Female copying and sexual selection in a marine isopod crustacean, *Paracerceis sculpta*

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Abstract. The opportunity for sexual selection on males can be influenced by 'female copying', a form of female mate selection in which females imitate the mate choices of other females. Female copying always increases the opportunity for sexual selection on males because it increases the number of males obtaining no mates, as well as the number of males obtaining many mates. *Paracerceis sculpta*, a marine isopod crustacean, breeds in intertidal sponges in the Gulf of California. In the field and in laboratory choice tests, females in this species do not exhibit male or sponge preferences, but do prefer to breed in spongocoels containing other females. This tendency for females to aggregate is a form of female copying. Males in this species occur as three genetically distinct morphotypes: large α-males defend breeding sites in intertidal sponges; small β-males resemble sexually receptive females in behaviour and body form; and tiny γ-males that are effective at entering spongocoels and engaging in sperm competition with other males. α-Males prefer to guard large aggregations of females. β-Males and γ-males prefer to invade spongocoels containing large female aggregations. This paper reports the degree of female copying that is sufficient to account for the observed distribution of females in spongocoels in the field. These results also indicate that while female copying increases variance in harem size among α-males, it also increases the opportunity for β- and γ-males to invade large breeding aggregations. Female aggregation behaviour thus creates a 'mating niche' for β-males and γ-males. The availability of this niche may partially explain the persistence of multiple male morphs in this species.

Bateman (1948) empirically demonstrated that male fruit flies, *Drosophila melanogaster*, exhibit greater variance in offspring numbers than females. He showed, moreover, that this difference was the result of variation among males in numbers of mates. Bateman thus identified a sex difference in the variance in reproductive success that permits selection to be stronger in males than in females. This sex difference in the variance in fitness was later given theoretical expression by Wade (1979) and by Wade & Arnold (1980).

Bateman's observations are often included in discussions of species under sexual selection (reviews in Thornhill & Alcock 1983; Clutton-Brock 1988). These discussions frequently use the variance in male reproductive success as a de-

scription of the intensity of sexual selection on males. Following Crow (1958, 1962), Wade (1979, 1987) has argued that statistical variance in male reproductive success is a necessary, but not a sufficient condition for sexual selection, and suggests instead that the 'opportunity for sexual selection', I_{males} (Wade & Arnold 1980), is a more appropriate index of the strength of sexual selection. 'Opportunity for sexual selection' is defined as

$$I_{males} = V_{RSmales}/(\bar{X}_{RSmales})^2 \qquad (1)$$

where $V_{RSmales}$ is the variance in the number of mates of males, and $\bar{X}_{RSmales}$ is the mean number of mates per male. The opportunity for selection thus measures the variance in relative fitness among males owing to male variation in mating success, similar to sexual selection as envisioned by Bateman (1948). Low values of I (approaching 0) indicate the sexual selection is weak and that there is little

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variation among males in mating success. Larger values of I (> 1) indicate stronger selection owing to greater variation among males in mating success (Wade 1979, 1987; Wade & Arnold 1980). Values of I near 1 occur when the variance in reproductive success is equal to the square of the mean in reproductive success, i.e. when the distribution of mates between males fits a Poisson distribution. Such distributions have been suggested as null models for the measurement of sexual selection in natural populations (Downhower et al. 1987; G. Cabana, personal communication).

Wade & Pruett-Jones (1990) have shown that the opportunity for sexual selection on males is influenced by 'female copying', a form of female mate selection in which females imitate the mate choices of other females. Related phenomena, termed 'conspecific cueing' (Kiester 1979), have been reported in lizards, *Anolis auratus* (Kiester 1979), fallow deer, *Dama dama dama* (Clutton-Brock et al. 1989), and the reef fish, *Serranus fasciatus* (Petersen 1987). Wade & Pruett-Jones (1990) suggest that female copying may explain some of the variance in male mating success in lekking birds because females in such species actively choose mates, but male characters and environmental correlates explain only part of the variance in male mating success (reviews in Bradbury 1985; Bradbury et al. 1985; Bradbury & Davies 1987). Wade & Pruett-Jones (1990) derive an explicit formula that demonstrates how this type of female mate selection behaviour can affect the variance in male mating success, and thus influence the opportunity for sexual selection. They conclude that since female copying always increases the variance in mate numbers among males, female copying always increases the opportunity for sexual selection on males.

