

Department of Zoology, University of California, Berkeley

Male Defense of the Breeding Cavity and Factors Affecting the Persistence of Breeding Pairs in the Stomatopod, *Gonodactylus bredini* (Manning) (Crustacea: Hoplocarida)

STEPHEN M. SHUSTER & ROY L. CALDWELL

SHUSTER, S. M. & CALDWELL, R. L. 1989: Male defense of the breeding cavity and factors affecting the persistence of breeding pairs in the stomatopod, *Gonodactylus bredini* (Manning) (Crustacea: Hoplocarida). *Ethology* 82, 192—207.

Abstract

In Caribbean Panama, nonreproductive male and female stomatopods are solitary and defend their own coral-rubble cavities. When breeding pairs form, however, males assume all responsibility for cavity defense. To compare success in cavity defense and defensive tactics among paired and unpaired males, and to examine the tendency for paired stomatopods to exchange their present mates for larger (higher quality) individuals, we introduced same-sized and 15 % larger male, and same-sized and 15 % larger reproductive female intruders to paired and unpaired male residents in a balanced design. Paired males were more successful at cavity defense than unpaired males, evidently because paired males strike intruders more than unpaired males, and because intruders fight less intensely against paired males than against unpaired males. Paired males occasionally attempted extrapair copulations, but showed little tendency to abandon their mates in favor of larger females. Paired females, however, mated readily with intruder males that evicted resident males. Population-wide female breeding synchrony and prolonged female receptivity before oviposition reduce variance in male mating success and may force males to guard the breeding cavity to assure their paternity. Uncertainty about the reproductive condition of intruder females may prevent males from exchanging mates.

Corresponding author: Stephen M. SHUSTER, Department of Ecology and Evolution, University of Chicago, 915 E. 57th St., Chicago, IL 60637, U.S.A.

Introduction

In many animal species, reproductive associations of one male and one female last well beyond the time necessary for the transfer of gametes (reviews in WRANGHAM 1979; WITTENBERGER & TILSON 1980; WICKLER & SEIBT 1981; RIDLEY 1983; THORNHILL & ALCOCK 1983). Although such associations are often considered monogamous, the term "monogamy" is accurate only if individuals mate exclusively with one other individual, or if individuals mate once in their lives

(WALKER 1980; THORNHILL & ALCOCK 1983). Since truly monogamous species in this sense are relatively rare (WITTENBERGER & TILSON 1980), the term "breeding pair" is more appropriate for reproductive associations that occasionally permit extrapair matings or that may dissolve between successive reproductive events.

Breeding pairs frequently establish a reproductive territory and defend space around it. The specific characteristics of such territoriality may vary depending on the degree to which parental care or mate guarding are the primary context for pair formation. Within the continuum bounded by species with obligate biparental care, and species in which nonparental males guard individual females only to protect their own paternity, three general categories of territory defense by breeding pairs are apparent: (1) cooperative territory defense, in which both members of a pair repel all conspecific invaders regardless of the invader's sex (LEFFELAAR & ROBERTSON 1984, 1986; BORSEMA & BEMUS 1985); (2) sex-specific territory defense, in which males repel male intruders and females repel female intruders [WRANGHAM 1979; FITCH & SHUGART 1983; MITANI 1984; LINSENMIR 1984; CARLSON et al. 1985; RAEMAEEKERS & RAEMAEEKERS 1985; SLAGSVOLD & LIFJELD 1986; male guarding of female to defend paternity is included in this category (SHUSTER 1981; RIDLEY 1983; DUNHAM 1986)], and (3) single-sex territory defense, in which one member of a pair consistently repels all conspecific intruders, regardless of the intruder's sex. Most examples of territory defense by breeding pairs fall into the first two categories. The third category is not well documented and is poorly understood.

Most research on territory defense by breeding pairs of animals has involved field observations with relatively little manipulation (MOLLER 1985; CARLSON et al. 1985; reviews in WITTENBERGER & TILSON 1981, WITTENBERGER 1981). This is not surprising because field manipulations are difficult to conduct and often preclude symmetrical experimental designs or controls (RAEMAEEKERS & RAEMAEEKERS 1985; BORSEMA & BEMUS 1985; MITANI 1984). Moreover, nearly all recent investigations of patterns of territorial defense by pairs have concentrated on the outcome of contests without considering how different agonistic behavior patterns may have influenced a resident's success in repelling an intruder. Concentration on outcome can mistakenly lead to the conclusion that paired individuals are more aggressive or fight more vigorously than nonpaired individuals. In fact, persistence rather than aggressiveness may be the most effective tactic in successful territory defense (MONTGOMERY & CALDWELL 1984).

In this paper we describe the pattern of breeding-cavity defense by pairs of stomatopod crustaceans (*Gonodactylus bredini*), a species apparently exhibiting single-sex territory defense. Agonistic behavior in these animals is easily observed and manipulated in the laboratory and is virtually identical to behavior observed in the field (review in CALDWELL 1986a). Here we specifically examine factors contributing to the persistence of breeding pairs at proximate and ultimate levels of causation.

At the proximate level, we asked four questions: (1) Is defense of cavities by stomatopods cooperative, sexspecific or single-sex? (2) Does pairing affect an individual's success in cavity defense? (3) What defensive tactics are used by

paired and unpaired individuals to defend their cavities? (4) How does the presence of a breeding pair in a cavity affect the behavior of intruders?

