

**THE REPRODUCTIVE BEHAVIOUR
OF α -, β -, AND γ -MALE MORPHS IN *PARACERCEIS SCULPTA*,
A MARINE ISOPOD CRUSTACEAN**

by

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(With 4 Figures)

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Summary

Males occur as three distinct morphotypes in *Paracerceis sculpta*, a marine isopod inhabiting the Gulf of California. Alpha-males are largest in body size ($\bar{x} \pm SD = 6.55 \pm 0.72$ mm, N = 63) and defend breeding sites in intertidal sponges. Beta-males are smaller ($\bar{x} \pm SD = 4.34 \pm 0.43$ mm, N = 59) and resemble sexually receptive females in behaviour and body form. Gamma-males are tiny ($\bar{x} \pm SD = 2.65 \pm 0.73$ mm, N = 23) and are capable of rapid movements. All three male morphs are sexually mature and successfully sire young in the field (SHUSTER, 1989a). Using artificial sponges to simulate natural breeding habitats, I examined (a) competitive interactions among α -males for access to breeding sites and sexually receptive females, (b) behaviours used by β - and γ -males to enter spongocoels, and (c) the tendency for β - and γ -males to discriminate breeding site quality in terms of the availability of sexually receptive females. I found that:

1. Resident and intruder α -males used their walking legs, uropods and body positioning to retain or gain access to breeding sites.
2. Intruders were consistently more aggressive than residents in contests, except when breeding sites containing sexually receptive females were limited.
3. Despite their relative quiescence, residents retained their spongocoels in most contests, apparently due to the positional advantage residents gain when situated in the spongocoel.
4. When interacting with α -males, β -males imitated female courtship behaviour, and

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α -males responded as if β -males were females. Tactile stimulation of α -males by β -males may thus be sufficient to release normal α -male courtship behaviour.

5. Beta-males preferred spongocoels containing α -males paired to sexually receptive females, over spongocoels containing α -males paired to gravid (nonreceptive) females.

6. Beta-males also preferred spongocoels containing high densities of receptive females over spongocoels containing low densities of receptive females.

7. However, β -males preferred to associate with unpaired α -males over α -males paired to gravid females. Since receptive females prefer established breeding sites (SHUSTER, 1990), this preference by β -males remains unexplained.

8. Gamma-males approached breeding sites occupied by α -males indirectly, and invaded spongocoels only after repeated attempts to slip around the resident α -male and into his spongocoel.

9. Alpha-males actively resisted such invasion attempts, and with considerable dexterity, used their uropods, the apex of their pleotelsons and their walking legs to evict γ -male intruders. Small body size may enhance a γ -male's ability to remain within breeding sites.

10. Unlike β -males, γ -males preferred only spongocoels containing α -males paired to sexually receptive females, and showed no preference for unpaired α -males or α -males paired to gravid females.

Introduction

Male reproduction in most animal species is limited by the availability of sexually receptive females (BATEMAN, 1948; WILLIAMS, 1966; WADE, 1979; CLUTTON-BROCK, 1988). Males must compete for access to mates, and characteristics that permit individuals to overpower, outmaneuver, outperform or exclude other males in reproductive competition are expected to be favoured by sexual selection (DARWIN, 1874; WADE & ARNOLD, 1980). If sexually receptive females become rare, male-male competition is expected to become intense and the cost of combat to become prohibitive for all but a few individuals. However, if certain males can acquire mates by less costly, unconventional means, male reproductive behaviours alternative to combat (also known as alternative reproductive strategies or tactics, depending on whether differences among males represent genetic or environmentally induced polymorphisms) are expected to arise and coevolve with the behaviour and/or morphology of conventional, combative males (GADGIL, 1972; DAWKINS, 1980; AUSTAD, 1984). This sequence of adaptations suggests that male polymorphism may arise in any species in which sexual selection occurs. It is therefore not surprising that male alternative reproductive behaviour has been documented in nearly every major animal taxon (SHUSTER *et al.*, in review).

The three male morphs in the marine isopod, *Paracerceis sculpta* (Fig. 1; SHUSTER, 1987a, 1989a), appear to represent this type of evolutionary progression. Most males in the northern Gulf of California population (82%, SHUSTER, 1987a; SHUSTER & WADE, 1991a) possess rugose

pleotelsons and elongated uropods. These α -males (SHUSTER, 1987a) establish breeding sites within intertidal sponges (*Leucetta losangelensis*, SHUSTER, 1987b). 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 (SHUSTER, 1987a; SHUSTER & WADE, 1991a), and as many as 52 females in multiple-male assemblages (SHUSTER, unpubl. data). Alpha-males compete for control of these aggregations, and body size confers an advantage in spongocoel defence and takeover (SHUSTER, 1990).

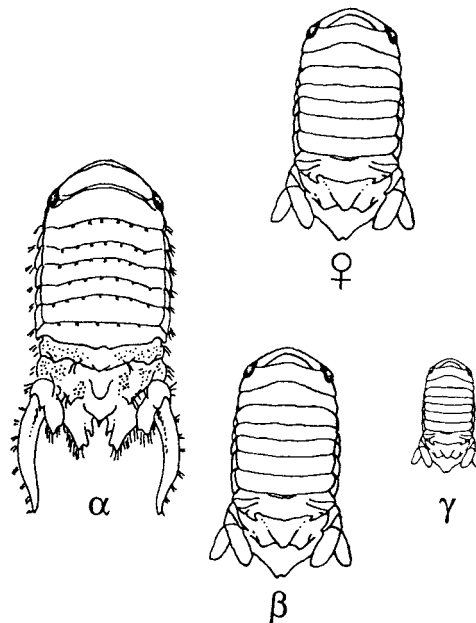


Fig. 1. The three male morphs in *Paracerceis sculpta*, (α) α -male (body length: $\bar{x} \pm SD = 6.55 \pm 0.72$ mm, $N = 63$); (β) β -male (body-length: $\bar{x} \pm SD = 4.34 \pm 0.43$ mm, $N = 59$); (γ) γ -male (body length: $\bar{x} \pm SD = 2.65 \pm 0.73$ mm, $N = 23$); (♀) female (body length: $\bar{x} \pm SD = 4.91 \pm 0.42$ mm, $N = 67$).

Beta-males are smaller than α -males and are relatively rare (4% of the male population: SHUSTER, 1987a; SHUSTER & WADE, 1991a). Beta-males lack pleotelsonic modification, resemble sexually receptive females in their external morphology, and appear to enter spongocoels by 'deceiving' α -males (SHUSTER, 1989b). Whereas mimicry of female reproductive behaviour as a form of intrasexual deception is well-documented

in many animal species (KODRIC-BROWN, 1986; review in SHUSTER, 1987a; GROSS, 1991), the details of this form of behaviour are poorly known among the Crustacea.

