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*Editado por:*

*Edited by:*

**GIOVANNI MALAGRINO - HERMILO SANTOYO**

Departamento de Biología Marina  
Universidad Autónoma de Baja California Sur  
La Paz, B.C.S., México.

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**Giovanni Malagrino-Hermilo Santoyo**  
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MALE BODY SIZE, NOT REPRODUCTIVE HABITAT CHARACTERISTICS,  
DETERMINES POLYGYNY IN A SEXUALLY DIMORPHIC INTERTIDAL  
ISOPOD CRUSTACEAN, *PARACERCEIS SCULPTA* (CRUSTACEA: ISOPODA)

STEPHEN M. SHUSTER\*

ABSTRACT

In the northern Gulf of California, the spongocoels of an intertidal sponge, *Leucetta losangelensis*, serve as reproductive habitat for an isopod crustacean, *Paracerceis sculpta*. Sexual dimorphism in this species is pronounced. Males are larger than females and possess elongated uropods and sculptured telsons. Females lack such modifications and lose functional mouthparts with a reproductive molt. Forty-five percent of adult males (N = 78) possess multiple mates, and large males are most successful at mate acquisition. Single, monogamous, bigamous and polygynous males differ significantly in body size, but spongocoels occupied by these males do not differ significantly in volume. In multiple regression, sponge volume, spongocoel location and the number of nearby occupied spongocoels do not predict harem size. Male body size, however, accurately predicts the number of female per male. Since male body size, not reproductive habitat characteristics, determines the degree of polygyny in *P. sculpta*, sexual selection is probably responsible for the evolution of large males in this species. This evolutionary trend, combined with selection for certain life history characteristics in females, may have led to the unique form of sexual dimorphism observed in *P. sculpta* and in several of its sphaeromatid relatives.

INTRODUCTION

The intertidal zone of the northern Gulf of California, near Puerto Peñasco, Sonora, Mexico, is characterized by coquina limestone reefs strewn with basaltic boulders. This rugged terrain provides attachment sites for a variety of sessile organisms, including a white calcareous sponge, *Leucetta losangelensis*. The sponges grow abundantly beneath rocks and shelves in permanent tide pools, and form discrete colonies with numerous large spongocoels. These spongocoels serve as reproductive habitat for *Paracerceis sculpta*, a sphaeromatid isopod crustacean. Brusca (1980) reported that *P. sculpta* breeds monogamously in *Leucetta* spongocoels, but few

details of the association of isopods and sponges are known.

Many animal species mate and rear young in distinct reproductive habitats (reviews in Wittenberger, 1981; Searcy, 1982; Oring, 1982). The amount of food available near nesting sites, or the extent to which nests are protected from predators or from physical forces may have a significant effect on the distribution and character of breeding aggregations (Oring, 1982). Reproductive habitats for most species, however, are difficult to delimit and quantify. Consequently, studies accurately assessing the effects of reproductive habitat characteristics on breeding aggregation characteristics are few (Pleszczyńska, 1978; Downhower and Brown, 1980).

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\* Dept. of Biology, University of New Mexico, Albuquerque, NM 87131, U.S.A.

Present Address: Dept. of Zoology, University of California, Berkeley, CA 94720, U.S.A.

Crustacean mating systems are poorly understood (Salmon, 1983). Studies examining the relationships between reproductive habitats and breeding aggregations are mostly qualitative (Borowsky, 1980; Christy, 1983), and isopod mating systems are virtually unknown (Schuster, 1981). Sponges used as reproductive habitat by *P. sculpta* consist of small discrete units that are easily collected and measured. The association of isopods with sponges, therefore, permits this crustacean's mating system to be examined in detail and the effects of reproductive habitat on breeding aggregations in this species to be clearly examined.

