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Chapter

Bateman Gradients and Alternative Mating Strategies in a Marine Isopod

Katharine M. Saunders and Stephen M. Shuster

Abstract

The "Bateman gradient" provides a means for estimating the strength of sexual selection. Although widely used for this purpose, this approach has not been applied to examine the covariance between mate numbers and offspring numbers among alternative mating strategies. Differences in this covariance could exist if the average fitnesses of different mating phenotypes were unequal, as has been suggested for "alternative mating tactics." We tested this hypothesis in *Paracerceis sculpta*, a sexually dimorphic marine isopod in which three male morphs coexist. We found no significant differences in sexual competency and no significant differences in Bateman gradients among morphs, that is, the average morph fitnesses were equivalent. However, with data pooled among morphs, we found a significant sex difference in Bateman gradients, as expected for dimorphic species; females gained no additional fitness from mating with multiple males, whereas male fitness increased with increasing mate numbers. In nature, the fitnesses of the three morphs are variable due to differences in the availability of receptive females. Our results suggest that differences in mate availability, not differences in sexual competency, are responsible for observed variance in fitness within, and for the equality of fitnesses among, the three male morphs in this species.

Keywords: measuring sexual selection, male polymorphism, Crustacea, Isopoda

1. Introduction

By definition, females produce few, large ova, whereas males produce many, tiny sperm. This sex difference in initial parental investment is widely viewed as the primary cause of sexual selection and intersexual conflict [1–4]. However, Bateman ([1], p. 363) also argued that, "Variance in number of mates is...the only important cause of the sex difference in the variance in fertility," and therefore that a sex difference in the variance in fertility provides "a measure of the sex difference in intensity of selection." This statement implies that selection within each sex, rather than between the sexes is responsible for sexual selection as well as for the evolution of sexual differences. The magnitude of the sex difference in fitness variance can be specifically quantified, not through proxies for selection intensity,

such as the ratio of sexually mature males to receptive females at any time (the Operational Sex Ratio, OSR [5]) or the ratio of maximum potential reproductive rates for each sex (PRR; [6]), but rather from actual estimates of selection's strength [7–12].

Such measures include the opportunity for selection ($V_W/W^2 = I$; [13]), the ratio of the variance in fitness to its squared average. This parameter, when measured using the mean and variance in mate numbers for each sex and adjusted by the sex ratio, quantifies the sex difference in the opportunity for selection, that is, the opportunity for sexual selection (I_M, [7, 8]; I_{mates} [9]; I_s [14]). Despite an early focus on mate numbers, the opportunity for sexual selection can be measured more precisely using the mean and variance in offspring numbers for each sex [9, 15, 16]. The Bateman gradient, β_{ss} [14, 16–19] provides a more specific estimator of the effect of mating success on fitness, by quantifying the standardized covariance between mate number and offspring number. Jones' Index, $\beta_{ss}\sqrt{I_s}$, combines these parameters and appears to provide a useful correction when the opportunity for sexual selection is expressed in terms of mate numbers rather than in terms of offspring numbers [14, 20].

The Bateman gradient is among the more precise methods for measuring sexual selection because it measures the slope, β_{ss}, of the statistical relationship between mate numbers and offspring numbers for members of each sex [16]. Thus, it estimates the intensity of sexual selection on the trait or traits that influence the sex difference in the variance in offspring numbers, provided that such traits can be identified. Although now widely used to compare sex differences in selection intensity [16–19, 21], the Bateman gradient has not been used to examine the covariance between mate numbers and offspring numbers among polymorphic mating phenotypes, also known as alternative mating strategies [9, 22, 23].

Polymorphisms in mating phenotype are considered by many researchers to provide examples of *fitness satisficing*, a current explanation for why alternative adult morphs persist within populations despite their experience of average fitness that is less than the average fitness of the conventional adult morph. According to this hypothesis, alternative phenotypes appear to "make the best of a bad job" [22–24]. One mechanism by which alternative phenotypes could experience less-than-average fitness is if Bateman gradients among the adult morphs are statistically distinct.

The Gulf of California sphaeromatid isopod, *Paracerceis sculpta*, has three distinct male morphs and breeds within the spongocoels of the sponge, *Leucetta losangelensis*, (**Figure 1**). Alpha males are largest and possess enlarged uropods, used for defending breeding sites. Beta males are smaller than α-males and resemble females in behavior and body form. Gamma males are the smallest and use their small size and agility to "sneak" into spongocoels [25]. Previous results indicate that variance in fitness within each of the three male morphs is large, whereas fitness differences among morphs are minute, a necessary condition for the persistence of genetic polymorphism [26].