At the level of ultimate causation, we asked two questions: (1) To what extent do male and female residents attempt extrapair matings when confronted with same-sized and larger male and female intruders (i.e., potentially higher quality mates)? (2) What aspects of female reproductive biology influence the nature of cavity defense by breeding pairs? Answers to these questions permit the pattern as well as the context for cavity defense by stomatopod pairs to be more clearly understood.

The Ecology and Reproductive Biology of *Gonodactylus bredini*

Stomatopod crustaceans are common, ecologically important predators in coastal tropical waters world-wide (CALDWELL et al. 1989). *Gonodactylus bredini*, a medium-sized (adults 25–60 mm standard length) gonodactylid stomatopod, inhabits intertidal and subtidal zones throughout the Caribbean Sea (MANNING 1969). As all gonodactylids, *G. bredini* possesses enlarged and hardened second maxillipeds, structures capable of delivering powerful, smashing blows, and used by stomatopods to capture and process hardbodied prey such as crustaceans and gastropods (CALDWELL et al. 1989). These raptorial appendages also serve as weapons in agonistic encounters with conspecifics, usually over access to cavities in coral rubble (CALDWELL & DINGLE 1976; BERZINS & CALDWELL 1983).

Cavities provide hard substrate for processing food, shelter from predators and a site for courtship, mating and rearing young. Typically, cavities are limited in number and quality due to the close relationship between a cavity's dimensions and its suitability for the above activities (STEGER 1987). Considerable competition occurs among stomatopods for access to this limited resource (CALDWELL & DINGLE 1976; STEGER 1987), and natural selection has evidently favored extreme aggressiveness and a complex repertoire of combat and display tactics associated with competitive interactions (DINGLE & CALDWELL 1969; CALDWELL 1979, 1987). The powerful weaponry possessed by stomatopods makes fighting dangerous, and individuals may be severely damaged or even killed in contests (BERZINS & CALDWELL 1983). Moreover, stomatopods must often move among nearby habitats in pursuit of food or mates, which makes cavity defense a frequent activity for most established individuals (CALDWELL et al. 1989).

Female *G. bredini* reproduce year-round in two- to four-month cycles, with oviposition occurring at full moon (CALDWELL 1986a). About 10 days before oviposition, females provision their eggs with yolk and develop thoracic sternal glands that provide cement for holding egg masses together. Sternal-gland development permits classification of females by reproductive condition (CALDWELL 1986a). Females also alter their agonistic responses to males at this time, evidently to facilitate pairing (CALDWELL 1986a). When females are established in cavities, pairing occurs only after males fight their way in. While such resistance may serve as a form of mate selection, fights resemble those with other females or between nonreproductive females and males (SHUSTER, pers. obs.). When reproductive females encounter males already established in cavities, however, few

aggressive acts are performed by either sex. Females in most cases move directly into the male's cavity and pairing occurs immediately (CALDWELL 1986a; SHUSTER, unpubl. data).

After pairs form, males and females copulate repeatedly over several days until the female spawns (usually within a week, CALDWELL 1986a). Males leave cavities shortly after oviposition and provide no direct parental care to young. Females, however, remain within the cavity after oviposition and defend their brood until the young disperse after the fourth stadial molt (DINGLE & CALDWELL 1972; MONTGOMERY & CALDWELL 1984). Reproduction during full moon, spring tides, results in considerable synchrony in female reproductive condition within local populations (CALDWELL 1986a), and pairs persist over the interval in which most receptive females are available. The combination of prolonged pairing and female reproductive synchrony may reduce variance in male reproductive success by restricting the number of successive pairings available to each male within one reproductive cycle (KNOWLTON 1979). The lack of conspicuous sexual dimorphism in this species is consistent with this hypothesis (MANNING 1969; SHUSTER & CALDWELL, unpubl. data).

Fighting success correlates with body size in *G. bredimi* (CALDWELL & DINGLE 1979; CALDWELL 1986a, b, 1987). Since growth in stomatopods is indeterminate, large stomatopods are generally older and have demonstrated their superior survival and/or feeding ability by simply existing (THORNHILL 1980; KODRIC-BROWN & BROWN 1984). As in most crustacea, large females are more fecund than small females (REAKA 1976). Thus, depending on their size and reproductive condition, intruders represent potential evictors that are variously threatening to residents, as well as potential mates of varying quality. With reproductive success of both members of a pair constrained by this species' reproductive synchrony, behavioral analysis of paired residents' reactions toward this variety of intruders provides insight into factors contributing to the persistence of breeding pairs.

Materials and Methods

This study was conducted at Galeta Marine Laboratory, Smithsonian Tropical Research Institution in the Republic of Panama between May and Sep. 1982, and between July and Sep. 1983. Stomatopods were collected from coral rubble and from artificial cavities in the intertidal and shallow subtidal zones near Galeta as described by DINGLE & CALDWELL (1969) and STEGER (1987). Stomatopods were transported to the lab, where each individual was sexed, measured to the nearest 0.5 mm and examined for injury sustained in collection or in agonistic encounters with other stomatopods. The reproductive condition of each individual was recorded as described in CALDWELL (1986a, b), and all animals larger than 35 mm standard length were marked by removing one antennule flagellum: right antennules were removed in females, left antennules were removed in males. As the eyes and antennules of individuals defending cavities are visible at the cavity entrance, this procedure permitted the sex of individuals defending cavities to be determined at a glance. All animals were maintained in 225-ml plastic cups and provided with food and seawater changes twice weekly.

