Divergence in male mating tactics between two populations of the soapberry bug: I. Guarding versus nonguarding

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I compared male allocation to prolonged mate guarding versus not guarding between two populations of the soapberry bug (*Jadera haematoloma*) that differ in adult sex ratio: Oklahoma, USA (mean ± SD adult sex ratio, 2.70 ± 0.95 males per female), and Florida, USA (1.09 ± 0.26 males per female). To predict the reproductive performance of each mating tactic in each population, I collected data on search time per mating, time required for guarding to be effective, sperm competition, female remating propensity, and female resistance to guarding. Search time alone differed significantly between the populations, being much greater in Oklahoma (estimated as 26.2 h per mate) than in Florida (estimated as 9.6 h per mate). For males in each region, these data were used to model the costs and benefits of guarding for different numbers of oviposition bouts versus not guarding. The reproductive rate of nonguarders in Oklahoma is exceeded by that of guarders who remain with a female for more than one oviposition bout, but in Florida, the reproductive rate of nonguarders is only exceeded by that of guarders who remain with a female for at least three ovipositions. Consistent with the model, Oklahoma males in field arenas guarded more frequently than did Florida males. However, nonguarding was common in both populations, and guarding durations were highly variable. *Key words:* geographic variation, mating systems, sex ratio, *Jadera haematoloma*, Rhopalidae, mate guarding, sperm competition, mate search. *[Behav Ecol 4:156–164 (1993)]*

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> *Darling, you got to let me know, should I stay or should I go?*—The Clash

Mating system theory predicts that whether males mate promiscuously or attempt to monopolize access to one or more females will be influenced by the operational sex ratio and the spatial and temporal distribution of receptive females (Bradbury and Vehrencamp, 1977; Brown, 1964; Emlen and Oring, 1977; Verner, 1964), as well as the tactics of competing males (Maynard Smith, 1982; Rubenstein, 1980). In general, promiscuity should be favored when or where receptive females can be easily located and sperm competition is not severe. In contrast, difficulty in locating mates, whether due to reasons of demography, distribution, or male–male competition, may favor relatively monogamous mate guarding, especially if sperm competition is severe.

Attempts to understand the factors that structure mating systems have proceeded along different but complementary pathways. One approach has been to examine correlations between habitat structure and mating systems in broad comparisons among species (e.g., Crook, 1965; Jarman, 1974; Orians, 1961, 1969). Another approach has focused more narrowly on alternative mating tactics within populations of single species (in insects, e.g., Alcock et al., 1977; Campanella and Wolf, 1974; Carroll, 1991; Hayashi, 1985; Johnson, 1982; Rubenstein, 1984; Sillén-Tullberg, 1981; Thornhill, 1981; Waage, 1973).

A third, intermediate approach, used more recently and with vertebrates, has been to compare populations or closely related species inhabiting different environments (e.g., Dhont, 1987; Kodric-Brown, 1981; Koenig and Stacey, 1990; Lott, 1991; Mousseau and Collins, 1987; Reyer, 1980; Sherman, 1989). This tactic differs from broad interspecific comparisons in that variation from phylogenetic differences is reduced, and the genetic environment of any evolutionary change should be similar between populations. It adds to intrapopulation studies in that beyond examining the details of tactical plasticity or polymorphism, it is the first step in asking whether populations have diverged behaviorally due to differences in selection.

The study reported in this paper takes advantage of a natural experiment to test the prediction that the mating system has diverged between two genetically isolated populations of an insect, the soapberry bug, *Jadera haematoloma* (Hemiptera: Rhopalidae), in Oklahoma and the Florida Keys, USA. Individual male soapberry bugs practice two alternative mating tactics to varying degrees: guarding and promiscuity (Carroll, 1988, 1991). A consistent difference in adult sex ratio between the Oklahoma and Florida Keys populations (Carroll, 1988) provides the opportunity to test for corresponding differences in male allocation to the two tactics. Specifically, male-biased sex ratios in Oklahoma aggregations should result in an increased cost for mate searching relative to the Florida Keys, where sex ratios approximate 1:1. Thus, mate guarding may be more commonly practiced in Oklahoma than in the Florida Keys.