Female mate choice involving female copying has been demonstrated in *Paracerceis sculpta*, a marine isopod crustacean that breeds in intertidal sponges, *Leucetta losangelensis*, in the northern Gulf of California (Shuster 1987a, 1990, 1991). Variance in harem size among males in this species appears significantly influenced by the tendency for females to prefer breeding aggregations consisting of more than one female (Shuster 1990). Here we use the methods of Wade & Pruett-Jones (1990) and data from Shuster (1986, 1989a, 1990) to estimate the degree of female copying that is sufficient to explain the observed distribution of females with males in a natural *P. sculpta* population.

METHODS

Reproductive Biology of *P. sculpta*

Male polymorphism

Males in this species occur as three distinct morphotypes that represent alternative reproductive strategies (Shuster 1987a, 1989b). α-Males possess enlarged pleotelsons and elongated uropods. β-Males are smaller than α-males, lack ornamentation and resemble sexually receptive females in their behaviour and morphology. γ-Males are also unornamented, are smaller than β-males, and use their tiny proportions and rapid movements to slip around α-males and into spongocoels (Shuster 1987a, 1990). While the three male morphs differ in their reproductive behaviour (Shuster 1989a, b, 1991), they do not differ in their abilities to sire young successfully when isolated with females (Shuster 1986, 1987a). Moreover, relative fertilization success among males in spongocoels varies with the density of receptive females, and evidently with the relative frequency of other male types in the population (Shuster 1989b).

Female behaviour at breeding sites

Most males in the northern Gulf of California population are α-males (82%, Shuster 1987a). α-Males establish breeding sites within spongocoels, females are attracted to spongocoels containing α-males (Shuster 1990), and polygynous breeding assemblages form that may include as many as 19 females per α-male ($\bar{X} \pm \text{SE} = 1.73 \pm 0.245$, $N = 212$; Shuster 1987a). Females initiate courtship that involves oral contact of α-males by females, and lifting and shaking of females by α-males. Despite this apparent mate assessment, females do not discriminate between α-males that differ by 10% in body length, by 30 days in age, or even among intact males and males lacking appendages used in courtship (Shuster 1990). In most cases, females simply pair with the first α-male they encounter.

In the field, large breeding aggregations contain a disproportionate number of recently inseminated females, suggesting that large harems are particularly attractive to sexually receptive females (Shuster 1990). Furthermore, multivariate analyses show no relationship between the physical characteristics of breeding sites and the size of female breeding aggregations (Shuster 1987b, 1991).

α-Males attempt to control such mating sites, and body size confers an advantage in spongocoel take-over (Shuster 1990). α-Males, moreover, show no reluctance to pair with any female that approaches their spongocoel (Shuster 1986).

Shortly after entering spongocoels, females undergo a moult that initiates their sexual receptivity (Shuster 1989a). Females mate in spongocoels at this time and begin brooding their embryos in a ventral brood pouch. Post-moult females lose functional mouthparts and cease to feed after they become gravid. Young isopods (mancae) emerge from females approximately 4 weeks after mating depending on water temperature, and all females die within 2 weeks of parturition (Shuster, in press). Thus, females in this, and evidently in at least 16 other sphaeromatid genera (Harrison 1984), are obligately semelparous.

Female copying in P. sculpta

Female mate selection in this species is noteworthy because females prefer to enter spongocoels occupied by other females (Shuster 1986, 1987b, 1990, 1991). As demonstrated by Wade & Pruett-Jones (1990), such behaviour in females can increase the variation in number of mates among males. α-Males, moreover, attempt to usurp sponges preferred by females from other α-males. This competition could further increase variance in the number of mates per male and thus increase the value of I_{males}.

In this paper, we use the model of Wade & Pruett-Jones (1990) to investigate: (1) the level of female copying necessary to explain the distribution of *P. sculpta* females in spongocoels in the field, and (2) the effect of this female copying on the strength of sexual selection, I_{mates}. We also discuss how the female aggregation behaviour permits β-males and γ-males to invade breeding aggregations by increasing the mating niche of these males.