Contest arenas consisted of plastic mouse cages (20 × 35 × 20 cm) filled with seawater. Each arena contained a concrete artificial cavity (construction described in STEGER 1985) embedded in a layer of fine sand on the cage bottom. A male was introduced to each arena and allowed 1 h to establish himself in the cavity. A same-sized reproductive female ($\pm 1\%$ of the male's total length)

was then introduced to each male and allowed 10 min to pair with the male. This sequence simulates pair formation in nature (CALDWELL 1986a, and above description), and in most cases stomatopods paired immediately. To standardize contests, cavity dimensions were scaled to match the body sizes of stomatopods (STEGER 1987), and pairs were allowed 1 h to adjust to their cavity and to each other before intruders were introduced.

Each pair faced the following four types of intruders in a balanced design: (1) a same-sized ($\pm 1\%$ total length) male; (2) a same-sized reproductive female; (3) a 15% larger male; (4) a 15% larger, reproductive female. A size difference of 10% is detectable by most animals (WALLACE 1987) and is usually sufficient to affect the outcome of stomatopod contests (CALDWELL & DINGLE 1979; CALDWELL 1986b). Single males established in cavities, facing the same intruder types in a balanced design, served as controls.

Before each contest, the position and sex of residents visible at the cavity entrance were noted. Intruders were introduced to the arena about 10 cm in front of the cavity entrance and agonistic interactions among stomatopods were recorded on tape for 10 min. Stomatopod fighting tactics were described and classified by intensity as in CALDWELL (1979).

To determine how differences in the fighting tactics of residents and intruders affected contest outcomes, the following comparisons were made among experimental (pairs vs. intruders) and control (single males vs. intruders) contests: whether the resident or the intruder performed (1) the first aggressive act; (2) the first escalated act; (3) the first strike in the contest; as well as (4) the elapsed time before the first strike by the resident, (5) the contest duration, (6) the fight intensity (the total number of escalated acts/the contest duration) for residents and for intruders, and (7) the ratio of strike/total aggressive acts by the resident and by the intruder. Strike ratios were arcsin transformed before analysis. Only residents that faced all four types of intruders were included in comparisons 1–7.

Variation among pairs and among controls was first examined using Cochran's Q test (analyses 1–3), Kruskal-Wallis tests (analyses 4–5), or ANOVA (analyses 6–7). Resident and intruder behavior patterns were compared using matched-pair t-tests, and pairwise comparisons of the behavior of paired and control individuals were then performed using 2x2 G-tests (adjusted for continuity), U-tests or t-tests (SOKAL & ROHLF 1981). To minimize the likelihood of Type I errors that may occur in repeated observations on experimental animals or in pairwise testing (MACHLIS et al. 1985), an alpha level of 0.01 was used for significance in Kruskal-Wallis tests, U-tests and in pairwise G- and t-tests.

To examine the occurrence of facultative polygyny by stomatopods in these experiments we recorded the frequency with which paired males attempted to copulate with intruder females as well as the frequency with which paired males permitted intruder females to enter their cavities. The tendency for paired individuals to exchange their present mates for opposite-sex intruders of potentially higher quality was examined by recording the frequency with which paired males or paired females exchanged mates when confronted with larger intruders of the opposite sex.

Contests were terminated in less than 10 min when intruders swam directly away from the cavity, or when both residents were evicted. If only one resident was evicted and the intruder entered the cavity, the arena was reexamined in 1 h. If the new pair was still intact, a mate exchange was assumed to have occurred. Pairs were allowed at least 1 h between successive contests, and no individual was used more than once as an intruder or in more than one set of contests as a resident.

Results

Characteristics of Cavity Defense by Pairs

1. Males Defend Cavities

In 82% of all pair-defense trials, males defended cavities against same-sized and larger intruders of both sexes ($n = 184$, Fig. 1). Females defended cavities only when the male had been evicted or when the intruder actually entered the cavity. Thus unlike many species breeding in pairs, single-sex territory defense consistently occurs in *G. bredini*.

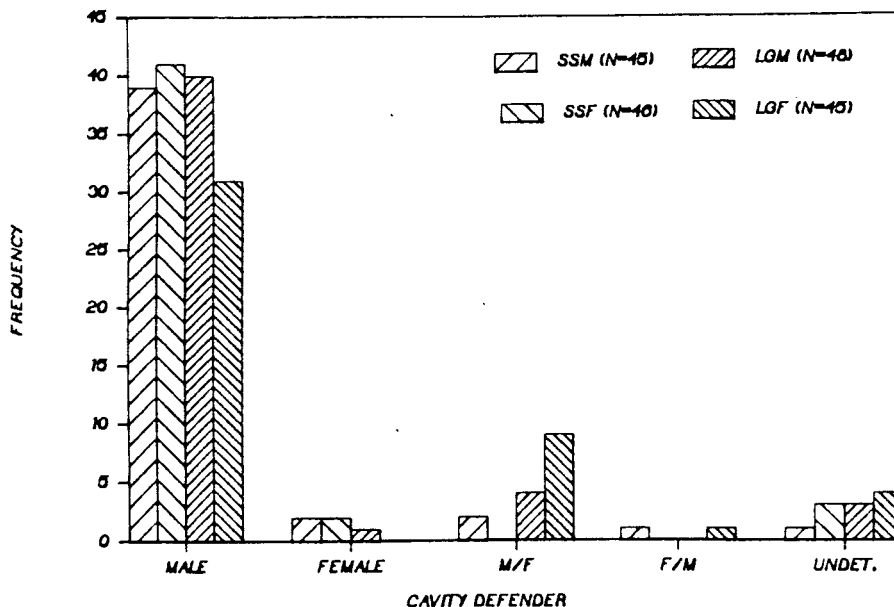


Fig. 1: Cavity defense by pairs of *G. bredini* ($n = 184$), vs. same-sized male (SSM), same-sized reproductive female (SSF), 15 %-larger male (LGM) and 15 %-larger reproductive female (LGF) intruders. Cavity defenses initiated by resident males and later assumed by resident females (M/F) comprised 8 % ($n = 15$) of contests. Cavity defenses begun by resident females and later assumed by resident males (F/M) comprised 1 % ($n = 2$) of contests. Cooperative defenses usually occurred when the first defender was evicted. Defenders were undetermined in 11 contests