In modeling the payoffs to mate guarding versus nonguarding, however, several additional biological parameters should be incorporated because they too are candidates for influencing fertilization opportunities. In addition to (1) the rate at which receptive, unguarded females are encountered, these parameters include (2) the probability that an unguarded female will become reinseminated before using a previous male's sperm, (3) the outcome of sperm competition, (4) the time required for guarding to be effective (e.g., the interval between ovipositions; Parker, 1970, 1974; Yamamura, 1986), and (5) the probability that a female will permit guarding for a particular duration. I report data on these features and use them to estimate fertilization rates for each tactic in both populations. Under the conditions currently prevailing in nature, guarding is predicted to be more successful in Oklahoma than in the Florida Keys. Data on the guarding times of males in each region are then used to test this prediction.

Differences between the populations in any of the parameters presented above could lead to tactical differences. Some factors that potentially influence the parameters values are "internal" to the mating system; in particular, typical guarding durations of a population will influence female availability in addition to any effect of sex ratio. The complex interactions between such factors in the evolution of mate guarding is the subject of Yamamura's (1986) dynamical evolutionarily stable strategy (ESS) model predicting equilibrium allocation frequencies. Sherman (1989) used a more tractable ESS model, in which a fundamental difference in female availability between groups was also used to predict differences in the payoffs to mate guarding versus nonguarding. Here, I build a similar model based on the candidate parameters that I predict determine the distribution of fertilization opportunities for males and the effectiveness of mate guarding versus nonguarding in using these opportunities. I compare tactical payoffs over a distribution of guarding durations from short to long. Even though female availability depends to a degree on the prevailing male tactics, this method still tests the soundness of the chosen parameters: assuming evolutionary equilibrium conditions in the study populations, the model is tested by comparing predicted versus observed behavior in field populations that differ absolutely in female availability.

My preliminary observations revealed that males in each population are both guarders and nonguarders (Carroll, 1991, unpublished data). The chief aim of this study is therefore to test for differences in the frequency and duration of allocation to one tactic versus the other.

Background and rationale

Reproductive ecology of the soapberry bug in Oklahoma and Florida

Adult sex ratio in Oklahoma is normally >2:1 male-biased due to greater female mortality, whereas in the Florida Keys it is 1:1 (Carroll, 1988; see below). Host plants are rare or absent in a disjunction of several hundred kilometers across the Gulf Coast region, and gene flow between populations in Oklahoma and Florida has probably been negligible for millenia (Carroll and Boyd, 1992).

The soapberry bug specializes on the mature seeds of sapindaceous plants for growth and reproduction (Carroll and Loye, 1987). In the south-central United States, the hosts are the native soapberry tree, *Sapindus saponaria*, and the introduced golden rain tree, *Koelreuteria paniculata*, and in southern Florida, the native balloon vine, *Cardiospermum corindum*. Although bug populations in each region differ slightly in several characters (Carroll, 1988; Carroll and Boyd, 1992; Carroll and Loye, 1987), they remain interfertile (Carroll SP, unpublished data). Adult soapberry bugs are 1–1.5 cm in length, bright red and black, and form aggregations of up to thousands of individuals on and near host plants. Individuals are protected from predators by a variety of noxious compounds (Aldrich et al., 1990); predation is essentially absent in U.S. populations (Aldrich et al., 1990), and no parasitoids have been observed at any phase of the life cycle (Carroll, 1988).

In Oklahoma, reproduction is highly seasonal and mainly limited to late summer and early autumn when host seeds ripen. Reproduction ceases in a cold weather diapause. In contrast, temperatures are perennially warm in the Florida Keys, and bugs breed year-round (Carroll, 1988). Florida Keys aggregations usually contain fewer bugs (hundreds of adults) than do those in Oklahoma (thousands) (Carroll, 1988). Sex ratios, although 1:1 at hatching, become strongly male biased in Oklahoma due to disproportional female mortality during most phases of the life cycle and at most times of year. In contrast, adult sex ratios in Florida average 1:1 (Carroll, 1988).

