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The American Naturalist, Vol. 144, Supplement: Sexual Selection in Plants and Animals (Aug., 1994), S126-S149.

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BATEMAN'S PRINCIPLES AND THE MEASUREMENT OF SEXUAL SELECTION IN PLANTS AND ANIMALS

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Abstract.—A. J. Bateman's approach to animal mating systems is generalized to provide a framework for studying sexual selection in plants and hermaphroditic animals. The key feature of this generalization is the realization that the relationship between fecundity and mating success can take a variety of forms beyond those observed in Bateman's data. Thus, under many circumstances, female animals, or the female function of a hermaphroditic plant or animal, can experience sexual selection. Path diagrams are used to show that sexual selection is a component of fecundity selection. Finally, statistical procedures are discussed for measuring sexual selection in plant and animal populations with separate or combined sexes.

In his important article on sexual selection, Trivers (1972) resurrected an insightful contribution by A. J. Bateman that had languished in the literature. In the years since 1972, various authors have attributed different ideas to Bateman (1948). All of these ideas have commonly been called Bateman's principle (Wilson et al. 1994). It is useful to recognize three principles in Bateman's (1948) article. It has been argued (Arnold and Duvall 1994) that one of Bateman's three principles is the key to understanding the operation of sexual selection in animals. The goal of the present article is to explore whether Bateman's third principle (described below) illuminates sexual selection in plants and hermaphroditic animals as well as in animals with separate sexes.

BATEMAN'S THREE PRINCIPLES

Bateman (1948) derived three principles from his *Drosophila* data and discussed their generality. Using genetic markers, he tabulated the numbers of mating partners and offspring for individual male and female fruit flies. Bateman's principles can be seen in a plot of his data, in which number of offspring is graphed against number of mating partners (fig. 1). "It can now be seen that the sex difference in variance of fertility, which is a sign of intra-masculine selection, is due to the effect of number of mates per fly on fertility" (Bateman 1948, p. 362). Thus, *Bateman's first principle* is that males show greater variance in number of offspring than do females. This sex difference is especially dramatic in the subset of data shown in figure 1 in which the fecundity variance of males is 15 times greater than the corresponding variance in females. Bateman (1948, p. 362) goes

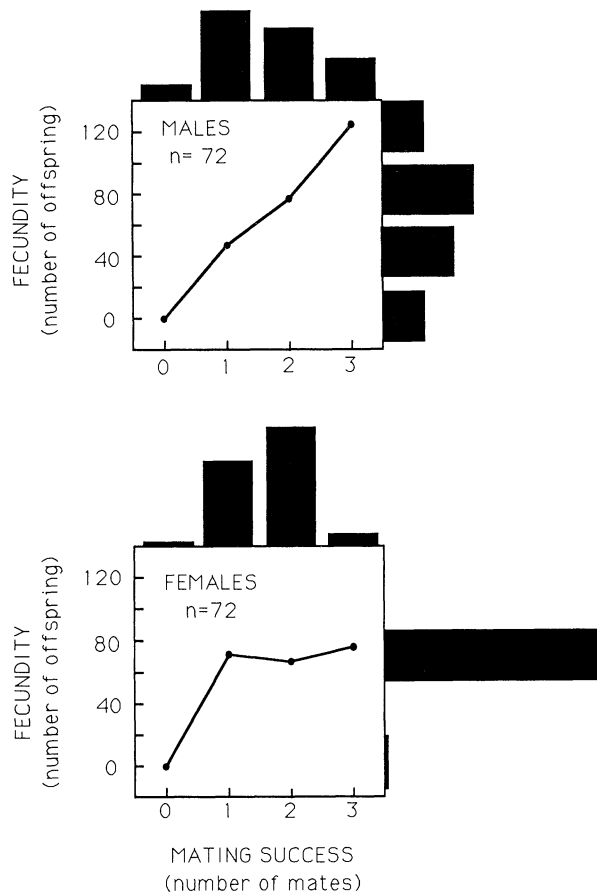


FIG. 1.—Fecundity as a function of mating success in *Drosophila melanogaster*. In each plot the histogram on the right shows the distribution of fecundity. The histogram at the top of each plot shows the distribution of mating success. Data are from Bateman (1948, series 5 and 6).

on to say that the effect of mating success on fecundity, and hence on variance of fecundity, works in two ways. The first way is described by *Bateman's second principle*: “(a) [t]he higher variance, in males, of the number of mates per fly. This is a sign of intra-masculine selection.” The second is described by *Bateman's third principle*: “(b) [t]he stronger correlation, in males, between number of mates and fertility. This is the cause of intra-masculine selection.” Bateman's second principle, the sex difference in variance of mating success, can be seen in figure 1 by comparing the marginal distributions of mating success. The sex difference in mating success variance is not as dramatic as the sex difference in fecundity variance; nevertheless, the male variance is twice as large as the female variance. Bateman's third principle, the dependency of fecundity on mating success, is shown in figure 1 by the lines that graph average fecundity as a function

of mating success. The relationship is linear in males, but in females the average number of offspring hardly changes as mating success increases beyond one mate.

Bateman's (1948) assertions that fitness variance is a sign of selection, whereas the dependency of fecundity on mating success is a cause of selection, must have been enigmatic to his audience in 1948. These assertions are considerably more transparent today. A little algebra reveals that fitness variance places a limit on the magnitude of directional selection, as well as on other kinds of selection (Crow 1958; Wade and Arnold 1980; Arnold 1986). The relationship of selection to Bateman's third principle is discussed below (see also Arnold and Duvall 1994). In short, the "sign" and "cause" interpretations that Bateman attached to his principles find support in subsequent work.