2. Relative Success in Cavity Defense by Paired and Control Males

Paired males were unusually successful at cavity defense, and were especially successful against larger opponents. Paired males won all but three contests against same-sized and larger male and reproductive female intruders and thus defended their cavities with approximately equal success over all intruder types (Cochran's Q-test, $p > 0.10$, Table 1). Successful cavity defense by control males was unequally distributed over intruder type; control males won most contests against same-sized male and same-sized reproductive female intruders, but were considerably less successful against larger opponents of both sexes (Q-test, $p < 0.001$, Table 1). This relationship was substantiated in pairwise-comparisons of the guarding success of paired and control males by intruder types; the guarding success of paired and control males in contests against same-sized male and same-sized, reproductive female intruders were not significantly different (G_{adj} tests, $p > 0.05$ and $p > 0.10$, respectively, Table 1). Paired males, however, were more successful than control males in defending their cavities against larger male and larger reproductive female intruders (G_{adj} -tests, $p < 0.001$, and $p < 0.001$, Table 1).

Table 1: Summary of guarding success by paired and control *G. bredini* males in contests vs. same-sized and 15% larger, male and reproductive female intruders

Resident male	Intruder type											
	Same-sized male			Same-sized female			Larger male			Larger female		
	R wins	I wins	n	R wins	I wins	n	R wins	I wins	n	R wins	I wins	n
Paired	20	0	20	19	1	20	18	2	20	20	0	20
Control	<u>31</u>	<u>4</u>	<u>35</u>	<u>28</u>	<u>7</u>	<u>35</u>	<u>12</u>	<u>23</u>	<u>35</u>	<u>20</u>	<u>15</u>	<u>35</u>
	51	4	55	47	8	55	30	25	55	40	15	55

Comparison	Intruder	Test	Value	n	p
Among pairs	all	Cochran's Q	3.678	80	> 0.10
Among controls			29.490	140	< 0.001
Pairwise: pairs × controls	SSM	G_{adj}	3.333	55	> 0.05
	SSF		2.486	55	> 0.10
	LGM		17.283	55	< 0.001
	LGF		16.010	55	< 0.001

Defensive Tactics of Paired and Control Residents

1. Vigilance, First Aggressive Act and First Strike

Against all intruders, paired males were observed at the entrance of cavities before the start of contests, i.e., were "vigilant," significantly more often than control males (G_{adj} -tests, $0.001 < p < 0.05$ for all intruders; among-paired male and among-control male differences were nonsignificant, Q-tests, $p > 0.50$, and $p > 0.10$). Despite their apparent motivation to fight, however, paired males did not initiate agonistic interactions in contests. There were no significant differences among paired males or among control males in tendency to perform the first aggressive act (Q-tests, $p > 0.05$ and $p > 0.70$) or the first escalated act (Q-tests, $p > 0.05$), and pairwise comparisons of such interactions among paired and control males were nonsignificant over all intruder types (G_{adj} -tests, $p > 0.10$ for all tests). Paired males were somewhat more aggressive against male intruders than against female intruders, but there were no significant differences among paired males or among control males in their tendency to perform the first strike against any intruder (Q-tests, $p > 0.50$ and $p > 0.20$). Pairwise G-tests among paired and control males by intruder type were also nonsignificant in contests against same-sized male and against same-sized and larger reproductive female opponents. Paired males, however, struck larger males somewhat more frequently than control males ($G_{adj} = 3.96$, $0.01 < p < 0.05$).

2. Time to First Strike and Contest Duration

The greater guarding success of paired males was unrelated to striking rapidly or to fighting longer. There were no significant differences among paired males or among control males in the time males took to deliver their first strike

(Kruskal-Wallis tests, $p = 0.91$, and $p = 0.84$), and pairwise comparisons among paired and control males by intruder type were nonsignificant (U-tests, $p > 0.13$ for all tests). Furthermore, there were no significant differences in contest duration among paired males or among control males. Pairwise comparisons of paired and control contests by intruder type were also nonsignificant (Kruskal-Wallis tests, $p = 0.59$ and $p = 0.09$, U-tests, $p > 0.06$ for all tests).

Fight Intensity and Strike Ratio

Contest outcome evidently was influenced, however, by fight intensity and differences in the ratio of strikes to total aggressive acts (strike ratio) among residents and intruders. These variables provide estimates of the overall character

Table 2: Fight intensity [(n strikes + n threats)/contest duration] for residents and intruders in contests involving paired and control males vs. same-sized and 15 %-larger, male and reproductive female intruders