In Oklahoma, copulations often last several hours or days (Carroll, 1988, 1991). This is well beyond the 10-min period sufficient for sperm transfer and suggests that prolonged copulation functions as mate guarding (Carroll, 1988, 1991). Males are anchored in the females with enlarged genital hooks. They are almost never displaced by other males, but cannot search for other matings while guarding (Carroll, 1988, 1991). In contrast to other aggregating hemipterans that use prolonged copulatory mate guarding after insemination (e.g., Harris and Todd, 1980; McLain, 1980; Sillén-Tullberg, 1981), male soapberry bugs continue to guard females during egg laying. Moreover, some pairs stay together for several ovipositions over days or weeks, up to about one half of the male adult life span (about 30 days; Carroll, 1988, 1991).

Costs and benefits of mate guarding versus not guarding

Assuming similar costs in energy and risk (and that the 10-min mating time required for ejaculate transfer is negligible), the reproductive success of both the guarding and nonguarding tactics may be estimated as the number of fertilizations per mate divided by the searching plus guarding time per mate. Thus, population differences in both search time and sperm competition will influence the relative fitness payoffs to mate searching and mate guarding.

In this study, I measured guarding times by monitoring the copulation histories of marked individuals in arenas in the natural habitat. Searching times required for mate acquisition were similarly measured from observations of unmated males in nature. Calculating the proportion of eggs fertilized via each tactic is more complex because of the interaction of female promiscuity, sperm competition, and variable guarding durations. The number of eggs fertilized per mate (f) are accounted with the formula

$$f_{m,k} = N \sum_{i=1}^{k} \sum_{l=0}^{m-i} x(y)^{l} \qquad (1)$$

for a male that guards for k of the m clutches that a female lays while carrying his sperm, each containing N eggs, from the ith oviposition for which he guards, where l denotes each successive clutch laid by the female, each of a particular reproductive value determined by x, the proportion of eggs he fertilizes per clutch while guarding, and y, the proportion of eggs he fertilizes after he ceases guarding and another male inseminates the female.

As indicated earlier, female reproductive behavior will also influence the fertilization rates of guarders and nonguarders. Tactical payoffs may differ between populations because of differences in the remating rates and receptivity of unguarded females, as well as in the average interval between mating and oviposition. These parameters were also measured in this study.

MATERIALS AND METHODS

Parameters affecting tactical payoffs: field studies

Sex ratio

I sampled aggregations in central and west-central Oklahoma from 1982 to 1987, and in the upper Florida Keys from 1985 to 1989. Sites are described in Carroll (1988). I measured aggregation sex ratios by counting all adult males and females (distinguished by visual inspection of the genitalia) encountered in a 20-min period. This included sampling both on the ground beneath the host plant and on the host plant. Both sexes are "tame," easily identified, active, and easily distinguished from the substrate, which reduces error in estimating sex ratios. The act of sampling did not disrupt mating pairs. Only aggregations in which >50 adults were sampled are included in analyses.

Searching for mates

Between censuses, I randomly chose single males in the arenas or in similar adjacent aggregations and observed them continuously for 6 min each. Any matings were recorded. I then painted a dot on each male to prevent resampling. I examined 1574 males in Oklahoma and 675 in Florida. Most locomotion by males appeared to function in mate searching, and, in a subset of 100 males from each population, I recorded the time spent in motion and the number of copulatory mounts on single females, mating pairs, and single males.

Time to remating by females

In an experiment to assess the probability that an unguarded female would mate before using the sperm of the deserting male, I removed mating males from their females (24 in Oklahoma, 25 in Florida) and measured the time interval until the females remated. This experiment was conducted after the conclusion of the censuses for the copulation duration study.