Gamma-males occur at low to intermediate frequency in the male population (14%: SHUSTER, 1987a; SHUSTER & WADE, 1991a). These males are also unornamented, are smaller than β -males, are capable of rapid movement, and appear to use their tiny proportions to 'sneak' into spongocoels established by α -males (SHUSTER, 1989a). Sneaker males are well-documented among animals (GROSS, 1985; DE JONGE & VIDELER, 1989, review in SHUSTER, 1987a), but as with female mimicry, the tactics such males use to acquire mates are not well understood in crustaceans (but see BOROWSKY, 1985; RA'ANAN & SAGI, 1985).

The three male morphs in *Paracerceis sculpta* do not differ in their abilities to successfully sire young when isolated with individual females (SHUSTER, 1989b). Moreover, relative fertilization success among males in spongocoels varies with receptive female density, and evidently with the relative frequency of other male types in the population (SHUSTER, 1989a; SHUSTER & WADE, 1991a, b). Beta- and γ -males in the field are found primarily in spongocoels containing α -males and at least one sexually receptive female (SHUSTER, 1987a; SHUSTER & WADE, 1991a). This suggests that β - and γ -males are capable of locating spongocoels containing receptive females, and can discriminate the relative density of receptive females within breeding assemblages.

In this paper, I examine four aspects of the behaviour of *Paracerceis sculpta* males around breeding sites: (1) competitive interactions among α -males for access to spongocoels, particularly for spongocoels containing sexually receptive females, (2) behaviours used by β - and γ -males to enter spongocoels, (3) whether β - and γ -males are attracted to α -males, receptive females or nonreceptive females, and (4) whether β -males can discriminate the relative density of receptive females in spongocoels.

General methods

Isopods were collected from *Leicetta losangelensis* spongocoels and maintained in the laboratory as described in SHUSTER (1989a). Alpha-males were individually identified by their relative body size (measured to the nearest 0.15 mm using an ocular micrometer), their age (this species has determinate growth, adult males rarely feed and male cuticular pigmentation fades at a regular rate as individuals age, SHUSTER, 1990), and by unique pigmentation patterns on their dorsal cuticles (SHUSTER, 1989b). No individual was used twice in the same experiment.

'Receptive' females in these experiments were females that had entered the spongocoels of α -males in the field, but had not yet undergone a reproductive moult. Such females

usually undergo their reproductive moults 6-50 hr after entering spongocoels (SHUSTER, 1991a). Isopod moults are biphasic (*i.e.*, the cuticle is shed in two halves) and females become available for mating only after shedding the posterior portion of their cuticle in their female preadult moult (SHUSTER, 1991b). 'Nonreceptive' females in these experiments were females that had completed their reproductive moult and had deposited embryos into their brood pouch (*i.e.* gravid females). Females in this condition can no longer be mated by males.

Artificial sponges used in experiments were of standardized dimensions (diameter = 20 mm; osculum diameter = 3 mm; spongocoel volume = 7.85 cm³; see SHUSTER, 1990 for details on artificial sponge construction), and were rinsed in fresh water between uses. This procedure removes any significant residual scent from previous spongocoel residents (SHUSTER, 1990). Cylindrical 225 ml white plastic cups containing seawater served as arenas for all behavioural experiment. All observations were conducted between 19:00 and 02:00 hr under red light.

Unless otherwise stated, the behaviour of individuals in containers was recorded on tape for 20 min after each trial had begun. This standardized interval allowed individuals to assess conditions within their container, and limited the number of behavioural interactions possible in each trial. For statistical analysis of interactions among males, each act was counted only once for each individual to prevent repeated acts by the same individual from inflating the total sample size. Actual behavioural sequences are described in the text. Twelve hours after behavioural observations were completed, containers were again examined and the positions of individuals within each container recorded.

Experiments

1. Interactions among α -males: The effects of sponge availability and the presence or absence of receptive females in spongocoels.

Methods

The following four experiments were conducted to examine the behaviour of α -males when unoccupied spongocoels were available or limited, and when receptive females were present or absent: (a) To examine the behaviour of α -males when unoccupied spongocoels were unavailable and receptive females were absent, 20 α -males were placed into separate arenas containing seawater and an artificial sponge. Alpha-males were allowed 24 hr to establish themselves in spongocoels. An identical, empty sponge was then submerged in each container, and 1 hr later a size- and age-matched α -male, an 'intruder' was introduced. (b) To examine the behaviour of α -males when sponges were limited and receptive females were absent, 25 α -males were placed into separate arenas, each of which contained seawater and one artificial sponge. After residents were established in spongocoels as described above, a size- and age-matched α -male intruder was released into each container. (c) To examine the behaviour of α -males when sponges were not limited and receptive females were present, 19 α -males were established in artificial sponges as described above, and were allowed to pair with a receptive female. Receptive females, when introduced to established α -males, usually paired within 1 hr (SHUSTER, 1990). After females had paired, an additional sponge was [placed into the container, and after an additional hr, a size- and age-matched α -male was introduced. (d) To examine the behaviour of α -males when sponges were limited and receptive females were present, 20 α -males were established in artificial sponges in separate arenas and allowed to pair with receptive females as described above. After 1 hr, a size- and age-matched intruder was introduced to each container.

Results

Experiment 1a.

Behavioural observations: When two sponges and no females were available to pairs of α -males, 14 of 20 intruders showed no behaviour in 20 min. Four intruders settled on the occupied sponge. Three of these intruders swam off without interacting with the resident. The fourth intruder contacted the resident, but turned and moved off the sponge immediately.

Two intruders settled first on the unoccupied sponge. One of these individuals left the sponge after wandering around the osculum for approximately one min; the other intruder established himself in the osculum. The intruder that earlier encountered and avoided the resident moved to the unoccupied sponge and established himself in the osculum approximately 2 min after the end of the 20 min observation period for that trial.

Positions of individuals after 12 hr: After 12 hr, one of 20 intruders was loose in its container, one intruder was situated on the occupied sponge, 12 intruders had established themselves in the unoccupied sponge, and one intruder had wedged himself into the resident's former sponge and the former resident was established in the previously empty sponge.

Overall, residents retained their positions in spongocoels in 15 of 20 trials (Binomial test, $p = 0.021$; Table 1), and although five residents were either evicted or moved of their own accord, all five of these individuals were able to reestablish themselves in the other sponge.

Experiment 1b.

Behavioural observations: With one sponge and no receptive females available, 12 of 25 intruders either remained motionless or moved haphazardly around the containers for 20 min. The remaining 13 intruders moved onto the resident's sponge. One intruder climbed onto the sponge and remained there for the duration of the experiment. The other 12 intruders wandered around the sponge surface, occasionally swimming off the sponge, returning, approaching within 1 cm of the osculum and then leaving the sponge ($N = 6$), or approaching within 1 cm of the osculum and turning away, but remaining on the sponge ($N = 6$). All of these intruders approached the edge of the osculum at least twice. Two of these intruders retreated from the osculum after approaching it the second time. The remaining four intruders initiated contact with the resident.