	Intruder type															
	Same-sized male				Same-sized female				Larger male				Larger female			
	Pairs		Controls		Pairs		Controls		Pairs		Controls		Pairs		Controls	
	R	I	R	I	R	I	R	I	R	I	R	I	R	I	R	I
n	20	20	35	35	19	19	35	35	20	20	35	35	19	19	34	34
Mean	.093	.068	.064	.106	.047	.069	.053	.079	.057	.049	.046	.074	.057	.065	.032	.086
2 SE	.056	.041	.020	.033	.023	.044	.017	.032	.039	.025	.011	.022	.035	.031	.011	.026
Comparison	Intruder				Test	Value	n	p								
Among pairs	all				ANOVA	0.837	78	0.47								
Among intruders vs. pairs						0.301		0.83								
Among controls						2.334	139	0.08								
Among intruders vs. controls						1.085		0.36								
Paired male vs. intruders	SSM				paired t-test	1.331	20	0.10								
	SSF					- 1.219	19	0.12								
	LGM					0.551	20	0.29								
	LGF					- 0.808	19	0.21								
Control male vs. intruders	SSM					- 2.175	35	0.02								
	SSF					- 1.219	35	0.12								
	LGM					- 3.933	35	<0.001								
	LGF					- 4.132	34	<0.001								
Pairwise: pairs × controls	SSM				pairwise t-tests	0.891	55	0.19								
	SSF					- 0.271	54	0.39								
	LGM					0.178	55	0.43								
	LGF					1.748	53	0.04								
Pairwise: intruders vs. pairs × intruders vs. controls	SSM					- 1.656	55	0.04								
	SSF					- 0.354	54	0.36								
	LGM					- 2.257	55	0.01								
	LGF					- 1.039	53	0.15								

of a contest among paired and control males as well as among residents and intruders. Thus such comparisons permit analysis of the influence of resident behavior, as well as the influence of intruder behavior, on contest outcome.

1. Fight Intensity

There were no significant differences in fight intensity among paired males and intruders (paired *t*-tests, $p > 0.10$ for all tests). Moreover, pairwise comparisons among paired and control males by intruder type were uniformly nonsignificant (*t*-tests, $p > 0.04$). Same-sized and larger male intruders, and larger reproductive female intruders, however, fought more intensely than control males (paired *t*-tests, $p = 0.02$, < 0.001 and < 0.001 , respectively, Table 2). Moreover, pairwise comparisons of intruder fight intensities in contests against paired males and against control males were nearly different against same-sized male intruders (*t*-test, $p = 0.04$) and were significantly different against larger male intruders (*t*-test, $p = 0.01$), with intruders fighting harder against control residents in both cases. There were no significant differences in the fight intensities among females fighting against paired males and against control males (Table 2), but like male intruders, female intruders fought more intensely against control males than against paired males. There were no significant differences in fight intensity among residents (ANOVA, $p = 0.47$, for paired males; $p = 0.08$ for control males), or among intruders ($p = 0.831$, for intruders against paired males; $p = 0.36$, for intruders against control males).

To summarize, paired males fought no more intensely than control males against all intruders, while intruders fought more intensely against controls than against pairs. This suggests that intruders may "hold back" in contests against paired male residents.

2. Strike Ratio

Paired males used significantly higher strike ratios against same-sized male, same-sized reproductive female and larger male intruders (paired *t*-tests, $p < 0.002$ for all comparisons, Table 3) than these intruders used against them. Paired males also used somewhat higher ($p = 0.019$) strike ratios against larger reproductive female intruders. With the exception of contests against same-sized male intruders, no such differences were found in comparisons of strike ratios among control males and intruders. In fact, control males showed somewhat lower strike ratios than larger male and larger reproductive female intruders. Furthermore, strike ratios of paired males were consistently higher than those of control males against all intruder types (pairwise *t*-tests, Table 3).

There were no pairwise differences in intruder strike ratios in contests against paired males and against control males ($p > 0.079$), and there were no differences in strike ratio among paired males or among intruders in contests against paired males (ANOVA, $p = 0.66$ and 0.14 , respectively). Strike ratios among control males and among intruders against control males, however, showed significant heterogeneity (ANOVA, $F = 2.832$, $p = 0.04$ and $F = 7.246$,

Table 3: Strike ratio (n strikes/total aggressive acts) for residents and intruders in contests involving paired and control males vs. same-sized and 15 %-larger, male and reproductive female intruders. All values arcsin-transformed for statistical comparison

	Intruder type															
	Same-sized male				Same-sized female				Larger male				Larger female			
	Pairs		Controls		Pairs		Controls		Pairs		Controls		Pairs		Controls	
	R	I	R	I	R	I	R	I	R	I	R	I	R	I	R	I
n	20	20	35	35	20	20	35	35	20	20	34	34	20	20	34	34
Mean	.285	.062	.268	.136	.269	.035	.098	.063	.365	.128	.213	.275	.315	.147	.147	.155
2 SE	.127	.075	.110	.079	.156	.049	.054	.042	.121	.092	.097	.079	.141	.095	.057	.022

Comparison	Intruder	Test	Value	n	p
Among pairs	all	ANOVA	0.530	79	0.66
Among intruders vs. pairs			1.877		0.14
Among controls			2.832	137	0.04
Among intruders vs. controls			7.246		0.001
Paired males vs. intruders	SSM	paired t-test	3.526	20	0.001
	SSF		3.214	20	0.002
	LGM		3.597	20	0.001
	LGF		2.223	19	0.019
Control males vs. intruders	SSM		2.509	35	0.008
	SSF		1.266	35	0.107
	LGM		- 1.267	34	0.107
	LGF		- 0.166	34	0.434
Pairwise: pairs × controls	SSM	pairwise t-tests	- 0.312	55	0.378
	SSF		- 2.347	55	0.011
	LGM		- 2.099	54	0.020
	LGF		- 2.367	54	0.011
Pairwise: intruders vs. pairs × intruders vs. controls	SSM		1.430	55	0.079
	SSF		0.863	55	0.196
	LGM		- 1.250	54	0.109
	LGF		0.217	54	0.415

$p = 0.001$, respectively). These differences were evidently the result of control males striking reproductive female opponents considerably less than they struck male opponents, and reproductive female intruders striking less than male intruders. For unpaired control males, perhaps attempting to pair with reproductive females, this result makes sense and further accentuates the fact that paired males delivered significantly more strikes, particularly at female opponents, than control males. This greater tendency for paired males to strike intruders, combined with the tendency for intruders to fight less intensely against paired males, may explain why paired males are exceptionally successful in guarding their cavities.

