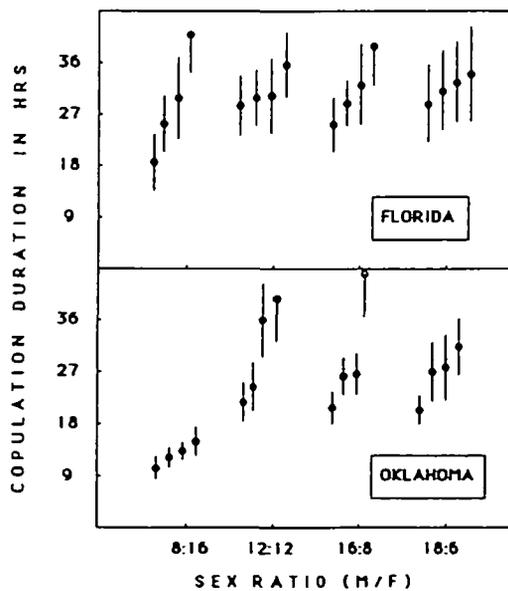


Figure 4
Mean (\pm SE) copulation durations by sex ratio replicate for Florida and Oklahoma pairs.

The costs and benefits of mate guarding will vary as a function of female availability (Carroll, 1993). At higher sex ratios, both the probability of finding a new mate and the likelihood that sperm deposited in a previous mate will be diluted increase (Yamamura, 1986). How the fitness of different guarding-nonguarding allocation tactics varies with sex ratio (the "environmental tolerance" for phenotypic variation, *sensu* Lynch and Gabriel, 1987) has not been explicitly modeled for soapberry bugs, and so we do not have specific allocation predictions for the populations. Theoretically, multiple tactics, each differing in the degree of behavioral specialization, may evolve within a population, depending on the form of selection and any costs associated with plasticity. At present, we cannot be certain that the tactical differentiation observed between the populations is adaptive. However, it is notable that, in response to our experimental variable, greater behavioral flexibility occurred as predicted in the population from the more variable environment.

Female choice and comparisons with field studies

Female reproductive interests play a major role in determining male mating options in many species (Ahnesjö et al., 1993), but based on evidence presented here and in previous articles (Carroll, 1991, 1993), it appears unlikely that female mating decisions had a major influence on the durations of individual pairings observed in this study. While females may resist prolonged copulations, they do so infrequently (Carroll, 1993). The most common point at which pairings terminate is shortly after oviposition (Carroll, 1988, 1991), and in this study, the average interval between ovipositions was nearly identical in the two populations at all sex ratios (Figure 1). Thus, most males have the option of remaining with a female for at least one oviposition, and the higher probability that Oklahoma males would leave their mates when females were in excess probably resulted from male, rather than female, decisions.

The patterns observed in this study differ in some interesting ways from those observed in the much larger field arenas (Carroll, 1993). In the field, individually marked bugs in Oklahoma were observed at a 3 : 1 M : F ratio, and bugs in Florida were observed at a 1 : 1 ratio. Under these conditions, Oklahoma males remained with (guarded) females for significantly longer periods than did the Florida males. Such a difference is not seen when comparing the patterns in this study at those two ratios. In fact, considering the result from all captive ratios, the Florida males showed a greater propensity to guard.

It is not clear that this result was due to some effect of captive existence, even though captive densities were somewhat greater than those in the field arenas (Carroll, 1993). The manner in which density might affect male mating decisions will depend on what cues males use to make decisions. For example, males could use the time it has taken them to find a mate as a cue to determined whether they should guard her. Search times in this study (estimable from the γ parameter in Table 3) increased with sex ratio, and the range exhibited in-

cludes the search times estimated for the field populations (approximately 10 h in Florida, and 26 h in Oklahoma; Carroll, 1993). This fact suggests that captive densities did not affect our results, at least on the basis of encounter rates. The reasons for a high guarding frequency in Florida males is unknown. However, the possibility that both populations show some form of plasticity in their allocation patterns, with different thresholds for shifting tactics, cannot be fully excluded by our results.

In addition, an uncontrolled variable that could also have affected adult behavior was the fact that we reared the captive populations on two different host species. Though host species could influence their behavior, we chose to use the appropriate native host for each population rather than rearing them on the same host species and thereby introducing another, less natural uncontrolled variable.

