The Evolution of Crustacean Mating Systems

Stephen M. Shuster
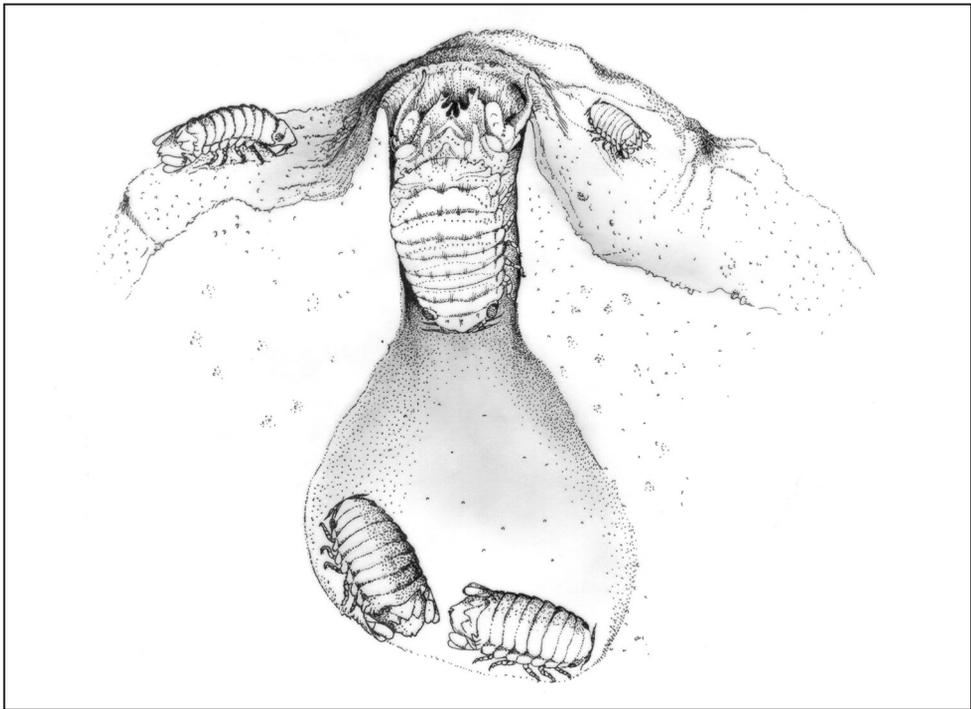
The alpha males of the isopod Paracerceis sculpta *allow reproductive females (here inside the sponge) to enter their host sponges; beta males and tiny gamma males, which are morphologically identical to females and juveniles, respectively (here seen on the outer sponge surface), attempt to sneak past the alpha male guarding the entrance to copulate with the females within.*

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There are two central issues in the study of animal mating systems: (1) the source of sexual selection and (2) the intensity of sexual selection. These issues are important because the approach researchers take to explore them determines (a) the processes that are presumed to cause sexual selection, (b) the procedures that are undertaken to observe these processes, and (c) the variables that are measured in hypothesis testing. The analysis of animal mating systems, until recently, has been based on the hypothesis that sex differences in parental investment are the source of sexual selection (reviewed in Shuster and Wade 2003; see also chapters 7, 9, 12). This emphasis was crystallized by Trivers (1972), who, following discussions by Darwin (1874), Bateman (1948), and Williams (1966), proclaimed, "What governs the operation of sexual selection is the relative parental investment of the sexes in their offspring" (p. 141).

Indeed, most studies of mating systems are consistent with parental investment theory (PIT). According to this view, female reproduction is limited by the availability of resources required for parental investment, and because these resources vary in their abundance in space and in time, male reproduction is limited by the spatial distribution of resources and by the temporal distribution of sexually receptive females. To estimate the degree to which these latter distributions influence the intensity of selection, Emlen and Oring (1977) defined two measures: the operational sex ratio (OSR) and the environmental potential for polygamy (EPP).

The OSR was originally defined by Emlen (1976, p. 283) as "the ratio of potentially receptive males to receptive females at any time." There have been multiple interpretations of this description, but in its simplest form, OSR = $R_o = N_\sigma/N_\varphi$, where N_σ and N_φ equal the number of males and females, respectively (Shuster and Wade 2003). With OSR > 1, females are rare and competition for mates is presumed to be intense, although this assumption depends on the degree to which male mating success or failure is consistent among males throughout the breeding season. With OSR < 1, females are abundant and competition for mates is presumably relaxed, although again, depending on the cause of a female-biased sex ratio, such conditions may still allow certain males to contribute disproportionately to the next generation (Shuster and Wade 2003). The EPP measures the degree to which social and ecological conditions allow males to monopolize females. However, appropriate methods for quantifying female distributions, and the scale on which EPP should be measured were never defined. As a result, while serving as a conceptual proxy for the intensity of sexual selection, the uncertain relationship between EPP and selection intensity makes comparisons within and among species imprecise (Shuster and Wade 2003).

Researchers emphasizing PIT have encountered further difficulties in putting its assumptions to rigorous empirical tests. Despite Trivers's (1972) prediction, a sex difference in relative parental investment has proven extremely difficult to compare within and among species. Not only are the relative amounts of energy, cost, and risk associated with relative parental investment difficult to quantify (Strohm and Linsenmair 1999; see also chapters 7–9), but also, the correlation between sex differences in parental investment and sexual dimorphism is dismal, particularly in species with sex role reversal (S.M. Shuster and M.J. Wade, unpublished data). Measures of sexual selection intensity based on PIT require laboratory conditions that are rarely encountered in nature (e.g., potential reproductive rate; Clutton-Brock and Vincent 1991) or make assumptions that underestimate the variance in mating success among

individuals (e.g., Q, which focuses on individuals "qualified" to mate; Ahnesjö et al. 2001). Moreover, like other research paradigms grounded in optimality theory (reviewed in Cheverud and Moore 1998), PIT has an unfortunate tendency to emphasize adaptive outcomes, wherein researchers declare to what "should" evolve due to sex differences in parental investment or in expected fitness returns, and then proceed to look for evidence of adaptations consistent with their initial predictions.