Various statements that have been labeled as "Bateman's principle" are best viewed as corollaries of the sex difference in the dependency of fecundity on mating success. First, male fecundity is generally limited by inseminations (rather than by sperm production), but female fecundity is usually limited by egg production (Bateman 1948, p. 364). Botanists are fond of the plant version of this statement (Charnov 1982; Stanton et al. 1986; Campbell 1989): female reproductive success is limited by resources (not by pollen), while male reproductive success is limited by pollinator visits. Second, because females produce fewer gametes than males, male gametes compete to fertilize female gametes (Bateman 1948, pp. 364–365). Some authors have seized on this idea to characterize sexual differences in selection in terms of gamete production times (Baylis 1981; Sutherland 1985; Clutton-Brock and Vincent 1991). Third, whichever sex has the strongest dependency of fecundity on mating success is the sex that experiences the strongest sexual selection (Queller 1983; Arnold and Duvall 1994). This statement is perhaps the most important but most neglected corollary and will be discussed in the next section.

THE DEPENDENCY OF FECUNDITY ON MATING SUCCESS

Some authors have assumed that Bateman's (1948) *Drosophila* relationships are universal. Such a viewpoint prejudices the case. A better perspective is to ask how the underlying features of Bateman's principles vary in other mating systems (Arnold and Duvall 1994; Wilson et al. 1994). As the underlying features vary, so should Bateman's principles. From an empirical standpoint, the outstanding problems are to discover what relationships between mating success and fecundity actually prevail in nature for each sex and to determine what types of male and female relationships coexist in particular mating systems.

Possible Relationships between Fecundity and Mating Success

Four possible relationships between fecundity and mating success are shown in figure 2A. First, the relationship might be linear (or nearly so), so that fecundity is a steadily increasing function of mating success. In Bateman's (1948) study, male *Drosophila* showed this kind of curve (fig. 1). Second, the relationship might be one of diminishing returns, so that progressively fewer offspring are gained with each additional mate. Third, the relationship might be asymptotic, so that

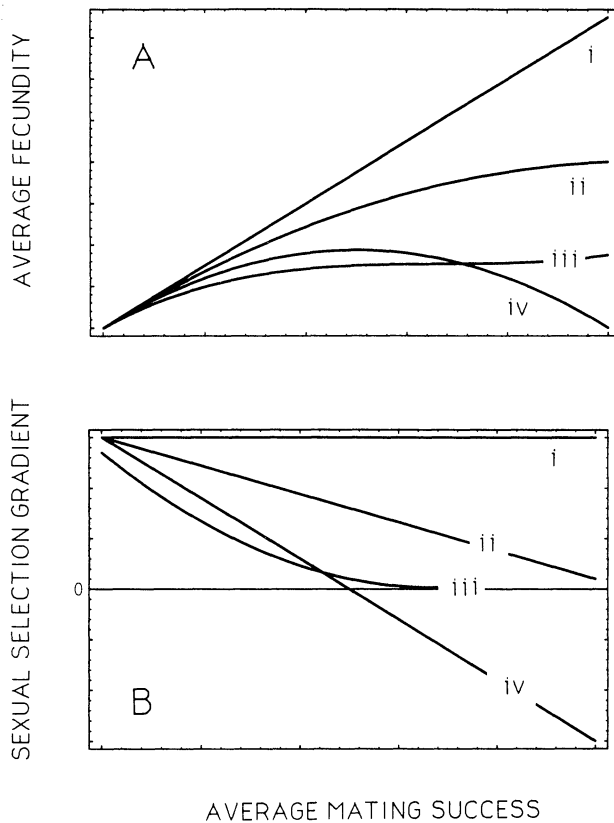


FIG. 2.—Average fecundity and sexual selection gradients as functions of average mating success. *A*, Four hypothetical relationships are shown: *i*, linear; *ii*, diminishing returns; *iii*, one-mate saturation; and *iv*, intermediate optimum. *B*, The sexual selection gradients are the first derivatives of the functions shown in *A*.

there is no increase in fecundity after mating once (single-mate saturation). Female *Drosophila* sometimes show this kind of curve (fig. 1). Fourth, the relationship might be curvilinear, with an intermediate optimum. In such a mating system, the largest number of offspring is produced at some intermediate level of mating success. A survey of possibilities in plants and animals (below) suggests that males or females might show any one of the relationships that we have considered. Thus, the two types of curves revealed in Bateman's (1948) data are just samples from a larger universe of possibilities.

The mathematics of reproduction impose some limits on the kinds of male and female relationships that can coexist in a mating system. In particular, the ratio of average male mating success to average female mating success must equal the ratio of average male fecundity to average female fecundity (because each successful mating involves one participant of each sex, and each offspring has exactly one mother and one father). As a consequence, if the curves in figure 2A represent averages, then the bivariate means of males and females are constrained to lie

on a straight line that passes through the origin (Arnold and Duvall 1994; figs. 5 and 6 below). In other words, the bivariate means of males and females can occupy only certain positions in superimposed plots of fecundity and mating success for the two sexes. Furthermore, if the superimposed curves for males and females cannot be intersected by a straight line through the origin, that pair of curves cannot represent nature.

Before turning to the possible relationships between fecundity and mating success in plants and animals, let us consider what those relationships tell us about sexual selection.

*What the Relationship between Fecundity and Mating Success
Says about Sexual Selection*

The relationship between fecundity and mating success is a key aspect of any mating system because it translates numbers of mates into numbers of offspring. This relationship is the connection between two important types of fitness currency. For example, if we know how tail length in peacocks affects male mating success, then knowing the relationship between mating success and fecundity enables us to express selection on the tail in units of offspring per millimeter of tail length. In any given mating system, however, data will be limited, and so the relationship between fecundity and mating success will be known imperfectly. Consequently, we must resort to statistics to extract the crux of the relationship.

Linear regression is a useful way to quantify the relationship between fecundity and mating success. In figure 1, for example, the regression slope of a straight line fitted to the male data tells us how many offspring are gained per mate. It is less obvious that linear regression is a good solution to quantifying the female data in figure 1, for clearly the data do not fall on a straight line. Figure 3 shows a hypothetical case in which the true relationship is curvilinear. The individual data points are shown in this plot as well (only the fecundity means of the mating success classes are available in Bateman's 1948 article). For any given mating success class in this plot, the dependency of fecundity on mating success can be visualized as the appropriate tangent to the *thin curve*. As we move from one mating success class to the next, from *left* to *right* in this plot, the tangents decrease in slope. A reasonable measure of average dependency could be obtained by taking the average of these tangents, weighting each one by the size of the appropriate mating success class. A simpler way to estimate the average tangent is to calculate the slope of the linear regression (Lande and Arnold 1983, eq. [9]). Furthermore, this estimate of average slope can be made without knowing the true relationship between fecundity and mating success. So far we have discussed only simple regression, but the same arguments apply with multiple regression in which, for example, we hold life span constant, while estimating the dependency of fecundity on mating success.