Evictions, Mate Exchanges and Extra-Pair Mating Attempts

1. Evictions

26 of 166 contests resulted in the eviction of one ($n = 16$) or both members ($n = 10$) of a pair. 8 of 10 double evictions were accomplished by larger intruders. In 10/16 single evictions (63 %) the usurping intruder paired with the remaining resident. Same-sized reproductive female intruders replaced female residents once ($p = 0.024$, $n = 41$), same-sized male intruders and larger reproductive female intruders each replaced male residents twice ($p = 0.048$, $n = 41$ and $p = 0.05$, $n = 40$, respectively), and larger male intruders replaced male residents five times ($p = 0.114$, $n = 44$).

2. Mate Exchanges

If stomatopods replace their present mates with higher quality (larger) individuals, the frequency with which mates are exchanged should be higher in contests against larger, opposite-sex intruders. This hypothesis was rejected, however, ($G = 3.15$, $p > 0.10$, $n = 166$), as exchanges occurred evenly across all intruder sexes and sizes. Thus neither paired males, nor paired females showed a significant tendency to exchange mates, even when opposite sex intruders were larger (i.e., of potentially higher quality). However, a substantial proportion of 15 %-larger male intruders evicted and replaced paired males ($p = 0.11$). In these cases, paired females made no attempt to prevent the larger male from entering the cavity, and remained paired with the larger males until oviposition.

3. Extra-Pair Copulation Attempts by Males

Attempts by paired males to copulate with intruder females were rare (3/91 trials, $p = 0.03$), but resident males exhibited two tactics that may permit extrapair matings in nature. Once, a paired male left his cavity when confronted with a same-sized female intruder. The male grasped the intruder female and copulated with her directly in front of the cavity entrance. After 20 s, the male abandoned the intruder female and re-entered the cavity, striking the intruder female when she attempted to follow him in. Two other paired males admitted intruder females into their cavities.

In the first of these two latter cases, a same-sized female intruder rushed into the cavity almost immediately after introduction to the arena. The paired resident male did not prevent her entry. Once the intruder had entered, however, several strikes were audible from inside the cavity and the intruding female (who was recognizable by stab wounds on her carapace, sustained before collection) was evicted. The resident male probably did not have time to copulate with the intruder female in this case. In the other case, a paired male permitted a 15 %-larger female to enter his cavity. The intruder remained within the cavity for nearly 2 h before evicting both members of the original pair. Whether the resident male was able to mate before eviction, however, was unclear.

Discussion

Cavity Defense by Males

Defense of the reproductive habitat in *Gonodactylus bredini* is almost entirely undertaken by males. In these experiments, moreover, paired males were significantly more successful against larger intruders than unpaired, control males. Although paired males were only slightly more successful than controls in defending their cavities against same-sized intruders, resident stomatopods have a positional advantage over intruders and typically win a majority of contests against same-sized opponents in any case (CALDWELL & DINGLE 1979; STEGER 1985). This positional advantage is therefore likely to obscure the magnitude of the increased defensive success paired males may experience over same-sized intruders.

Fighting Tactics of Paired Males

The tactical reasons for greater guarding success of paired males seem unrelated to initial acts of aggression. While paired males were more vigilant than control males, paired males neither threatened intruders more nor escalated contests faster than control males. Furthermore, paired males did not prolong contests and fought no more intensely than control males. Paired males did, however, include a higher proportion of strikes in their fight repertoires than unpaired males, making fights with paired males particularly dangerous. Perhaps to avoid injury against such aggressive opponents, intruders fought less intensely against paired males than against control males.

The Behavior of Paired Males Toward Reproductive Female Intruders

Paired males used essentially the same fighting tactics against male intruders that they used against female intruders. This was unexpected given that all intruder females in this experiment had advanced sternal-gland development and were sexually receptive. Paired males, however, seldom attempted to mate with intruder females and almost never allowed these females into their cavities. The constraints of cavity volume and possible deleterious effects of oxygen depletion within cavities may in general dissuade females from joining, and thus prevent males from attempting to form polygynous breeding aggregations. That paired males actually attacked intruder females, however, suggests it may be costly for paired males merely to permit female intruders to remain near their cavities. That same-sized, and particularly larger, intruder females were capable of evicting pairs from cavities, moreover, indicates that paired males have good reason to concentrate on avoiding eviction rather than on securing additional mates.

Factors Affecting the Persistence of Stomatopod Pairs

The vigorous defense of coral-rubble cavities by nonreproductive stomatopods is testimony to the value of this resource to both males and females (STEGER 1985, 1987). Stomatopod females require a cavity in which to brood and defend their developing young after oviposition (CALDWELL 1986a). Both mem-

bers of a breeding pair might therefore be expected to take active roles in cavity defense. The pattern of female receptivity in this species, and circumstances necessary for successful reproduction by males, however, suggest that the cost of eviction is unequally borne among members of breeding pairs. It follows that the risks of cavity defense are likely to be assumed by the individual that stands to lose more if one or both members of the pair are evicted.