In this chapter, I explain the utility of a quantitative approach for measuring the source and intensity of sexual selection (see also Shuster and Wade 2003). Using ecological, life history, and behavioral data that are commonly available for sexual species, here, using crustaceans as examples, I show how the magnitude of the sex difference in fitness variance, estimated using measurements of *actual* male and female fitness, can be used to classify mating systems. I also show how the sex difference in fitness variance is influenced, by the spatial and temporal crowding of receptive females, by female life history, by male and female reproductive behavior, and by runaway processes in various forms. My goal is to suggest an empirical framework for the study of sexual species that measures the selective forces responsible for sex differences in adult phenotype.

The Sex Difference in Fitness Variance

Most research on sexual selection and its effects on mating systems, including that of Darwin (1874) himself, has focused either on the *context* in which sexual selection occurs (i.e., via male combat or female choice) or on the evolutionary *outcome* of sexual selection (i.e., on descriptions of sexual dimorphism or mating behavior). These approaches, while interesting in their own right, consider neither the process nor the degree to which sexual selection may achieve its evolutionary effects. Shuster and Wade (2003) asked, "How can sexual selection be strong enough to counter the combined, opposing forces of male and female viability selection?" (p. 10). This Quantitative Paradox is resolved by measuring the fitness variance for males and females within and among species. This method illustrates when and why sexual selection can be strong enough to overwhelm the effects of natural selection and therefore how it produces the phenotypes its researchers find so compelling.

Consider a hypothetical crustacean population consisting of 20 individuals. If each of the 10 females in the population produces a clutch of 10 ova, and if each clutch is fertilized by a single male, then the total number of offspring produced is $N_{o\text{total}} = (10 \text{ ova}) \times (10 \text{ females}) = 100$. Because each mating pair produces 10 offspring, the total offspring produced by all females, $N_{o\female}$, equals the total offspring produced by all males, $N_{o\male} = 100$. Because there are 10 females and 10 males in our population, the average number of offspring per female, $O_{\female} = N_{o\text{total}}/N_{\female}$ is 10, which equals the average number of offspring per male, $O_{\male} = N_{o\text{total}}/N_{\male}$. Also, because each individual produces the same number of offspring (10), no variance in offspring numbers exists for either sex. Thus, $V_{o\female} = V_{o\male} = 0$. Separately calculating the mean and variance in offspring numbers for each sex shows how differences in mate numbers between the sexes may influence these parameters.

Now consider a case in which 1 of the 10 males secures more than one mate (e.g., 3) as might occur in harpacticoid copepods (Stancyk and Moreira 1988) or in

cypridinid ostracods (Morin and Cohen 1991). The total offspring produced by our population, $N_{ototal} = 100$, remains unchanged. Similarly, because $N_\male = N_\female = 10$, the average offspring number per male, $O_\male = N_{ototal}/N_\male = 10$, equals the average offspring number per female, $O_\female = N_{ototal}/N_\female = 10$. Because each female still secures one mate with whom she produces a single brood, the variance in offspring numbers for females, $V_{o\female}$, is 0. However, because one male has three mates, two males must be excluded from mating. That is, for every k mates obtained by one male, there must be k—1 males who are unable to mate. When this happens, the variance in offspring numbers among males, $V_{o\male}$, must increase.

How can we quantify this increase in fitness variance among males? If paternity data are available, we could simply calculate the statistical variance in offspring numbers for males (Shuster and Wade 1991). Unfortunately, such data can be difficult to obtain (see chapter 9). An alternative approach is to partition the variance in offspring numbers within and among the classes of mating and nonmating males. The data necessary to do this, the mean and variance in mate numbers for males, and the mean and variance in offspring numbers for females, are often available in standard life history analyses. Why should we do this? This approach allows us to measure the *fitness variance* within each sex, which is proportional to the *intensity of selection*. Measures of fitness variance provide direct estimates of selection intensity, and the sex difference in selection intensity estimates the degree to which the sexes will diverge in phenotype.

We begin by identifying the classes of mating males and their population frequencies. There are three such classes: males who do not mate, p_o (= 2/10 males = 0.2), males who mate once, p_1 (= 7/10 males = 0.7), and males who mate three times, p_3 (= 1/10 males = 0.1). Here, we represent the proportion of the male population in each mating class as p_j, where j represents the number of females in the jth mating class. The sum of all mating classes, $\Sigma p_j = (0.2 + 0.7 + 0.1) = 1$. We next use these values to identify the average number of offspring produced by males in each jth mating class, $O_{\male j}$, as well as the average number of offspring produced by all males, $O_\male$. The average number of offspring that males in each mating class produce equals the average number of offspring per female, $O_\female$, multiplied by the number of mates, j, that males in each jth mating class secures, or $O_{\male j} = j(O_\female)$. Thus, the average number of offspring produced by males who do not mate, $O_{\male o}$, is $(0)(10) = 0$. For males who mate once, $O_{\male 1} = (1)(10) = 10$. And, for males who mate three times, $O_{\male 3} = (3)(10) = 30$. The average number of offspring produced by *all* males, $O_\male$, is equal to the number of offspring produced by the average female, $O_\female$, multiplied by the number of females mated by males in each mating class, j, multiplied by the fraction of the males belonging to that mating class, p_j, and summed over all mating classes, or

$$O_\male = \Sigma p_j j(O_\female) \tag{1}$$

Using the values in our example above, $O_\male = 10$. Note that although mates are unevenly distributed among males, the average number of offspring among all males remains unchanged compared to the initial case in which all males have equal mate numbers.