*P. sculpta* is strongly sexually dimorphic. Males are larger than females, are often brightly pigmented and possess sculptured telsons and elongated uropods. Females are drab in color and lack such structural modifications. This pattern of sexual dimorphism is observed in a number of sphaeromatid species besides *P. sculpta* (Hansen, 1905; Holdich, 1978; Iverson, 1982). Holdich (1971) speculated that telsonic modification in males is associated with crypsis and possibly with male parental care in *Dynamene bidentata*, but provided only anecdotal data to support his claim. The adaptive significance of sexual dimorphism in the Sphaeromatidae, thus remains obscure.

Slatkin (1984) considers sexual dimorphism in most animal species to have arisen (1) from life history differences between the sexes, such as when fecundity advantages accrued to large females lead to divergence in male and female body size, or (2) from sexual selection favoring morphological attributes of males that confer advantages in mate acquisition. Slatkin argues that genetic similarities between the sexes probably restrict males and females from evolving toward different adaptive peaks in the same environment, and that ecological competition between the sexes, while documented in some species (Selander, 1966; Schoener, 1969), is by itself rarely intense enough to select for significant male-female divergence. Sexual dimorphism in monogamous species is interesting because with monogamy, variance in male mating success approximately equals variance in female mating success (Wade and Arnold, 1980). Sexual selection is therefore weak in such species and observed morphological differences between the sexes are most likely ecologically derived.

I will address 3 questions: (1) What is the mating system of *P. sculpta*? (2) How do characteristics of this species reproductive habitat effect the distribution and form of breeding

aggregations? (3) How does selection in these contexts, combined with life history differences between the sexes explain the existence of sexual dimorphism in this species. My conclusions relate broadly to the evolution of animal mating systems and specifically to the evolution of sexual dimorphism in the Sphaeromatid Isopoda.

## MATERIALS AND METHODS

In 1978 I collected 30 sponges from the intertidal zone east of Puerto Peñasco, Sonora, México. I removed sponges from rocks and split each spongocoel longitudinally with a scalpel. If a spongocoel was occupied by isopods I noted their relative positions within, pushed the spongocoel back together, and measured the osculum diameter with vernier calipers to the nearest 0.01 mm. I then reopened the spongocoel and removed and measured the occupants to the nearest 0.01 mm. Finally, I measured a line that described the maximum linear dimension of the spongocoel interior to the nearest 0.01 mm. In most cases, spongocoels were roughly cylindrical in shape with the diameter of the osculum approximating the diameter of the cylinder. Using these dimensions, I estimated the volume of each spongocoel as:

$$V_s = (\pi d_s / 2)^2 \cdot l_s$$

where  $V_s$  = spongocoel volume,  $d_s$  = spongocoel diameter and  $l_s$  = spongocoel length.

In 1979 I collected 25 sponges as described for the previous year. On each sponge I established longitudinal, latitudinal and altitudinal axes and recorded sponge dimensions along these lines to the nearest 0.01 mm. I split spongocoels and removed and measured isopods as previously described. I determined the relative locations of each occupied spongocoel by measuring the distance from the extreme edge of the sponge to the center of each occupied spongocoel along the 3 predetermined axes. A statistic,  $T$ , was calculated as:

$$T = 1 - 1 / \{ (l_1 - l_2) (w_1 - w_2) (h_1 - h_2) \}$$

where  $l_1$ ,  $w_1$  and  $h_1$  represented the measurements along the 3 axes.

The reciprocal transformation normalized the data for individuals occupying different sized sponges, and subtracting from 1 placed  $T$  between 0 and 1. I then used multiple regression to examine how harem size for each male was

influenced by 4 independent variables: male body length (MLENGTH), sponge volume (SPV), spongocoel location (T) and the number of nearby occupied spongocoels (OTHERM). I selected as independent variables reproductive habitat characteristics and male characteristics that seemed most likely to determine the distribution and form of breeding aggregations. Body size may influence a male's ability to attract or control mates. Sponge volume and spongocoel location may assess the relative protection that physical structure of sponges provides. Large sponges may be less easily damaged by wave action, or may be less easily invaded by predators than small sponges. Spongocoels located at the center of sponges may be more protected than spongocoels located at the periphery. Alternatively, spongocoels situated on the periphery of sponges may be more easily located by females than spongocoels situated in the center. The number of other nearby breeding aggregations may assess the relative benefit that isopods obtain by breeding in groups. Spongocoels surrounded by or at least associated with other occupied spongocoels may be individually less vulnerable to predation in the same way that birds nesting colonially are more protected than when nesting alone.