TABLE 1. Effects of sponge availability and the presence or absence of premoult females on the guarding success of resident α -males¹

	Receptive female				N
	Absent		Present		
	2 Sponges	1 Sponge	2 Sponges	1 Sponge	
Resident retains	15	18	17	17	67
Resident evicted	5	7	2	3	17
Totals	20 ²	25 ³	19 ⁴	20 ⁵	84

¹ $G_{adj[df=3]}=2.78$, $p > 0.10$. ² Binomial test, $p = 0.021$. ³ Binomial test, $p = 0.022$. ⁴ Binomial test, $p < 0.001$. ⁵ Binomial test, $p = 0.001$.

Residents responded to initial contact with intruders by withdrawing into their spongocoels. All four intruders moved away from the osculum when residents withdrew. In two cases, residents splayed their uropods within the spongocoel and worked the tips of these appendages into the cavity walls. Both intruders abandoned their attempts to evict these apparently secure residents. The remaining two intruders attempted to enter the residents' spongocoel.

In eight total cases, intruders attempted to enter the spongocoel. These intruders included the four individuals that remained on the sponge after settling there, and four individuals that swam away from the sponge and later returned. Five intruders attempted to force their way between the resident and the spongocoel wall, a behaviour that was successfully blocked by each resident. One of these intruders abandoned the sponge, while three other intruders moved away from the osculum after several attempts at entering. The remaining intruder grasped the resident with his walking legs, braced his uropods against the sponge, and pulled vigorously on the resident's body. The behaviour was also used by three other intruders after they had contacted the resident.

Only one of the four grasped residents was evicted by an intruder in this experiment. The successful intruder secured a grip on the resident's dorsal surface, pulled steadily for approximately 17 min and then abruptly extracted the resident from his spongocoel. The resident was allowed to fall down the side of the sponge, while the intruder assumed the resident's place in the osculum. The evicted resident did not attempt to recover his position for the duration of the experiment.

Positions of individuals after 12 hr: After 12 hr, eight intruders were loose in their containers, and two intruders were situated on the resident's sponge

near the osculum. In 10 cases, both the resident and the intruder were wedged into the same osculum, and in two of these cases, intruders held the innermost position, effectively evicting the resident. In five cases, the resident was completely evicted. Overall, residents successfully retained their spongocoels in 18 of 25 trials (Binomial test, $p = 0.022$; Table 1).

Experiment 1c.

Behavioural observations: When spongocoels were not limited and residents were paired to receptive females, nine of 19 intruders showed no behaviour in 20 min. Four of the 10 remaining intruders climbed onto the unoccupied sponge and either remained there for several minutes, or immediately moved off the sponge and wandered about the container. Six intruders climbed onto the resident's sponge, but four of these males moved onto and off of the sponge repeatedly.

Five of the 10 active intruders approached the resident's osculum. Two intruders turned away from the resident after encountering him, but remained on the sponge. The three other intruders attempted to force their way into the spongocoel. Two of these intruders were successfully blocked by residents. The third intruder wedged himself into the resident's osculum and remained there for the rest of the 20 min observation period.

Positions of individuals after 12 hr: After 12 hr, the intruder that attempted a forced entry was still wedged in the resident's osculum. Five intruders were loose in their containers, one intruder was situated near the resident's spongocoel, and ten intruders had established themselves in the unoccupied spongocoel. Residents were evicted or left their spongocoels in two cases, and one of these residents established himself in the empty sponge. Overall, 17 of 19 residents retained their spongocoels (Binomial test, $p < 0.002$; Table 1).

Experiment 1d.

Behavioural observations: When sponges were limited and residents were paired to receptive females, 10 of 20 intruders showed no behaviour in 20 min. The remaining 10 intruders climbed onto the residents' sponges. Several intruders left and returned to the sponge repeatedly; one intruder left the sponge and remained in the container for the duration of the experiment.

Intruders approached the resident's osculum eight times. One of these intruders immediately retreated, and then approached and retreated from the osculum four additional times. One intruder remained motionless at the osculum, and one intruder was blocked by the resident. Blocking residents sealed the osculum of their spongocoels with their pleotelsons and warded off intruders with their uropods. Shifts in position by the intruder were followed by the blocking resident, who oriented his dorsum toward the intruder, simultaneously projecting his uropods upward and over his dorsum.

Six intruders contacted residents and attempted to force their way into the spongocoel. Residents either blocked intruders with their bodies, or gripped intruders with their uropods and attempted to lift them off of the sponge. Four intruders were gripped and lifted immediately after they contacted residents. Lifting was accomplished by residents rapidly flexing their dorsal musculature after grasping the intruder. Lifted intruders were simply dropped off the sponge ($N = 1$), or were violently shaken by residents and then dropped ($N = 2$), or were thrown clear of the sponge with another rapid dorsal flex by the resident ($N = 1$).

Intruders able to avoid being displaced, blocked or thrown, seized residents with their walking legs, braced downward with their own uropods and began tugging on residents. Intruders alternated between pulling on residents and attempting to force their way into ascula. One intruder gave up after pulling on the resident for eight min. Another intruder successfully extracted the resident, dropped him off the sponge and quickly climbed into the spongocoel.

Positions of individuals after 12 hr: After 12 hr, four intruders were loose in their containers, five intruders were situated on the resident's sponge, eight intruders had wedged themselves into the resident's spongocoel with the resident, and three intruders had evicted and replaced residents. Overall, 17 of 20 residents retained their spongocoels (Binomial test, $p = .001$; Table 1).

Summary of experiment 1 results.

Block (resident blocks intruder with his pleotelson), *grip* (resident grasps intruder with his uropods), *lift* (resident lifts intruder off the sponge with his uropods), *shake* (resident shakes the lifted intruder), and *throw* (resident tosses intruder away from the sponge), were considered aggressive acts performed by residents against intruders. When paired to receptive

TABLE 2. Effects of sponge availability and the presence or absence of receptive females on aggressive acts performed by resident α -males against intruder α -males¹

Aggressive act	Receptive female			
	Present		Absent	
	2 Sponges	1 Sponge	2 Sponges	1 Sponge
Block	5	8	0	5
Grip	1	4	0	1
Lift	0	4	0	0
Shake	0	2	0	0
Throw	0	1	0	0
Total acts	6	19 ²	0	6 ³

¹ Fisher's exact test, $p = 0.240$. ² Binomial test, $p = 0.007$. ³ Binomial test, $p = 0.016$.

TABLE 3. Effects of sponge availability and the presence or absence of receptive females on aggressive acts performed by intruder α -males against resident α -males¹

Aggressive act	Receptive female			
	Present		Absent	
	2 Sponges	1 Sponge	2 Sponges	1 Sponge
Approach	5	8	1	12
Contact	3	6	1	8
Forcible entry	3	6	0	5
Grasp/pull	1	2	0	4
Evict	1	1	0	1
Total acts	13	23 ²	2	30 ³

$G_{adj} = 9.37$, $p < 0.05$. ² $G_{adj} = 2.78$, $p > 0.10$. ³ Binomial test, $p < 0.001$.

females and when alone in spongocoels, residents showed more aggressive responses toward intruders when sponges were limited than when sponges were available (Binomial test, $p = 0.007$ and $p = 0.016$, respectively, Table 2). Although paired residents in arenas containing a single sponge performed more aggressive acts and appeared to escalate contests more than other types of paired and unpaired residents, there was no significant interaction between sponge availability and female reproductive condition in aggressive behaviour by residents (Fisher's exact test, $p = 0.24$, Table 2).

