

BATEMAN GRADIENTS AND ALTERNATIVE MATING STRATEGIES



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Abstract

Among the available methods for estimating the intensity of sexual selection, the Bateman gradient is considered one of the most accurate, because it specifically measures the standardized covariance between mate numbers and offspring numbers for members of each sex. Although widely used to compare sex differences in selection intensity, it has yet to be used to examine the covariance between mate numbers and offspring numbers among alternative mating strategies. We allowed marine isopods (*Paracercis sculpta*) representing the 3 genetically distinct male morphs in this species to mate from 1 to 5 times, and we allowed females to mate 1, 3 and 5 times. We compared the total number of offspring produced by each mating or sequence of matings using 2-way ANOVA. We found that females gained no additional fitness from mating with multiple males, whereas male fitness increased with increasing mate numbers. There were no significant differences in the Bateman gradients for α -, β - and γ -males, and no significant differences in the fitnesses of α -, β - and γ -males allowed to mate with 1-9 females in succession. In nature, the fitnesses of the 3 morphs are highly variable, apparently due to differences in the availability of receptive females. Our results suggest that differences in mate availability, not differences in sexual competence, are responsible for observed variance in fitness within, and for the equality of fitnesses among, the 3 male morphs in this species.

Introduction

Parental Investment Theory holds that the source of sexual selection is a sex difference in initial parental investment (Bateman 1948; Williams 1966; Trivers 1972; Alcock 2005). Yet Bateman (1948) himself showed that sexual selection arises instead from a sex difference in the variance in fitness (Wade 1979; Wade & Arnold 1980; Shuster & Wade 2003; Wade & Shuster 2005). The magnitude of this latter sex difference can be specifically quantified, not as proxies for selection intensity, such as the ratio of sexually mature males to receptive females at any time (OSR; Emlen & Oring 1977) or the ratio of maximum potential reproductive rates for each sex (PRR; Clutton-Brock & Vincent 1991), but rather from actual estimates of selection. Such measures include the ratio of the variance in fitness to its squared average ($V_{\text{fitness}}/W^2 = I_{\text{selection}}$; Shuster & Wade 2003), i.e., the opportunity for sexual selection, or more specifically, from estimates of the standardized covariance between mate number and offspring number, what is now known as the Bateman gradient, β_B (Arnold & Duvall 1994; Jones et al. 2000, 2004).

The Bateman gradient is considered among the most accurate ways to measure sexual selection because it measures the slope, β_B , of the statistical relationship between mate numbers and offspring numbers for members of each sex. Thus, it directly measures the intensity of sexual selection on the trait or traits that influence the sex difference in the variance in offspring numbers. For the Bateman gradient, the trait considered is the number of mates that males and females acquire. Although now widely used to compare sex differences in selection intensity (Arnold & Duvall 1994; Jones et al. 2000, 2004, 2005; Bjork & Pitnick 2006), this parameter has yet to be used to examine the covariance between mate numbers and offspring numbers among alternative mating strategies. Polymorphisms in mating phenotypes are considered by many to provide examples of fitness satisfying, in which one or more phenotypes "make the best of a bad job" (Dawkins 1980; Gross 1996; Tomkins & Hazel, in press). If this is indeed the case, Bateman gradients among morphs are likely to be statistically distinct.

The Gulf of California sphaeromatid isopod, *Paracercis sculpta*, breeds within the spongoecells of the sponge, *Leucetta losangelensis*, and has three distinct male morphs (Fig. 1). Alpha males are largest and possess enlarged uropods for defending breeding sites. Beta males are smaller than α s and resemble females in behavior and body form. Gamma males are the smallest and use their small size and agility to "sneak" into spongoecells (Shuster 1987). Previous results indicate that variance in fitness within the 3 male morphs is large, whereas fitness differences among morphs are minute; a necessary condition for the persistence of genetic polymorphism (Shuster & Wade 1991; Fig. 2), but the causes of within-morph fitness variance remain unclear. Here, we measure the Bateman gradient for α -, β - and γ -males, and females, in *P. sculpta* to determine if there is a significant difference in the covariance between mate numbers and offspring numbers for males of each phenotype and for females in this species.

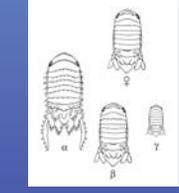


Figure 1. The alpha, beta, and gamma male morphs compared to a female in *Paracercis sculpta* (from Shuster 1982).

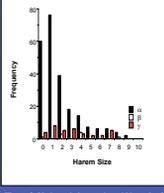


Figure 2. Variance in harm size within each of the 3 male morphs is much larger than the variance in harm size among the 3 morphs (redrawn from morphs in Shuster & Wade 1991).



Figure 3. Copulation: an alpha male and a female.