Future directions and general conclusions

Differences among the replicates of a given sex ratio for each population show that some variability in male mating tactics remains unexplained by the proposed model. Genetic differences among replicates probably do not account for this, because siblings were nearly uniformly distributed throughout the treatments and replicates. Moreover, while the populations have diverged in several aspects of their feeding and reproductive ecology (Carroll, 1988, 1993; Carroll and Boyd, 1992; Carroll and Loye, 1987), it is not clear that any of these characters impinge strongly on individual or population differences in mating strategy. Males are similar in their activity rates, and the diel distributions of mating events are similar between the populations (Carroll, 1993; Carroll S and Corneli P, unpublished data). Potentially important variables, such as predation (Sivinsky, 1980; Travers and Sih, 1991; Walker, 1980) and parasitism (Cade, 1975; McLain, 1980) are essentially absent from both populations (Aldrich et al., 1990; Carroll, 1988). Possible effects of male and female condition and experience, and more complex aspects of social competition or sperm competition over time, should be investigated in greater detail. In addition, to control for any unaccounted effects of captive conditions, sex ratios should also be manipulated in the field.

Jong (1989) hypothesized that populations historically exposed to little environmental variation should not exhibit phenotypic plasticity in relevant traits. Even if the species has previously experienced variable conditions, the costs of possessing phylogenetically derived plasticity may make it maladaptive in relatively invariant environments, such that it is not maintained, or, in the absence of selection, plasticity may be eliminated by genetic drift. At the same time, unpredictable variability (e.g., when there is no capacity for assessment) may select for monomorphic reproductive strategies (McGinley et al., 1987). In the soapberry bug, the variable, male-biased sex ratios observed in Oklahoma at the northern edge of the species range are probably atypical and novel demographic conditions in the sociobiology of this mainly tropical species (Carroll, 1988; Carroll and Boyd, 1992). Male soapberry bugs may have evolved tactical plasticity sometime in the past several thousand years as their host plants have recolonized the south central Unit-

Table 6

LRT statistics testing for homogeneity among replicates of each ratio for the two populations

Ratio	Oklahoma	Florida
	$-2 \ln \gamma$	$-2 \ln \gamma$
8:16	29.5*	34.8*
12:12	22.3*	56.0*
16:8	28.9*	14.5
18:6	16.0	8.9

Null hypothesis: the four replicates within a ratio do not differ.

The statistic, $-2 \ln \gamma$, is distributed as χ^2 with 9 degrees of freedom (asymptotically).

* $p < .05$.

ed States (post-glacially), where environmental conditions produce variable sex ratios (Carroll, 1988).

Differences in behavioral plasticity between the populations imply that their genetic responses to changes in selection over evolutionary time, and their evolutionary potential, will also be different (sensu Bradshaw, 1965; Slobodkin and Rapoport, 1974; Thoday, 1953; West-Eberhard, 1989; Wright, 1931). In particular, the behavior of Oklahoma males should be adaptive over a wider range of conditions than that of Florida males, such that some types of environmental change might be more likely to produce genetic changes in the Florida population (sensu Stearns, 1989; Wright, 1931). In contrast, Morgan (1896), Waddington (1953), Wcislo (1989), and West-Eberhard (1989) have all argued that plasticity greatly alters a taxon's evolutionary potential, such that the creative behavior of Oklahoma males may increase their likelihood of entering novel phenotypic spaces that foster genetic polymorphism, and perhaps speciation. At present, the biological relationship between behavioral plasticity and genetic variation remains a largely unexplored but important area of evolutionary biology (Carroll and Corneli, in press).

APPENDIX A

Markov chain inference

The underlying theory and the general expressions of the likelihood-ratio tests for Markov chain inference used for this analysis are presented by Billingsley (1961). The tests were derived entirely from this source, unless otherwise cited. Except as noted, the entire analysis [recoding the data, calculation of maximum likelihood estimators (MLEs), and the likelihood-ratio statistics] was performed using a spreadsheet package (Wingz, Informix Software, Inc.) on a Macintosh IIfx microcomputer.