The distribution of females across all classes of mating males is equal to the population sex ratio, R (= $1/R_o$, where R_o = OSR; Shuster and Wade 2003), which is

calculated as the number of females mated by males in each mating class, j, multiplied by the fraction of the males in each mating class, p_j, and summed over all classes of males, or, $R = \Sigma j\, p_j = 1$. Because the distribution of all females with all males equals the average mates per male, R also equals $N_\female/N_\male = 1$. Thus, by substitution, we see that the average number of offspring per male, $O_\male$, equals the average mates per male, R, multiplied by the average number of offspring per female, $O_\female$, or $O_\male = RO_\female = 10$. Note, again, that although the distribution of females is now uneven among males, the average mates per male, R, the average offspring number per female, $O_\female$, and the average offspring number per male, $O_\male$, *remain unchanged* relative to our initial mating conditions.

With these expressions defined, we can now express the total variance in offspring numbers for males, $V_{o\male}$. As in analyses of variance (ANOVA), the total variance in male fitness equals the sum of two components: (1) the average variance in offspring numbers for males *within* the classes of males who sire offspring, and (2) the variance in average number of offspring sired by males *among* these same categories (Shuster and Wade 2003). The first component of variance in male offspring numbers is calculated in three steps. First, for each mating class of males, the variance in female offspring numbers, $V_{o\female}$, is multiplied by the number of mates obtained by males in each jth mating class. Next, this product is multiplied by the proportion of males in the population, p_j, that belong to each jth mating class. Last, these products are summed over all mating classes. Thus, the variance in offspring numbers within the classes of mating males equals

$$V_{o\male(\text{within})} = \Sigma p_j(jV_{o\female}) \tag{2}$$

In this example, because there is no variance in offspring numbers among females ($V_{o\female} = 0$, and all females produce 10 offspring), the variance in offspring numbers within the classes of mating males is zero ($V_{o\male(\text{within})} = 0$). We will return to this point shortly.

The second component of variance in male offspring numbers, the variance in the average number of offspring sired by males *among* these same categories, is calculated in four steps. First, for each mating class of males, we calculate the difference between the average number of offspring per male, $O_\male$, and the average number of offspring produced by that mating class, $O_{\male j}$ (= $O_\male - O_{\male j}$). Next, we square each difference. Third, we multiply each squared difference by the fraction of males belonging to each mating class, p_j, and last, we sum across all classes to obtain

$$V_{o\male(\text{among})} = \Sigma p_j(O_\male - O_{\male j})^2 \tag{3}$$

Substituting in the values from above, we have $V_{o\male(\text{among})} = 60$. Thus, the total variance in offspring numbers among males is the sum of the within- and among-male components in offspring numbers, or

$$V_{o\male} = \Sigma p_j(jV_{o\female}) + \Sigma p_j(O_\male - O_{\male j})^2 \tag{4}$$

Because there is no variance in offspring numbers for females, $V_{o\female} = 0$, and the first term in Eq. 4 drops out. Because $V_{o\male(\text{among})} = V_{o\male}$, we can easily see that the variance

in fitness among males goes from 0 to 60 when a single male mates with three females instead of one. Note, too, that the increase in fitness variance comes *entirely* from the among-male component of total fitness variance (Wade and Shuster 2004). If one male mates with all 10 of the females in this population, the mean and variance in offspring numbers for females, again, remain unchanged ($O_♀ = 10$, $V_{o♀} = 0$). Also, there is no change in either the sex ratio, $R = 1$, or the average number of offspring per male, $O_♂ = 10$. However, because one male mates 10 times, nine males do not mate at all (here $k = 10$, so $k - 1 = 9$); thus, $p_{♂o} = 9/10 = 0.9$, $p_{♂1}$ to $p_{♂9} = 0$, and $p_{♂10} = 1/10 = 0.1$. When these values are substituted into Eq. 4, we see $V_{o♂}$ now increases 15-fold to 900.

Three Rules

This exercise shows three simple rules. First,

> When the sex ratio equals 1, both sexes have equal average fitness.

This is true whether or not individual males and females have different mate numbers. It means that the average mate numbers, as well as the average offspring numbers, must be equal for each sex (Wade and Shuster 2002, 2005). When the sex ratio does not equal 1, the average fitness of the minority sex will increase (Eq. 1). However, as explained below, biases in sex ratio are only one component of sexual selection. This is an important consideration for studies of crustacean mating systems in which fluctuating or biased sex ratios are common (Shuster et al. 2001; see also chapter 7). As discussed below, this is also why, contrary to most mating system analyses conducted in accord with PIT, it is not sufficient to measure OSR alone to understand the intensity of sexual selection.

The second rule is:

> When some individuals are excluded from mating, the variance in
> offspring numbers within that sex will increase.

