

THE EFFECT OF FEMALES ON MALE-MALE COMPETITION IN THE ISOPOD,
PARACERCEIS SCULPTA: A REACTION NORM APPROACH TO BEHAVIORAL PLASTICITY

Stephen M. Shuster and Emily M. Arnold

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011-5640, U.S.A.
(Stephen.shuster@nau.edu);

Current address: Department of Integrative Biology, University of California, Berkeley, California 94720-3140, U.S.A.
(emarnold@berkeley.edu)

A B S T R A C T

In *Paracerceis sculpta*, a Gulf of California isopod, α -males usually defend aggregations of breeding females within the spongocoels of intertidal sponges. Breeding isopods are also found in habitats other than sponges, but interactions among individuals in these locations are poorly known. To investigate plasticity in male-male interactions associated with mate acquisition in breeding habitats other than sponges, we examined the behavior of pairs of α -males in two distinct environments; those in which breeding sites were absent, but females were present, and those in which both breeding sites and females were absent. We established males as residents in the presence and in the absence of females by allowing them to occupy arenas for 1 h before intruders were introduced. Residents and intruders engaged in significantly more total acts and grappled more in the presence of females than when females were absent. In the presence of females, residents became active first in most cases, and gripped females more than intruders. Latency to activity was significantly longer when receptive females were present than when they were absent. However, residents seldom interacted with intruders when females were lacking. Our results suggest that in locations other than sponges, α -males compete for females and can recognize their status as residents and as intruders. These results also suggest that, as in many vertebrate and invertebrate species, *P. sculpta* α -males attempt to mate opportunistically, and that contests for mates in atypical breeding habitats may be common in nature. We discuss the importance of distinguishing rare and highly contingent behaviors from those likely to represent adaptive behavioral plasticity, and we propose a simple criterion of commonality for their identification in behavioral analyses.

INTRODUCTION

In most animal species, male reproduction is limited by the availability of sexually receptive females (Bateman, 1948; Williams, 1966; Wade, 1979; Clutton-Brock, 1988; Shuster and Wade, 2003). Males must compete for access to mates, and sexual selection is expected to favor male characteristics that permit individuals to overpower or exclude other males in reproductive competition (Darwin, 1874; Wade and Arnold, 1980). Because ecological circumstances favor particular sets of male and female characteristics, mating systems are usually characterized by the specific circumstances that attend breeding pairs (Emlen and Oring, 1977; Thornhill and Alcock, 1983). Species are typically described as “harem forming” or “socially monogamous,” depending on the types and durations of male-female bonds that are most common in the natural population (review in Shuster and Wade, 2003).

When circumstances allowing reproduction are more variable, breeding pairs may form under conditions that appear species atypical (Elnor and Beninger, 1995; Jormalainen and Shuster, 1999; Shine et al., 2003). While seemingly adaptive, and often treated as such (Sih et al., 2004), the observed behavior need not represent what is often called “adaptive behavioral plasticity” (Clark et al., 1997; Shuster and Wade, 2003; see below). Unusual behaviour could represent the activities of aberrant individuals who are destined to be removed from the population by selection. They could also represent aberrant activities stimulated by unfamiliar surroundings. Distinguishing adaptation from aberrancy is a common problem for behavioral biologists. We know of no widely recognized criterion for making this distinction.

In the northern Gulf of California, the sphaeromatid isopod, *Paracerceis sculpta* breeds primarily within the spongocoels of calcareous sponges (*Leucetta losangelensis*, Shuster, 1987a, b). Most males in this population, 81% (Shuster and Wade, 1991) possess rugose pleotelsons and elongated posterior appendages (uropods) that are used in contests with other males. These “ α -males” usually establish breeding sites within sponges, females are attracted to spongocoels occupied by α -males, and breeding assemblages form that may include as many as 19 females per α -male in single-male assemblages, and as many as 52 females in multiple-male assemblages (Shuster, 1987a; Shuster and Wade, 1991; Shuster, unpublished data). Alpha-males compete for control of these aggregations, and body size confers an advantage in spongocoel defence and takeover (Shuster, 1990). However, after females enter sponges, males spend little time guarding individual mates (Shuster, 1992). The details of male polymorphism in this species, including descriptions of β - and γ -males, which comprise 4% and 15% of the male population, respectively, are available in Shuster et al. (2001), and Shuster and Wade (2003).

Reproductive behavior occurring outside of sponges is poorly known in *P. sculpta*, although reproductive individuals, including mature males, as well as mature, premolt females and females bearing developing young, are regularly collected from subtidal algae (Shuster, 1986). In the northern Gulf of California, sponge populations crash in midsummer, forcing breeding individuals into habitats not usually occupied by this species, e.g., demosponges (*Haliclona*), tunicates, and rocky substrates (Shuster, 1986,

Table 1. Results of a 3-way ANOVA to examine the effects of male experience class (CLASS = used once; used twice), male identity (ID = resident; intruder), and experimental treatment (TMT = female present; female absent) on the total number of acts performed by each male in our experiments; * indicates statistical significance.

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	7	77.77	11.11	2.16	0.047*
Error	74	379.84	5.13		
Total	81	457.61			

Source	DF	Sum of Squares	F Ratio	Prob > F
CLASS	1	12.52	2.44	0.12
ID	1	1.18	0.23	0.63
TMT	1	61.68	12.02	<0.001*
CLASS*ID	1	0.003	0.0006	0.98
ID*TMT	1	0.07	0.01	0.91
CLASS*TMT	1	0.68	0.13	0.72
CLASS*ID*TMT	1	0.26	0.05	0.82

1991). Isopods from this population readily mate and brood young in laboratory containers (Shuster, 1990, 1991, 1992). *Paracerceis sculpta* is also known to be an invasive species, with populations recorded worldwide from a range of intertidal and subtidal locations (review in Ariyama and Otani, 2004). These results suggest that reproduction by *P. sculpta* may not be exclusive to infaunal habitats.