Approach (intruder approaches resident's osculum), *contact* (intruder contacts resident with some part of his body; usually with mouthparts), *forcible entry* (intruder attempts to force his way into the resident's osculum), *grasp/pull* (intruder grasps the resident with his walking legs, braces his uropods against the sponge and pulls on the resident), and *evict* (intruder removes resident from the spongocoel), were considered aggressive acts performed by intruders. When residents were paired to a receptive female, intruders were equally aggressive toward residents regardless of whether one or two sponges were present ($G_{\text{adj}} = 2.78$, $p > 0.10$, Table 3). When receptive females were absent from arenas, however, intruders were more aggressive toward residents when sponges were limited than when sponges were available (Binomial test, $p < 0.001$, Table 3). The interaction between sponge availability and the presence of receptive females in spongocoels on the aggressive behaviour of intruders was significant ($G_{\text{adj}} = 9.37$, $p < 0.005$, Table 3).

Despite proportionally greater guarding success experienced by residents paired to receptive females than by unpaired residents, 12 hr after experiments were begun, there were no significant differences in guarding success by residents among the four treatments ($G_{\text{adj}[\text{df}=3]} = 2.78$, $p < 0.10$, Table 1).

2. Interactions between α - and β -males, and β -male discrimination of female reproductive condition.

Methods

Experiment 2a.

To examine interactions among α - and β -males at spongocoels, and to determine whether β -males discriminate the reproductive condition of females situated within spongocoels, two sets of β -males were placed into individual 225 ml containers in which each male was allowed to choose between two standardized sponges: (1) The first set of β -males ($N = 20$) chose between a sponge containing an unpaired α -male and a sponge containing a size- and age-matched α -male paired to a receptive female. (2) The second set of β -males ($N = 23$) chose between a sponge containing an unpaired α -male and a sponge containing a size- and age-matched α -male paired to a nonreceptive female. Behavioural observations were recorded as described above.

Experiment 2b.

To determine if β -males discriminate the relative density of receptive females, 20 β -males were placed in separate containers and allowed to choose between two sponges. In each trial, one sponge contained an β -male and one receptive female, the other sponge contained a size- and age-matched α -male and three receptive females. The positions of individuals in each container were recorded after 12 hr.

Results

Experiment 2a. 1.

Behavioural observations: Of 20 β -males allowed to choose between spongocoels containing unpaired α -males and α -males paired to receptive females, nine β -males were inactive during the 20 min observation period. Four of the 11 active β -males settled first on the sponge containing the unpaired α -male, and seven β -males first settled on the sponge containing the mated α -male. All but two of these 11 active β -males moved between the two sponges before interacting with α -males.

Twelve of 20 β -males approached the oscula of α -males mated to receptive females. Three of these β -males advanced and retreated from the spongocoel repeatedly before interacting with the α -male. Two β -males left the sponge entirely after approaching the asculum. Seven β -males briefly contacted some part of the α -male's pleotelson, and six of these β -males initiated oral contact with one of the α -male's uropods.

Beta-males initiating oral contact pulled and appeared to chew on α -male uropods with their mouthparts for up to 30 sec, occasionally pausing and then resuming contact, or moving away from the osculum. Alpha-males slowly moved or twitched their uropods or pleotelsons at this time, but were otherwise passive. All β -males that began such interactions eventually moved between the uropods of α -males, occasionally pausing en route, but usually proceeding deliberately onto the crest of the α -male's pleotelson.

Once β -males had moved onto α -male's pleotelsons, α -males grasped β -males with their uropods, rapidly and forcefully jerked their pleotelsons up and down along a sagittal plane for several cycles, and then placed the β -male back onto the sponge. Beta-males often paused again at this point, and either reinitiated oral contact with the α -male's uropod or remained in place until the α -male gripped and shook them again. However, most β -males, after completing these interactions backed up and off of the α -male's pleotelson. Alpha-males responded by lifting their pleotelsons slightly and beating their pleopods. Beta-males responded, in turn, by crawling into the spongocoel beneath the α -male. Alpha-males usually twitched their pleotelson after the β -male had entered the spongocoel. This behavioural sequence was virtually identical to the courtship sequence observed between α -males and sexually receptive females (SHUSTER, 1990).

Six of 20 β -males approached unpaired α -males. Three of these β -males approached the resident and leaned one-half body length into the

osculum before moving away. Only one of these β -males initiated oral contact with an unpaired α -male. Interactions between this β - and α -male were essentially the same as those described in the previous paragraph.

Positions of individuals after 12 hr: After 12 hr, one β -male was loose in the container (*i.e.*, not associated with either sponge), five β -males were situated near the osculum of the paired α -males' sponge and eight β -males were situated within the paired α -male's spongocoel. Two β -males were situated near the osculum of the unpaired α -male's sponge, and four β -males were situated within the unpaired α -male's spongocoel. Overall, 14 of 20 β -males associated with α -males paired to receptive females, five β -males associated with unpaired α -males and one β -male showed no association (Fig. 2). Thus, β -males showed a significant preference for spongocoels containing α -males paired to receptive females over spongocoels containing unpaired α -males.

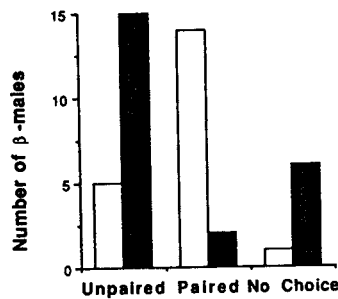


Fig. 2. Results of choice tests in which β -males were allowed to choose between unpaired α -males and α -males paired to receptive females (white), and between unpaired α -males and α -males paired to nonreceptive females (hatched). Beta-males preferred to associate with α -males paired to receptive females and with unpaired α -males when receptive females were unavailable ($G_{adj} = 9.91$, $p < 0.01$, $N = 43$).

Experiment 2a. 2.

Behavioural observations: Of 23 β -males allowed to choose between unpaired α -males and α -males paired to gravid females, 10 β -males were not active during the 20 min observation period. Two of the 13 active β -males settled first on sponges containing α -males paired to gravid females. These β -males did not approach the spongocoel, and left the sponge within a few minutes. The remaining 11 active β -males each settled first

on the unpaired α -male's sponge. Seven of these β -males approached the osculum and made contact with the α -male, although three of these β -males advanced and retreated several times before interacting with the resident α -male. Two β -males, after breaking off interactions with the α -male further along in the courtship sequence, reapproached and reinitiated contact with the α -male.