1. The Pattern of Female Receptivity

Unlike many crustaceans, sexual receptivity in female stomatopods is not associated with molting (CALDWELL 1986a). Not only is mating possible throughout the female's breeding cycle but females can store viable sperm for at least one month (CALDWELL, pers. obs.). Males copulate with females within a few min after females enter their cavity, and mating occurs repeatedly before oviposition (CALDWELL, pers. obs.). Little is known about sperm competition in stomatopods, but the breeding biology of these animals suggests that considerable potential for such competition exists (PARKER 1970).

2. The Costs of Eviction to Males and to Females

If evicted from a cavity, both sexes experience the risk of predation, and time and energy lost in locating a new cavity. Evicted males not only lose their present mate, but since reproductive females are likely to mate again (CALDWELL 1986a; SHUSTER, unpubl. data) evicted males also lose the time and energy invested in guarding a particular female prior to eviction. If the evicted male is to mate again, he must locate and control a new cavity. Since suitable cavities are limited in number (STEGER 1987), and since residents have a positional advantage over intruders, even if the evicted male is successful in usurping another cavity, the new cavity is likely to be lower in quality than the one he previously held. An evicted male might locate an unpaired reproductive female in a cavity, but the time available for acquiring a mate in this manner is limited due to populational synchrony in female receptivity. Depending on how long the male has held his previous cavity, the likelihood of pairing with another female progressively diminishes. Thus if no other females are available, an evicted male loses his current reproductive effort and must wait at least a month for another opportunity to breed.

Reproductive females evicted from cavities suffer few of these costs because they are less restricted in gaining a new cavity than males. Reproductive females seldom engage in escalated aggression when confronting single males established in cavities, and typically move in with little trouble. Once inside, females copulate with and are protected by their new mates. If previously paired females cannot locate a cavity occupied by a single male they, like evicted males, must locate a vacant cavity or take over an occupied cavity. However, since previously paired females are already inseminated they, unlike males, need not locate another mate to reproduce. Selection undoubtedly favors males that are strongly motivated to defend their reproductive habitat against any intruder attempting to enter and possibly take over their cavity. Moreover, while females still experience some

risk of eviction by intruders, by exploiting the extreme motivation of cavity-defending males, females gain protection and avoid the risks of cavity defense themselves.

The substantial risks incurred by the guarding males may further explain why males show little tendency to replace their mates with other, even larger, females. If a male has successfully guarded a female throughout her receptive period, a male's present mate provides greater paternity assurance than any female intruder. Moreover, the reproductive condition of the mated female is certain. Intruder females are known to behave as if they are receptive, enter cavities, and subsequently evict the male resident without copulating (CALDWELL 1986b). Weighed against the possible benefits of increased fecundity, the risks of cavity loss seem considerable. Males show little tendency to relinquish their present mates for larger reproductive females, and while males engage in extrapair mating attempts that seem unlikely to jeopardize their present holdings, such activity is seldom observed.

Female Reproductive Biology and Animal Mating Systems

Defense of the breeding cavity by male stomatopods appears to have evolved in response to the pattern of female receptivity in this species. This pattern of receptivity evidently increases a female's chances of acquiring a cavity for brooding developing young. Discussions of male guarding behavior often imply that by monopolizing females, males somehow control female reproduction. Patterns of female receptivity, and thus of male guarding behavior, however, are fundamentally influenced by selective forces creating variance in female reproductive success. If environmental factors shaping female reproductive biology are indeed the prime movers of mating-system evolution, then males, rather than being in control of female reproduction, are often substantially controlled themselves.

Acknowledgments

Logistical support for this research was provided by John CUBIT and the staff of the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute. George K. RODERICK assisted in collecting specimens and provided useful discussions on the concept and design of these experiments. H. Elizabeth BRAKER, George W. BARLOW, Michael SALMON and an anonymous referee provided suggestions that substantially improved the quality of the manuscript. Financial support was provided by National Science Foundation grants BNS-8023414, BNS-8517573, and BSR-8700112, and by the Center for Latin American Studies, University of California, Berkeley.

Literature Cited

- BERZINS, I. K. & CALDWELL, R. L. 1983: The effect of injury on the agonistic behavior of the stomatopod, *Gonodactylus bredini* (Manning). *Mar. Behav. Physiol.* 10, 83—96.
- BORSEMA, I. & BEMUS, R. F. 1985: Territorial defense and intra-pair cooperation in the carrion crow (*Corvus corone*). *Behav. Ecol. Sociobiol.* 16, 99—104.
- CALDWELL, R. L. 1979: Cavity occupation and defensive behaviour in the stomatopod *Gonodactylus festai*: evidence for chemically mediated individual recognition. *Anim. Behav.* 27, 194—201.