Our goal in these experiments was to observe the pre-mating behavior of male isopods in two distinct environments. Our experimental design considered the behavior we observed as norms of reaction; i.e., as the interaction between individual genotype and environmental conditions that produces a recognizable phenotype (Roff, 1996; Shuster and Wade, 2003). Our two environments were those in which breeding sites were absent, but females were present, and those in which both breeding sites and females were absent. Our specific aims were to determine whether males performed recognizable behavior in each of these circumstances, as well as whether the behavior of males in each situation differed in measurable ways.

In our experiments, we described the fractions of individuals who responded similarly to two types of environmental cues. The first cue was the absence of breeding sites. The second cue was the availability of sexually receptive females. We tested three specific hypotheses regarding the effects of these cues on male-male competition: 1) if males found these experimental circumstances unfamiliar, we expected to observe no consistent patterns in male behaviour, 2) if males who were established first in arenas recognized themselves as "residents," we expected these males to behave more aggressively than "intruder" males introduced later, and 3) if males allowed to associate with potential mates recognized themselves as residents, we expected resident males to compete with intruder males more readily and more intensely in the presence of females than in their absence.

Our results showed that α -males do exhibit consistent behavioral patterns in arenas that lack usual breeding sites, and that these activities differed from those usually observed at breeding sites. Furthermore, α -males competed for females in such circumstances, and appeared to recognize their status as residents and as intruders. Opportunistic mating attempts by males in many species appear to be

adaptive, but few studies have documented the details of male mating behavior in locations other than normal breeding habitat. Our results show that *P. sculpta* α -males behave in particular ways when they encounter receptive females outside of sponges. We suggest that contests for mates in these locations are sufficiently common in nature to have favored the evolution (or retention) of contact mate guarding behavior in a crustacean species that usually breeds within cavities.

MATERIALS AND METHODS

To examine the behavior of α -males when sponges were unavailable and receptive females were present (Treatment 1), 20 field collected α -males (residents) were placed into separate 250 ml cylindrical polyethylene arenas containing seawater and a receptive female for 1 h before each trial. When within sponges, receptive females usually pair with α -males within this time (Shuster, 1992). Because all females used in these experiments were behaviorally receptive, but had not yet undergone their reproductive molts (Shuster, 1992), our experiments focused exclusively on male interactions that occurred before mating.

After 1 h, a size- and age-matched α -male (an intruder), was introduced to the resident's arena (see Shuster, 1990, 1992 for further details on this protocol). For 20 min, all behaviors were recorded by one of us (SMS) on audio tape, including latency to first act, contact (a low intensity act directed toward a male or female), male-male grappling with uropods or walking legs (an aggressive act initiated by one toward the other male), rolling up (a defensive posture in response to contact or a grappling attempt), and gripping of the female by a male in a contact guarding posture (Shuster, 1981; Jormalainen and Shuster, 1999).

To examine the behavior of α -males when sponges and receptive females were absent (Treatment 2), 20 field collected α -males were established in separate arenas. After 1 h, a size- and age-matched α -male intruder was introduced to each container. All behaviors occurring within 20 min were recorded as described above. Ten of the 20 residents and 10 of the 20 intruders were used in both treatments. The order in which males experienced each treatment was balanced across both treatments, and no individuals were used twice in the same treatment. All contests in both treatments were observed between 18:00 and 02:00 hrs under red light. All individuals were handled, maintained and returned to their habitats as described in Shuster (1990, 1991, 1992).

To determine whether: 1) the behavior of males used in both treatments differed from that of males used in only one treatment, 2) the behavior of residents differed from that of intruders, and 3) the presence of females influenced male behavior, we used 3-way ANOVA to examine the effects of male experience class (CLASS = used once; used twice), male identity (ID = resident; intruder), and experimental treatment (TMT = female present; female absent) on the total number of acts performed by each male in our experiments. We used 2-way ANOVA to examine the effects of male identity and treatment on the number of times males grappled. To compare the number of interactions by residents and intruders with females, and the latency to first activity by residents, we used 1-way ANOVA. Lastly, we used $R \times C$ and 2×2 G-tests to compare the number of trials in which residents and intruders initiated activity in the presence and in the absence of females. To minimize observer bias, data analyses were conducted by only one of us (EMA).

RESULTS

Our 3-way ANOVA to examine variation in total male acts was significant overall ($F_{[7,81]} = 2.16$, $P = 0.047$). However, only experimental treatment (TMT; $F = 12.02$, $P < 0.001$; Table 1) had a significant effect on the total number of acts performed by individual males. Stated differently, the presence of females appeared to significantly increase the activity of males regardless of male identity and experience (Fig. 1), but neither the number of times a male was used (CLASS: $F = 2.44$, $P = 0.12$) nor the male's identity as resident or intruder (ID: $F = 0.23$, $P = 0.63$) significantly influenced overall male activity. Furthermore, none of the