While the possible causes of variance in mating success within α-males are relatively well understood [27–32], the causes of within-morph fitness variance for β- and γ-males are less clear. Here, we measured Bateman gradients 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 the four adult phenotypes in this species. Our results reveal the precision of this approach for measuring the difference in sexual selection intensity and suggest an alternative method for investigating fitness differences among morphs in species with sexual polymorphisms.

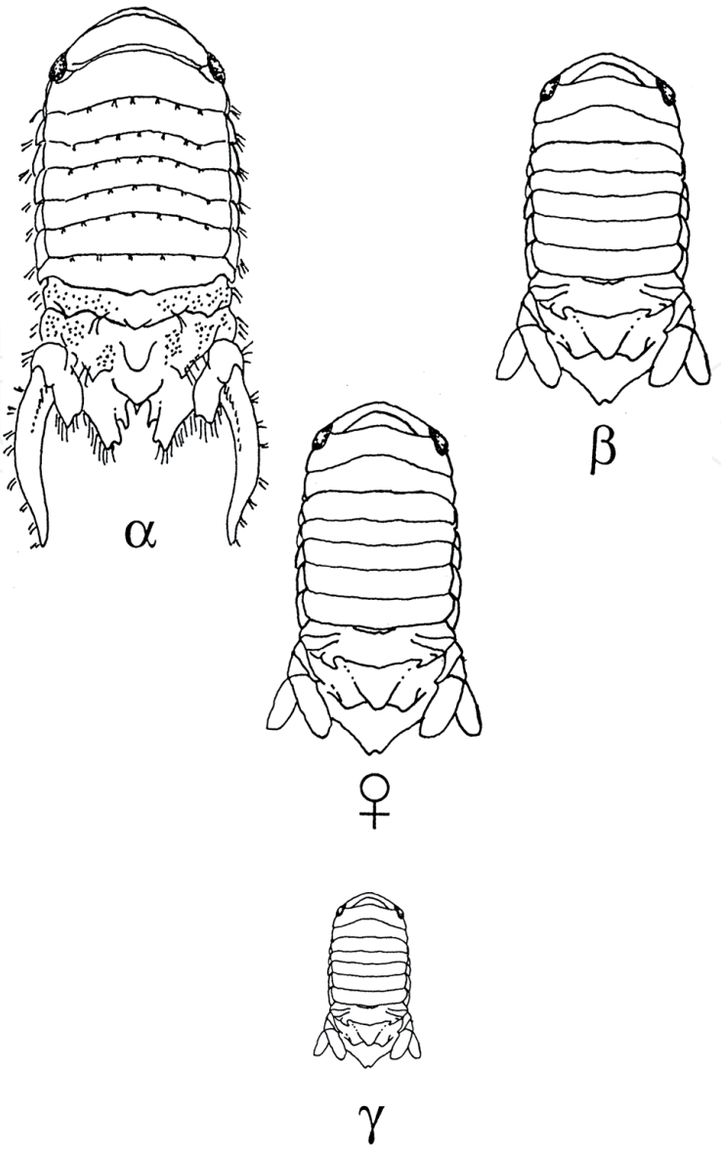

Figure 1.
The α-, β-, and γ-male and female morphs in Paracerceis sculpta (redrawn from Shuster [30]).

2. Materials and methods

2.1 Sexual receptivity, mating, and gestation in *P. sculpta*

Females are attracted to breeding sites in sponges when their ovaries and brood pouches mature [29]. Sexual receptivity in these S_1 females is initiated when they shed the posterior half of their cuticle and expose genital openings at the base of each fifth walking leg [27]. Females in S_2 (half molted) condition remain receptive for 24 h before shedding their anterior cuticles, ovipositing into internal brood pouches and becoming non-receptive (S_3). Females do not feed during gestation (S_4–S_7; [27]). Males complete a mating sequence with receptive females by inserting their appendix masculina and ejaculating into one, and then into the other of their mate's vaginas. Fertilization occurs and zygotes are brooded internally for 3 weeks before being released as fully formed juveniles (mancas; [27–29]).

2.2 Field collections

We collected several hundred isopods from the spongocoels of the intertidal sponge, *Leucetta losangelensis*, in the northern Gulf of California [30]. All individuals

were sexed, scored by reproductive condition, measured to the nearest 0.125 mm, and identified by unique cuticular pigmentation patterns [27, 28]. We retained unmolted, sexually mature (S_1) females (N = 92), as well as α-, β-, and γ-males (N = 41) from samples and placed these individuals into 225-ml plastic cups containing seawater. All other individuals were returned to collection sites within 24 h.