## RESULTS

In both collections (Table 1), isopods were found singly and in monogamous breeding aggregations (Table 2). Isopods were also found, however, in bigamous and in polygynous aggregations (Table 2). Since in both years more mating aggregations contained multiple females

than would be expected by chance alone (1978: N=11, 46%; 1979: N=24, 44%), the mating system of *P. sculpta* should be considered polygynous rather than monogamous. Both mated and unmated males were situated at the osculum of their spongocoels, partially occluding the opening with their bodies and protruding their telsons and uropods outward. Female were clustered within spongocoels and were in no noticeable orientation.

As expected, males and females from both collections were morphologically quite distinct. Males were significantly larger than females (*U*-test,  $P < 0.001$  for 1978 and 1979, figs. 1 and 2), and variance in male body length was significantly greater than variance in female body length (Table 3). All females possessed brood pouches filled with embryos in various stages of development. Development stages ranged from completely undifferentiated embryos to fully developed juveniles isopods. All females possessed reduced and atrophied mouthparts. The mouthparts of males, however, were well-formed and appeared fully functional.

A significant positive correlation was found between male body length and the number of females per male (Spearman  $r_s = 0.628$ ,  $P < 0.002$ ,  $N = 24$ , fig. 3). Moreover, single, monogamous, bigamous and polygynous males were significantly different in body size for the 1978 collection (Kruskal-Wallis test,  $P < 0.05$ , Table 4). Assuming that the number of females per male accurately reflects male mating success, large males experienced significantly greater mating success than small males. No significant size differences were found between females mated to single, monogamous, bigamous and

Table 1. *Leucetta losangelensis* sponges and *Paracerceis sculpta* isopods collected at Puerto Peñasco, Sonora, Mexico, 1978, 1979.

	1978	1979
Sponges Examined	30	25
Spongocoels Occupied	41	64
Isopods Collected	76	145

Table 2. Breeding aggregations of *P. sculpta* from *L. losangelensis* spongocoels.

	1978		1979	
	Males	Females	Males	Females
Single	6	17	13	11
Monogamous	7	7	12	12
Bigamous	8	16	10	20
Polygynous	3	12	11	51
Largest Harem		5		5
% Polygynous		46%		44%

Table 3. Body length parameters for male and female *P. sculpta* (mm).

	1978		1979	
	Males	Females	Males	Females
N	24	51	51	94
Median	6.60	5.50	7.40	6.00
Range	5.80-8.50	3.90-6.60	5.50-9.35	4.10-7.55
$\bar{x}$	6.60	5.55	7.32	5.94
SD	1.49	0.58	0.83	0.65
$s^2$	2.23**	0.33	0.68*	0.42

\*F=1.99, P < 0.003.

\*\*F=6.46, P < 0.0005.

polygynous males (Kruskal-Wallis test,  $P > 0.50$ , Table 5). Furthermore, no relationship was found between spongocoel volume and harem size (Spearman  $r_s = 0.278$ ,  $P < 0.50$ ,  $N = 17$ ). Finally, no significant differences were found between spongocoels occupied by single, monogamous, bigamous and polygynous males (Kruskal-Wallis test,  $P > 0.25$ , Table 6). Clearly, while male body size and harem size were significantly correlated, spongocoel volume and harem size were not.

Multiple regression (1979) showed a signifi-

cant relationship between harem size and the 4 independent variables, male body length, sponge volume, spongocoel location and nearby occupied spongocoels. Of these variables, however, only male body length explained a significant amount of the variation in harem size (Table 7). Reproductive habitat attributes that seem associated with predator avoidance or protection from physical forces evidently do not influence the number of females per male. Only male body length accurately predicts harem size.

Table 4. Comparison of male body length for P. sculpta.