This increase in fitness variance indicates that selection is occurring within that sex. Such selection can lead to the evolution of specialized behaviors or structures associated with mating. For example, in rhizocephalan barnacles, parasitic copepods, and epicaridean isopods, only a small fraction of females locate hosts successfully (Høeg 1991; see also chapter 12). Such extreme variance in female fitness appears to favor high fecundity and grotesquely large body size. Because females in these species tend to be widely dispersed in space, only a small fraction of males successfully locate females and mate (Kabata and Cousens 1973). Extreme variance in male fitness appears to favor rapid maturation and the ability to locate and remain with individual females. The extreme fitness variance in both sexes appears to explain the remarkable sexual dimorphism in many of these crustaceans, even in species in which apparent monogamy occurs (Shuster and Wade 2003; see also chapter 12).

The third rule is:

> If the fraction of individuals excluded from mating is larger in one sex
> than it is in the other, a sex difference in the variance in offspring
> numbers will arise.

This sex difference in the variance in offspring numbers is the source of sexual selection. In the above example, $V_{o\male} - V_{o\female} = 900 - 0 = 900$. Because the variance in offspring numbers is proportional to the strength of selection, the magnitude of this sex difference in offspring numbers determines the intensity of sexual selection. Strong, single-sex selection leads to sexual dimorphism because traits associated with high fitness are disproportionately transmitted to the next generation. Strong, single-sex selection also represents a functional bias in sex ratio (Shuster et al. 2000). Such biases are often equalized by the evolution of alternative mating strategies (Shuster and Wade 1991, 2003). The existence of nonmating individuals of one phenotype creates a "mating niche" that can be invaded by individuals expressing alternative mating phenotypes, for example, in isopods (*Paracerceis sculpta*; Shuster 1992), amphipods (*Microdeutopus gryllotalpa*; Borowsky 1980), and decapods (*Rhynchocinetes typus*; Correa et al. 2000). Such invasions act to reduce the functional bias in sex ratio and thereby reduce the sex difference in fitness variance.

The Opportunity for Sexual Selection

Crow (1958) noted that the variance in absolute fitness, V_W, divided by the squared average fitness, W^2, equals the variance in *relative* fitness, or $V_W/W^2 = V_w$. Crow also called this value, I, the "opportunity for selection." This ratio provides a dimensionless, empirical estimate of selection's maximum strength, placing an upper bound not only on the change in mean fitness due to selection but also on the change in the standardized mean of every other trait (Wade 1979, Shuster and Wade 2003). As stated above, it is the sex difference in the variance in fitness that determines whether and to what degree the sexes will diverge in character, because fitness variance is proportional to selection intensity. For this reason, the opportunity for selection approach is useful for understanding the strength of selection within each sex. The value of I for each sex is expressed as the ratio of the variance in offspring numbers, V_o, to the squared average in offspring numbers, O^2, among members of that sex. Thus, $I_\male = V_{o\male}/O_\male^2$ and $I_\female = V_{o\female}/O_\female^2$. These expressions are linked through the sex ratio and mean fitness, which must be equal for both sexes (Wade and Shuster 2002). Thus, there is a fundamental algebraic relationship between the opportunity for selection on males, $I_\male$, and the opportunity for selection on females, $I_\female$.

How can we express this relationship for a natural population? Rewriting Eq. 4, substituting values from Eqs. 2 and 3, and rearranging terms (Shuster and Wade 2003), we have

$$V_{o\male} = RV_{o\female} + O_\female^2 V_{\text{mates}} \tag{5}$$

When $R = 1$, Eq. 5 shows that the variance in fitness for males, $V_{o\female}$, equals the variance in fitness for females, $V_{o\female}$, *plus* the quantity $O_\female^2 V_{\text{mates}}$. This latter term equals the average female fitness squared, $O_\female^2$, multiplied by the variance in mate numbers among males, V_{mates} $[=\Sigma p_j(R - j)^2]$. For the above example, $O_\female^2 V_{\text{mates}} = 900$, which shows that the sex difference in fitness variance is due to the fitness effects of a sex difference in the variance in mate numbers (Wade 1979). Recall that $I = V_W/W^2$ (Crow 1958). We can obtain an analogous expression for the variance in fitness for

males in terms of offspring numbers, $V_{o\sigma}$, by dividing Eq. 5 by $(RO_{\female})^2$, that is, by the squared average offspring number for males. We now have

$$I_{\sigma} = (1/R)(I_{\female}) + I_{\text{mates}} \qquad (6)$$

or $I_{\sigma} = (R_o)(I_{\female}) + I_{\text{mates}}$ because R equals $1/\text{OSR}$ ($= 1/R_O$; Shuster and Wade 2003).

   These expressions show, contrary to recent discussions of mating systems based on PIT (Reynolds 1996, Correa et al. 2000, Ahnesjö et al. 2001), that the sex ratio is only *part* of the total opportunity for selection. In particular, OSR ($= R_o = 1/R$) has its strongest influence on the sex difference in fitness when $I_{\text{mates}} = 0$. When the sex ratio equals 1 ($R = 1/R_o = 1$), subtracting $I_{\female}$ from both sides of Eq. 6 yields $I_{\sigma} - I_{\female} = I_{\text{mates}}$, demonstrating that the sex difference in the opportunity for selection, that is, the opportunity for *sexual* selection, is due to differences in mate numbers between the sexes (Wade 1979, Shuster and Wade 2003).