Quantifying the dependency of fecundity on mating success with a regression slope also provides a bridge to formal selection theory. This bridge is important because it makes the powerful machinery of selection theory and statistics applicable to particular empirical problems. A regression concept of selection is used in predictive equations from quantitative genetics. These equations predict how

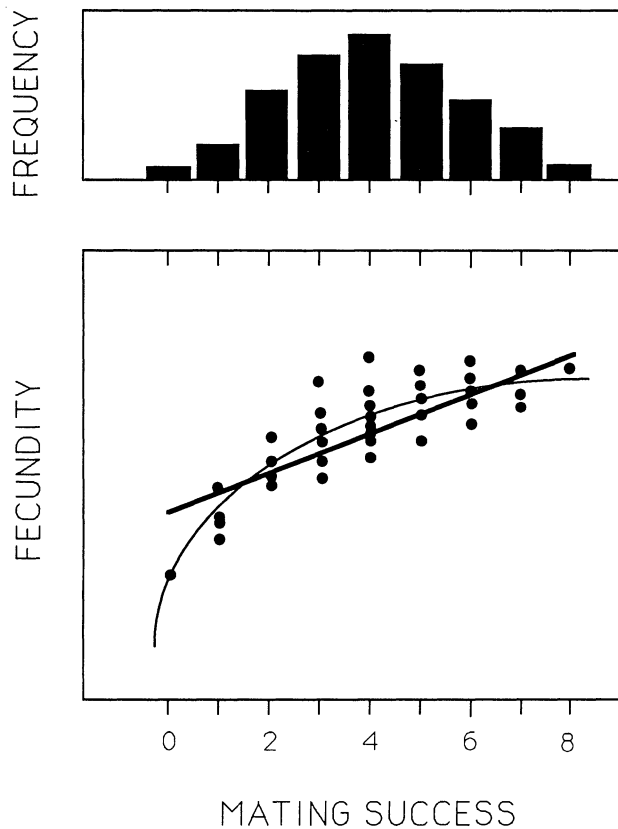


FIG. 3.—The sexual selection gradient estimated as the slope of the regression line that relates fecundity to mating success. The plot shows hypothetical data. The *solid dots* are hypothetical data points for individual organisms from a single population. The *thin curved line* shows the true relationship between fecundity and mating success. The *solid straight line* shows the linear regression equation that has been fitted to the data. The histogram above shows the distribution of mating success.

much the average phenotype evolves from one generation to the next (Lande 1979, 1982; Lande and Arnold 1983; Charlesworth 1993). In this family of equations, selection is modeled as a sensitivity of fitness to changes in average value of a phenotypic character—a selection gradient. This selection gradient is mathematically equivalent to a partial regression of fitness on the value of one phenotypic character, while holding the values of other characters constant. The realization that our most general concept of selection is a statistical parameter has wide-ranging consequences. It means that we can approach the analysis of selection as a statistical problem.

The dependency of fecundity on mating success has two things to say about sexual selection. First, our regression slope measures the intensity of selection on mating success. Thus, a comparison of the male and female regression slopes for Bateman's *Drosophila* data (fig. 1) tells us that selection on male mating

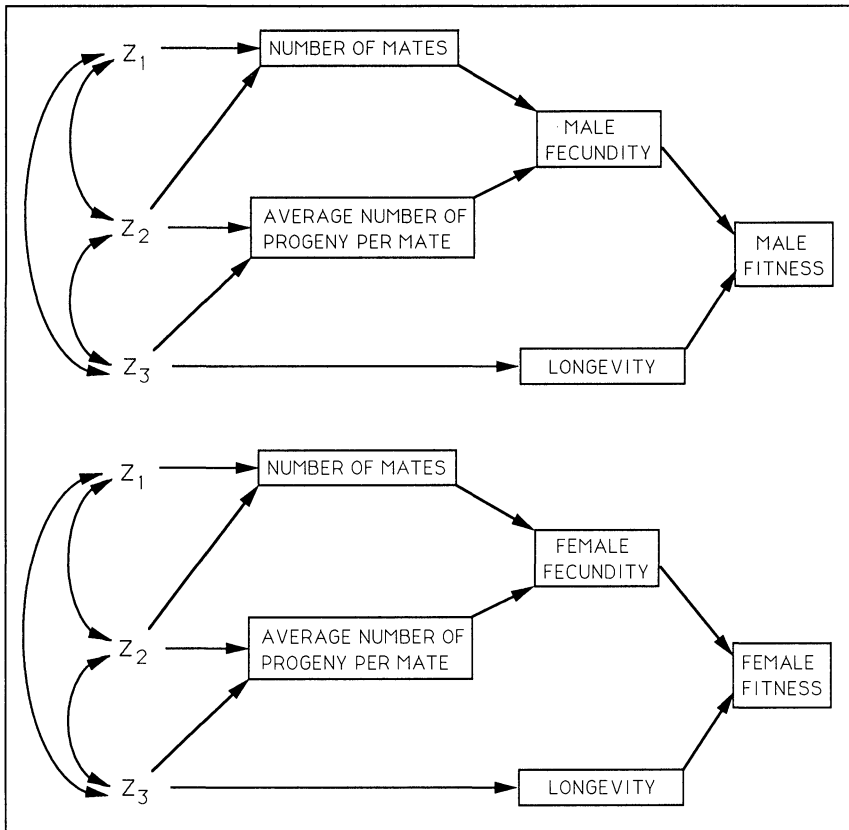


FIG. 4.—Selection in a population with separate sexes represented as two path diagrams, one for each sex. Three hypothetical traits are denoted z_1 , z_2 , and z_3 . Single-headed arrows represent direct effects (selection gradients); double-headed arrows represent covariances between phenotypic traits. For simplicity, arrows representing residual effects on number of mates, average number of progeny per mate, and longevity in each sex have been omitted. There are no residual effects on male or female fecundity because their determinants are components of fecundity.