After contacting α -males, three β -males immediately began oral contact with the α -male's uropods. These β -males then climbed onto the α -male's pleotelson and between his uropods. Five β -males mounted the α -male's pleotelson after initial contact, and two of these males then began oral contact with the α -male's uropods. One β -male entered the spongocoel immediately after pulling on the α -male's uropods with his mouthparts.

Two β -males were blocked by α -males after initiating contact. After being blocked, one β -male paused and attempted to reinitiate oral contact, but when blocked again, moved off the sponge. The other β -male appeared to be weakly blocked by the α -male during oral contact. This β -male backed up, then reestablished himself on the α -male's pleotelson. The α -male ceased to occlude the osculum with his body, gripped and released the β -male, and then allowed the β -male to enter his spongocoel.

Two β -males paused after being shaken by the α -male and began the entire courtship sequence over again. All other β -males, however, backed off the pleotelson of α -males after being shaken and released, and moved directly beneath the α -male and into his spongocoel. Alpha-males, as previously described, beat their pleopods and moved their pleotelson up and down while β -males entered their spongocoels.

Positions of individuals after 12 hr: After 12 hr, six β -males were not associated with either sponge, one β -male was situated near the osculum of the paired α -male's sponge and one β -male was situated inside of the paired α -male's spongocoel. Three β -males were situated near the osculum of the unpaired α -male's sponge and 12 β -males were situated inside of the unpaired α -male's spongocoel. Overall, two of 23 β -males associated with α -males paired to nonreceptive (gravid) females, 15 β -males associated with unpaired α -males, and six β -males showed no association with α -males (Fig. 3).

Summary of experiment 2a results.

Block resident α -male blocks β -male intruder with his body or pleotelson) and *evict* (resident α -male grasps and evicts β -male intruder from his

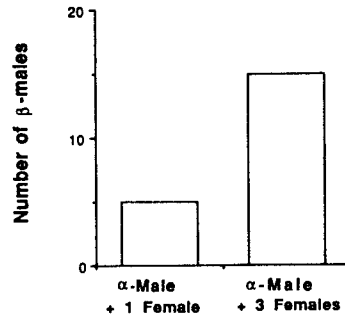


Fig. 3. Results of choice tests in which β -males were allowed to choose between α -males paired to one receptive female and α -males paired to three receptive females. Beta-males preferred the higher density of females (Binomial test, $p = 0.02$, $N = 20$).

spongocoel) were considered aggressive acts performed by resident α -males against β -males. Only unpaired α -males ($N = 2$) attempted to block β -males, and no α -males were observed to attempt eviction of β -males after β -males had entered their spongocoels.

Approach (β -male approaches resident α -male's osculum), *contact* (β -male contacts the resident α -male), *uropod-pull* (β -male grasps the α -male's uropod with his mouthparts and pulls), *mount* (β -male mounts the α -male's pleotelson), and *enter* (β -male enters the α -male's spongocoel) were considered acts performed by β -males that were associated with invading α -male's spongocoels. When allowed to choose between unpaired α -males and α -males paired to receptive females, β -males directed significantly more invasion activity toward paired α -males, and entered only paired α -male's spongocoels during the 20 min observation period ($G_{\text{adj}} = 16.38$, $p < 0.001$, Table 4). When allowed to choose between unpaired α -males paired to nonreceptive females, β -males directed significantly more invasion activity toward unpaired α -males, and entered only unpaired α -males' spongocoels during the 20 min observation period (Binomial test, $p \ll 0.001$, Table 4). The interaction effect of female reproductive condition and the presence or absence of receptive females on the pattern of invasion activity by β -males was significant ($G_{\text{adj}} = 53.10$, $p < 0.001$, Table 4).

After 12 hr, the positions of β -males in and on sponges was consistent with their above preference for spongocoels containing α -males paired to receptive females over unpaired α -males, as well as their preference for unpaired α -males over α -males paired to nonreceptive females ($G_{[\text{df}=2]} = 19.11$, $p < 0.001$, $N = 43$, Fig. 2).

TABLE 4. Effects of female reproductive condition on spongocoel invasion acts performed by β -males against α -male residents¹

Invasion act	Female receptive		Female non-receptive	
	Present	Absent	Present	Absent
Approach	12	6	2	7
Contact	7	3	0	7
Uropod pull	6	1	0	6
Mount	6	0	0	8
Enter	6	0	0	9
Total acts	37	10 ²	2	37 ³

¹ $G_{adj} = 53.10$, $p < 0.001$. ² $G_{adj} = 16.38$, $p < 0.001$. ³ Binomial test, $p \ll 0.001$.

Experiment 2b.

After 12 hr, 15 of 20 β -males had entered spongocoels containing α -males paired to three receptive females. The remaining five β -males had entered sponges containing α -males paired to one receptive female. Thus, β -males showed a significant preference for spongocoels in which receptive female density was relatively high (Binomial test, $p = 0.002$, Fig. 3).

3. Interactions between α - and γ -males and γ -male discrimination of female reproductive condition.

Methods

To examine interactions among α - and γ -males around spongocoels, and to determine if γ -males discriminate the reproductive condition of females in spongocoels, two sets of γ -males were placed into individual 225 ml containers. Within each container, each γ -male was allowed to choose between two standardized sponges: (a) The first set of γ -males ($N = 35$) chose between a sponge containing an unpaired α -male, and a sponge containing a size- and age-matched α -male paired to a receptive female; (b) The second set of γ -males ($N = 38$) chose between a sponge containing an unpaired α -male and a sponge containing a size- and age-matched α -male paired to a gravid female. Behavioural observations were recorded as described above.

Results

Experiment 3a.

Behavioural observations: Of 33 γ -males allowed to choose between sponges containing unpaired α -males and α -males paired to receptive females, 18 γ -males were inactive during the 20 minute observation period. Four of

the remaining 15 γ -males settled on the unpaired γ -male's sponge and approached the spongocoel osculum. Two of these four γ -males swam off the sponge before encountering the resident α -male, one γ -male was blocked by the α -male as he approached the osculum, and one γ -male moved directly into the spongocoel with no apparent reaction from the resident α -male.

Eleven of 33 γ -males settled first on the sponges of α -males paired to receptive females, and all but one of these γ -males approached the osculum. Four of these 10 γ -males approached and retreated from the osculum several times before interacting with the resident α -male. Five γ -males left the sponge, then returned, then approached and retreated from the osculum several times before attempting to enter. One γ -male approached the osculum directly.

Four γ -males left the sponge after several approaches and retreats. These individuals were apparently undetected by the α -male. Four γ -males apparently were detected by the α -male during their approach, because in each case the α -male quickly sealed his osculum with his pleotelson and directed his uropods at the intruder. Gamma-males responded by circling around the osculum, and at irregular intervals, rushing forward in apparent attempts to squeeze past the α -male and into the spongocoel. In one of these attacks, an α -male caught a γ -male between his uropods and backed out the spongocoel while holding the γ -male in a forceps-like grip. The intruder was deposited over the edge of the sponge and the α -male returned to his spongocoel.