Parameters affecting tactical payoffs: laboratory studies

Sperm competition

I studied sperm competition in each population by mating virgin females twice, once to normal males and once to males irradiated with 12 krad of X-rays. Preliminary studies showed 12 krad to be the minimum dosage necessary to cause 100% embryonic mortality. I used this dosage to minimize any impact of irradiation on the competitive ability of sperm. I assumed that sperm are released from the spermatheca at the time of oviposition, as is typical of insects (Chapman, 1982). In each experimental pairing, a female and male were held together in isolation for 24 h (approximating the average mating duration). To augment the probability of exclusively sampling pairs with adequate sperm transfer, the only pairs included in the analysis were copulating in at least three of the four observations taken at 6-h intervals (including an observation shortly after the pair was placed together). (Sperm sufficient to fertilize 10 or more clutches of eggs are transferred in less than 10 min; Carroll, 1991.) Subsets of the females were mated first either to normal males ($N = 10$ for Oklahoma, 5 for Florida) or irradiated males ($N = 8$ for Oklahoma, 6 for Florida) as a check for differences in competitive ability. I housed the females in 9-oz (270 ml) plastic drinking cups ringed inside the rim with Fluon AD-1, with filter paper bottoms, water in a cotton-stoppered vial, and golden rain tree seeds for Oklahoma bugs, or balloon vine seeds for Florida bugs. They laid their eggs in the bottoms of the cups, and I collected them once per day with an aspirator and placed the clutches individually in vials until hatching. I checked clutches daily for hatching.

I assigned paternity to eggs on the basis of hatching success, modified for a 7% average infertility rate for eggs from control normal males ($N = 5$ females mated to separate normal males for each population). Thus, in the case of matings of normal, and then irradiated males, the proportion of fertilizations attributed to the second male (P_2) equals 1.0 minus the proportion of eggs hatching divided by the fertility rate (0.93), and in the case of matings to irradiated and then normal males, P_2 equals the proportion of eggs hatching divided by the fertility rate. Detailed results for individual experimental matings in the Oklahoma population are given in Carroll (1991).

Interval between ovipositions

I placed marked individuals raised in captivity from Oklahoma and Florida grandparents in greenhouse arenas at a series of sex ratios (M:F 1:2, 1:1, 2:1, and 3:1) and censused them at 3-h intervals for 7 days. Four replicates were performed for each ratio. This experiment provided data addressing several related questions; in this paper, data are reported on the intervals between ovipositions. Relevant methods are presented here; Carroll SP and Corneli PS (submitted) provide a more detailed description.

I collected the grandparents of the bugs used in this experiment from the field sites described above. Newly molted (virgin) F_2 adults were given individual numbers as in the field studies (below). Arenas were clear plastic boxes 33 × 24 × 11 cm high, lined on the interior rim with Fluon AD-1, floored with filter paper, and covered with clear plastic lids which had mesh-covered ventilation portals 7.5 cm in diameter. I placed 24 individuals in each arena. Light and temperature conditions simulated those in the field (13.5 h light:10.5 h dark, "daylight" fluorescent tubes; 30°C average in daytime, 26°C average at night). Unlimited food from the appropriate host and water in cotton-stoppered vials were provided.

For all females (168 from each population), I recorded relative egg load (on a 0–4 scale of increasing abdominal expansion) and the presence of oviposition behavior in each observation period. Reductions in egg load from one period to the next were recorded as ovipositions in the event that oviposition was not directly observed. I replaced individuals that died during the study with sexually mature virgins of the same sex. The sex ratio in each arena had little effect on the interval between ovipositions; these data are pooled and presented as means for each population.

Estimation of fertilization rates

Sperm competition interacts with mating competition to determine the fertilization rates of guarding and nonguarding in each population, and the tactical payoffs can be estimated for each from the data for each relevant parameter and Equation 1, simplified with the following provisions. Rates of sperm displacement, female remating rates, and the total number of mates per female were similar in both populations (data below), so the costs of nonguarding will be similar. In addition, the times required for insemination (≤ 10 min in Oklahoma; Carroll, 1991) and oviposition (<30 min; Carroll, 1988) are assumed to be negligibly brief in both populations. Also, sperm from a single mating are assumed to be sufficient to fertilize a female's eggs for about 25 days (Carroll, 1991).