success is 17 times more intense than comparable selection in females. Second, the dependency of fecundity on mating success represents part of the selection that acts on any sexually selected trait (Arnold and Duvall 1994). This second point is easiest to see in a path diagram that shows the statistical connections among traits, fitness components, and fitness (fig. 4). We can think of the total selection that acts on a trait as a sum of paths that connect the trait with fitness (Arnold 1983). Sexual selection is represented by those paths that pass through mating success en route to fitness. For any such path, the dependency of fecundity on mating success is a common denominator. More exactly, total sexual selection on a trait can be represented as the product of the selection coefficients (partial regression slopes) that lie along the path from the trait to mating success to fitness. (These arguments are developed in more detail in the last section of

this article.) Thus, the dependency of fecundity on mating success represents the final common path for sexual selection on any trait, and in this sense it is a factor in all sexual selection. For these two reasons, the dependency of fecundity on mating success (ideally measured as a partial regression slope) has been called the *sexual selection gradient* (Arnold and Duvall 1994). Thus, in Bateman's (1948) data, even if body size had comparable effects on mating success in male and female *Drosophila*, the difference in their sexual selection gradients means that males would experience 17 times more intense sexual selection on body size than would females.

The regression slope descriptor of the dependency of fecundity on mating success is also equivalent to the first derivative of the *curves* shown in figure 2A. These *curves* show average fecundity as a function of average mating success. A population occupies a particular position along such a curve. The sexual selection gradient for that population is equivalent to the first derivative of the curve evaluated at that position (Lande 1979; Lande and Arnold 1983). Figure 2B shows the first derivatives (sexual selection gradients) for each *curve* as functions of average mating success in a population. In other words, this figure shows how the sexual selection gradient would change as a population displays different average values of mating success and fecundity. Thus, in figure 2B, we see that the sexual selection gradient can be positive and constant (*i*); it can gradually decelerate, while remaining positive (*ii* or *iii*); or it can become negative above a critical level of average mating success (*iv*). This partial derivative view of the sexual selection gradient will be useful as we survey various animal and plant examples of the *curves* shown in figure 2A.

The goal of the next section is to consider the factors that produce different relationships between fecundity and mating success. Elsewhere Duvall and I (Arnold and Duvall 1994) approached this issue by making formal models for both sexes in a few different animal mating systems. The present approach is less ambitious. I will not present formal models, nor will I tackle the technical details of articulating the curves for the two sexes that comprise a mating system. Instead, I focus on the sexes separately in a broad survey of both animal and plant mating systems.

BATEMAN'S THIRD PRINCIPLE IN ANIMALS WITH SEPARATE SEXES

Darwin's (1871, 1874) discussions of sexual selection mainly focused on the males of animals with separate sexes. Darwin admitted the possibility of sexual selection in females only when he discussed species in which the female was more brightly colored than the male and the male nurtures offspring (Darwin 1874, pp. 214, 225, 347, 480). By taking a statistical perspective on sexual selection, we can envision many other situations in which sexual selection will act on females.

In an animal population with separate sexes, sexual selection can occur in males, females, or both sexes. A particular trait can influence mating success in males, females, or both sexes (fig. 4). In the following survey I will focus on sexual selection gradients, the paths that connect mating success to fecundity in males and females in figure 4. My goal in this survey is not to argue that some

types of relationships between fecundity and mating success are inherently implausible, even though this may be the case. Instead, my goal is to encourage more empirical work by showing that a variety of different relationships are at least conceivable. In the following sections on males and females, the subheadings refer to the shape of the curve that relates fecundity to mating success (fig. 2A).

Males

Linear.—When multiple mating imposes no penalties on the fecundity of mates, the relationship between fecundity and mating success may be linear. In other words, the number of progeny that a male can expect to sire with a mate is the same when the male has few mates or many. Within this category, the steepest relationship (hence the greatest sexual selection gradient) results when males can monopolize the paternity of their mates, either because the male effectively guards females against insemination by rivals or because a physiological system of single-male paternity prevails in the population (see Arnold and Duvall 1994, eq. [12a]). The sexual selection gradient does not vary with average mating success.

Diminishing returns.—When the number of offspring that a male can expect to sire with a mate progressively declines, the relationship between fecundity and mating success will be one of diminishing returns (fig. 2A). Such a decline in expected offspring per mate may result from an erosion in mate fecundity, deterioration in ability to give parental care, or an exhaustion of materials required for insemination. Thus, the male may be limited in his ability to supply nuptial gifts that the female converts into offspring. For example, in arthropods the female may feed on the prey supplied by the male, the male's spermatophore, or special male body parts, or she may consume the male himself. As the male's supply of nuptial gifts declines, he may make a smaller contribution to the fecundity of his mates (Arnold and Duvall 1994). Likewise, in species with paternal care, later broods may receive less care and be smaller than earlier broods (Arnold and Duvall 1994, eq. [15b]). Finally, any of the material ingredients for successful insemination (sperm, seminal fluids, spermatophore materials, etc.) may be limited, so that the male sires fewer offspring from the insemination of later mates. In any of these situations, the sexual selection gradient acting on males progressively declines as average mating success increases in the population.

Single-mate saturation.—Suppose that the male is capable of siring some limited number of progeny. When the male has multiple mates, the maternity of those progeny is simply divided among the females that he inseminates. Mating with additional females does not increase the male's fecundity. This kind of situation may prevail in those species in which the paternal care places a limit on the number of offspring that the male can sire. In pipefishes and sea horses, for example, the male broods his offspring in a pouch of limited size. If a male's first mate can fill his pouch and later mates displace the ova of earlier females, then the relationship between fecundity and male mating success might be of the single-mate saturation variety (fig. 2A).