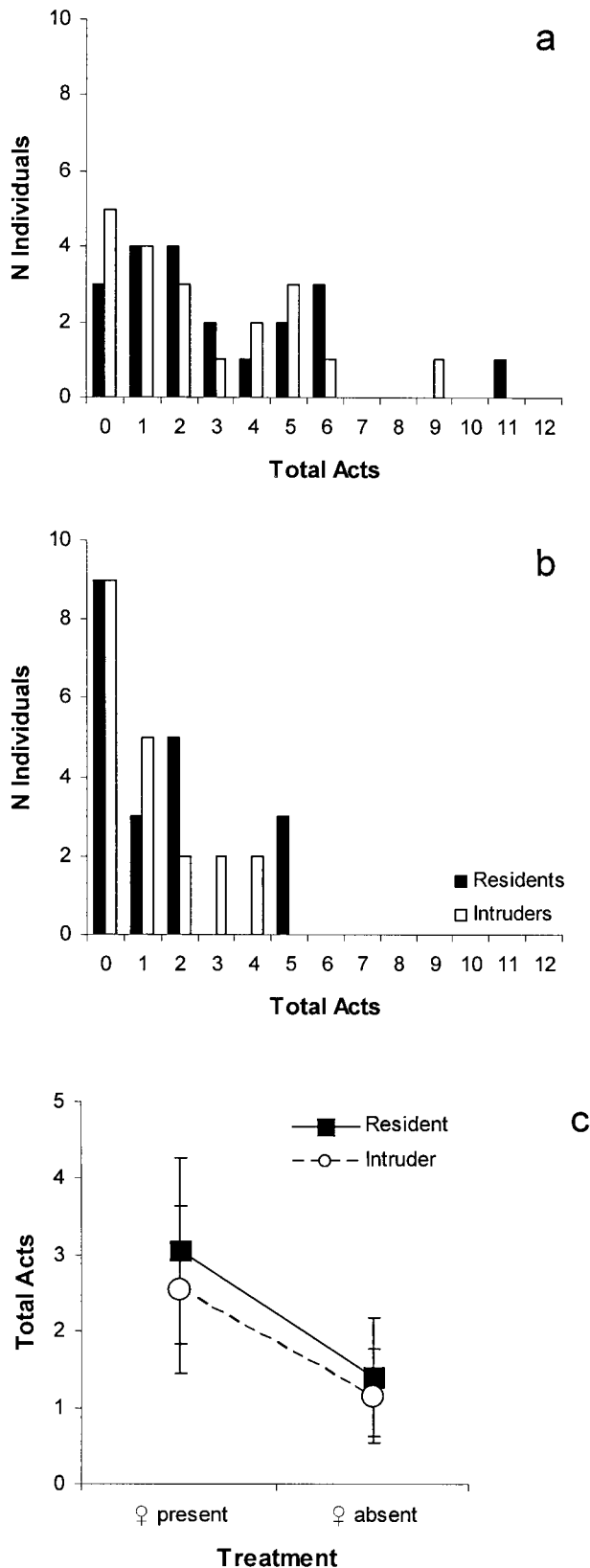


Fig. 1. The total number of acts performed by residents (black columns) and intruders (white columns). a, Treatment 1, females present (mean \pm 95%CI: residents 3.05 ± 1.22 ; intruders 2.55 ± 1.10), b, Treatment 2, females absent (mean \pm 95%CI: residents 1.40 ± 0.77 ; intruders 1.15 ± 0.61). c, There was no significant difference in the average number of acts

possible interactions among the main effects (CLASS*ID: $F < 0.001$, $P = 0.98$; CLASS*TMT: $F = 0.13$, $P = 0.72$; ID*TMT: $F = 0.01$, $P = 0.91$; CLASS*ID*TMT: $F = 0.05$, $P = 0.82$; Table 1) significantly influenced overall male activity.

The details of behavior performed by residents and intruders were distinct, in the presence and in the absence of females, both in the ways residents and intruders associated with females as well as in their responses to each other. Resident males in all cases ($N = 20$; Treatment 1) associated themselves closely with females, either maintaining a contact guarding position similar to that observed in non-cavity dwelling sphaeromatids (Shuster, 1981; Jormalainen and Shuster, 1999), or remaining within a body length of the female. When females were present (in Treatment 1), 12/20 (60%) of residents contacted intruders, 9/20 (45%) of residents grappled with intruders and 14/20 (70%) of residents gripped and retained the female during the trial. Also in Treatment 1, 13/20 (65%) of intruders contacted residents, 11/20 (55%) grappled with residents and 4/20 (20%) of intruders attempted to grip the females during the trial but were repulsed by the resident. Neither residents nor intruders rolled up during any of these trials. When females were present, there was no significant difference in the average number of acts performed by individual residents (mean \pm 95%CI = 3.05 ± 1.22 , $N = 61$) and intruders (2.55 ± 1.10 , $N = 51$; Fig. 1a), and there was no significant difference in the average number of grapples engaged in by residents (1.15 ± 0.47) and intruders (1.45 ± 0.73 ; Fig. 2a).

Females were absent in Treatment 2. Here, 10/20 (50%) of residents contacted intruders, 5/20 (25%) of residents grappled with intruders, and 3/20 (15%) of residents rolled up during the trial. Also in Treatment 2, 9/20 (45%) of intruders contacted residents, 4/20 (20%) of intruders grappled with residents and 4/20 (20%) of intruders rolled up during the trial. When females were absent, there was no significant difference in the average number of acts performed by individual residents (mean \pm 95%CI = 1.40 ± 0.77) and intruders (1.15 ± 0.61 ; Fig. 1b), and no significant difference in the average number of grapples engaged in by residents (0.40 ± 0.33) and intruders (0.25 ± 0.24 ; Fig. 2b).

Our 2-way ANOVA to compare the number of times resident and intruder males grappled in contests with and without females was significant ($F_{[3,79]} = 5.00$, $P = 0.003$), with a significant effect of treatment ($F = 14.16$, $P < 0.001$), but no significant effect of male identity ($F = 0.08$, $P = 0.77$) and no significant interaction ($F = 0.75$, $P = 0.39$). Thus, the presence of females significantly increased the male tendencies to grapple regardless of their identity as residents or intruders (Fig. 2c).