Female Copying: the Model

Consider a population in which m is the number of males, f is the number of females and R is the sex ratio (note that $R = f/m$). If the size of the population is large, the sex ratio is near unity and mating is random, the probability of a female mating with any male is $1/m$. Moreover, after all females have mated, the distribution of females among males will

be Poisson as f becomes very large. The mean number of mates per male is f/m, which equals the sex ratio, R. In the absence of female copying, the variance among males in the number of mates per male, V_{mates}, equals

$$f(1/m)(1 - 1/m) \qquad (2)$$

or

$$f(m - 1)/m^2 \qquad (3)$$

The opportunity for sexual selection on males, I_{males}, equals the variance in male mating success divided by the square of mean male mating success, thus

$$I_{\text{males}} = [f(m - 1)/m^2]/(f/m)^2 \qquad (4)$$

which equals 1 when $R = 1$, f is large and mating is random. Henceforth, I_{males} will be referred to simply as I.

If females copy the mate choices of other females, the magnitude of this tendency can be represented by s. Thus, when a female selects a mate, the probability of her mating with a male already mated to another female is increased above $(1/m)$ by s. Similarly, the probability of her mating with an unmated male is decreased below $(1/m)$ by s. Since the probability that a female will mate with a particular male increases as the number of females preferring that male increases, the probability that the ith mating female will choose to mate with a particular male can be expressed as

$$P(i) = (1 + hs)/[m + (i - 1)s], \qquad (5)$$

where h is the number of other females already mated to that male. The larger the value of s, the greater the tendency of females to mate with already-mated males and to avoid mating with unmated males. (Further discussion of this model and its relationship to Polya's Urn Models as well as the formula for the expected mean and variance of this probability distribution (equation 5) can be found in Wade & Pruett-Jones (1990).) The value for the opportunity for sexual selection on males incorporating the effects of female copying may then be calculated as

$$I = (m - 1)(m + fs)/f(m + s) \qquad (6)$$

It is easy to see from this equation that I is always increased (and is always greater than 1) with positive values of s. Therefore, female copying always
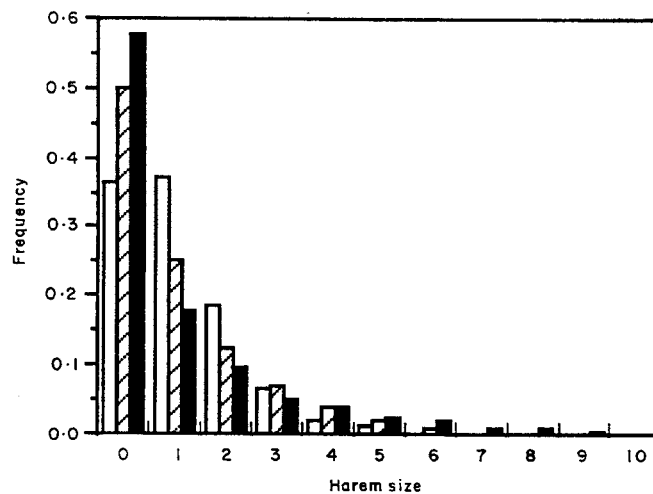
Figure 1. The distribution of females with males if females associate randomly with males and if females copy the mate choices of other females. $\square$: $s = 0$; $\boxtimes$: $s = 1 \cdot 0$; $\blacksquare$: $s = 2 \cdot 0$. The population consists of 50 males and 50 females (redrawn with permission from Wade & Pruett-Jones 1990).

increases the opportunity for sexual selection over random mating.

The distribution of harem sizes using this model of female mate choice is different from that generated by females choosing males randomly. If the distribution of females with males is plotted using values of s from 0 to 2 (Fig. 1), it is clear that with increasing values of s, the 0 class of males (unsuccessful males) and the classes of extremely successful males both increase with increasing s. Note also that most of the males lie in the 0 or 1 classes (unsuccessful males and males mated to exactly one female, respectively). Since the ratio of these classes of males, $Pr(x = 0)$ to $Pr(x = 1)$ equals $s + (1/R)$, Wade & Pruett-Jones (1990) suggested that the significance of s may be determined by comparing the expected values of the 0 and 1 mate classes (calculated using the random distribution formula) with those values observed in the field by means of a chi-squared test. The ratio of the proportions also provides an estimate of s, i.e. an estimate of the degree of female copying sufficient to account for the deviation from random mate choice.