2.3 Matings for males

To examine the relationship between mate number and fertility for the three male morphs, and to compare the fertility of females mated to each of the three male morphs (see below), we allowed α-males (N = 14), β-males (N = 14), and γ-males (N = 13) to mate with 1–5 females in succession ($N_{females}$ = 86). We allowed each male to remain with each female for the duration of her 24-h period of receptivity. We then separated individuals and placed them in separate 225-ml cups containing seawater. Males were then placed with another S_2 female, allowed to mate for 24 h, and the sequence was continued until males either died or mated five times. All S_3 females were maintained in containers until parturition when we counted all mancas and undeveloped zygotes, if present.

To determine whether the fertility of males differed or decreased with increasing mating frequency, as well as to determine whether the fertility of the females mated by α-, β-, and γ-males was statistically distinguishable, we first calculated the residuals for the regression of offspring number on female body size to account for the positive effect female body size has on fertility ($F_{[1,85]}$ = 98.14, P < 0.0001). Then, we analyzed these residuals using a two-way ANOVA to examine the influences 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 ($F_{[1,68]}$ = 0.67, P = 0.42).

2.4 Matings for females

To examine the relationship between mate number and fertility for females, we allowed S_2 females to complete one mating sequence each with either 1 (N = 2), 3 (N = 1), or 5 (N = 3) α-males in succession. Pairs of isopods were given a maximum of 20 min 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 min before the next male was introduced. The entire mating sequence for each female never exceeded 2 h. S_3 females were maintained in their containers until parturition, when all mancas were counted. Again, the numbers of undeveloped zygotes, if present, were also counted.

To investigate whether the fertility of females who mated 1–5 times over 2 h, was different from each other as well as from the fertility of the 86 females, we allowed unlimited matings with males over 24 h (see "Matings for males" section), we first calculated the residuals for the regression of offspring number on female body size to account for the positive relationship between female size and fertility ($F_{[1,5]}$ = 15.98, P = 0.02). Next, because of the small sample size of females mated within 2 h (N = 6), we compared the residuals of the fertility of females mated 1, 3 and 5 times using a Kruskal-Wallis test. Because this test was non-significant ($X^2_{[2,6]}$ = 0.86, P = 0.65), we pooled these females for our analysis and compared their fertility as a group, with those of females who were allowed unlimited matings for 24 h. Note that these latter females ($N_{females}$ = 86) were the same females whose fertility was compared when mated with α-, β-, and γ-males above.

Using two-way ANOVA, we then examined the influences of female body length (FBLENG), the time available for mating (DURATION; 1–5 matings in 2 h; unlimited matings in 24 h), and their interaction (FBLENG*DURATION) on the number of offspring produced by females. We performed a similar analysis on the number of undeveloped zygotes per female. As in the previous analysis of undeveloped zygotes, we did not calculate residuals for this analysis because there was no significant relationship between female body length and the number of undeveloped zygotes ($F_{[1,73]} = 1.27$, $P = 0.26$).

2.5 Bateman gradients

We used two-way ANOVA to examine the influences of adult phenotype (ADULTP), mate number (NMATES), and their interaction (ADULTP*NMATES) on the number of offspring produced by α-, β-, and γ-males, and females. We then subdivided our data by sex and used two-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 criterion for significance, $\alpha = 0.05/2 = 0.025$. Lastly, we pooled the data for all males and used two-way ANOVA to examine the influences of sex (SEX), mate numbers (NMATES), and their interaction (SEX*NMATES) on the number of offspring produced by all males and all females. For individual Bateman gradients, we calculated the least squares regression of offspring numbers on mate numbers for each adult morph [16].