Our 1-way ANOVA of the number of interactions with females, which usually involved gripping the female, showed that resident α -males had significantly more of

←

performed by individual residents and intruders within each treatment ($F = 0.36$, $P = 0.55$), but relative to Treatment 2, the presence of females significantly increased the activity of males in Treatment 1 ($F = 12.25$, $P = 0.001$).

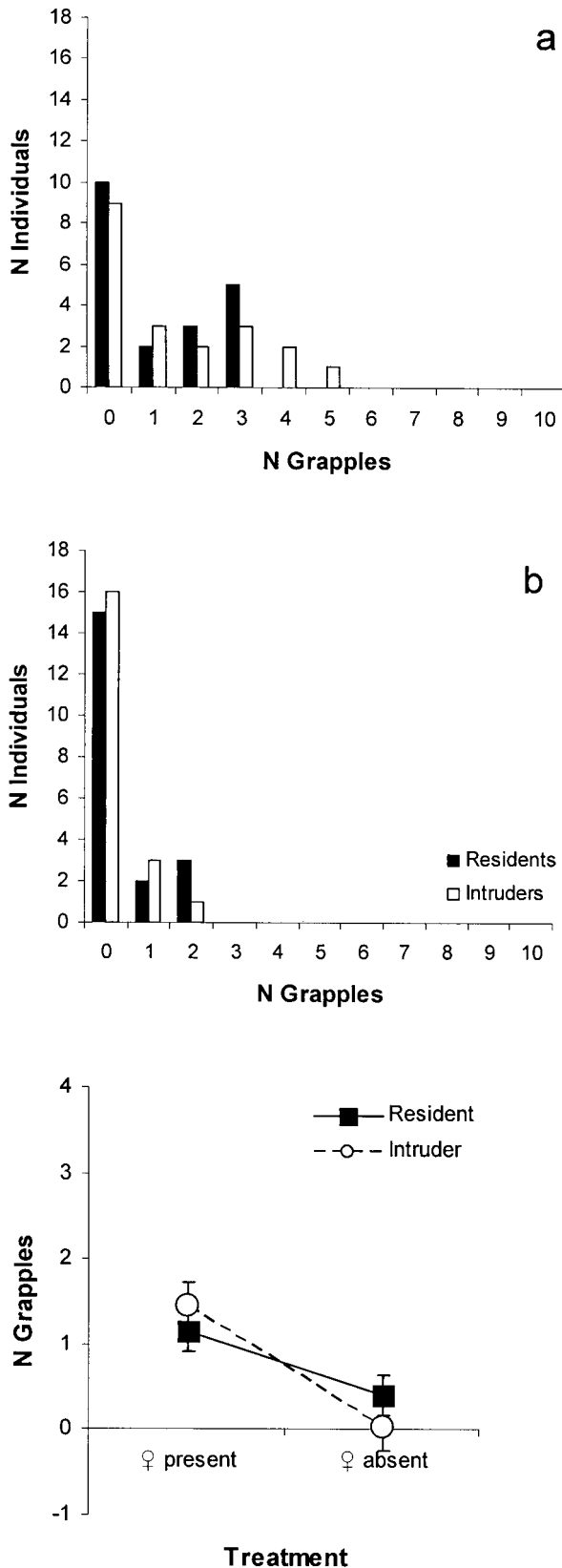


Fig. 2. The total number of grapples performed by residents (black columns) and intruders (white columns). a, Treatment 1, females present (mean \pm 95%CI: residents 1.15 ± 0.47 ; intruders 1.45 ± 0.73). b, Treatment 2, females absent (mean \pm 95%CI: residents 0.40 ± 0.33 ;

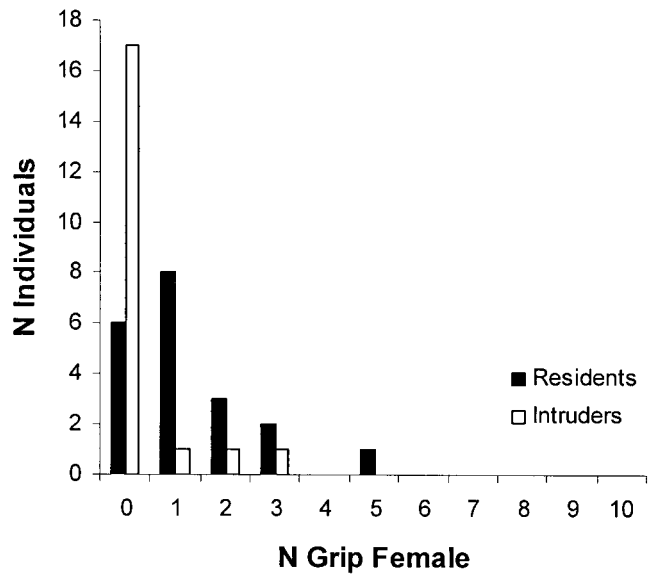


Fig. 3. In Treatment 1, resident α -males (black columns; 1.15 ± 0.57) interacted with females significantly more often than intruder α -males (white columns; 0.30 ± 0.57 ; $F = 5.90$, $P < 0.02$).

these interactions (1.15 ± 0.57) with females than intruder α -males (0.30 ± 0.57 ; $F = 5.90$, $P < 0.02$; Fig. 3). Our 1-way ANOVA to compare latency to first activity by residents between treatments showed longer latency by resident males when receptive females were present than when females were absent ($F = 9.17$, $P = 0.008$). Across all trials, there was a significant effect of the presence or absence of females on resident and intruder behavior ($G_{adj} = 10.98$, $P < 0.001$, $d.f. = 2$; Fig. 4a). Interactions between males occurred more often when females were present than when females were absent ([resident acts + intruder acts] vs no acts, $G_{adj} = 6.21$, $P < 0.025$, $d.f. = 1$). Furthermore, among those trials in which interactions occurred ($N = 29$), resident α -males initiated interactions with α -male intruders more often when females were present in arenas (14/20), than when females were absent (4/20), whereas intruder α -males initiated interactions with α -male residents more often when females were absent (7/20) from arenas than when females were present (4/20; $G_{adj} = 4.68$, $P < 0.05$, $d.f. = 1$, Fig. 4b).