Materials and Methods

Sexual Receptivity, Mating and Gestation in *P. sculpta*. Females are attracted to breeding sites when their ovaries and brood pouches mature. Sexual receptivity in this species is initiated when she sheds the posterior half of her cuticle and exposes genital openings at the base of each 5th walking leg. Females in S₁ (full moult) condition remain receptive for 24 hrs before shedding their anterior cuticle, ovipositing into internal brood pouches and becoming non-receptive (S₂). Females do not feed during gestation (S₂S₃). Males complete a mating sequence with receptive females by inserting their appendages masculinized and ejaculating into it, and then into the other of their male's vaginas (Fig. 3). Fertilization occurs and zygotes are brooded internally for 3 wks before being released as fully formed juveniles (manacs; Shuster 1989, 1990).

Field Collections: We collected isopods from the spongoecells of the intertidal sponge, *Leucetta losangelensis*, in the northern Gulf of California as described in Shuster (1992). All individuals were sexed, scored for reproductive condition, and measured to the nearest 0.125 mm, and identified by unique cuticular patterns (Shuster 1989a, b). We retained unmated, sexually mature S₁ females, as well as α -, β - and γ -males from samples and placed these individuals into 225 ml plastic cups containing seawater. All other individuals were returned to collection sites within 24 hrs.

Matings for Males: To examine the relationship between mate number and fertility for the 3 male morphs, we allowed α -males (N=14), β -males (N=14) and γ -males (N=13) to mate with 1-5 females in succession (N_{mates}=86). We allowed each male to remain with a female for the duration of her 24 hr period of receptivity. We then separated individuals and placed them into separate 225 ml cups containing seawater. Males were placed with another S₁ female. All S₁ females were maintained in containers until parturition when we counted all manacs and undeveloped zygotes, if present. To determine whether the fecundities of males differed with increasing mating frequency, as well as to determine whether the fecundities of females mated by α - and γ -males were statistically distinguishable, we first calculated the residuals for the regression of offspring number on female body size to account for the positive relationship between these variables, then we used 2-way ANOVA to examine the influence of male morph (MORPH), the order of females in the mating queue (ORDER) and their interaction (MORPH*ORDER) on the number of offspring produced by individual females mated by α -, β - and γ -males. We performed a similar analysis on the number of undeveloped zygotes per female but did not calculate residuals for this analysis because there was no significant relationship between female body length and the number of undeveloped zygotes ($F_{1,86} = 0.61$, $p > 0.42$).

Matings for Females: To examine the relationship between mate number and fertility for females, we allowed S₁ females to complete one mating sequence with 1 (N=2), 3 (N=1) or 5 (N=3) α -males in succession. Pairs of isopods were given a maximum of 20 minutes to begin mating. To prevent re-mating, we removed males after mating, changed the water in the cup and allowed each female to recover for 5 minutes before the next male was introduced. The entire mating sequence for each female took less than 2 hrs. S₁ females were maintained in containers until parturition when all manacs were counted. Again, the numbers of undeveloped zygotes, if present, were counted. To compare the fecundities of females who mated 1-5 times over 2 hrs with the fecundities of females allowed unlimited matings over 24 hrs, we used 2-way ANOVA to examine the influence of female body length (FLENGTH), the time available for mating (DURATION; 1-5 matings in 2 hrs; 24 hrs), and their interaction (FLENGTH*DURATION) on the number of offspring females produced.

Bateman Gradients: We used 2-way ANOVA to examine the influence of adult phenotype (ADULTPH), mate number (NMATES) and their interaction (ADULTPH*NMATES) on the number of offspring produced by α -, β - and γ -males, and females. We then subdivided our data by sex and used 2-way ANOVA to examine the influence of male morph (MORPH), mate number (NMATES) and their interaction (MORPH*NMATES) on the number of offspring produced by α -, β - and γ -males. Because males were analyzed separately from females, we used a Bonferroni correction to reduce our criteria for significance $\alpha = 0.052 = 0.025$. Lastly, we pooled our data for all males and used 2-way ANOVA to examine the influence of sex (SEX), mate numbers (NMATES) and their interaction (SEX*NMATES) on the number of offspring produced by all males and all females.

Results and Conclusions

Our 2-way ANOVA of the residuals for offspring number on female body length, to determine whether the fertilities of the 3 male morphs differed or decreased with increasing mating frequency, was non-significant overall ($F_{2,835} = 0.25$, $P = 0.94$) with non-significant effects of male morph ($F_{[MORPH]} = 0.42$, $P = 0.66$) and mate order ($F_{[ORDER]} = 2.21$, $P = 0.64$) and a non-significant interaction between these factors ($F_{[MORPH*ORDER]} = 0.15$, $P = 0.86$). This result indicated that, although they do appear to invest different amounts of energy to somatic and gametic functions (Shuster 1989a), the 3 male morphs did not differ in their sexual competency with multiple matings. This result also confirmed that there were no significant differences in the fecundities of females mated with α -, β - and γ -males, and consistent with Shuster (1989a), there were no significant differences in the numbers of undeveloped zygotes among females mated by α -, β - and γ -males ($F_{[5,67]} = 0.18$, $P = 0.97$; $F_{[MORPH]} = 0.31$, $P = 0.73$; $F_{[ORDER]} = 0.01$, $P = 0.95$; $F_{[MORPH*ORDER]} = 0.18$, $P = 0.83$).