- — 1986a: Withholding information on sexual condition as a competitive mechanism. In: Behavioral Ecology and Population Biology (DRICKAMER, L. C., ed.) Privat, I.E.C., Toulouse, pp. 83—88.
- — 1986b: The deceptive use of reputation by stomatopods. In: Deception: Perspectives of Human and Non-human Deceit (MITCHELL, R. W. & THOMPSON, N. S., eds.) State Univ. of New York Press, New York, pp. 129—145.
- — 1987: Assessment strategies in stomatopods. Bull. Mar. Sci., in press.
- — & DINGLE, H. 1976: Stomatopods. Sci. Am. 234, 80—89.
- — & DINGLE, J. 1979: The influence of size differential on agonistic encounters in the mantis shrimp, *Gonodactylus viridis*. Behaviour 69, 255—264.
- —, RODERICK, G. K. & SHUSTER, S. M. 1989: Studies of predation in *Gonodactylus bredini*. Boll. Zool., in press.
- CARLSON, A., HILLSTROM, L. & MORENO, J. 1985: Mate guarding in the wheatear, *Oenanthe oenanthe*. Ornis Scand. 16, 113—120.
- DINGLE, H. & CALDWELL, R. L. 1969: The aggressive and territorial behavior of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). Behaviour 33, 115—136.
- — & CALDWELL, R. L. 1972: The aggressive and territorial behavior of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). Biol. Bull. 142, 417—426.
- DUNHAM, P. 1986: Mate guarding in amphipods: a role for brood pouch stimuli. Biol. Bull. 170, 526—531.
- FITCH, M. A. & SHUGART, G. W. 1983: Comparative biology and behavior of monogamous pairs and one male-two female trios of herring gulls. Behav. Ecol. Sociobiol. 14, 1—7.
- KNOWLTON, N. 1979: Reproductive synchrony, parental investment and the evolutionary dynamics of sexual selection. Anim. Behav. 27, 1022—1033.
- KODRIC-BROWN, A. & BROWN, J. H. 1984: Truth in advertising: the kind of traits favored by sexual selection. Am. Nat. 124, 309—323.
- LEFFELAAR, D. & ROBERTSON, R. J. 1984: Do male tree swallows guard their mates? Behav. Ecol. Sociobiol. 16, 73—80.
- — & — — 1986: Equality of feeding roles and the maintenance of monogamy in tree swallows. Behav. Ecol. Sociobiol. 18, 199—206.
- LINSENAIR, K. E. 1984: Comparative studies on the social behavior of the desert isopod *Hemilepistus reaumuri* and of a *Porcellio* species. Symp. Zool. Soc. Lond. 53, 423—453.
- MACHLIS, L., DODD, P. W. D. & FENTRESS, J. C. 1985: The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z. Tierpsychol. 68, 201—214.
- MANNING, R. B. 1969: Stomatopod crustacea of the western Atlantic. Stud. Trop. Oceanogr. Miami 8.
- MITANI, J. C. 1984: The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). Behav. Ecol. Sociobiol. 15, 225—230.
- MOLLER, A. P. 1985: Mixed reproductive strategy and mate guarding in a semi-colonial passerine, the swallow, *Hirundo rustica*. Behav. Ecol. Sociobiol. 17, 401—406.
- MONTGOMERY, E. L. & CALDWELL, R. L. 1984: Aggressive brood defense in females by the stomatopod, *Gonodactylus bredini*. Behav. Ecol. Sociobiol. 14, 247—251.
- PARKER, G. A. 1970: Sperm competition and its evolutionary consequences in insects. Biol. Rev. 45, 525—567.
- RAEMAEEKERS, J. J. & RAEMAEEKERS, P. M. 1985: Field playback of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species specific responses. Anim. Behav. 33, 481—493.
- REAKA, M. L. 1976: The ecology and evolution of molting, life history patterns and agonistic behavior in stomatopod crustaceans. Ph. D. Diss. Univ. of California, Berkeley.
- RIDLEY, M. 1983: The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating. Oxford Sci. Publ., Oxford.
- SHUSTER, S. M. 1981: Sexual selection in the Socorro isopod, *Thermosphaeroma thermophilum* (Cole and Bane) (Crustacea: Peracarida). Anim. Behav. 28, 698—707.
- SLAGSVOLD, T. & LIJELD, J. T. 1986: Mate retention and male polyterritoriality in the pied flycatcher, *Ficedula hypoleuca*. Behav. Ecol. Sociobiol. 19, 25—30.
- SOKAL, R. R. & ROHLF, F. J. 1981: Biometry. 2nd ed. W. H. Freeman, and Co., New York.

- STEGER, R. 1985: The behavioral ecology of a Panamanian population of the stomatopod, *Gonodactylus bredini* (Manning). Ph. D. Diss. Univ. of California, Berkeley.
- — 1987: Effects of refuges and recruitment on gonodactylid stomatopods, a guild of mobile prey. *Ecology* 68, 1520—1533.
- — & CALDWELL, R. L. 1983: Intraspecific deception by bluffing: a defense strategy of newly molted stomatopods (Arthropoda: Crustacea). *Science* 221, 558—560.
- THORNHILL, R. 1976: Sexual selection and parental investment in insects. *Am. Nat.* 110, 153—163.
- — 1980: Competitive, charming males and choosy females: was Darwin correct? *Fla. Entomol.* 63, 5—30.
- — & ALCOCK, J. 1983: *The Evolution of Insect Mating Systems*. Harvard Univ. Press, Cambridge.
- WALKER, W. F. 1980: Sperm utilization strategies in non-social insects. *Am. Nat.* 115, 780—799.
- WALLACE, B. 1987: Ritualistic combat and allometry. *Am. Nat.* 129, 775—776.
- WICKLER, W. & SEIBT, U. 1981: Monogamy in crustacea and man. *Z. Tierpsychol.* 57, 215—234.
- WITTENBERGER, J. F. 1981: *Animal Social Behavior*. Duxbury Press, Boston.
- — & TILSON, R. L. 1980: The evolution of monogamy: hypotheses and evidence. *Ann. Rev. Ecol. Syst.* 11, 197—232.
- WRANGHAM, R. 1979: On the evolution of ape social systems. *Soc. Sci. Info.* 18, 335—368.

Received: May 20, 1988

Accepted: February 11, 1989 (G. Barlow)