Collection of Isopods

Sponges containing isopod breeding aggregations occur beneath boulders in permanent tide pools in the mid-intertidal zone near Puerto Peñasco, Sonora, Mexico (Shuster 1991). Between October 1983 and November 1985, monthly

samples were collected from 15 randomly selected 0·25-m plots along a 100-m transect, situated within the zone of greatest sponge density and oriented parallel to the shore. All the sponges within each plot were removed from rocks, and spongocoels within each sponge were opened and examined for isopods. In most cases, spongocoels were discrete, thus membership of a particular breeding aggregation was easily assigned. Individuals contained within converging spongocoels were considered a single breeding aggregation. All isopods were removed from spongocoels, examined under a stereomicroscope and sexed. Mature males were identified by their external genitalia (Shuster 1987a) and seminal vesicles visible through the ventral cuticle. Females were identified by their possession of a marsupium filled with embryos, or by mature ovaries visible through the ventral cuticle.

Estimating Female Copying

To estimate the degree of female copying that occurred in the population between October 1983 and November 1985, adjacent monthly samples were pooled to yield 12 samples over 2 years. The total number of males (m), the total number of females (f), and the population sex ratio ($f/m = R$) were then calculated for each of the 12 samples. Using the equations derived above, the values for s and I were also calculated. To test the significance
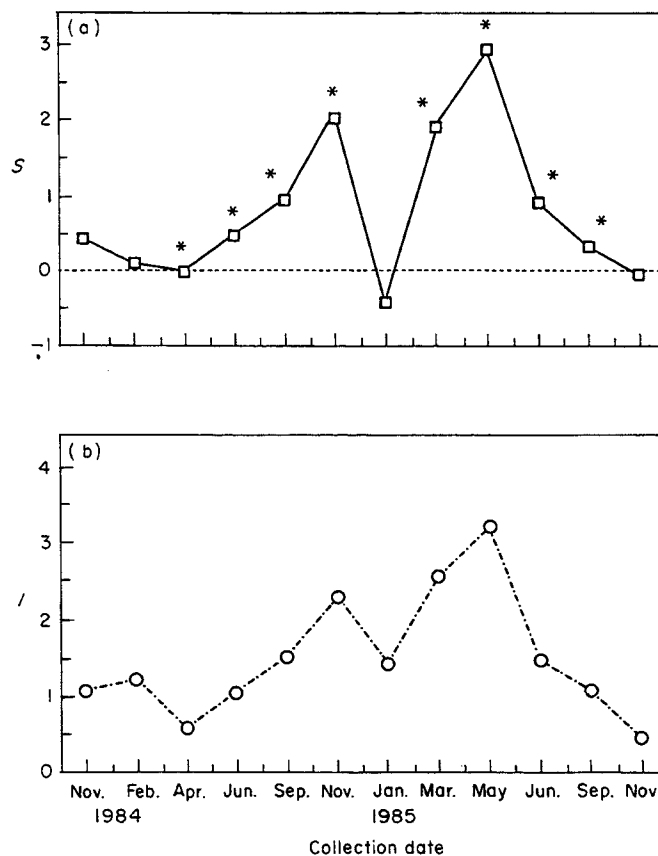
Figure 2. (a) Seasonal variation in the value of s, the degree of female copying, for samples of *P. sculpta* adults collected between October 1983 and November 1985. *Values of s that deviate significantly (chi-squared test, $df=1$, $P<0.05$) from values predicted by a random distribution of females with males. (b) Seasonal variation in the value of I, the opportunity for selection on males, over the same duration as in (a).

of s for each pooled sample, the observed and expected values for unmated males collected from spongocoels ($Pr(0)$), and for males collected from spongocoels that were mated to exactly one female ($Pr(1)$) were compared using a chi-squared test with one degree of freedom. Pooling of adjacent monthly samples was necessary on statistical grounds to generate expected values for the 0 and 1 classes of males that were equal to or greater than 5, as is required for a chi-squared test (Siegel 1956). On biological grounds, pooling on this scale is appropriate because the tenure of an adult α-male is approximately 2 months (Shuster 1986).