The reproductive success of a nonguarder is the fraction of each mates' offspring fathered per time spent in searching, multiplied by the number of females he inseminates. For each mating, the male will fertilize a diminishing portion of each of the female's subsequent clutches as a function of the sperm displacement rate (Equation 1). Similarly, the reproductive success of a guarder is the fraction of a mates' offspring fathered per time spent in guarding plus time spent in searching, multiplied by the number of females inseminated.

I calculated fertilization rates for model guarders in each population that remain with a female for one to eight ovipositions. It is assumed that additional sperm are displaced by a male each time he recopulates after an oviposition. These fertilization rates are compared with those of nonguarders in each population.

Guarding and nonguarding in field arenas

I estimated guarding and nonguarding frequency and guarding duration by monitoring the copulation behavior of marked individuals twice a day in a field arena at Boiling Springs State Park, near Woodward, Oklahoma (latitude 36°25′ N, longitude 99°24′ W; September 1987), and on Plantation Key, Florida (latitude 25°10′ N, longitude 80°17′ W; February 1988). Arenas were walled with plastic lawn edging placed in the ground, circling a host plant. I chose the focal host plants because they were producing seeds and grew from uncluttered short grass and soil (Oklahoma) or sand (Florida Keys) substrate. The lawn edging was treated above ground level (10 cm high) with Fluon AD-1 (a low-friction resin, ICI Americas Corp.) to prevent marked bugs from walking out and to prevent unmarked bugs from walking in. Because all life-cycle activities take place in the immediate vicinity of fruiting plants (Carroll, 1988), restriction to arenas imposed little change on the insects' normal habits.

I modified aggregations slightly to contain 210 adult males and 70 adult females in Oklahoma, and 50 adult males and 50 adult females in Florida. These experimental populations retained the sex ratio characteristics of the original populations. The surface areas of the arenas were adjusted to create identical densities in each (14 m^2 in Oklahoma and 5 m^2 in Florida). I retained surplus adults for replacement of any individuals that died during the course of the study ($< 2\%$), and I removed juveniles from the arenas. In Oklahoma, bugs were further prevented from walking out of the arena by a band of Fluon-treated tape placed around the tree trunk 1.5 m above the ground. In Florida, the host vine was <1 m in height, so no similar barricade was necessary. Bugs did not fly from the arenas.

I sexed each adult and gave it a unique number on the thorax and proximal forewings (elytra). Numbering involved two steps: first, a square of white Tek-Pen glass-marking ink, thinned with turpentine, was painted on each bug's dorsum. When this dried (<5 min), I wrote the number in the square with a fine-point Sharpee permanent marker. Preparation of the arena plus marking and release was accomplished over 2 days in Oklahoma and in 1 day in Florida. During marking, I separated bugs at each site by sex and held them in plastic boxes with moist cotton for drinking water. I then released the bugs together into each arena, where censuses began 12 h later.

Marking the dorsum with white paint did not affect body temperature. In Florida, the internal thoracic temperatures of nine marked and nine unmarked (black) individuals were measured with a needlelike thermoprobe and a Sensortek B-12 thermometer. The mean of marked bugs was 36.2°C ± 1.4°C, and that of unmarked bugs was 36.1°C ± 1.8°C. Simultaneous shade air temperature was 28.0°C 1 m above the ground and 30.0°C 1 cm above the ground.

I censused all individuals in the arenas twice per day, at 0630–0730 h and 1730–1830 h, for 10 days. In each census I recorded the mating status (mating or single) and the identity of the mate. Dim flashlights with red lenses were used for observations in low light. Presence or absence of female resistance to copulation (vigorous shaking and kicking) was also recorded for each paired female, and for single females that were mounted by males at the instant of censusing. I removed unmarked individuals from the arenas upon detection. Pairings recorded only in the first census or last census were excluded from analyses.