   Inserting the values from the above example into this latter equation shows that when males and females have equal mate numbers, $I_{\text{mates}} = 0$. When males vary in mate numbers, $I_{\female}$ still equals 0, so *all* of the opportunity for selection on males is due to sexual selection, $I_{\sigma} = I_{\text{mates}}$. If $V_{o\female}$ becomes nonzero, $I_{\female}$ increases and I_{mates} will be eroded, to a degree determined by the relative magnitudes of I_{σ} and $I_{\female}$ (see below). The point is this: I_{mates} can be estimated for *any* population for which the mean and variance in offspring numbers among females, and the mean and variance in mate numbers among males are known (for worked examples using the marine isopod *Paracerceis sculpta*, see Shuster and Wade 2003). However, because data on offspring and mate numbers may be every bit as difficult to obtain as parentage data, yet another type of data may be used to estimate the sex difference in the opportunity for selection.

The Spatial and Temporal Crowding of Mates

Emlen and Oring (1977) observed that female reproductive ecology determines the degree to which males may monopolize females or the resources on which breeding females depend. Wade (1995) used mean crowding, Lloyd's (1967) ecological mea-sure of density-dependent competition, to relate the clustering of receptive females at resources, to the strength of sexual selection. When females are patchily distributed on resources, and when males defend patches to mate with the females on them, the mean and the variance in harem size increase as females become increasingly clumped in space. For this reason, the mean spatial crowding of females, m^*, provides a *direct* estimate of the opportunity for sexual selection, I_{mates}. In short, m^* equals I_{mates}.

   Calculating m^* is straightforward. The average density of females per patch, m, equals the sum of all females over all m_i patches, divided by the total number of patches containing one or more females, M, or $m = \Sigma m_i/M$. The variance in the number of females per patch equals the squared difference of average female density and the density of females on the ith patch [$= (m - m_i)^2$], multiplied by the fraction of the total patches, p_i, that each ith patch comprises, summed over all patches, or $V_m = \Sigma p_i(m - m_i)^2$. The mean spatial crowding of females on resource patches, m^*, equals $m + [(V_m/m) - 1]$ (Wade 1995). The value of the variance, V_m, relative to the

mean number of females per patch, m, indicates whether females are clumped (m^* large; $V_m > m$), dispersed (m^* small; $V_m < m$), or randomly distributed in space ($m^* = m$; $V_m = m$).

The *temporal* distribution of female sexual receptivity also affects the sex difference in the opportunity for selection. Shuster and Wade (2003) derived t^*, an expression similar to m^*, for describing the mean crowding of female sexual receptivity over intervals of the breeding season. When the breeding season is divided into intervals of duration equal to the average duration of female receptivity, the mean temporal crowding of sexually receptive females during the breeding season, t^*, is $t + [(V_t/t) - 1]$, where t and V_t equal the average and variance in the number of receptive females per interval, respectively. The mean temporal crowding of females, t^*, quantifies the number of other receptive females the average female experiences for the period when she herself is sexually receptive. The value of the variance, V_t, relative to the mean number of females per interval, t, indicates whether females are clumped (t^* large; $V_t > t$), dispersed (t^* small; $V_t < t$), or randomly distributed in time ($t^* = t$; $V_t = t$).

Both m^* and t^* provide direct estimates of the opportunity for sexual selection, I_{mates}. But, the relationship between the spatial patchiness of receptive females and I_{mates} is linear, whereas the relationship between the temporal crowding of receptive females and I_{mates} is reciprocal (Shuster and Wade 2003). Thus, when females become *synchronous* in their sexual receptivity, the ability of certain males to mate with multiple females decreases, as it does in mass-mating cumaceans (*Mancocuma*; Guewuch and Croker 1973) or in pair-bonded snapping shrimp (*Alpheus*; Knowlton 1980). In contrast, when females become *asynchronous* in their sexual receptivity, it is possible for certain males to become serially polygynous, as occurs in brine shrimp (*Branchinecta*; Belk 1991) and in lobsters (*Homarus*; Cowan 1991).

Because of the different relationships between m^*, t^*, and I_{mates}, temporal variations in the OSR fail to describe the actual intensity of sexual selection. When female receptivities are asynchronous, OSR measured at any time can be large and sexual selection may *seem* strong. However, such measurements of OSR do not quantify the *consistency* of male mating success over time, that is, the covariance among intervals in male mating success. It is only when *particular* males mate successfully across the breeding season that high OSR leads to strong sexual selection (see chapter 10). When a *different* male mates with each female that becomes receptive, apparently intense sexual selection (high OSR) is actually diminished.

The I_{mates} Surface

When either m^* or t^* accurately reflects the variance in mate numbers among males, its measurement alone is sufficient to estimate I_{mates}. However, because female spatiotemporal distributions can lead to highly dynamic responses by males (e.g., in the isopod *Paracerceis sculpta*; Shuster 1992), it is often necessary to measure m^* and t^* simultaneously to visualize the actual intensity of sexual selection. Multiple measurements of m^* and t^* throughout a breeding season create a three-dimensional surface describing I_{mates} for a particular species, a surface whose shape and orientation will vary depending on how the spatial and temporal distributions of females interact