The following assumes that a finite first-order, three-state Markov chain describes the process, and that the chain has stationary (time-homogeneous) transition probabilities p_{ij} . The p_{ij} s have the form $p_{ij}(\theta)$, where $\theta = (\alpha, \beta, \gamma)$, and the parameter to be estimated is θ . For a chain describing the sequence of male mating behaviors, the likelihood and log-likelihood functions are respectively:

$$L = \alpha^{n_{11} + n_{22}} \beta^{n_{21} + n_{12}} \gamma^{n_{33}} (1 - \alpha - \beta)^{n_{13} + n_{23}} (1 - \gamma)^{n_{33}},$$

$$\ln L = (n_{11} + n_{22}) \ln \alpha + (n_{21} + n_{12}) \ln \beta + n_{33} \ln \gamma + (n_{13} + n_{23}) \ln(1 - \alpha - \beta) + n_{33} \ln(1 - \gamma),$$

where n_{ij} is the number of transitions from state i to state j .

The MLEs were found by maximizing the log-likelihood function with respect to α , β , and γ (Anderson and Goodman, 1957; Basawa and Rao, 1980). Thus, the MLEs are the simultaneous solutions to the set of equations

$$\begin{aligned} \delta \ln L / \delta \alpha &= 0, \\ \delta \ln L / \delta \beta &= 0, \\ \delta \ln L / \delta \gamma &= 0. \end{aligned}$$

Solving the system of equations yielded the maximum-likelihood estimators, which were simply calculated by dividing cell frequencies by row totals ($n_{ij} / \sum_j n_{ij}$). Computation of the MLEs for the testing of various hypotheses required the transition frequency counts to be summed over the appropriate groups, with the corresponding MLEs calculated from the summed counts.

For the null hypothesis (H_0) that the transition probabilities do not differ among the four ratios, the maximum likelihood estimators the three-parameter null model were determined by summing the transition frequency tables over the four ratios within a population (all 16 tables: four replicates of each ratio). For the alternative 12-parameter model, MLEs were determined for each ratio (transition frequency tables were summed over the replicates within a ratio).

The log-likelihood for the null hypothesis, $\ln L_0$, is the likelihood function evaluated at the MLEs for the null model, and for the alternative hypothesis, $\ln L_1$, it is the likelihood function evaluated at the MLEs for the alternative model. The log-likelihood ratio statistic for this test of homogeneity among the four groups of soapberry bugs is

$$\begin{aligned} -2 \ln \lambda &= -2 \ln(L_0/L_1) = 2(\ln L_1 - \ln L_0) \\ &= 2\{\sum_k [(n_{11k} + n_{22k}) \ln \alpha_k \\ &\quad + (n_{21k} + n_{12k}) \ln \beta_k + n_{33k} \ln \gamma_k \\ &\quad + (n_{13k} + n_{23k}) \ln(1 - \alpha_k - \beta_k) \\ &\quad + n_{33k}(1 - \gamma_k)] \\ &\quad - [\sum_k n_{11k} + n_{22k}) \ln \alpha_0 \\ &\quad + (\sum_k n_{21k} + n_{12k}) \ln \beta_0 \\ &\quad + \sum_k n_{33k} \ln \gamma_0 \\ &\quad + (\sum_k n_{13k} + n_{23k}) \ln(1 - \alpha_0 - \beta_0) \\ &\quad + \sum_k n_{33k} \ln(1 - \gamma_0)]\} \end{aligned}$$

which, under the null hypothesis, is asymptotically χ^2 distributed with 9 degrees of freedom. The number of degrees of freedom for a test is the difference between the number of independent parameters in the null model for the alternative model.

For testing the hypotheses that within a ratio, Oklahoma and Florida males do not differ, the null model supposes that one Markov chain with three

independent parameters best describes the two populations while the alternative model has six parameters (three for each Markov chain). The test is the same as above except that summations for the MLEs and the LRT statistic were over the $k = 2$ populations. Under the null model, $-2 \ln \lambda$ is asymptotically χ^2 distributed with 3 degrees of freedom.

Test statistics for individual parameters included a null likelihood function (L_0) for which the parameter of interest (γ , or α , β , and δ) was held constant while the others were allowed to vary with the sex ratio. Since altering the MLE of α meant altering the MLE of β as well, it was not possible to hold one of these parameters constant for the purposes of testing it individually. The parameter γ was a univariate response, while α , β , and δ were considered to be a multivariate response and were tested together.