In two cases, γ -males approached within one cm of the osculum, then suddenly leaped onto the α -male's pleotelson and rushed down the α -male's body toward the spongocoel. Alpha-males blocked these attempts by pinning the γ -male against the spongocoel wall with their bodies and then moving outward, shoving the γ -male out of the spongocoel as well. Alpha-males also used the apex of their pleotelsons (which are equipped with sharp spines, Fig. 1) to pin γ -males against the spongocoel wall and then flick the intruders out of the osculum.

Five of 33 γ -males successfully entered spongocoels containing α -males paired to receptive females during the 20 min observation period. Two of these γ -males entered spongocoels with little reaction from the α -male. The other three γ -males had already been blocked by α -males, and met considerably more resistance before they successfully entered spongocoels. In each of these cases, resident α -males became agitated immediately after the γ -male entered, twitching and delving into their spongocoels in apparent attempts to capture the intruder. If the resident was

successful in grasping the γ -male, the intruder was passed to the osculum in the α -male's walking legs and placed into the current created by the resident's beating pleopods. This propulsive force served to propel the γ -male out and away from the spongocoel. What γ -males lacked in size they did not lack in persistence. Even after eviction, two γ -males returned and attempted entry (two and four attempts respectively). In each case, α -males grasped and evicted γ -males using the behaviours described immediately above.

Positions of individuals after 12 hr: After 12 hr, six γ -males were not associated with either sponge, 11 γ -males were situated near the osculum of the paired α -male's sponge and 12 γ -males were situated inside of the paired α -male's spongocoel. All but two of these latter γ -males were located deep within the spongocoel, usually in a small depression in the spongocoel wall. This behaviour matches well with that of γ -males in the field, which are usually found deep within spongocoels, evidently beyond the reach of α -males (SHUSTER, 1987a, 1989a). Three γ -males were situated on the sponge of the unpaired α -male, and only one γ -male was situated inside of the spongocoel of the unpaired α -male. Overall, 23 γ -males associated with an α -male paired with a receptive female, four γ -males associated with an unpaired α -male, and six γ -males showed no association (Fig. 4).

Experiment 3b.

Behavioural observations: Of the 38 γ -males allowed to choose between sponges containing unpaired α -males, and sponges containing α -males paired to nonreceptive females, 19 γ -males were not active during the 20 min observation period. Six γ -males settled first on the unpaired α -male's sponge, and 13 γ -males settled first on the paired α -male's sponge. Unlike the previous experiment, γ -males moved frequently between the two sponges.

All of the γ -males that settled first on the unpaired α -males sponge eventually approached the osculum, but as described above, did so only after advancing and retreating from the osculum, or repeatedly leaving and returning to the sponge. One γ -male approached the osculum and entered the spongocoel without reaction by the α -male. Two other γ -males approached the osculum and contacted the α -male. One of these γ -males left the sponge after contact. The other γ -male attempted to enter the spongocoel and was blocked by the α -male. Although the γ -male

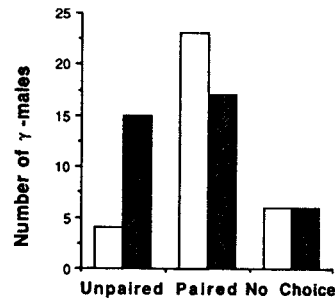


Fig. 4. Results of choice tests in which γ -males were allowed to choose between unpaired α -males and α -males paired to receptive females (white), and between unpaired α -males and α -males paired to nonreceptive females (hatched). Gamma-males preferred to associate with α -males paired to receptive females ($G_{adj} = 7.72$, $p < 0.01$, $N = 71$).

eventually succeeded in invading the spongocoel, this intruder, as well as the γ -male previously allowed into a spongocoel, were evicted by α -males within the 20 min observation period. These γ -males did not attempt to reenter the spongocoel.

Five γ -males settling on sponges occupied by α -males paired to nonreceptive females remained inactive for the entire 20 min observation period. Eight other γ -males settled on and eventually approached the osculum of α -males paired to nonreceptive females. Three γ -males left the sponge after approaching the resident. Five γ -males interacted with the α -male. One of these γ -males contacted the α -male, met no response and moved off the sponge. Two other γ -males approached the osculum, were blocked by the α -male and retreated off the sponge. Two γ -males attempted to enter the spongocoel directly. One of the γ -males was immediately grabbed and tossed out of the spongocoel by the α -male, the other γ -male was shoved out of the spongocoel on the α -male's pleotelson. The latter γ -male attempted to reenter the spongocoel, but was again successfully excluded by the α -male and retreated off the sponge.

Positions of individuals after 12 hr: After 12 hours, six γ -males were not associated with either sponge. Four γ -males were situated outside of the osculum of the paired α -male's spongocoel. As described above, γ -males that successfully invaded spongocoels were usually situated in depressions deep within the spongocoel, evidently beyond the reach of α -males. Five γ -males were situated on the sponges of unpaired α -males, and 10 γ -males were situated inside of the spongocoels of unpaired α -males. Overall, 17

γ -males associated with α -males paired to nonreceptive females, 15 γ -males associated with unpaired α -males and six γ -males showed no association (Fig. 4).

Summary of experiment 3 results.

Block (resident α -male blocks γ -male intruder with his body or pleotelson) and *evict* (resident α -male grasps, and using his pereopods, uropods or telson, evicts γ -male intruder from his spongocoel) were considered aggressive acts performed by resident α -males against intruding γ -males. Alpha-males paired to receptive females performed significantly more aggressive acts than unpaired α -males against intruding γ -males (Binomial test, $p = 0.035$, Table 5), whereas α -males paired to nonreceptive females and unpaired α -males were equally aggressive toward γ -male intruders (Binomial test, $p = .50$, Table 5). There was no significant interaction between female reproductive condition and the presence or absence of females in spongocoels on aggressive acts performed by residents α -males (Fisher's exact test, $p = 0.231$, Table 5).

TABLE 5. Effects of female reproductive condition on the frequency of aggressive acts performed by α -male residents against γ -male intruders¹

Aggressive act	Female receptive		Female non-receptive	
	Present	Absent	Present	Absent
Block	4	1	2	1
Evict	3	0	2	2
Total acts	7	1 ²	4	3 ³

¹ Fisher's exact test, $p = 0.231$. ² Binomial test, $p = 0.035$. ³ Binomial test, $p = 0.50$.