Our 2-way ANOVA to compare the fecundities of females who mated 1-5 times over 2 hrs vs. the fecundities of females allowed unlimited matings over 24 hrs, was significant overall ($F_{[1,81]} = 34.56$, $P < 0.0001$) with a significant effect of body length ($F_{[FLENGTH]} = 7.34$, $P = 0.008$), but no significant effect of the time available for mating ($F_{[DURATION]} = 1.03$, $P = 0.31$) and no significant interaction between female body length and the time available for mating ($F_{[FLENGTH*DURATION]} = 0.35$, $P = 0.55$), indicating that the size-adjusted fecundities of females allowed to mate 1-5 times were no different from those of females allowed unlimited access to matings over 24 hrs.

Our 2-way ANOVA comparing the relationship between mate numbers and offspring numbers, for each of the 3 male morphs and females, was significant ($F_{[7,39]} = 8.71$, $P < 0.001$) with significant effects of adult phenotype ($F_{[ADULTPH]} = 5.13$, $P = 0.04$) and mate numbers ($F_{[NMATES]} = 32.60$, $P < 0.0001$), and with a significant interaction between adult phenotype and mate numbers ($F_{[ADULTPH*NMATES]} = 3.25$, $P = 0.032$). This result indicated that a sex difference in Bateman gradients does exist for *P. sculpta*, but it did not reveal the source of the difference.

We then separated males into categories to explore differences among the male morphs. Our 2-way ANOVA of males alone, even with Bonferroni correction, was significant overall ($F_{[5,35]} = 8.91$, $P < 0.0001$), with a significant effect of male morph ($F_{[MORPH]} = 1.59$, $P = 0.22$) and no significant interaction between male morph and mate numbers ($F_{[MORPH*NMATES]} = 0.17$, $P = 0.85$), indicating that the Bateman gradients for the 3 male morphs were indistinguishable. This result justified pooling all males for re-analysis of the relationship between mate numbers and offspring numbers for males and females. Alpha-, β - and γ -males coexist at different frequencies in nature and appear to differ in their mating success in different social circumstances, but that fact that their Bateman gradients are statistically indistinguishable indicated that under our experimental conditions the fitnesses of the 3 male morphs were equal.

The pooled-male analysis was significant overall ($F_{[1,38]} = 19.09$, $P < 0.001$) with a significant effect of sex ($F_{[SEX]} = 11.81$, $P = 0.001$), a significant effect of mate numbers ($F_{[NMATES]} = 10.14$, $P = 0.003$) and a significant interaction between sex and mate numbers ($F_{[SEX*NMATES]} = 9.26$, $P = 0.004$), a result further confirming that a sex difference in Bateman gradients exists for *P. sculpta*. Although the slope of the relationship for females was non-negative, the large difference between the sexes in the number of offspring produced with increased numbers of mates suggests that sexual conflict could exist within this species. However, the magnitude of this difference also suggests that natural selection on females is unlikely to allow females to respond evolutionarily to possible exploitation by males.

The significant sex difference in Bateman gradients for *P. sculpta* shows that the intensity of sexual selection is much higher for males than for females in this species, but does not differ among the 3 male morphs. This result corroborates other results (Shuster & Wade 1991, 2003) indicating that fitness satisfying does not occur among the male morphs in *P. sculpta*, and that differences in mate availability, not differences in sexual competence, are responsible for observed variance in fitness within, and for the equality of fitnesses among, the 3 male morphs in this species.

Table 1. Bateman Gradients for Each Adult Phenotype

	α male	β male	γ male	female	pooled males
β_{SS} (SE)	87.60 (25.33)	80.46 (11.96)	69.48 (26.16)	1.78 (3.475)	78.92 (12.23)
P	0.0047 **	<0.0001 **	0.022*	0.636 NS	<0.0001 **

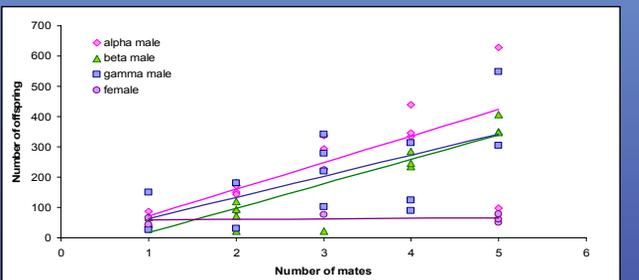


Figure 4. Bateman gradients estimated for each adult phenotype in *P. sculpta*. For the male matings, there were α -males (N=14), β -males (N=14), γ -males (N=13). For the female matings there were female mating once (N=2), 3 times (N=3) or 5 times (N=3) (alpha male $r^2 = 0.499$, beta male $r^2 = 0.790$, gamma male $r^2 = 0.391$, female $r^2 = 0.081$).

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Acknowledgments

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