Note that single-mate saturation is not the same as having a single mate that

lasts a season or lifetime. The parasitic male angler fish is monopolized by his mate for a lifetime, but the relationship between fecundity and mating success in males is linear, with only two mating classes in the population (no mates or one). The relationship is not asymptotic. The two essential features of single-mate saturation are that total fecundity of the male is saturated after a single successful mating and that this total fecundity is unchanged by additional matings.

Intermediate optimum.—A negative association between mating success and the average fecundity per mate can cause the curve graphed in figure 2A to have an intermediate optimum. In marmots (*Marmota flaviventris*), males maintain harems of females. Downhower and Armitage (1971) found that the average number of offspring per female declined with increasing harem size. Consequently, the total fecundity of a male is low when he has few or many females in his harem and shows the highest value when his harem is of intermediate size. The negative covariance between mating success and mate fecundity that is at the root of the intermediate optimum can be caused by interference among females and other forms of competition that impair fecundity. Downhower and Armitage (1971) argued that marmot females compete for food within the harem. In such a mating system, the sexual selection gradient becomes negative once average mating success passes beyond a critical point (corresponding to the location of the intermediate optimum). Once this situation is achieved, selection favors lower male mating success (i.e., smaller harems, in the case of the marmots).

Females

Ten different hypotheses for the evolutionary maintenance of multiple mating in females have been reviewed elsewhere (Halliday and Arnold 1987). Only some of these will be discussed in the sections that follow. Ridley (1988) reviews the empirical literature on multiple mating by female insects.

Linear.—When mating success is the primary factor limiting fecundity, the relationship between fecundity and mating success may be linear (fig. 2A). Such a relationship is most likely when total fecundity is not limited by maternal expenditure, body size, or similar factors. Thus, in lineages in which males alone perform parental care (e.g., many fish, some dendrobatid frogs, jacanas, phalaropes), it is conceivable that mating success might limit female fecundity. In this circumstance, and when the relationship between average fecundity and average mating success is linear, the female sexual selection gradient is positive and a constant.

Diminishing returns.—Under a wide variety of circumstances a female can increase her fecundity by mating with more than one male, but the fecundity gain diminishes with each additional mate (fig. 2A). Additional matings may increase the size of the female's clutch if she receives a nuptial gift from each male (Thornhill 1976; Gwynne 1984; Gwynne and Simmons 1990), if each male's ejaculate is insufficient to sire the whole clutch (Gromko et al. 1984), or if each male takes up some of the burden of parental care (Hrdy 1977; Stacey 1982; Davies 1985). In any of these circumstances, however, the female's total clutch size is likely to be limited by her body size or physiological condition. Consequently, the fecundity gain from multiple matings will be of diminishing returns as the female approaches her physical or physiological limit. In insect species in which

females normally mate more than once, repeated mating is usually required to achieve the fecundity limit (Ridley 1988). Under this condition, sexual selection on females will be greatest when average female mating success is low. Sexual selection will gradually decrease as fecundity reaches the limit set by factors other than mating success.

Single-mate saturation.—Suppose that a single mating is sufficient to sire a female's entire clutch. When the female mates with additional males, her clutch size is unaffected, but paternity is divided among the inseminating males. These conditions specify a single-mate saturation relationship between fecundity and mating success (fig. 2A). In a review of the insect literature, Ridley (1988) finds little evidence for the proposition that a single mating is sufficient to sire the female's entire clutch. Thus, the curve displayed by Bateman's (1948) *Drosophila* data (fig. 1) may be exceptional. Should single-mate saturation prevail in a population, sexual selection on females vanishes if average female mating success is greater than one (Arnold and Duvall 1994).

Intermediate optimum.—A negative association between the average fecundity per mate and female mating success could produce an intermediate optimum in the curve that relates total fecundity to mating success (fig. 2A). By analogy with the situation in which males are polygynous (see above), we might expect such negative covariance to arise in polyandrous species in which a female maintains a harem of males (e.g., jacanas, phalaropes). Thus, competition or interference among the males within a harem might reduce the average clutch size tended by males, so that average clutch size decreases with harem size. Such circumstances may be exceptional. A somewhat more plausible scenario might apply when males engage in lengthy postcopulatory amplexus or other forms of mate guarding. Such engagements could conceivably drain the female's resources and reduce her fecundity, which would cause an intermediate optimum in the curve that relates total fecundity to mating success.

BATEMAN'S THIRD PRINCIPLE IN HERMAPHRODITIC ANIMALS

Modern attention to hermaphroditic animals has focused on three issues: defining the conditions under which hermaphroditism will be favored over separate sexes, the optimal allocation of resources to male as opposed to female function, and the best age at which to change sex (Maynard Smith 1971; Warner et al. 1975; Charnov et al. 1976; Heath 1977; Charnov 1979, 1988; Morgan 1994). The ecological conditions associated with hermaphroditism have been discussed by Ghislen (1969) and Strathmann et al. (1984). Jarne and Charlesworth (1993) have reviewed the topic of selfing in animals. None of these important topics will be my primary concern. Instead, I focus on the more limited objective of characterizing sexual selection in hermaphrodites.

Darwin (1874) felt that sexual selection did not occur in hermaphroditic animals or at least played no important role in their evolution. "In the lower divisions of the animal kingdom, Sexual Selection seems to have done nothing: such animals are often affixed for life to the same spot, or have the sexes combined in the same individual, or what is still more important, their perceptive and intellectual