For testing the assumption that a first-order Markov chain described the data better than independence (0-order Markov chain), the log-likelihood statistic, $-2 \ln \lambda$, was

$$\begin{aligned} 2\{[(n_{11} + n_{22}) \ln \alpha + (n_{21} + n_{12}) \ln \beta \\ + (n_{13} + n_{23}) \ln(1 - \alpha - \beta) + n_{33} \ln(1 - \gamma)] \\ - [(n_{.1} + n_{.2}) \ln \alpha_0 + n_{.3} \ln(1 - \alpha_0)]\}, \end{aligned}$$

where $n_{.j} = \sum_i n_{ij}$. The MLE for the independence (null) hypothesis was $\alpha_0 = (n_{.1} + n_{.2})/n$, because only two states, mating and nonmating were possible. So assuming the null hypothesis was true, then $-2 \ln \lambda$ was asymptotically χ^2 distributed with 1 degree of freedom.

APPENDIX B

Modeling transition probability parameters as linear functions of sex ratio

A variety of models were analyzed for goodness-of-fit using GLIM3.77 (Royal Statistical Society), a statistical package for interactively investigating generalized linear models. The null model of these regression analyses assumes that the parameter does not change as a linear function of sex ratio.

Because the parameter γ is a proportion, appropriate linear regression models included the binomial logit model and the complementary log-log models. Several transformations of the explanatory variable were also tested for improved fit, including $\log(\text{ratio})$, ratio^{-1} , and ratio^2 . Using a method described by Aitken et al. (1989: 225-236) a multinomial logit model of the parameters α , β , and δ as a function of ratio was compared to the null model.

The relative fits of these models, including the null model of no linear relationship between the parameter and ratio, were determined by noting the relative magnitudes of the scaled deviances (a likelihood ratio statistic) for each model. The difference between the scaled deviances of two models is asymptotically χ^2 distributed (Aitken et al., 1989). An examination of Pearson residuals provided additional information for model criticism.

Among the models tested, the following best described the data. The binomial logit model for the Oklahoma parameters was:

$$\begin{aligned}\text{logit}(\gamma) &= \log(\gamma/(1 - \gamma)) \\ &= 0.0746 - 0.7957(\text{ratio})\end{aligned}$$

and for Florida was:

$$\text{logit}(\gamma) = -0.8385 - 0.6038(\text{ratio}).$$

The multinomial logit model for Oklahoma was:

$$\text{logit}(\alpha) = \log(\alpha/\alpha) = 0$$

$$\text{logit}(\beta) = \log(\beta/\alpha) = -0.5476 - 1.130(\text{ratio})$$

$$\text{logit}(\delta) = \log(\delta/\alpha) = -2.898 + 0.1486(\text{ratio})$$

and for Florida:

$$\text{logit}(\alpha) = \log(\alpha/\alpha) = 0$$

$$\text{logit}(\beta) = \log(\beta/\alpha) = -1.759 - 0.7113(\text{ratio})$$

$$\text{logit}(\delta) = \log(\delta/\alpha) = -3.660 + 0.3157(\text{ratio}).$$

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REFERENCES

- Ahnesjö I, Vincent A, Alatalo R, Halliday T, Sutherland WJ, 1993. The role of females in influencing mating patterns. *Behav Ecol* 4:187-189.
- Aitken M, Anderson D, Francis B, Hinde J, 1989. *Statistical modelling in GLIM*. Oxford: Oxford University Press.
- Alcock J, Jones CE, Buchmann SL, 1977. Male mating strategies in the bee, *Centris pallida* Fox (Hymenoptera: Anthophoridae). *Am Nat* 111:145-155.
- Aldrich JR, Carroll SP, Lusby WR, Thompson MJ, Kochansky JP, Rudmann AA, 1990. Sapindaceae, cyanolipids, and bugs. *J Chem Ecol* 60:199-210.
- Anderson TW, Goodman LA, 1957. Statistical inferences about Markov chains. *Ann Math Stat* 28:89-110.
- Basawa IV, Rao BLS, 1980. *Statistical inferences for stochastic processes*. New York: Academic Press.
- Berven KA, 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.
- Berven KA, Gill DE, 1983. Interpreting geographic variation in life history traits. *Am Zool* 33:609-623.
- Berven KA, Gill DE, Smith-Gill SJ, 1979. Countergradient selection in the green frog *Rana clamitans*. *Evolution* 33:609-623.
- Billingsley P, 1961. *Statistical inferences for Markov processes*. Chicago: University of Chicago Press.
- Bradbury JW, Vehrencamp SL, 1977. Social organization and foraging in emballonurid bats. III. Mating systems. *Behav Ecol Sociobiol* 2:1-17.
- Bradshaw AD, 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* 13:115-155.
- Cade W, 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket songs. *Science* 190:1312-1313.
- Campanella PJ, Wolf LL, 1974. Temporal licks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera). I. *Plathemis lydia* (Drury). *Behaviour* 51:49-87.
- Carroll SP, 1988. Contrasts in the reproductive ecology of temperate and tropical populations of *Jadera haematoloma* (Rhopalidae), a mate-guarding hemipteran. *Ann Ent Soc Am* 81:54-63.
- Carroll SP, 1991. The adaptive significance of mate guarding in the soapberry bug, *Jadera haematoloma* (Hemiptera: Rhopalidae). *J Insect Behav* 4:509-530.
- Carroll SP, 1993. Divergence in male mating tactics between two populations of the soapberry bug: I. Guarding versus nonguarding. *Behav Ecol* 4:156-164.
- Carroll SP, Boyd C, 1992. Host race radiation in the soapberry bug: natural history, with the history. *Evolution* 46:1052-1069.
- Carroll SP, Corneli PS, in press. The evolution of behavioral flexibility as a problem in ecological genetics: theory, methods and data. In: *Geographic diversification of behavior: an evolutionary perspective* (Foster SA, Endler JA, eds). Oxford: Oxford University Press.
- Carroll SP, Loye JE, 1987. Specialization of *Jadera* (Hemiptera: Rhopalidae) species on seeds of Sapindaceae (Sapindales), and coevolution of defense and attack. *Ann Ent Soc Am* 80:373-378.
- Clark SJ, 1988. The effects of operational sex ratio and food deprivation on copulation duration in the water strider (*Gerris remigis* Say). *Behav Ecol Sociobiol* 23:317-322.
- Dhont AD, 1987. Polygynous blue tits and monogamous great tits: does the polygyny threshold model hold? *Am Nat* 129:213-220.
- Dingle H, 1994. Genetic analyses of animal migration. In: *Quantitative genetic studies of behavioral variation* (Boake CRB, ed). Chicago: University of Chicago Press.
- Dingle H, Blau WS, Brown VK, Hegmann JP, 1982. Population crosses and the genetic structure of milkweed bug life histories. In: *Evolution and genetics of life histories* (Dingle H, Hegmann JP, eds). New York: Springer-Verlag.
- Emlen ST, Oring LW, 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- Endler JA, 1986. *Natural selection in the wild*. Princeton, New Jersey: Princeton University Press.
- Falconer DS, 1981. *Introduction to quantitative genetics*, 2nd ed. New York: Longman.
- Foster SA, Endler JA (eds), in press. *Geographic variation in behavior: an evolutionary perspective*. Oxford: Oxford University Press.
- Harvey PH, Pagel MD, 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hayashi K, 1985. Alternative mating strategies in the water strider *Gerris elongatus* (Heteroptera, Gerridae). *Behav Ecol Sociobiol* 16:301-306.
- Hebert PDN, Grewe PM, 1985. *Chaoborus*-induced shifts in the morphology of *Daphnia ambigua*. *Limnol Oceanogr* 30:1291-1297.
- Houde AE, Endler JA, 1990. Correlated evolution of female mating preference and male color patterns in the guppy *Poecilia reticulata*. *Science* 248:1405-1408.
- Kodric-Brown A, 1981. Variable breeding systems in pupfishes (Genus *Cyprinodon*): adaptations to changing environments. In: *Fishes in North American deserts* (Naiman RJ, Soltz DL, eds). New York: Wiley.
- Koenig WD, Stacey PB, 1990. Acorn woodpeckers: group-living and food storage under contrasting ecological conditions. In: *Cooperative breeding in birds* (Stacey, PB, Koenig WD, eds). Cambridge: Cambridge University Press.
- Kres H, 1983. *Statistical table for multivariate analysis* (Wadsack P, trans). New York: Springer-Verlag.
- Johnson LK, 1982. Sexual selection in a tropical brentid weevil. *Evolution* 36:251-262.
- Jong G de, 1989. Phenotypically plastic characters in isolated populations. In: *Evolutionary biology of transient unstable populations* (Fontdevila A, ed). New York: Springer-Verlag.