Approach (γ -male approaches resident α -male's osculum), *contact* (γ -male contacts the resident α -male's body), *rush* (γ -male attempts to rush around the α -male and into his spongocoel), and *enter* (γ -male enters the α -male's spongocoel) were considered acts associated with spongocoel invasion that were performed by γ -males. When allowed to choose between unpaired α -males and α -males paired to receptive females, γ -males directed significantly more invasion activity toward paired α -males (Binomial test, $p = 0.001$, Table 6), whereas invasion activity directed toward unpaired α -males and toward α -males paired to nonreceptive females was not significantly different (Binomial test, $p = 0.339$, Table 6). There was no significant interaction effect between female reproductive condition

TABLE 6. Effects of female reproductive condition on spongocoel invasion acts performed by γ -males against α -male residents¹

Invasion act	Female receptive		Female non-receptive	
	Present	Absent	Present	Absent
Approach	10	4	8	6
Contact	2	0	1	2
Rush	6	0	2	1
Enter	5	1	2	1
Total acts	21	5 ²	13	10 ²

¹ $G_{\text{adj}} = 3.290$, $p > 0.05$. ² Binomial test, $p = 0.001$. ³ Binomial, test, $p = 0.339$.

and the presence or absence of females in spongocoels on aggressive acts performed by γ -males ($G_{\text{adj}} = 3.29$, $p > 0.005$, Table 6).

After 12 hr, γ -males showed a significant preference for spongocoels containing α -males paired to receptive females over spongocoels containing unpaired α -males ($G_{[\text{df}=2]} = 7.33$, $p < 0.05$, $N = 71$, Fig. 4), but showed no apparent preference for α -males paired to nonreceptive females, over unpaired α -males.

Discussion

The relative activity of isopods in the laboratory.

In these experiments, behavioural interactions among α -, β - and γ -males were characterized by long periods of relative quiescence punctuated by brief periods of activity. Immediate responses by residents to newly introduced (and by intruders to residents) were rare, and nearly half of all individuals introduced to containers were inactive for the entire 20 min of observation. An artificial environment and a lack of appropriate sensory cues may have been responsible for such inactivity. However, individuals that initiated behavioural interactions did so in a deliberate manner. Moreover, similar sequences of interactions between intruders and residents were observed in independent trials within the same experiment. Within 12 hours, the orientation of α -, β - and γ -males with respect to receptive females and available artificial spongocoels, was consistent with that encountered in the field (SHUSTER, 1987a, 1989a; SHUSTER & WADE, 1991a). Thus, despite the artificiality of the laboratory environment, the behaviour observed in these experiments appears unlikely to differ significantly from that occurring in nature.

The fact that *Paracerceis sculpta* normally inhabits a predator-rich environment may partly explain the inactivity of these experimental animals.

An evolutionary history of fish predation on this species is evidenced by this species' nocturnality and the exceptionally cryptic coloration of juveniles and prereproductive adults inhabiting coralline algae (SHUSTER, 1991a). Conspicuous movement by isopods, which lack the ability to swim rapidly, and which also lack mechanical means for defense against predators, is probably strongly disfavoured by selection (although α -males appear to gain some protection from fish predation by splaying their uropods laterally when attacked; SHUSTER, unpubl. data). Thus, long periods of inactivity in *P. sculpta* are likely to be quite normal, and 20 min observation periods were perhaps too brief to reveal significant differences in rates of behavioural interactions among males.

Interactions among α -males.

Intruding α -males elicited little response from resident α -males during brief tactile interactions. In most cases, residents simply drew more deeply into their spongocoels and avoided further interaction. However, as intruders became more persistent in their attempts to enter spongocoels, residents became increasingly active in defending their territories. Residents were usually successful in blocking intruders by using their enlarged pleotelsons and sharp uropods to barricade the spongocoel entrance. Moreover, residents were remarkably agile within their cavities as they moved to foil invasion attempts by intruders.

Escalated defensive acts by residents were rare and appeared to be context-specific. Residents were observed to grip, shake and throw intruders away from their spongocoels only when receptive females were present within the spongocoel. These acts appeared not only to prevent intruders from entering spongocoels, but also seemed aimed at physically removing intruders from the vicinity of the breeding site. Although displaced intruders merely fell to the bottom of containers in the laboratory, in nature, intruders displaced from sponges are probably carried away from the sponge in currents, or fall a considerable distance away from the sponge within the tide pool.

Interactions between α - and β -males.

Beta-males moved back and forth between sponges containing unpaired α -males, and sponges containing α -males paired to receptive females. This apparent assessment behaviour may have provided β -males with information on the presence or absence of potential mates. After 12 hr, β -males showed a significant preference for α -males mated to receptive

females over unpaired α -males, as predicted by the distribution of β -males in spongocoels in the field (SHUSTER & WADE, 1991a). Consistent with this hypothesis, β -males did not exhibit assessment behaviour when allowed to choose between unpaired α -males and gravid females, and after 12 hr, β -males preferred to associate with unpaired α -males over α -males paired to nonreceptive females.

Why β -males associated with unpaired α -males is unclear. In nature, β -males may anticipate the arrival of receptive females in such circumstances. However, since receptive females prefer to breed in established spongocoels (*i.e.* spongocoels already containing females; SHUSTER, 1990; SHUSTER & WADE, 1991a), unpaired α -males seem less, rather than more likely to attract receptive females, and thus might be unattractive to β -males. Beta-males show a weak tendency to associate with unpaired β -males in field samples (SHUSTER, 1986), but the majority of β -males appear in population samples when receptive females are abundant in the population as a whole. Beta-males may have little difficulty locating α -males mated to receptive females at these times, and any tendency for β -males to associate with unpaired α -males in the field may be obscured. Since β -males are female mimics, they may by themselves be attractive to females and therefore tolerated in spongocoels by α -males. This aspect of spongocoel selection by β -males and how it affects the behaviour of other males and females bears further study.

Beta-males closely imitated the sequence of courtship behaviours performed by females, and thus appear to be true female mimics, rather than simply small males that lack large male ornamentation. The mechanism by which β -males were able to accomplish their 'deception', however, is uncertain. Mechanical stimulation of α -males by β -males in ways similar to stimulation usually provided by females may have been sufficient to release normal α -male courtship behaviour. Beta-males are rare in natural populations (4%, SHUSTER, 1987a), thus, under most circumstances, α -males responding positively to generalized 'male-like' stimuli may accumulate larger harems than males that are less willing to allow females into their spongocoel. The rarity of β -males corroborates evidence that frequency-dependent selection operates among males in this species (SHUSTER & WADE, 1991).

Interactions between α - and γ -males.

Like β -males, γ -males also assessed sponges containing paired and unpaired α -males before attempting to enter the spongocoel. The actual ap-

proach of γ -males to spongocoel oscula, however, differed markedly from the approach behaviour of β -males. Gamma-males approached α -males indirectly and appeared to circle the osculum, perhaps in attempts to remain beyond the α -male's ability to detect intruders, or seeking an advantageous position from which to rush into the spongocoel. The latter seems most likely, since in five cases, α -males detected γ -males at a distance and used their pleotelsons to seal their oscula against γ -males before these intruders completed their approach. Alpha-males in nature and in these experiments situated themselves head-down when established in spongocoels, with their cephalons oriented toward the sponge interior. Thus, visual detection of approaching γ -males is prevented. The means by which α -males detected γ -males, therefore seems likely to have involved smell, vibration or some yet unknown sensory modality.