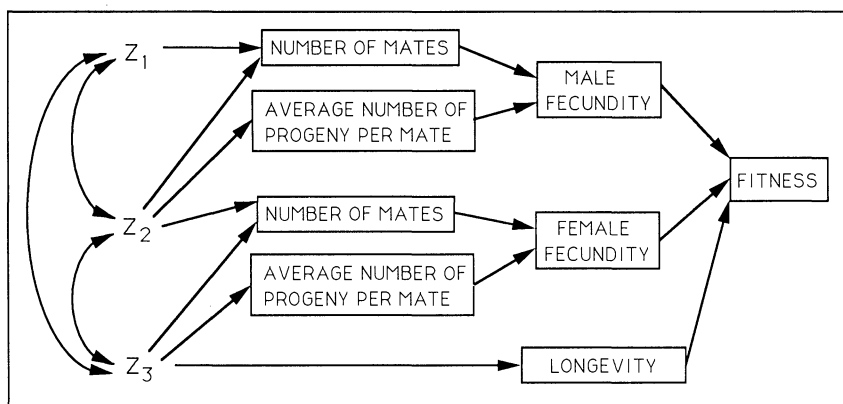


FIG. 5.—Selection in a population of hermaphrodites represented as a path diagram. Conventions are as in fig. 4.

facilities are not sufficiently advanced to allow of the feelings of love and jealousy, or of the exertion of choice" (Darwin 1874, p. 613). In another passage, Darwin (1874, p. 260) stressed the same three reasons for failure of sexual selection in animal hermaphrodites: secondary sexual characters cannot be expressed when the two sexes are combined in the same individual; permanent attachment to a support eliminates the possibility of sexual search and struggle; and because of poorly developed senses and mental abilities, lower animals (including most hermaphrodites) cannot exercise mate choice or feel rivalry. While these three factors may restrict the expression of sexual selection in hermaphrodites, they will not eliminate sexual selection (Morgan 1994).

The most important feature in the mating system of a hermaphroditic animal is that each individual possesses both male and female components of reproductive success. Two statistical consequences of this feature can be appreciated by considering a flowchart of total fecundity and its components (see fig. 5). One consequence is that selection on a particular trait may act through both male and female components of fecundity. (Of course, in the simplest case, selection might act only through male or female functions.) In a hermaphroditic snail, for example, large body size might enhance male fecundity, perhaps by increasing the number of mating partners that receive sperm. Large body size also might allow the snail to accommodate more eggs and so enhance female fecundity. Because these effects act in the same individual, they contribute to the second statistical consequence. That consequence is that male and female components of reproduction may not be statistically independent, as they necessarily are in organisms with separate sexes. In the hypothetical snail just considered, if body size were the only determinant of male and female fecundity, then those two components would be positively correlated. Alternatively, male and female fecundity may be negatively correlated when a fixed level of resources must be allocated between male and female functions (as in the models in Charnov et al. 1976 and Heath 1977). Morgan (1994) has made the important point that such nonindependence of male

and female traits and components constrains possible evolutionary trajectories in hermaphrodites.

The consequence of nonindependence of male and female characters for sexual selection gradients is that we must hold both male and female features constant while considering the relationship between fecundity and mating success. For example, to evaluate the male sexual selection gradient in figure 5 (i.e., the path from number of female mating partners to male fecundity), we would need to regress male fecundity on number of female mating partners, while holding constant both average number of progeny per female mating partner and female fecundity of the individual in question. These statistical operations are described in more detail in the last section of this article. These operations imply that we have a data set in which we have scored both the male and female components of reproductive success for each individual in a reasonably large sample. Working with the hermaphroditic snails of the genus *Bulinus*, Jarne et al. (1992) have made major strides toward this daunting empirical goal.

Two other features of animal hermaphrodites seem especially likely to influence relationships between fecundity and mating success. The first of these is reciprocity in gamete transfer. For example, in simultaneous hermaphroditic fishes of the genus *Hypoplectrus*, the individuals in a spawning pair take turns fertilizing each other's eggs, a phenomenon that Fischer (1980, 1981) calls *egg trading*. Likewise, in at least some pulmonate snails, both individuals transfer sperm to one another during copulation (Jarne et al. 1992). Fischer (1981) has pointed out that such reciprocity will stabilize a hermaphroditic mating system against invasion by pure males. To evaluate the constraint that reciprocity in gamete transfer imposes on sexual selection, we would need to know whether at least some of the sperm received from each partner is used to sire progeny and whether such reciprocity is an unbroken rule. A second feature of consequence is the breeding sex ratio (the ratio of the number of breeding males to the number of breeding females, including physiologically capable individuals that happen to produce no offspring). In animals with separate sexes, breeding males can outnumber breeding females or vice versa; in hermaphrodites, however, the breeding sex ratio is necessarily one. A breeding sex ratio of unity greatly constrains the values that male and female sexual selection gradients can assume in a particular population. The constraint arises because the average values of fecundity and mating success for male and female functions must lie on a line through the origin of a plot such as figure 3 (as discussed above). A breeding sex ratio of one fixes the position of that line (see Arnold and Duvall 1994, fig. 5C).

Although the sexual selection gradients in hermaphrodites will be constrained by nonindependence of male and female traits, reciprocity in gamete transfer, and unity of breeding sex ratio, the nature and importance of these constraints still needs to be established.

Other conspicuous features of hermaphroditic animals seem less likely to complicate a gradient view of sexual selection. For example, the phenomenon of selfing in some hermaphrodites (McCracken and Selander 1980; Jarne and Charlesworth 1993) poses no obstacles to our perspective on sexual selection gradients. The self may be included in a tally of the number of mating partners.

The significance of selfing, from the standpoint of sexual selection, is that it provides insurance against mating failure. Selfing guarantees that no individual fails to mate and produce progeny and so means that the sexual selection gradient is zero in a population with a single-mate saturation curve (fig. 2). The fact that selfed progeny are often inferior to outcrossed progeny (inbreeding depression) should not be ignored (Charlesworth and Charlesworth 1987*a*), but inbreeding need not complicate the business of measuring sexual selection. Likewise, the sessile nature of many hermaphrodites (e.g., barnacles, tunicates, tapeworms) does not rule out the possibility of sexual selection or even challenge our statistical picture of sexual selection. The formal logic of sexual selection in sessile hermaphrodites is the same as in mobile hermaphrodites (e.g., turbellarians, oligochaetes, leeches, gastropods), even though opportunities for active pursuit of mating partners are limited. Although barnacles are sessile, they possess remarkable intromittent organs (Darwin 1854) that suggest a persistent history of sexual selection on male function. Finally, the continuum from simultaneous to sequential hermaphroditism can be readily accommodated within the framework that has been outlined. Sequential hermaphrodites (e.g., parrot fishes, wrasses) probably escape from some of the constraints that limit sexual selection in simultaneous hermaphrodites. Nevertheless, male and female functions still can be statistically coupled even though they are separated in time.