within and among seasons (Fig. 2.1a). Species-specific differences in the "ellipsoids" of points that appear on the "I_{mates} surface" are likely to be identifiable (Fig. 2.1b), and because I_{mates} is dimensionless (Shuster and Wade 2003), comparisons of its value within and among breeding seasons for particular species, as well as in phylogenetic comparisons, are permitted. Because changes in the spatiotemporal distributions of females change the intensity, as well as the evolutionary effects of sexual selection, related species are expected to show more similar I_{mates} ellipsoids, whereas ellipsoids for species within larger taxa should be predictably divergent in three-dimensional I_{mates} space (Fig. 2.1c).
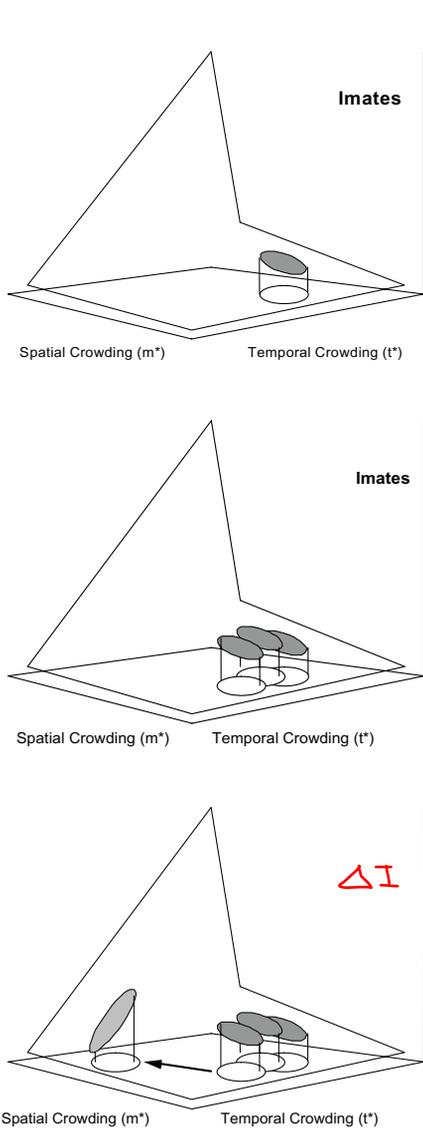
Figure 2.1 (a) Multiple measurements of m^* and t^* throughout a breeding season creates a three-dimensional surface describing I_{mates} for a particular species, a surface whose shape and orientation will vary depending on how the spatial and temporal distributions of females interact within and among seasons. (b) Species-specific differences in the "ellipsoids" of points that appear on the "I_{mates} surface" are likely to be identifiable. (c) Changes in the spatial and temporal distributions of females, the effects of female life history, and behavioral responses of each sex to these distributions may make mating system evolution a dynamic process. Thus, related species are expected to show similar ΔI ellipsoids, whereas ellipsoids for divergent species within larger taxa should be predictably divergent in value and position in three-dimensional space. Redrawn from Shuster and Wade (2003).

The marine isopod *Paracerceis sculpta* provides the single published example in which the values of m^* and t^* are calculated (see chapters 2 and 3 in Shuster and Wade 2003). The spatial distribution of females in this species was easily estimated because females breed within clearly defined territories (e.g., spongocoels of intertidal sponges). The temporal distribution of *P. sculpta* females was also easily estimated, based on the known duration of female receptivity and the rate at which females proceed through the stages of their reproductive cycle. This information allowed the approximate number of females in the population that were receptive during each interval (~24 hours) within the breeding season to be estimated with considerable accuracy. However, the I_{mates} surface defined in terms of m^* and t^* provides information only on how the spatial and temporal distributions of matings influences I_{mates}. It says nothing about how fitness variance among females influences the total opportunity for selection, or how behavioral responses of each sex to these distributions make mating system evolution a dynamic process.

Sources of Fitness Variance for Males and Females

As explained above, when males mate more than once, other males are excluded from mating and variance in offspring numbers among males appears. For females, fitness variance arises from three sources: (1) females mate either once or more than once (monandry vs. polyandry), (2) females reproduce either once or more than once (semelparity vs. iteroparity), and (3) iteroparous females reproduce either repeatedly within a single season or repeatedly within multiple seasons. When a female mates once and produces only one clutch of offspring, she awards her entire complement of ova to a single male. However, when a female mates more than once, barring rigid patterns of sperm precedence, she divides her clutch of eggs into subclutches, equal in number to the number of males who succeed in fertilizing ova. The overall effect on I_{mates} of polyandrous matings by females is, when each mating male sires a fraction of the offspring of each mate he secures, the variance in fitness among males is *reduced* (see chapter 10).

Reduction in the variance in mate numbers that results from multiple matings by females is the likely context for the evolution of male mate guarding (Shuster and Wade 2003; see also chapters 7, 8). Males who defend their mates for the duration of their receptivity ensure their exclusive paternity of that female's brood, whereas male promiscuity, particularly when sperm mixing occurs, is usually favored only when the rate at which males may encounter and mate unguarded, receptive females is extremely high. A surprising prediction of this hypothesis is that male mate guarding in some form will be favored for nearly all spatial and temporal distributions of females. Mate guarding effectively prevents sperm competition; thus, where it does not occur, other forms of male paternity assurance appear to have evolved. In calanoid copepods, males attach individual spermatophores that cover female genitalia and prevent reinsemination (Subramoniam 1993). Female brachyuran crabs may receive multiple mates and/or store sperm, but males place secretions within females' spermathecae that seal off these other ejaculates (Diesel 1991; see also chapter 9). There are few behaviors more characteristic of crustacean sexuality than mate guarding (Jormalainen 1998; see also chapter 8). The near ubiquity of this behavior despite considerable variation in crustacean mating systems (see chapter 12) lends support to these predictions.