	1978*			1979**		
	N	Median	Range	N	Median	Range
Single	6	6.15	5.90-7.10	18	6.88	5.60-9.10
Monogamous	7	6.40	5.80-7.50	12	6.97	5.50-7.70
Bigamous	8	7.00	6.10-8.50	10	7.55	6.80-9.35
Polygynous	3	7.60	6.86-7.60	14	7.69	6.25-8.70

Kruskal-Wallis test: \*1978:  $P < 0.05$   
 \*\*1979:  $P < 0.005$ .

Table 5. Comparison of female body length for P. sculpta.

	1978			1979		
	N	Median	Range	N	Median	Range
Single	17	5.60	4.60-6.50	11	6.10	5.00-7.55
Monogamous	7	6.10	4.10-6.40	12	6.05	4.10-7.20
Bigamous	16	5.50	3.90-6.50	20	6.00	4.80-7.00
Polygynous	12	5.55	4.80-6.60	51	5.95	4.50-7.40

Kruskal-Wallis test: 1978:  $P = 0.50$ , N.S.  
 1979:  $P = 0.90$ , N.S.

Table 6. Comparison of the Calculated Volumes (mm<sup>3</sup>) of spongocoels occupied by *P. sculpta* males 1978.

	Breeding Situation			
	Single	Monogamous	Bigamous	Polygynous
N	2	5	7	.3
Median Volume	233.93	337.67	215.79	462-01
Range	130.29 -337.56	42.10 -657.79	129.36 -2136-15	326.10 -480.49

Kruskal-Wallis test:  $P > 0.25$

Table 7. Results of multiple regression (1979) to determine the influence of male body length (MLENGTH), sponge volume (SPV), spongocoel location (T) and the number of other males on the same sponge (OTHERM) on the log-transformed value of harem size for each male.

ANOVA	df	Sum of Squares	F	P
Regression	4	1.0659	4.7029	<0.010
Residual	46	2.6064		

$R^2 = 0.2903$

Contribution of Each Variable to the Regression.

	$R^2$	$R^2$ Change	F	P
MLENGTH	0.1443	0.1443	11.3500	<0.005
SPV	0.2596	0.1153	3.1510	>0.050
OTHERM	0.2828	0.0232		
T	0.2903	0.0075		



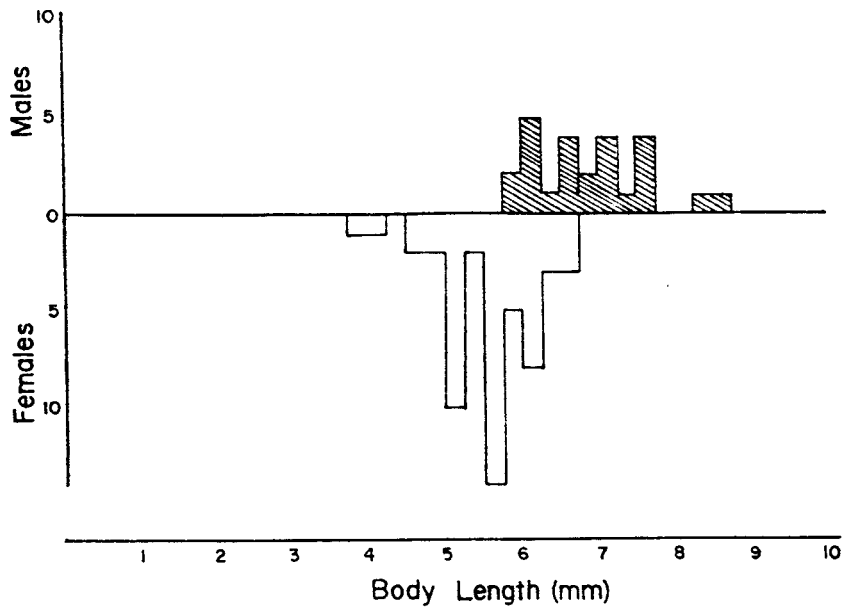


Fig. 1. Body lengths of male and female *P. sculpta* collected from spongocoels, 1978. Males (N=24; median=6.6 mm, range=5.8-8.5 mm) are significantly larger than females (N=51; median=5.5 mm, range=3.9-6.6 mm), U-test,  $P < 0.001$ .