3. Results

Our two-way ANOVA of the residuals for offspring number on female body length, to determine whether the fertility of the three male morphs differed or decreased with increasing mating frequency, was non-significant overall ($F_{[5,85]} = 0.25$, $P = 0.94$) 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 the three male morphs did not differ in their sexual competency with multiple matings. This result also confirmed that there were no significant differences in the fertility of females mated with α-, β-, and γ-males, and confirmed that 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 two-way ANOVA to compare the fertility of females who mated 1–5 times over 2 h vs. the fertility of females allowed unlimited matings over 24 h was significant overall ($F_{[3,81]} = 34.56$, $P < 0.0001$) with a significant effect of body length ($F_{[FBLENG]} = 7.34$, $P = 0.008$), 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 ($F_{[FBLENG*DURATION]} = 0.35$, $P = 0.55$). This result indicated that the size-adjusted fertility of females allowed to mate 1–5 times was no different from those of females allowed unlimited access to matings over 24 h. This result was corroborated by our finding that there were no significant differences in the numbers of undeveloped zygotes among females mated 1–5 times compared with females allowed unlimited matings over 24 h. ($F_{[3,73]} = 0.63$, $P = 0.60$; $F_{[FLENG]} = 1.07$, $P = 0.30$; $F_{[DURATION]} = 0.04$, $P = 0.84$; $F_{[FBLENG*DURATION]} = 0.33$, $P = 0.57$).

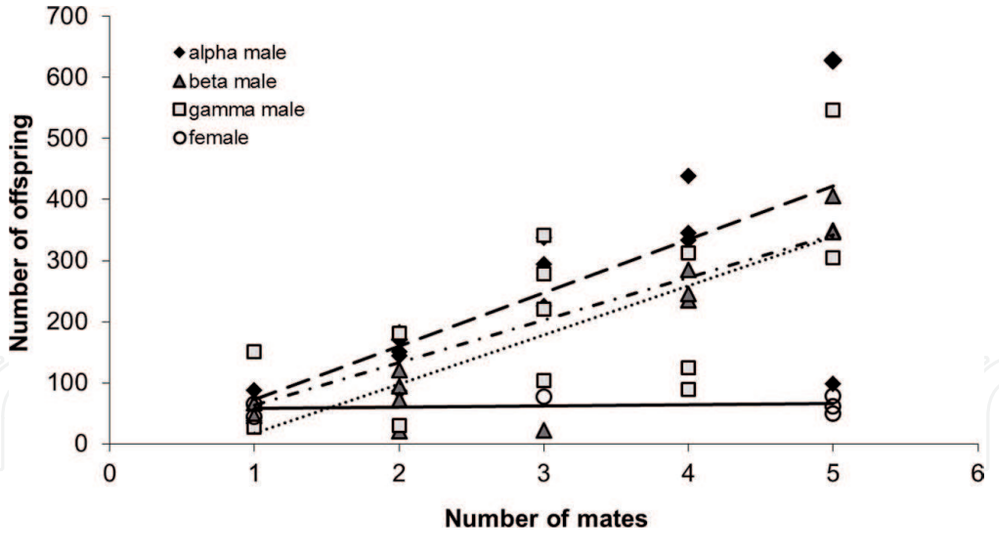

Figure 2.
Bateman gradients estimated for each adult phenotype in P. sculpta: α-males (βss ± SE = 87.60 ± 25.33, N = 14; P = 0.005; black diamonds, dashed line); β-males (βss ± SE = 80.46 ± 11.96, N = 14, P < 0.0001; dark gray triangles, dashed and dotted line); γ-males (βss ± SE = 69.48 ± 26.16, N = 13, P = 0.022; light gray squares, dotted line); females (βss ± SE = 1.78 ± 4.48, N = 6, P = 0.64; open circles, solid line); and pooled males (βss ± SE = 78.92 ± 12.23, N = 41, P < 0.0001; open circles); details of this analysis are described in the text.

Our two-way ANOVA comparing the relationship between mate numbers and offspring numbers for each of the three male morphs and females (**Figure 2**) was significant ($F_{[7, 39]} = 8.71$, $P < 0.001$), with a significant effect of adult phenotype ($F_{[ADULTP]} = 5.13$, $P = 0.004$), a significant effect of mate numbers ($F_{[NMATES]} = 32.60$, $P < 0.0001$), and with a significant interaction between adult phenotype and mate numbers ($F_{[ADULTP*NMATES]} = 3.25$, $P = 0.032$). This result indicated that a phenotype difference in Bateman gradients does exist for *P. sculpta*, but it did not reveal the source of the difference.

That source was revealed by two successive tests. Our two-way ANOVA of males alone, to identify the source of the difference in Bateman gradients among the adult phenotypes, was significant overall ($F_{[5, 35]} = 8.91$, $P < 0.0001$), with a significant effect of mate numbers ($F_{[NMATES]} = 40.66$, $P < 0.0001$). However, we found no 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 Bateman gradients for the three 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.