DISCUSSION

Interactions Among *P. sculpta* Males and Females

In our experiments, we found consistent male behaviors associated with mate defense and acquisition that were distinct from those displayed in typical breeding habitat (Shuster 1990, 1991, 1992, see below). These results also suggest that, as in many vertebrate and invertebrate species,

intruders 0.25 ± 0.24). c, there was no significant difference in the average number of acts performed by individual residents and intruders within each treatment ($F = 0.08$, $P = 0.77$), but relative to Treatment 2, the presence of females significantly increased the activity of males in Treatment 1 ($F = 14.21$, $P < 0.001$).

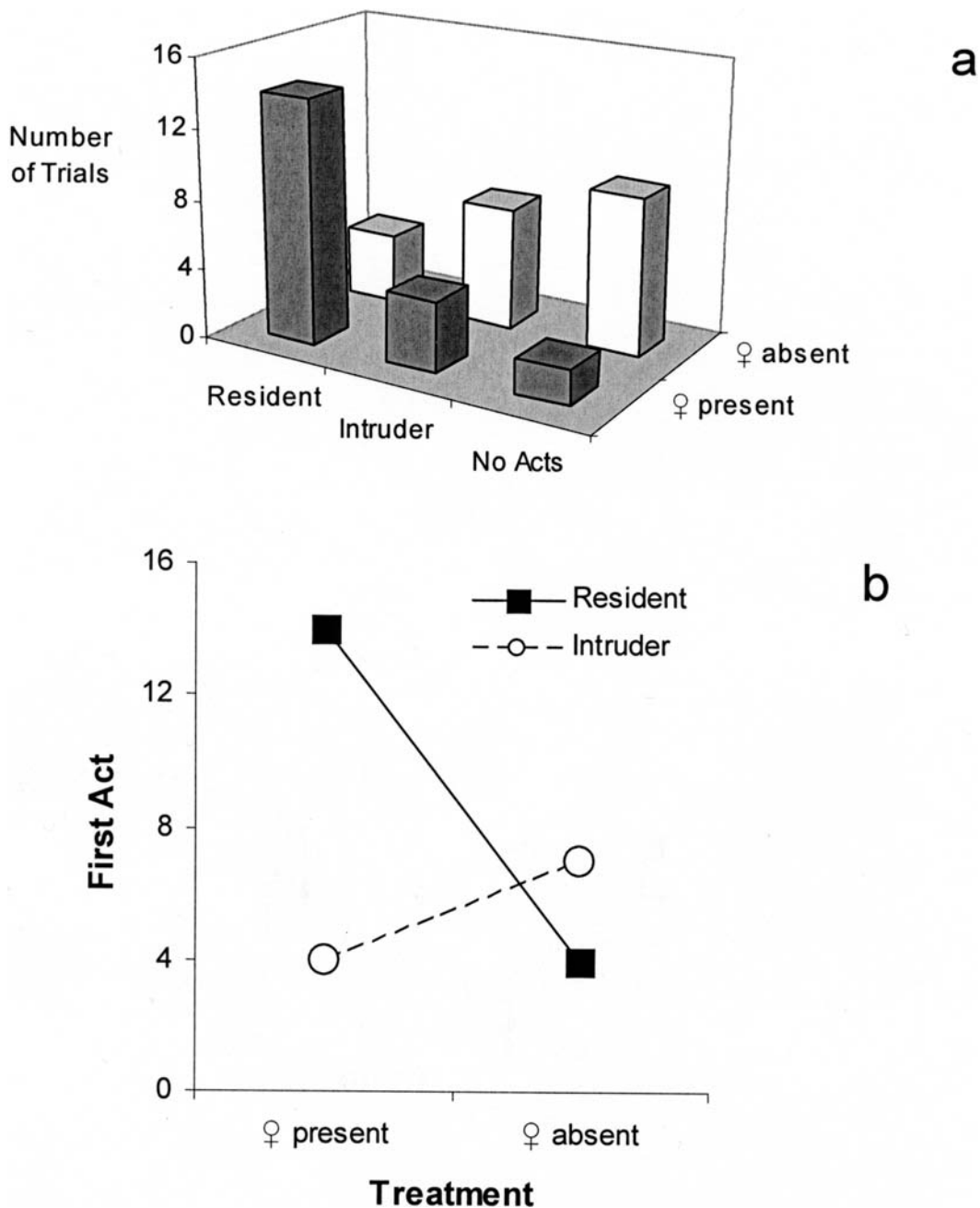


Fig. 4. a, There was significant heterogeneity in how activities were initiated by males when females were present in arenas (black columns), compared to when females were absent in arenas (white columns; $G_{adj} = 10.98$, $P < 0.001$, $d.f. = 20$); in particular, interactions between males occurred more often when females were present than when females were absent ([resident acts + intruder acts] vs no acts, $G_{adj} = 6.21$, $P < 0.025$, $d.f. = 1$); the height of each column represents the number of trials in each treatment; total trials per treatment = 20. b, Considering only trials in which interactions occurred ($N = 29$), resident α -males initiated interactions with α -male intruders more often when females were present in arenas, whereas intruder α -males initiated interactions with α -male residents more often when females were absent from arenas ($G_{adj} = 4.68$, $P < 0.05$, $d.f. = 1$).