- Lott DF, 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge: Cambridge University Press.
- Lynch CB, 1992. Clinal variation in cold adaptation in *Mus domesticus*: verification of predictions from laboratory populations. *Am Nat* 139:1219–1236.
- Lynch M, Gabriel W, 1987. Environmental tolerance. *Am Nat* 129:283–303.
- McGinley MA, Temme DH, Geber MA, 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *Am Nat* 130:370–390.
- McLain DK, 1980. Female choice and the adaptive significance of prolonged copulation in *Nexara viridula* (Hemiptera: Pentatomidae). *Psyche* 87:325–336.
- Morgan CL, 1896. On modification and variation. *Science* 4:733–740.
- Mousseau TA, Collins NC, 1987. Polygyny and nest site abundance in the slimy sculpin (*Cottus cognatus*). *Can J Zool* 65:2827–2829.
- Parker GA, 1970. The reproductive behaviour and nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *J Anim Ecol* 39:205–228.
- Parker GA, 1978. Searching for mates. In: Behavioural ecology: an evolutionary approach (Krebs JR, Davies NB, eds). Oxford: Blackwell.
- Reyer H, 1980. Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis rudis* L.). *Behav Ecol Sociobiol* 6:219–227.
- Riechert SE, 1986. Between population variation in spider territorial behavior: hybrid-pure population line comparisons. In: Evolutionary genetics of invertebrate behavior (Huettel MD, ed). New York: Plenum.
- Rubenstein DI, 1980. On the evolution of alternative mating strategies. In: Limits to action, the allocation of individual behavior (Staddon JER, ed). New York: Academic Press.
- Rubenstein DI, 1984. Resource acquisition and alternative mating strategies in water striders. *Am Zool* 24:345–353.
- Schlichting CD, 1986. The evolution of phenotypic plasticity in plants. *Annu Rev Ecol Syst* 17:667–693.
- Sherman PW, 1989. Mate guarding as paternity assurance in Idaho ground squirrels. *Nature* 338:418–420.
- Sillén-Tullberg B, 1981. Prolonged copulation: a male “post-copulatory” strategy in a promiscuous species, *Lygaeus equestris* (Heteroptera: Lygaeidae). *Behav Ecol Sociobiol* 9:283–289.
- Sivinski J, 1980. The effects of mating on predation in the stick insect *Diaperomera veliei* Walsh (Phasmatodea: Heteronemiidae). *Ann Entomol Soc Am* 73:553–556.
- Slobodkin LB, Rapoport A, 1974. An optimal strategy of evolution. *Q Rev Biol* 49:181–200.
- Sterns SC, 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* 39:436–445.
- Strong DR Jr, 1973. Amphipod amplexus, the significance of ecotypic variation. *Ecology* 54:1383–1388.
- Sultan SE, 1987. Evolutionary implications of phenotypic plasticity in plants. In: Evolutionary biology, vol. 21 (Hecht MK, Wallace B, Prance GT, eds). New York: Plenum.
- Thoday JM, 1953. Components of fitness. *Symp Soc Exp Biol* 7:96–113.
- Thornhill R, 1981. *Panorpa* (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource defense polygyny and alternative male reproductive efforts. *Annu Rev Ecol Syst* 12:355–386.
- Thornhill R, Alcock J, 1983. The evolution of insect mating systems. Cambridge, Massachusetts: Harvard University Press.
- Travers SE, Sih AJ, 1991. The influence of starvation and predators on the mating behavior of a semiaquatic insect. *Ecology* 72:2123–2136.
- Via S, 1984. The quantitative genetics of polyphagy in an insect herbivore. I. Genotype–environment interaction in larval performance on different host plant species. *Evolution* 38:881–895.
- Via S, 1991. The genetic structure of host plant adaptation in a spatial patchwork: demographic variability among reciprocally transplanted pea aphid clones. *Evolution* 45:827–852.
- Waage JK, 1973. Reproductive behavior and its relation to territoriality in *Calopteryx maculata* (Beauvois) (Odonata: Calopterygidae). *Behaviour* 47:240–256.
- Waddington CH, 1953. Genetic assimilation of an acquired character. *Evolution* 7:118–126.
- Walker WF, 1980. Sperm utilization strategies in non-social insects. *Am Nat* 115:780–799.
- Wcislo WT, 1989. Behavioral environments and evolutionary change. *Annu Rev Ecol Syst* 20:137–169.
- West-Eberhard MJ, 1989. Phenotypic plasticity and the origins of diversity. *Annu Rev Ecol Syst* 20:249–278.
- Wright S, 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.
- Yamamura N, 1986. An evolutionarily stable strategy (ESS) model of postcopulatory guarding in insects. *Theor Popul Biol* 29:438–455.