This pooled-male analysis was significant overall ($F_{[3,38]} = 19.09$, $P < 0.001$) 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 confirming that a sex difference in Bateman gradients exists for *P. sculpta* (**Figure 2**). In this analysis, the sex difference in the covariance between mate numbers and offspring numbers was over 40-fold larger for males than for females (**Figure 2**).

4. Discussion

Our results showed that although they appear to invest different amounts of energy toward somatic and gametic functions [27, 28], the three male morphs in *P. sculpta* do not differ in their sexual competencies with multiple matings. This result also demonstrated that individual females mated with α-, β-, or γ-males do

not differ in their fertility when allowed to mate with these males *a bene placito* over a 24-h period. Here, we confirmed this finding using the number of live young produced, *as well as* the number of undeveloped zygotes remaining within female brood pouches, thus considering the possibility of the positive, as well as the negative influences that multiple mating may have on female fertility. We also showed that the size-adjusted fertility of females allowed to mate 1–5 times was no different from those of females allowed unlimited access to matings over 24 h. This result justified our comparison of multiple matings by females with multiple matings by males of each of the three male phenotypes in our analysis of Bateman gradients.

Our results further showed that while the three male morphs do not exhibit distinct Bateman gradients, a sex difference in Bateman gradients does exist for *P. sculpta* when adult male and female phenotypes are compared. α-, β-, and γ-males coexist at different population frequencies in nature (α: 0.81; β: 0.15; γ: 0.04; N = 555; [26]) and appear to differ in their mating success in different social circumstances [28, 29]. However, the fact that their Bateman gradients are statistically indistinguishable indicates that under our experimental conditions the fitnesses of the three male morphs were equal. Although the sample size for the females was small relative to females who mated once, as many as five matings had no effect on the number of offspring females in our study produced. Moreover, the fertility of these females, with variable numbers of matings, was no different from the fertility of a larger sample of females (N = 86) with unlimited numbers of matings.

In contrast, within each of the three morphs, male fitness increased linearly with increasing numbers of matings (**Figure 2**). The large difference between the sexes in the number of offspring produced with increased numbers of mates suggests that intersexual conflict (c.f., [1–4, 12]) *could* exist within this species. Indeed in this study, the sex difference in the intensity of selection was over 40 times greater in males than in females (see also [10]). However, the magnitude of this difference also suggests that while intersexual conflict could exist, natural selection on females is considerably weaker than sexual selection on males. An evolutionary response by females to possible sexual exploitation by males, that is, an intersexual arms race of the sort envisioned in intersexual conflict scenarios [1–4, 12], might therefore be undetectable [9]. Despite the possibility of sexual exploitation by males, we found no evidence of that females were negatively affected by multiple matings.

The significant sex difference in Bateman gradients for *P. sculpta* suggests that sexual selection acts much more intensely on males than it does on females in this species. However, this result also indicates that sexual selection does not act differentially among the three male morphs through differences in mate number alone. This result corroborates other results [9, 26] indicating that fitness satisficing does not occur among the male morphs in *P. sculpta* in this context, and that differences in mate availability, not differences in sexual competency, are responsible for observed variance in fitness within, and for the equality of fitnesses among the three male morphs in this species. When β- and γ-males are present with α-males in the spongocoels in which these isopods breed, they tend to be more successful than α-males, particularly when harem sizes are large [9, 26, 28]. These results suggest that β- and γ-males may be more effective in tactics that enhance fertilization success, such as mate guarding or repeated inseminations, than α-males [26].

If this is indeed the case, then as is widely acknowledged, the number of matings individual males acquire need not translate linearly toward that male's overall fitness. More specifically, in nature, multiple Bateman gradients among male morphs may exist that each depend on the number of available mates *as well as* the number of different mating males representing each morph that are present within breeding sites at any given time. Such variation is likely to be widespread among species exhibiting reproductive polymorphisms (reviews in [17, 22, 33–40]). Under

such circumstances, it is unlikely that any given subset of fitness gradients among morphs accurately represents the entire population, particularly if that subset focuses on males who are successful at mating and tends to ignore males who are unsuccessful. Field samples that disproportionately focus on successfully mating males tend to overestimate the fitness of males in the mating class, making it easier to conclude that males expressing alternative mating phenotypes are "making the best of a bad job [9, 40]."

For this reason, we recommend, when male polymorphisms exist, that the fitness for a large number of males of each morph be measured, and their relative fitness outcomes be considered in proportion to the average fitness that all males in the population achieve. This approach is consistent with studies of this and other species [26, 40], in which equal average fitnesses exist among male morphs over multiple generations.

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