P. sculpta males guard their mates and may attempt to mate opportunistically, suggesting that contests for mates outside of normal breeding habitat may be common in nature. The presence of sexually receptive females clearly affected male-male competition by α -males in *P. sculpta*. Males had significantly more total interactions with each other and grappled more in the presence of females than when females were absent from arenas. Furthermore, the increase in the

distributions of acts and grapples by residents and intruders in the presence of females was not due to the influence of a few individuals (Figs. 1-2). Instead, the presence of females in Treatment 1 appears to have stimulated a larger proportion of males to increase their activity and to grapple more than when females were absent. There was no significant effect of using some males as residents in Treatment 1 and as intruders in Treatment 2.

Resident males gripped females more than intruder males. Such activity may be a form of mate guarding (Jormalainen, 1998) because residents, by definition, had previously associated with females in these trials for at least 1 h. This latter observation is noteworthy because within *Leucetta* sponges in nature as well as within artificial sponges in the laboratory, *P. sculpta* males tend not to engage in extensive contact guarding of mates, and tend not to retain females after copulation (Shuster, 1989, 1990). In contrast, males in other non-cavity dwelling sphaeromatid species tend to engage in prolonged mate guarding, both before and after copulation (review in Jormalainen and Shuster, 1999). Although we did not observe mating because only premolt females were used in these experiments, contact guarding by *P. sculpta* males was more extensive than has been observed in spongocoels in other experiments (Shuster, 1990, 1991, 1992), suggesting that increased male tendencies to physically defend their mates may also constitute a behavioral response to mating opportunities occurring outside of sponges.

Although resident males usually initiated activity when females were present (Treatment 1), contrary to our expectations, latency to first activity by resident males was significantly greater when females were present than when they were absent. This difference may be explained by the small number of residents who initiated activity in this treatment. However, intruders initiated activity more often than residents when females were absent, but seldom initiated activity when females were present, suggesting that males recognized their status as intruders and residents, and sought or avoided contests accordingly. Residents and intruders rolled up only in Treatment 2, suggesting that this act may represent a defensive posture observed only in low intensity interactions. In 5/20 Treatment 1 trials (25%), the female initiated contact with the resident male, suggesting that mate guarding in this species may involve some cooperation by females.

Neither residents nor intruders were passive during these experiments, suggesting that treatment conditions did not inhibit resident or intruder behavior in recognizable ways. Furthermore, in each set of experiments, significant proportions (15-70%) of the individuals designated as residents and intruders performed the activities we monitored. The presence of more individuals in each arena in Treatment 1 (females present) may have simply increased the overall activity of these individuals relative to individuals in Treatment 2 (females absent). However, this conclusion is mitigated by three observations: 1) latency to first act in Treatment 2 exceeded that in Treatment 1, 2) resident males in Treatment 1 directed their guarding activities toward females and their aggressive activities toward intruding males, and 3) defensive behavior by resident and intruder males appeared only in Treatment 2. If three vs. two individuals per arena simply caused greater disturbance, more defensive activities are likely to have been observed. These results corroborate our assertion that the behaviors we identified were typical of males in these circumstances; that is, in situations in which breeding opportunities exist outside of isopods' usual breeding habitats.

A Criterion for Investigating Behavior in Atypical Circumstances

When individuals are placed into circumstances that differ from those they usually encounter, as male isopods were in these experiments, they may behave in two possible ways. Individuals may perform completely aberrant behaviors because the novel environment is unfamiliar to them in all respects, or, individuals may perform a "recognizable" set of behaviors, that are identifiable by the experimenter because multiple individuals within the experimental population express them.

How can unfamiliar circumstances stimulate seemingly integrated sets of responses in different individuals? One possible explanation is that the "novel" experimental circumstances, in fact, resemble circumstances encountered by ancestral members of the experimental organisms' population, and, because these ancestors responded to such circumstances in a way that enhanced their fitness, the tendency for extant members of the population to respond in kind persists. This hypothesis views behavioral plasticity as a quantitative trait that has been shaped by past selection (Roff 1996; Shuster and Wade 2003). As such, an individual's behavioral phenotype is part of a distribution of similar phenotypes within a population, whose expression represents the interaction between genetic factors that permit the behavior, and environmental cues that stimulate it.

If the genetic factors influencing the expression of a behavioural phenotype are normally distributed—a reasonable assumption if behavior is influenced by many genes of individually small effect—then the fraction of the population that responds to an environmental cue will depend on the cue's intensity (Dempster and Lerner 1950; Gianola and Norton 1981). When cues are weak or absent, few or no individuals in the population will respond to it. In contrast, as the cue becomes more intense, an increasing fraction of the population will respond. The relative fitness of individuals who respond appropriately, given the average cue intensity, will determine the average genotype for that population, which in turn, will determine how readily the average individual in that population responds to a given environmental cue.

"Behavioral plasticity" describes flexibility in behavioural responses to variable environments and is generally presumed to be common (Bonnet et al., 2005; Badyaev, 2005). Shuster and Wade (2003) have argued that the evolution of behavioral plasticity requires three conditions: 1) inheritability; the existence of genetic factors underlying particular behavioral variants, 2) predictability; the frequent appearance of environments favoring reproduction by these variants, and 3) consistency; consistent, positive selection, relative to other evolutionary forces acting on the population, favoring behavioral variants that are capable of plastic responses to environmental variation. Contrary to the circumstances in which it is usually described (see West-Eberhard, 2003; Sih et al., 2004), this view suggests that adaptive behavioral plasticity evolves only in environments that are common, highly predictable, and which favor the reproduction of a significant proportion of the total population.