BATEMAN'S THIRD PRINCIPLE IN HERMAPHRODITIC PLANTS

If we consider Darwin's discussions of sexual selection in lower animals, it is easy to understand why he never wrote about sexual selection in plants. In Darwin's view, sexual selection was unimportant in lower animals because their sexes were combined, they were sessile, and, most importantly, they were incapable of mate choice and feelings of jealousy (see above). For these same reasons, sexual selection in plants must have been a non sequitur for Darwin. Sexual selection in plants is a concrete possibility, however, if we take a statistical perspective and use Bateman's third principle.

Most flowering plants are hermaphrodites with flowers that possess both male organs (stamens) and female organs (carpels) (Darwin 1877; Yampolsky and Yampolsky 1922; Jarne and Charlesworth 1993). Consequently, in the following survey I will concentrate exclusively on such plants.

The recognition that fecundity in hermaphroditic plants consists of both male and female parts (see, e.g., Lloyd 1972; Willson and Burley 1983; Morgan 1992*a*, 1992*b*) is fundamental to an analysis of sexual selection. We can ask whether features of the corolla and sepals affect male fecundity, female fecundity, or both (Morgan 1992*a*). We can also ask whether the effects on fecundity (in either sex) are mediated through mating success or the average number of progeny per mating partner (fig. 5). I refer to effects of the former kind as sexual selection (Arnold 1994). Such a distinction between sexual and fecundity selection seems not to have been made in the botanical literature.

Wilson et al. (1994, fig. 1) present a flowchart that is superficially similar to figure 5. In their scheme, however, the fecundity of each sex is broken down into

a single series of multiplicative components. In contrast, the fecundity of each sex in figure 5 is broken down into two multiplicative series, one involving mating success and the other involving the average fecundity of mates. Consequently, fecundity selection can be represented as the sum of two parts: sexual selection and mate fecundity selection (see below). It is not apparent which (if any) coefficients in the Wilson et al. (1994) scheme represent what I call sexual selection. Likewise, models for allocation of effort in hermaphroditic plants use a different scheme for subdividing fitness than is used here. In those allocation models (Charnov 1979, 1982; Charlesworth and Charlesworth 1987*b*; Lloyd 1987*a*, 1987*b*; Schoen and DuBuc 1990), total fecundity is broken down into male and female parts, but within each sex, a mating success component of fecundity is not recognized. Consequently, those allocation models do not make a distinction between sexual and fecundity selection.

My goals in the following sections are to survey the different relationships that might prevail between fecundity and mating success in plant mating systems and to discuss what those relationships imply about sexual selection. The subheadings under male and female function refer to the shapes of the *curves* in figure 2*A*. Only a couple of possibilities are discussed under each subheading; an exhaustive inventory is not presented.

Male Function

Linear.—A male's fecundity can be a linear function of the number of mates that his pollen reaches, if his expected share in paternity upon reaching a mate is constant in time and space. Systematic trends in paternity share will tend to make the relationship between fecundity and mating success nonlinear. Thus, for a linear relationship to prevail, the transport of pollen to mates (by wind, water, or animal vectors) would be random with respect to the proximity of mates.

Diminishing returns.—The relationship between fecundity and mating success can be of the diminishing returns type when fecundity returns are related to proximity of mates. Consider a population in which the closest mate yields the highest fecundity returns for a male; the next closest, the next highest; and so forth. Fecundity per mate could be dependent on mate proximity in roughly this way in both wind and animal pollination systems. This dependency could yield a diminishing returns curve such that the sexual selection gradient progressively declines with increasing average mating success (fig. 2).

Single-mate saturation.—Consider the following model. If a male pollinates a single female, that female mate receives all of the male's pollen. If a male pollinates two females, the females share paternity, but the male's fecundity is not increased. If a third female is pollinated, all three females share paternity, but the male's fecundity remains the same as before, and so forth. This model yields a curve that is of the single-mate saturation kind. For this model to apply, however, we must assume that a male's fecundity is limited by his pollen production rather than by the number of females that he succeeds in pollinating. In other words, the male's fecundity is some function of his pollen production, and that fecundity is merely divided among the females that he pollinates. Such a mating system seems implausible, but, should it prevail, there is some limited scope for

sexual selection on male function. Sexual selection can arise if some (but not all) males fail to mate. See the ensuing discussion (also Arnold and Duvall 1994, eq. [12b]).

Intermediate optimum.—An intermediate optimum in the curve relating fecundity to mating success could arise if a negative covariance prevails between the average fecundity per mate and mating success. Although the source of such negative covariance is not easy to imagine, such sources should not be dismissed out of hand. Consider a hypothetical plant species in which pollen is packaged into pollinia that vary in size from individual to individual. If large pollinia are less successful in reaching mating partners than are small pollinia, but larger pollinia reap a higher share of paternity once they contact a stigma, then a negative covariance might be produced, and our curve might show an intermediate optimum. In such a case, the sexual selection gradient is negative when average mating success exceeds a certain level (fig. 2). In our hypothetical example, this negative gradient would encourage evolution toward smaller pollinia.

Female Function

Restrictions on female fecundity are commonly discussed under the topic of pollen limitation (see, e.g., Willson and Burley 1983; Snow 1986; Young and Young 1992). In those discussions, female fecundity is related to pollen deposition or pollinator visits. My aim in the following sections, however, is to relate female fecundity to mating success (number of mating partners). That relationship will dictate connections to sexual selection theory. Thus, one would need to monitor the number of mating partners, not just the number of pollinator visits, to distinguish among the following possibilities.