However, there is also abundant evidence that multiple mating occurs and that sperm compete for fertilizations (Diesel 1991, Koga et al. 1993; see also chapter 9). Shuster and Wade (2003) showed that the intensity of sperm competition can be quantified as the mean crowding of ejaculates within females, m^*_P, which is directly affected by female promiscuity (see chapter 4 in Shuster and Wade 2003). For sperm competition to lead to sexual selection, males who mate with disproportionate success must *also* have sperm that are disproportionately successful within *each* of the females with whom they mate. Otherwise, multiple mating weakens rather than intensifies sexual selection. Also, while both sexes must have equal average fitness, when males gain more offspring by repeated matings than do females, a sex difference in the covariance between promiscuity and offspring numbers can exist. Sex differences in this covariance are the likely source of perception that "males are promiscuous and females are coy" (see chapter 12). In fact, because the average fitnesses of males and females must be equal (Eq. 1), a sex difference in average promiscuity cannot exist (Wade and Shuster 2002, 2005).

When a female is semelparous, that is, when she produces only one clutch of offspring in her lifetime, no variance exists *within* females in the number of offspring produced. All of the variance exists *among* females. However, when a female produces more than one clutch, the variance in offspring numbers can be partitioned into within- and among-female components. Just as male fitness is influenced by mate numbers and offspring per mating, the corresponding two components of female fitness are clutch numbers and offspring per clutch. Each of these sources of variance acts to decrease the sex difference in fitness variance (Eq. 6). Thus, multiple reproductive episodes by females erode I_{mates} because as clutch number increases, I_{mates} becomes a smaller fraction of the total variance in offspring numbers.

These patterns generate specific predictions about the overall effects of female life history on the opportunity for sexual selection. In particular, the effects of sexual selection (= sexual dimorphism) will be proportional to the magnitude of I_{mates}. In general, I_{mates} will be eroded least in monandrous, semelparous species and eroded most in polyandrous, iteroparous species. Indeed, within the sphaeromatid Isopoda, the most extreme sexual dimorphism appears in genera in which females are semelparous (*Dynamene*, Holdich 1968; *Paracerceis*, Shuster 1992; *Cymodopsis*, Hurley and Jansen 1977), whereas sexual dimorphism is reduced in genera in which females are iteroparous (*Sphaeroma* and *Parasphaeroma*, Hurley and Jansen 1977; *Thermosphaeroma*, Jormalainen et al. 1999). Yet even when $V_{o\female}$ seems large, its effects may be dwarfed by I_{mates}. In *P. sculpta*, sexual selection on males is nearly 20 times stronger than natural selection on females (Wade and Shuster 2004). Such conditions reduce the ability of females to respond evolutionarily to sexual conflict, even when the negative consequences of conflict on female fitness seem severe.

Factors Affecting ΔI

The value of I_{mates}, after the effects of female life history are considered, equals ΔI, the total opportunity for sexual selection (Shuster and Wade 2003). However, additional influences on the sex difference in the opportunity for selection are possible that make mating system evolution a dynamic process. ΔI is enhanced by any female tendency to copy the behavior of other females. Mutual attraction to patchily

distributed sources of food or shelter may cause females to become more spatially clumped. Although male mate guarding restricts female opportunities to engage in mate copying, genetic covariance between female tendencies to copy each other and males tendencies to guard their mates can favor, depending on the values of m^* and t^*, either the explosive breeding aggregations observed in land crabs (*Geocarcinoides*; Seeger 1996) or the formation of female aggregations that are defended by large males as in freshwater prawns (*Macrobrachium*; Kuris et al. 1987). A similar runaway process may favor males who display in groups, as well as females who are attracted to these signals, as in bioluminescent ostracods (*Vargula*; Morin and Cohen 1991) or in structure-building fiddler crabs (*Uca*; Christy 1983, Kim et al. 2004; see also chapter 10).

Similar processes may lead males to defend feeding sites, nesting sites, or display sites that are conspicuous to females. When males defend such sites, males are likely to become sedentary and females may become mobile. Nest site defense will depend on the degree to which nest control influences male mate numbers. When male mating effort and male parental effort both enhance offspring number for males, the opportunity for sexual selection on males can become extreme, and males may attempt to attract the attention of transient females by visual, auditory, or chemical displays. However, when males have few options for multiple mating or when particular males become highly successful at mating, male–female pairs are likely to arise and persist (see chapter 12).

Future Directions

The framework of Shuster and Wade (2003) combines these various processes to generate a classification scheme that defines mating systems in terms of the causal processes that produce them, rather than in terms of the presumed outcomes of male competition and female mate choice. The method begins by summarizing the spatial and temporal distributions of sexually receptive females. An estimate of the opportunity for sexual selection on males, I_{mates}, is obtained from (A) the mean spatial crowding of receptive females, m^*, and (B) the mean temporal crowding of receptive females, t^*. As explained above, each pair of m^* and t^* coordinates generates a unique value of I_{mates} arising from the spatial and temporal distribution of matings for each species (Fig. 2.1). The effects of female life history characters on the opportunity for sexual selection are then summarized using two additional parameters: (C) the opportunity for selection due to the effects on female clutch size of matings by individual sires, $I_{cs,sires}$, and (D) the opportunity for selection due the effects on female clutch size of multiple reproductive episodes by females, $I_{cs,clutch}$ (see chapter 5 in Shuster and Wade 2003).

From the resulting value of ΔI, it is possible to predict specific details in behavior and morphology that allow each combination of traits to be classified as a mating system. These predictions include (1) the degree to which sperm competition may occur, based on whether males are likely or unlikely to guard their mates; (2) whether female mate copying is likely, based on the spatial and temporal distribution of females; and (3) the estimated magnitude of the adjusted opportunity for sexual selection, ΔI, arising from combinations of factors 1 and 2 and factors A–D above. Empirical estimates of ΔI go beyond mere verbal predictions based on assumptions of optimality. Because they estimate the strength of selection directly,

Table 2.1. Representative examples of the major categories and subcategories of crustacean mating systems (see Shuster and Wade 2003).