RESULTS

Figure 2a shows seasonal variation in the value of s. Eight of the 12 samples deviated significantly from

the random expectation (Table I), as did the pooled distribution of harem sizes across all samples ($\chi^2 = 28.53$, $df=1$, $P<0.001$, Table I). The deviations of observed and expected distributions among samples, however, was heterogeneous ($\chi^2 = 54.14$, $df=10$, $P<0.001$, Table I).

Figure 2b shows variation in the value of I calculated from equation (6). As predicted by Wade & Pruett-Jones (1990), there is correspondence between the value of I and the value of s (Fig. 2a). Increased female copying coincides with increased values of I, although it is noteworthy that deviations in the sex ratio may confound this effect. The highly male-biased sex ratio occurring in the (12/1984) sample (Table I) generated considerable variance in harem size among males ($I=1.43$, Table I). Female copying at this time, however, was not evident ($s = -0.43$, NS, Table I), perhaps because males in

Table I. Parameters used for calculation of s, I and the significance of female copying determined from population samples of *P. sculpta* collected between October 1983 and November 1985

Sample date	m	f	N	$R(f/m)$	Observed $Pr(0)$	Observed $Pr(1)$	s	Expected $Pr(0)$	Expected $Pr(1)$	χ^2	I
10/1983–11/1983	39	58	97	1·49	11	10	0·43	8·64	13·20	1·42	1·06
12/1983–02/1984	36	31	67	0·86	15	12	0·09	15·03	13·32	0·13	1·21
03/1984–04/1984	81	137	218	1·69	14	24	−0·01	8·28	17·19	6·65*	0·58
05/1984–06/1984	66	108	174	1·64	15	14	0·46	6·52	13·53	11·06*	1·05
07/1984–09/1984	72	118	190	1·64	17	11	0·94	6·94	14·62	15·46*	1·50
10/1984–11/1984	33	72	105	2·18	10	4	2·04	2·72	6·53	20·42*	2·28
12/1984–01/1985	32	17	49	0·53	16	11	−0·43	17·75	10·06	0·25	1·43
02/1985–03/1985	47	58	105	1·23	19	7	1·90	13·50	17·02	8·14*	2·55
04/1985–05/1985	32	43	75	1·34	11	3	2·92	7·33	10·74	7·43*	3·25
06/1985–07/1985	23	34	57	1·48	8	5	0·92	5·07	7·84	4·01*	1·47
08/1985–09/1985	54	69	123	1·28	11	10	0·32	6·16	11·37	5·49*	1·07
10/1985–11/1985	40	79	119	1·98	5	11	−0·05	3·33	7·74	2·22	0·44
Sum	555	824	1379	—	152	122	—	101·28	143·16	82·67*	—
$\bar{X}$	46·3	68·7	114·9	1·45	12·7	10·2	0·79	8·44	11·93	—	1·49
SD	17·4	35·3	51·6	0·43	3·9	5·3	0·96	4·46	3·36	—	0·79

m: Number of males; f: number of females; N: total N; R: sex ratio; $Pr(x)$: frequency of 0 or 1 class males.
*$P<0·05$.

spongocoels were overdispersed (S. M. Shuster, personal observation). The combination of widely separated breeding sites and relatively few (usually one) females per spongocoel may have made detection of established breeding sites difficult or impossible for unmated females.

The estimated value of s for the distribution of females among males for the (9/1984) sample was 0·94 ($\chi^2 = 15·46$, $df = 1$, $P < 0·001$, Fig. 3); near the mean value, 0·79 of the 12 estimates of s. In this sample (9/1984), note the deviation of observed harem sizes from the expected distribution of females. Both the 0 class and highly polygynous classes of males are inflated relative to random expectation, leading to the increased variance among males in mate numbers. This distribution of females with males increases the opportunity for sexual selection on males above random expectation ($I = 1·50$, Table I).