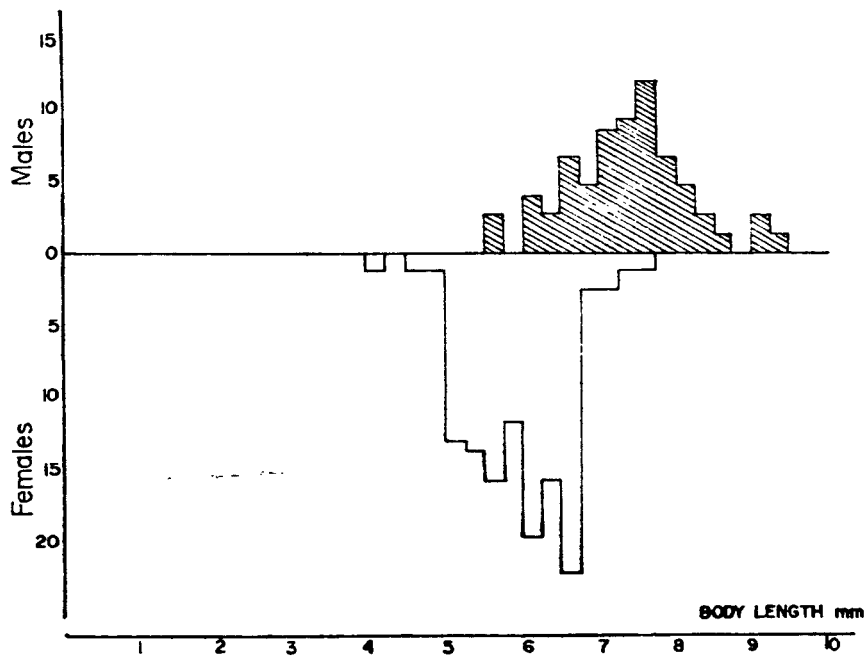
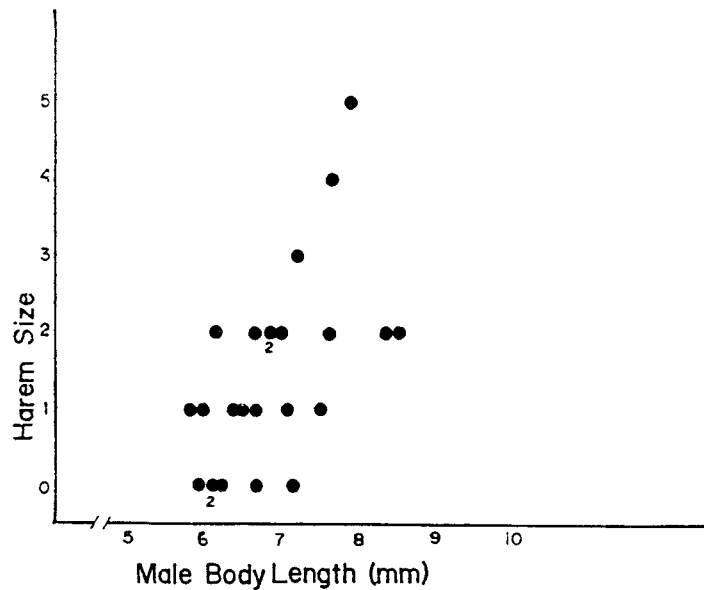


Fig. 2. Body lengths for male and female *P. sculpta* collected from spongocoels 1979. Males (N=51; median=7.40 range=5.50-9.35 mm) are significantly larger than females (N=94; median=6.00 mm, range=4.10-7.55 mm), U-test,  $P < 0.001$ .

Fig. 3. Relationship between male body length and the number of females per male (Spearman  $r_s = 0.628$ ,  $P < 0.002$ ,  $N = 24$ ).