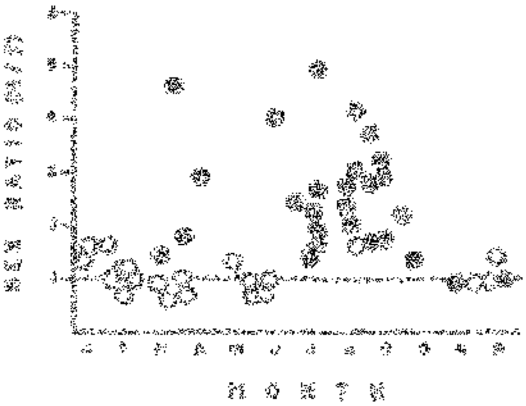


Figure 1
Adult sex ratios in reproductive aggregations of soapberry bugs in Oklahoma (filled circles) and the Florida Keys (open circles). The dotted line indicates the 1:1 primary sex ratio (Carroll, 1988).

Sex ratios

Adult sex ratios varied widely among aggregations in Oklahoma, ranging from 1:1 to 5:1 and averaging (±SD) 2.10 ± 1.25 males/female in reproducing aggregations (March–early October, $N = 35$). Adult sex ratios were restricted to about 1:1 in Florida, averaging 1.09 ± 0.31 males/female ($N = 19$; Figure 1). Sex ratio values for 16 of the 35 reproductive aggregations in Oklahoma differed significantly from 1:1 in chi-square goodness-of-fit tests, while none differed in Florida. The sex ratios of three nonreproductive, overwintering aggregations in Oklahoma were close to 1:1. Considering all sex ratio values, those in Oklahoma ($N = 35$) were significantly greater than those in Florida ($N = 19$) ($Z_c = 4.16$, $p < .0001$, Mann-Whitney U test).

Mate searching and male activity rates

The time required by a searching male to find a receptive female was much greater in Oklahoma than in Florida. Searching males in Oklahoma mated with females in 12 of 1574 5-min observation periods, whereas those in Florida mated with females in 14 of 675 such periods ($\chi^2 = 5.60$, $p < .025$). From these observations, the average search time required for a male to find a mate in Oklahoma is estimated as 10.9 h; for Florida it is 4.0 h. Because males are much less active at night, the real time required to find a mate by a male with 12 h of daylight was approximately 21.8 h for males in Oklahoma and 8.0 h for males in Florida.

The populations also differed in the frequency with which males encountered and mounted single females, mating pairs, and single males (Table 1). Oklahoma males were in motion significantly less frequently than were Florida males, but encountered all other individuals, pooled, at a greater rate (Table 1).

Number of mates and time to remating by females

Almost all individually marked females in the field arena mated with several males during the 2-day observation periods. Oklahoma females mated with an average of 6.5 ± 1.9 males (range = 3–11, mode = 5.5). Florida females mated with an average of 8.9 ± 2.8 males (range = 5–17, mode = 8). All females experimentally separated from their mates remated within 75 min (Figure 2). The average intervals between separation and remating were similar in both populations (Oklahoma: 12.8 ± 15.7 min, $N = 24$; Florida 20.7 ± 16.4 min, $N = 23$).

Female resistance to copulatory approaches

Female resistance was rare in both populations. Resistance occurred in 14 of 744 (1.9%) heterosexual encounters observed in Oklahoma, and in 17 of 879 (1.9%) heterosexual encounters observed in Florida.

Sperm competition

Males exposed to sperm competition had lower fertilization rates in both populations. The order of mating (sterile-irradiated versus fertile/untreated) did not affect the outcome of sperm competition (Table 2). The percentage of eggs fertilized by the second male, averaged for both types of matings, was 61.8 ± 23.5 for Oklahoma ($N = 17$), and 71.7 ± 19.2 for Florida ($N = 11$, Mann-Whitney $U = 87.0$, $p = .18$).

Intervals between oviposition

For captive females from Oklahoma, observed in groups at 8-h intervals, the mean (± SD) interval between ovipositions of egg clutches was 21.9 ± 8.6 h ($N = 1270$ ovipositions). Given the constraints of the time required to guard a female until oviposition, this is negligibly greater than the average of 18.9 ± 6.3 h for Florida females ($N = 887$ ovipositions).