Gamma-males that were not immediately blocked by α -males attempted to rush around α -males and into their spongocoels. Alpha-males quickly responded to these assaults and defended their spongocoels vigorously. Although α -males did not appear to apply lethal force to γ -males, α -males squeezed, blocked, scraped and teased γ -males from their spongocoels with remarkable precision, suggesting that selection has favoured dexterity among α -males in removing potential reproductive competitors. Gamma-males seemed capable of remaining in spongocoels only if they sequestered themselves beyond the α -male's reach. Extremely small body size probably increases an α -male's ability to resist eviction from reproductive habitat by α -males, and thus is also probably favoured by sexual selection.

Unpaired α -males and α -males paired to nonreceptive females did not seem as vigorous as α -males paired the receptive females in excluding γ -males from their spongocoels. Concordantly, γ -males seemed most persistent in attempting to invade spongocoels containing sexually receptive females. As expected, γ -males preferred to associate with α -males paired to receptive females, over unpaired α -males. Unlike β -males, however, γ -males showed no preference for unpaired α -males over α -males paired to nonreceptive females. Despite their lack of preference between these latter spongocoel types, γ -males still invaded rather than avoided spongocoels in most cases.

Coevolution of male polymorphism in *Paracerceis sculpta*.

The external morphology of α -males is similar to that of males in other '-cerceid' isopod species (HOLMES, 1904; IVERSON, 1982). The aggressive

behaviour of α -males in *Paracerceis sculpta* may therefore be typical of males in these other species as well. If such morphology has evolved in the context of male-male competition for mates, and if male polymorphism evolves as proposed by GADGIL (1972), as yet undescribed males, resembling β - and γ -males in their morphology and behaviour, may occur widely among the sphaeromatid Isopoda.

The reproductive behaviours of β - and γ -males in *P. sculpta* are functionally similar to female-mimicking and 'sneaker' behaviours that are widely reported in other animal species (reviews in GROSS, 1991; RYAN *et al.*, 1992). These alternative reproductive strategies and tactics appear to permit noncombative or nonterritory-holding individuals to gain access to mates. Whereas males employing alternative reproductive behaviours in most animal species appear to "make the best of a bad lot" in terms of their relative reproductive success (EBERHARD, 1982), β - and γ -males achieve fitnesses equal to that obtained by α -males (SHUSTER & WADE, 1991b; see also GROSS, 1991; RYAN *et al.*, 1992). Since selection acts more strongly within the male morphs than between the male morphs in *P. sculpta* (SHUSTER & WADE, 1991b), is not surprising that selection has produced a high degree of sophistication in female mimicry by β -males, and in stealth by γ -males. In species in which males appear to achieve marginal fitness via 'alternative' reproductive behaviour, however, it is difficult to see how selection could refine the effectiveness with which these activities are carried out. These observations call into question, therefore, whether many apparent examples of alternative reproductive tactics indeed represent behavioural adaptations at all.

Interactions between β - and γ -males remain unexamined. Although β - and γ -males do co-occur in spongocoels, they appear in less than 1% of all spongocoels containing isopod breeding aggregations (SHUSTER & WADE, 1991b). While apparently rare, these associations may occur frequently enough to favour the evolution of agonistic behaviour or other competitive adaptations among males. Whatever the details of such interactions prove to be, the co-occurrence of three discrete male reproductive behaviours and morphologies in *P. sculpta* indicates that male polymorphism in this species represents a long-standing, tightly coevolved system in which β -males and γ -males parasitize the reproductive efforts of α -males.

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Resumen

Existen tres morfotipos distintos en los machos de *Paracerceis sculpta*, un isópodo del Golfo de California. Los machos alfa (α -) son los mayores ($\bar{x}\pm SD = 6.55\pm 0.72$ mm, $N = 63$) y defienden espacios de reproducción en esponjas del intermareal. Los machos beta (β -) son más pequeños ($\bar{x}\pm SD = 4.34\pm 0.43$, $N = 59$) y parecen hembras receptoras tanto por su comportamiento como por la forma del cuerpo. Los machos gamma (γ -) son minúsculos ($\bar{x}\pm SD = 2.56\pm 0.73$ mm, $N = 23$) y son capaces de moverse rápidamente. Los tres tipos de machos son sexualmente maduros y producen prole en su medio natural (SHUSTER, 1989a). Usando esponjas artificiales para simular espacios de reproducción, se examinan: (a) las interacciones competitivas entre machos α para obtener espacios de reproducción o hembras, (b) las tácticas usadas para introducirse en las cavidades de las esponjas por los machos β y γ , y (c) la habilidad de los machos β y γ para discriminar entre distintas calidades de espacios de reproducción en base al número de hembras receptoras que estos contenían. Encontré lo siguiente:

1. Los machos α , tanto los residentes como los intrusos, utilizan sus patas, uropodos, y varias posturas corporales defensivas para conservar o conquistar espacios de reproducción.
2. Los intrusos son siempre más agresivos que los residentes en la mayoría de los encuentros excepto cuando se limita el número de espacios de reproducción que contenían hembras receptoras sexualmente.
3. A pesar de su aparente inactividad, los residentes consiguen mantener sus cavidades de las esponjas en la mayoría de los encuentros, aparentemente, a causa de la ventaja posicional de los residentes cuando se encuentran en el interior de la cavidad.
4. En interacciones con machos α , los machos β imitan el comportamiento de cortejo de la hembra hasta el más pequeño detalle, y los machos α se comportan como si los machos β fuesen hembras. Una estimulación táctil puede, por consiguiente, ser suficiente para provocar el comportamiento de cortejo de los machos α .
5. Los machos β prefieren cavidades de las esponjas que contienen machos α emparejados con hembras receptoras sexualmente, a las cavidades que contienen machos α y hembras grávidas (no receptoras sexualmente).
6. Los machos β prefieren asociarse con machos α no emparejados antes que con machos emparejados con hembras grávidas. Como las hembras receptoras prefieren espacios de reproducción establecidos (SHUSTER, 1990), no se encuentra explicación para esta preferencia.
7. No obstante, los machos β prefieren asociarse con machos α no emparejados antes que con machos emparejados con hembras grávidas. Como las hembras receptoras prefieren espacios de reproducción establecidos (SHUSTER, 1990), no se encuentra explicación para esta preferencia.

8. Los machos γ se aproximan indirectamente a los espacios de reproducción ocupados por machos α , e invaden cavidades de las esponjas solo tras repetidos intentos de colarse ante el macho α que guarda la entrada de la cavidad.
9. Los machos α resisten activamente los intentos de invasión, y usan sus urupodos, la punta de sus pleotelsons, y sus patas con considerable destreza para expulsar machos γ intrusos. El pequeño tamaño de los machos puede aumentar la habilidad de los machos γ para permanecer dentro de espacio de reproducción.
10. Al contrario que en los machos β , los machos γ prefieren solo cavidades con machos α emparejados con hembras sexualmente receptivas, no demostrando preferencia alguna por machos α emparejados con hembras grávidas.