DISCUSSION

Why might *P. sculpta* females copy the mate choices of other females? The simplest explanation is provided by considering the influence of natural selection on female life history characteristics in this species (Shuster 1991). To reproduce successfully, females must migrate from feeding sites in coralline algae to breeding sites in sponges. During this trip, females experience considerable predation pressure from reef fish (Thompson & Lehner 1976; Shuster 1991). Risks incurred during mate or breeding site selection are thought to diminish
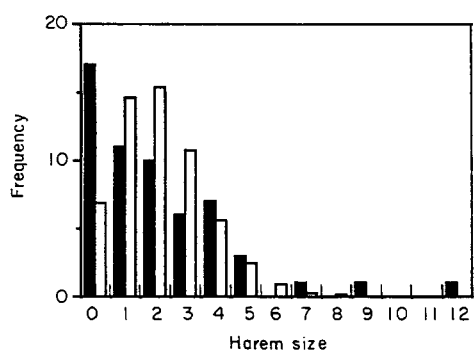
Figure 3. The observed (■) and expected (□) distributions of harem sizes for *P. sculpta* adults collected between July and September 1984. The observed distribution deviates significantly from the expected distribution ($\chi^2 = 15\cdot46$, $df = 1$, $P < 0\cdot001$, $N = 66$).

opportunities for females to discriminate between potential mates (Kirkpatrick 1987). Thus, it may be costly to females in this species, owing to predation, to move extensively among breeding sites to discriminate male and/or sponge characteristics. Females may instead use the scent of other females in spongocoels as an indication of the quality of breeding sites. This tactic would permit females to move towards established (and thus perhaps relatively safe) breeding sites with minimal exposure to predation.

Clearly, the tendency for females to copy other females increases the variance in mate numbers among α-males in this species. α-Males capable of locating and defending breeding sites preferred by females are thus likely to experience greater mating success than randomly searching, non-guarding males. α-Males can detect females in spongocoels from a distance, and prefer to occupy spongocoels containing several females (Shuster 1990). Moreover, α-males fight for access to such locations, large α-males win most contests over spongocoels, and α-male uropods appear important in successful spongocoel takeover (Shuster 1990). The tendency for females to aggregate with other females thus appears to have created the arena in which large body size and elongated uropods among α-males evolved.

The presence of several females in a spongocoel is also attractive to β- and γ-males. In the field, β- and γ-males are found in spongocoels containing an α-male and an average of 3·27 sexually receptive females, whereas the average harem size of α-males is 1·47 females (S. M. Shuster, unpublished data).

As the number of receptive females increases, the probability that β- and γ-males occur in such spongocoels increases significantly (Shuster 1986). Laboratory choice tests show that β- and γ-males prefer spongocoels containing sexually receptive females (Shuster 1986). Moreover, when given a choice, β-males show a preference for higher female densities.

Laboratory tests also show that fertilization success among genetically marked β- and γ-males in spongocoels of α-males increases with increasing female density, at the expense of α-male success (Shuster 1989b). β-Males and γ-males enjoy enhanced mating success in spongocoels containing several females, evidently because such breeding sites permit these males to encounter multiple mates and compete successfully with α-males. The aggregation behaviour of the females increases the frequency of multi-female spongocoels above that expected if females chose mating sites at random. In this way, female aggregation, or 'copying', creates a 'mating niche' for the β- and γ-males that may contribute to the maintenance of multiple male morphs in the population (direct measurements of male reproductive success for the different male morphs in the field are underway).

We have shown how the model of Wade & Pruett-Jones (1990) may be used to estimate the magnitude of female copying sufficiently to explain an observed distribution of females in the field. The model provides a simple and easily executed method for assessing the influence of a particular female behaviour pattern on the opportunity for selection in males. We have shown that female copying alone, independent of characteristics of males, can influence sexual selection in *P. sculpta*. Moreover, while certain α-males in this species may acquire extremely large harems as a result of female copying, these harems become vulnerable to invasion by β- and γ-males.

Aggregation behaviour on the part of females may contribute to the co-existence of multiple male mating strategies in these isopods by creating a 'mating niche' for β- and γ-males. Aggregations of receptive females as a result of conspecific cueing may also occur in polygynous birds, fish and mammals (Bradbury & Davies 1987; Petersen 1987). Males in these, and perhaps in similar species, exhibit alternative reproductive tactics. Female copying creates aggregations of reproductive females that may be susceptible to invasion by unconventional male phenotypes. This mating

niche created by the behaviour of females may explain the occurrence of alternative male reproductive strategies in other animal species.

ACKNOWLEDGMENTS

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