## DISCUSSION

Female availability limits male reproduction in most animal species, forcing males to compete among themselves to obtain mates (Emlen and Oring, 1977). Males may compete by monopolizing resources crucial to female reproduction or by monopolizing females directly. Since resources or females are often unevenly distributed, males that monopolize clumps of resources or group of females become polygynous. Variance in the number of females per male is determined by variability in the quality of resources or in the size of female groups monopolized by different males (Oring, 1982).

*P. sculpta* males associate with a resource that seems crucial to female reproduction. Variability in sponge quality, however, does not seem sufficient to effect the number of females per male. None of the physical attributes of sponges examined determined harem size, and sponges cannot serve as food sources since females are incapable of feeding once they become gravid. Since variance in male mating success seems unrelated to reproductive habitat characteristics, it is unlikely that males compete to monopolize certain sponges based on the physical attributes of sponges alone.

Harem size correlated with male body size in both samples. Large size could confer an advantage to males monopolizing female groups,

but males evidently do not seek aggregations of receptive females. No such aggregations were found in either collection. Moreover, the developmental stages of embryos carried by different females in the same harem ranged widely. This suggests that females were mated sequentially, as if they had entered spongocoels at different times, rather than that individual males had located and mated with a preassembled group of receptive females. Finally, both mated and unmated males assumed the same prominent position at the entrance of their spongocoels, suggesting that rather than actively searching for females, males wait for females to approach them. Thus males may monopolize females by excluding other males from their spongocoels. Large males may be more successful at osculum defense than small males, and protuberant telsons and elongated uropods may be useful in fending off conspecifics. Similar interactions between male dynastine beetles (*Podischnus agenor*) are described in fascinating detail by Eberhard (1979). Male beetles guard sexually receptive females in tubes constructed in sugar cane stalks, and use horns on their head and prothorax, not only to defend their own tubes, but also to usurp tubes occupied by other males. Large males are most successful at both maneuvers.

Males may also use their size and telson appendages to protect females and their young from predators (Holdich 1968, 1971). If large, horny males are more effective spongocoel defenders, females may prefer such males as

mates. Males that display their size and protuberances to approaching females may experience greater mating success than non-displaying males, perhaps explaining why males assume conspicuous, and presumably dangerous, positions in spongocoels.

While sexual selection via male-male combat or female mate preferences may explain large size and ornamentation in males, certain female attributes do not seem sexually selected. Females are incapable of feeding after their reproductive molt, and are severely depleted of all stored resources after releasing young. Their cuticles are brittle, they lack pereopod musculature and viscera, and their hepatopancreases are reduced to small stumps. Such females do not molt and regain their mouthparts, and die without reproducing again (Shuster, unpublished data).

Selection should stabilize body size in semelparous females so that the benefits of a large body cavity and consequent increased fecundity equal the costs of somatic maintenance. That is, females should be as large as possible given their ecological constraints, and variation in female body size should be minimal (Williams, 1966). *P. sculpta* females fit this description. Semelparity in *P. sculpta* females also explains mouthpart and pigmentation differences between adult males and females. Females may simply channel all stored energy, including that contained in muscles and cuticular pigments into developing embryos. Why females reproduce only once is unclear. Isopods feed on intertidal algae (Shuster, unpublished data) that is often remote from reproductive habitat. Intertidal predators may be so abundant that successful trips by breeding females from feeding sites to nest sites *and back* are extremely unlikely. If the probability of successful iteroparity is low, selection should favor females which invest heavily in their first brood and semelparity should soon evolve.

*P. sculpta* is clearly polygynous. Reproductive habitat characteristics evidently do not significantly influence variance in male mating success, while male body size predicts harem size accurately. Females reproduce only once and apparently invest all of their stored resources in developing young. Sexual dimorphism in *P. sculpta* therefore seems to have evolved through sexual selection on males and through selection for semelparity in females. Sphaeromatid isopods exhibiting morphologies similar to that exhibited by *P. sculpta* may face similar selective regimes, and may provide useful tests of current sexual selection and life history theory.

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