For most behavioral analyses, separating potentially adaptive from non-adaptive variation can be difficult. It is usually impossible to measure the heritability, frequency and fitness for behavioral traits without detailed laboratory or field analyses. Adaptation is indeed, an “onerous concept” (Williams 1966). For this reason, we suggest the following simple criterion for initially distinguishing potentially adaptive behaviors from mere phenotypic variants: the expression of the behavior must be recognizable in a significant fraction ($> 5\%$) of individuals within the population when a common stimulus is applied. This criterion was met for all of the behaviors documented for *P. sculpta* in the experiments described above.

This criterion serves an important and often neglected function. It eliminates from further evolutionary consideration certain aberrant behaviors, such as attempts by males to copulate with inanimate objects (Dickerman, 1960; Thornhill and Alcock, 1983; Lehner, 1988; Meshaka, 1996), or remarkable feats of skill or agility performed by single individuals (Patterson et al., 1991; West-Eberhard, 2003). Unless extraordinary fitness gains can also be shown to attend these unusual activities, there is little chance that they will be increased in frequency by selection.

This criterion is neither arbitrary nor easily met (Shuster and Wade, 2003). For example, suppose that in a given environment, a particular behavior is expressed by 5% of the population, and that by performing the behavior, individuals gain a positive fitness advantage, b . In the same environment, suppose that the remaining 95% of the population, because they do not perform the behavior, experience a fitness cost, c . In the absence of drift, migration or mutation, the rare behavioral trait can increase in frequency within the population only if its average effect on individual fitness is positive, i.e., if $(0.05b + 0.95c) > 0$. In this case, the fitness advantage gained by performing the behavior must be more than 19 times greater than the fitness cost of not performing it. If the trait is sex-limited, and therefore is exposed to selection in only half of the population, the fitness advantage conferred must be nearly 40 times greater than the cost. The simple rule is this: the rarer the trait, the more of a fitness advantage it must confer to persist within the population.

This criterion of “commonality” satisfies, at least until more detailed analyses can be conducted, all three requirements for the evolution of behavioral plasticity (Shuster and Wade, 2003). Genetic inheritability is the simplest explanation for the appearance of a behavior within a population at frequencies greater than expected by chance (Darwin, 1859). Environmental predictability and evolutionary consistency are also revealed, for the same reason, when more than 5% of a population responds in the same way to a particular stimulus. The appearance of a common behavioral phenotype suggests that the stimulus eliciting the behavior has been experienced by a significant fraction of the population at some time in the past, and furthermore, that the observed, common response has been favored in a consistent way by selection. The criterion of commonality does not guarantee that a behavioral variant meeting it is indeed an evolved trait; it simply provides sufficient justification for investigating the variant further as such. More

importantly, it provides a simple way for experimenters to avoid seeking adaptive explanations for the existence of rare individuals.

Certainly, behavior by its very nature is polymorphic, and distinct behavioral phenotypes may in some cases persist at frequencies less than 5% (Shuster, 1987a; Sinervo, 2001; West-Eberhard, 2003). However, such cases are explained by the necessary relationship between a phenotype’s relative fitness and its population frequency (Shuster and Wade, 2003). To persist within a population, rare phenotypes, particularly those appearing in less than 5% of the population, must confer disproportionate fitness advantages. Furthermore, the circumstances in which these advantages are gained must be common, or selection will be infrequent and thus weak. For example, in *Paracerceis sculpta*, two other genetically distinct male phenotypes, β -males and γ -males, coexist with α -males (Shuster et al., 2001). Beta-males do not appear in most population samples, and less than 4% of the male population may consist of β -males over time (Shuster, 1989). However, when aggregations of females with α -males become large and β -males invade these aggregations, they obtain an average of 60% of the available fertilizations (Shuster, 1992; Shuster and Wade, 1991). Despite their low population frequency, the extremely high fitness that β -males obtain within breeding sites appears to allow this highly specialized phenotype to persist.

The behavioral results presented here for *Paracerceis sculpta* meet the criterion of commonality. Although the behaviors we observed were not performed under the usual circumstances in which this species breeds, α -males consistently recognized themselves as residents and as intruders. They responded to the presence of females in consistent ways and they attacked each other in ways likely to enhance their mating success. Our results indicate that as in many other animal species, *P. sculpta* α -males attempt to mate opportunistically, and that contests for mates outside of normal breeding habitat are likely to be common in nature.

ACKNOWLEDGEMENTS

This research was funded by The Research Experience for Undergraduates program funded by the National Science Foundation, grant DBI-0243814 and by NSF grant DEB-0425908; we are grateful to Emily Omana, Steven Vuturo, Amber Shows and two anonymous reviewers for their comments on earlier versions of this manuscript. Permission to study *P. sculpta* populations in the Gulf of California was granted by Mexican Government, permits 412.2.1.3.0.2315, A00-702-06296, and DAN 02384.

REFERENCES

- Ariyama, H., and M. Otani. 2004. *Paracerceis sculpta* (Crustacea: Isopoda: Sphaeromatidae), a newly introduced species into Osaka Bay, central Japan. *Benthos Research* 59: 53-59.
- Badyaev, A. V. 2005. Stress-induced variation in evolution: from behavioral plasticity to genetic assimilation. *Proceedings of the Royal Society, Biological Science*, London 272: 877-886.
- Bateman, A. J. 1948. Intrasexual selection in *Drosophila*. *Heredity* 2: 349-368.
- Bonnet, X., F. Aubret, O. Lourdaux, M. Ladyman, D. Bradshaw, and S. Maumelat. 2005. Do ‘quiet’ places make animals placid? Island vs. mainland tiger snakes. *Ethology* 111: 573-592.
- Clark, D. C., S. J. DeBano, and A. J. Moore. 1997. The influence of environmental quality on sexual selection in *Nauphoeta cinerea* (Diptera: Blaberidae). *Behavioral Ecology* 8: 46-53.