Estimates of fertilization rates for guarding and nonguarding

For clarity, the values for the four parameters used for estimating fertilization rates are summarized in

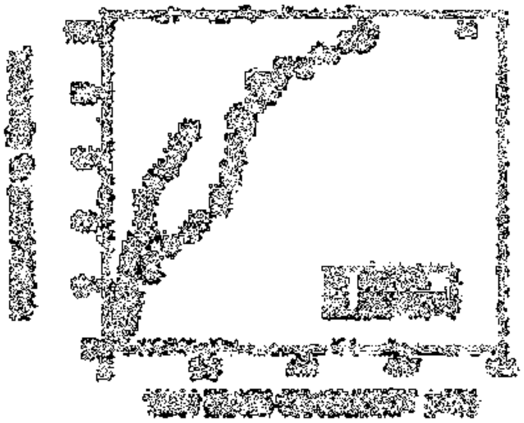
Table 1
Locomotion frequencies and sexual encounter rates of male soapberry bugs in Oklahoma and Florida

Trait	Mean ± SD		Z^a
	Oklahoma	Florida	
% Time walking	52 ± 27	69 ± 25	3.0**
Single female encounters/male	2.05 ± 0.19	0.95 ± 0.96	2.4*
Mating pairs encountered/male	0.47 ± 0.59	0.37 ± 0.58	1.5
Single males encountered/male	0.54 ± 0.25	0.39 ± 0.44	2.5*
Total encounters/male	1.15 ± 0.52	0.51 ± 0.62	3.5**

[a] Values are calculated from Mann-Whitney U analysis.

* $p < .05$.

** $p < .001$.



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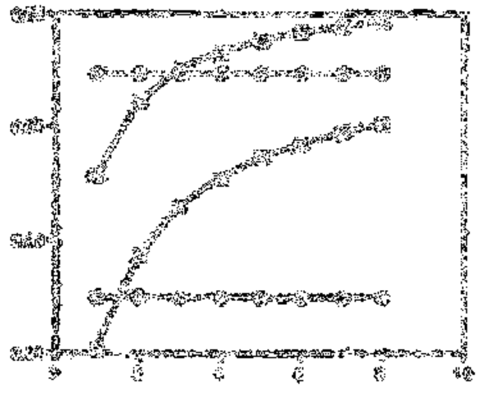
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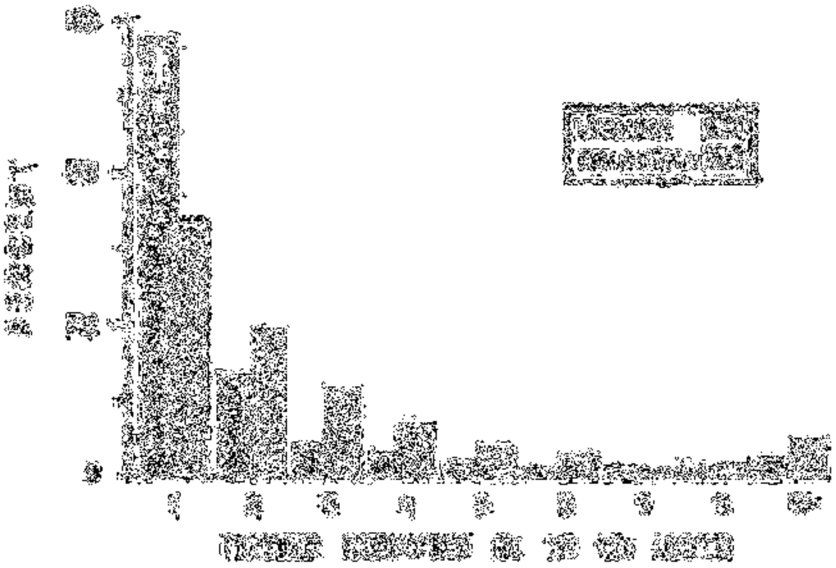

makes it difficult to precisely predict the frequencies of any genetically based behavioral phenotypes in each population; moreover, domination by any one tactic, or the evolution to any stable equilibrium, may be unlikely (sensu Maynard Smith and Brown, 1986). However, the results of my study suggest that by comparing populations in which the expected payoffs to alternative tactics are dissimilar, it is possible to accurately predict the direction of differentiation.

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