Major Category/Subcategory	Taxon	Reference
Sedentary pairs		
Eumonogamy	*Hemilepistus* (Isopoda)	Baker 2004
Persistent pairs	*Spongiocola* (Stenopodidea)	Hayashi and Ogawa 1987
Sequential pairs	*Gonodactylus* (Stomatopoda)	Shuster and Caldwell 1989
Itinerant pairs		
Attendance polygyny	*Eulimnadia* (Anostraca)	Belk 1991
Attendance polygynandry	*Euterpina* (Copepoda)	Stancyk and Moreira 1988
Attendance androdioecy	*Triops newberryi* (Notostraca)	Sassaman et al. 1997
Attendance polyandry	*Salmincola* (Copepoda)	Kabata and Cousens 1973
Coercive polygynandry	*Thermosphaeroma* (Isopoda)	Jormalainen et al. 1999
Mass mating		
Semelparous mass mating	*Mancocuma* (Cumacea)	Guewuch and Croker 1973
Mass mating with male parental care	*Pullosquilla* (Stomatopoda)	Jutte 1998
Iteroparous mass mating	*Geocarcinoides* (Brachyura)	Seeger 1996
Polygamy		
Cursorial polygyny	*Moina* (Branchipoda)	Forr'o 1993
Polygamy	*Pandalus* (Caridea)	Charnov 1982
Iteroparous classic leks	NA	
Male dominance		
Dominance polygyny	*Dynamene* (Isopoda)	Holdich 1968
Dominance polygynandry	*Macrobrachium* (Caridea)	Barki et al. 1992
Social pairs		
Pair-bond polygyny	NA	
Pair-bond polygamy	NA	
Pair-bond polygynandry	*Alpheus* (Caridea)	Knowlton 1980
Mating swarms		
Eumonogamy	NA	
Persistent pairs	NA	
Polyandrous mating swarms	NA	
Polygynous mating swarms	*Vargula* (Ostracoda)	Morin and Cohen 1991
Polygynandrous mating swarms	*Uca* (Brachyura)	Kim et al. 2004
Leks		
Semelparous exploded leks	NA	
Semelparous classic leks	NA	

Table 2.1. (*Contd.*)

Major Category/Subcategory	Taxon	Reference
Iteroparous exploded leks	NA	
Iteroparous classic leks	NA	
Feeding sites		
Semelparous feeding site polygyny	NA	
Semelparous classic leks	NA	
Iteroparous feeding site polygyny	NA	
Iteroparous classic leks	NA	
Nesting sites with female care		
Semelparous harem polygynandry	*Elaphognathia* (Isopoda)	Tanaka and Aoki 1999
Iteroparous harem polygynandry	*Microdeutopus* (Amphipoda)	Borowsky 1980
Nesting sites with male care		
Semelparous nest site polygynandry	NA	
Iteroparous nest site polygynandry	NA	
Polyandrogyny		
Eumonogamy	*Lernaeodiscus* (Rhizocephala)	Høeg 1991
Cursorial polyandrogyny	NA	
Mass mating with male parental care	NA	
Dominance polyandrogyny	NA	
Pair-bond polyandrogyny	*Synalpheus* (Caridea)	Duffy and MacDonald 1999
	Sacculina (Rhizocephala)	Høeg 1991
Harem polyandrogyny	*Leidya* (Isopoda)	Markham 1992

NA, no data available.

they allow precise predictions about (4) the likely form of male–female associations at breeding sites, (5) the degree and form of sexual dimorphism, (6) the tendency for males to provide parental care, (7) whether and how sexual conflict may arise between the sexes, and (8) whether as well as in what form alternative mating strategies are likely to exist. With this information it is possible to assign (9) a detailed descriptive category that summarizes each suite of male and female adaptations to each mating system, before, lastly, (10) classifying the mating system under this scheme (Table 2.1).

Although only a single attempt has been made to use this framework to classify crustacean mating systems (*Paracerceis sculpta*), a preliminary review of the literature suggests that crustacean representatives appear in nearly all 12 major mating system categories (Table 2.1; see also chapters 7–10, 12). I refer the interested reader directly to chapter 9 of Shuster and Wade (2003) for details on why I have classified some of these species as I have. This list is not exhaustive, and I hope that the above discussion stimulates research designed to fill the conspicuous gaps, such as the apparent lack of crustacean leks. My tentative hypothesis in this regard is that mate guarding occupies individual males sufficiently that extreme variance in male mating success is prevented. I invite those sufficiently motivated regarding why I have made my less obvious choices either to direct further discussion toward refining this scheme or, better yet, to use the methods discussed above to measure the components of ΔI and classify these species themselves.

Summary

In this chapter, I describe a quantitative approach for mating system analysis that measures the source and intensity of sexual selection. Using data commonly available from ecological, life history, and behavioral analyses and using crustaceans as specific examples, I show how the magnitude of the sex difference in fitness variance can be used to classify the mating systems of any sexual species. I also show how a sex difference in the opportunity for selection is influenced by the spatial and temporal crowding of matings, variation in female life history, male and female reproductive behavior, and runaway processes in various forms. My goal is to suggest an empirical framework for the study of crustacean and other mating systems that emphasizes the measurement of selective forces responsible for the evolution of male–female differences, an approach that is easier to test and interpret than current frameworks emphasizing optimality or parental investment theory.

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