- Clutton-Brock, T. E. (ed.), 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago. 538 pp.
- Darwin, C. R. 1859. On the Origin of Species. Facsimile of the first edition 1964. Harvard University Press, Cambridge, Massachusetts. 513 pp.
- . 1874. The Descent of Man and Selection in Relation to Sex. second edition. Rand McNally and Co., N.Y., republished by Gale Research Co., Detroit, Michigan, 1974, 672 pp.
- Dempster, E. R., and I. M. Lerner. 1950. Heritability of threshold characters. *Genetics* 35: 212-236.
- Dickerman, R. W. 1960. Davian behavior. *Journal of Mammalogy* 41: 403.
- Elner, R. W., and P. G. Beninger. 1995. Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: Physiological pathways and behavioral plasticity. *Journal of Experimental Marine Biology and Ecology* 193: 93-112.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223.
- Gianola, D., and H. W. Norton. 1981. Scaling threshold characters. *Genetics* 99: 357-364.
- Jormalainen, V. 1998. Precopulatory mate guarding in crustaceans: Male competitive strategy and intersexual conflict. *Quarterly Review of Biology* 73: 275-304.
- , and Shuster, S. M. 1999. Female reproductive cycles and sexual conflict over precopulatory mate-guarding in *Thermosphaeroma* isopods. *Ethology* 105: 233-246.
- Lehner, P. N. 1988. Avian Davian behavior. *Wilson Bulletin* 100: 293-294.
- Meshaka, W. E., Jr. 1996. Anuran Davian behavior: A Darwinian dilemma. *Florida Scientist* 59: 74-75.
- Patterson, F. G. P., C. L. Holts, and L. Saphire. 1991. Cyclic changes in hormonal, physical behavioral, and linguistic measures in a female lowland gorilla. *American Journal of Primatology* 24: 181-194.
- Roff, D. A. 1996. The evolution of threshold traits in animals. *Quarterly Review of Biology* 71: 3-35.
- Shine, R., T. Langkilde, and R. T. Mason. 2003. The opportunistic serpent: Male garter snakes adjust courtship tactics to mating opportunities. *Behaviour* 140: 1509-1526.
- Shuster, S. M. 1981. Sexual selection in the Socorro Isopod, *Thermosphaeroma thermophilum* (Cole and Bane) (Crustacea: Peracarida). *Animal Behaviour* 29: 698-707.
- . 1986. The reproductive biology of *Paracerceis sculpta* (Holmes). Unpublished Ph.D. Dissertation, University of California, Berkeley, 279 pp.
- . 1987a. Alternative reproductive behaviors: three discrete male morphs in *Paracerceis sculpta*, an intertidal isopod from the northern Gulf of California. *Journal of Crustacean Biology* 7: 318-327.
- . 1987b. Male body size, not reproductive habitat characteristics predicts polygyny in a sexually dimorphic intertidal isopod crustacean, *Paracerceis sculpta*. pp. 71-80. In, G. Maligrino and H. Santoyo (eds.), *Memorias del Simposium Biología Marina de Universidad Autónoma de Baja California Sur, 5 Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, Mexico*.
- . 1989. Courtship and female mate selection in a semelparous isopod crustacean (*Paracerceis sculpta*): The use of genetic markers to measure differences in fertilization success among α -, β -, and γ -males. *Evolution* 34: 1683-1698.
- . 1990. Courtship and female mate selection in a semelparous isopod crustacean (*Paracerceis sculpta*). *Animal Behaviour* 40: 390-399.
- . 1991. The ecology of breeding females and the evolution of polygyny in *Paracerceis sculpta*, a marine isopod crustacean. pp. 91-110. In, R. Bauer and J. Martin (eds.), *Crustacean Sexual Biology*, Columbia University Press, New York.
- . 1992. The reproductive behavior of α , β -, and γ -males in *Paracerceis sculpta*, a marine isopod crustacean. *Behaviour* 121: 231-258.
- , and M. J. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350: 606-611.
- , J. O. W. Ballard, G. Zinser, C. Sassaman, and P. Keim. 2001. The influence of genetic and extrachromosomal factors on population sex ratio in *Paracerceis sculpta*. pp. 313-326. In, R. C. Brusca and B. Kensley (eds.), *Isopod Systematics and Evolution, Crustacean Issues*. Vol. 13. Balkema Press, Amsterdam.
- , and M. J. Wade. 2003. *Mating Systems and Strategies*. Princeton University Press, Princeton, New Jersey, 522 pp.
- Sih, A., A. Bell, and J. Chadwick Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* 19: 372-378.
- Sinervo, B. 2001. Selection in local neighborhoods, graininess of social environments, and the ecology of alternative strategies. pp. 191-226. In, L. A. Dugatkin (ed.), *Model Systems in Behavioral Ecology*. Princeton University Press, Princeton, New Jersey.
- Thornhill, R., and J. Alcock. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, Massachusetts, 547 pp.
- Wade, M. J. 1979. Sexual selection and variance in reproductive success. *American Naturalist* 114: 742-746.
- , and S. J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behavior, female choice and sperm precedence. *Animal Behaviour* 28: 446-461.
- West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. Oxford University Press, Oxford, United Kingdom. 794 pp.
- Williams, G. C. 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, Princeton, New Jersey, 307 pp.

RECEIVED: 28 July 2006.

ACCEPTED: 18 November 2006.