Linear.—If females are so pollen limited that each male's pollen fertilizes an uncontested set of ovules, then a female's fecundity might be a linear function of the number of mates that pollinate her. Thus, pollen limitation generates sexual selection on female function. (Apparently contradictory statements by Willson and Burley [1983] and Snow [1986] arise from a focus on how pollen limitation affects sexual selection not on females but on males.) Factors that increase the expected number of progeny per mate will increase the female sexual selection gradient and so increase the force of sexual selection on female function.

Diminishing returns.—Consider the following model. The first mate fertilizes some number of ovules (but not the whole set); the next mate fertilizes some smaller number; the next mate, a smaller number still; and so forth. The population characterized by such a model can have a curve that is of the diminishing return variety (fig. 2). In such a population, female function experiences sexual selection (provided that the position occupied by the population on the curve is not on an asymptote). Female function experiences the strongest sexual selection when mating success is low.

An increase in fecundity with supplemental pollination is a common result in hand pollination studies. Young and Young (1992) found significant enhancement of fecundity in 42% of the 99 studies that they surveyed. These results suggest that populations often are poised on a linear or diminishing returns curve such that female function experiences sexual selection. As Haig and Westoby (1988)

point out, hand pollination with small increments of pollen could be used to establish the shape of the curve.

Single-mate saturation.—Suppose that the following mating system prevails. The first male fertilizes all ovules if no other males arrive. If a second male arrives, the two males share paternity. If a third male arrives, all three males share paternity, and so forth. Regardless of the rule for sharing paternity among pollinating males, the female's curve is of the single-mate saturation kind. The specification that a single male can monopolize the female's fecundity means that the model is most likely to apply if individuals have a single stigma. As the number of flowers and stigmas per individual increases, single-mate saturation becomes increasingly more difficult. Single-mate saturation provides less scope for sexual selection on female function than the linear or diminishing returns models. Sexual selection on female function vanishes if all individuals are successfully pollinated by at least one mate.

Hand pollination studies commonly show that supplementary pollination does not increase female fecundity (Young and Young 1992). Such results imply that the population is positioned on the asymptote of the curve relating fecundity to mating success. Paternity assays would be required to determine whether the asymptote is reached with a single mating partner.

Intermediate optimum.—In a review of 99 studies, Young and Young (1992) reported that, in 17 cases, hand pollination reduced female reproductive success. These results suggest that an intermediate optimum in the curve relating female fecundity to mating success may be common. Young and Young (1992) also reviewed three explanations that have been offered for reduction of fecundity associated with high mating success: interference of pollen tube growth at high densities, attraction of pollen thieves by high pollen loads, and damage to stigmas by enhanced pollinator visits. When an intermediate optimum prevails under natural conditions, female function can experience sexual selection for reduced mating success.

Other Factors Affecting Sexual Selection Gradients in Hermaphroditic Plants

Some features of hermaphroditism will affect sexual selection gradients of plants in much the same way as in animals. For instance, the simultaneous expression of male and female fecundity means that male features must be held constant while assessing female gradients and vice versa (see below). Likewise, a breeding sex ratio of unity constrains the expression of male and female sexual selection gradients.

Other features of plant hermaphroditism also have some impact on sexual selection viewed as a gradient. Thus, partial selfing in hermaphrodites may affect the means of traits in progeny (Charlesworth and Charlesworth 1987a). Such inbreeding depression is a separate issue from mating success, which is a count of mates producing progeny at the zygote stage. Thus, the view of sexual selection employed here eliminates postzygotic events such as ovule abortion and inbreeding depression from consideration as a matter of definition. Nevertheless, postzygotic mortality may complicate the assessment of mating success, so that sexual selec-

tion is confounded to some extent with viability selection and inbreeding depression in the offspring generation. For example, if inbreeding affects the germination of seeds from some parents more than others, then estimates of sexual selection gradients may be distorted.

THE MEASUREMENT OF SEXUAL SELECTION

A partial regression view of selection provides a framework for thinking about sexual selection. This framework is built on several elements. The first is the proposition that selection can be represented by the slope coefficients in a partial regression equation that relates fitness to a series of phenotypic traits (Lande and Arnold 1983). The second element in the framework is the recognition that fitness can be represented as a hierarchy of components (Falconer 1989). Thus, fitness is a product of fecundity and longevity, fecundity can be represented as a product of mating success and average mate fecundity, and so forth (Arnold and Duvall 1994). The principal advantage of breaking fitness into components (i.e., parts that completely constitute fitness) is that all variation in fitness can be accounted for by variation in its components. Most arbitrary decompositions of fitness will not have this property. The third element in our framework is the realization that the hierarchy of components can be defined so that it represents a nested series of regression equations. Consequently, the partial regression view of selection can be applied at each level in the component hierarchy. The resulting hierarchy of equations can be visualized as a path diagram (Wright 1934; Arnold 1983; Kingsolver and Schemske 1991). Thus, to view sexual selection from a partial regression perspective, we need to define a hierarchy of fitness components so that sexual selection is isolated from other paths between traits and fitness. One such hierarchy is shown in figure 6.

An advantage of the partial regression view of selection is that sexual selection can be clearly distinguished from other kinds of selection. Thus, in figure 6 I have used a theorem from path analysis (Wright 1934, 1968; Li 1975; Arnold 1983) to subdivide total fecundity selection on a particular trait, z_i , into component parts. This subdivision follows directly from the prior step of breaking fecundity into its component parts. A formal subdivision of fecundity selection allows us to label the parts of fecundity selection and see that sexual selection is a part of fecundity selection. Morgan's (1994) partitioning of the fecundity selection differential for a trait is consistent with the subdivision presented here.

The partial regression view of selection also suggests what kind of data will be required to measure sexual selection. Consider first the sexual selection gradient, which is the slope of the partial regression relating fecundity to mating success. This gradient can be visualized as the path from mating success to fecundity in figure 6. The ideal form of data for estimation of this gradient would consist of tallies of numbers of mates and offspring for a large sample of adult males and females in a single population. Such data might be obtained by using molecular markers to diagnose the paternity and maternity of each individual in a large sample of offspring (Meagher 1986, 1991; Gibbs et al. 1990). A useful tabulation of such data is to arrange them in a parental table in which rows represent individ-

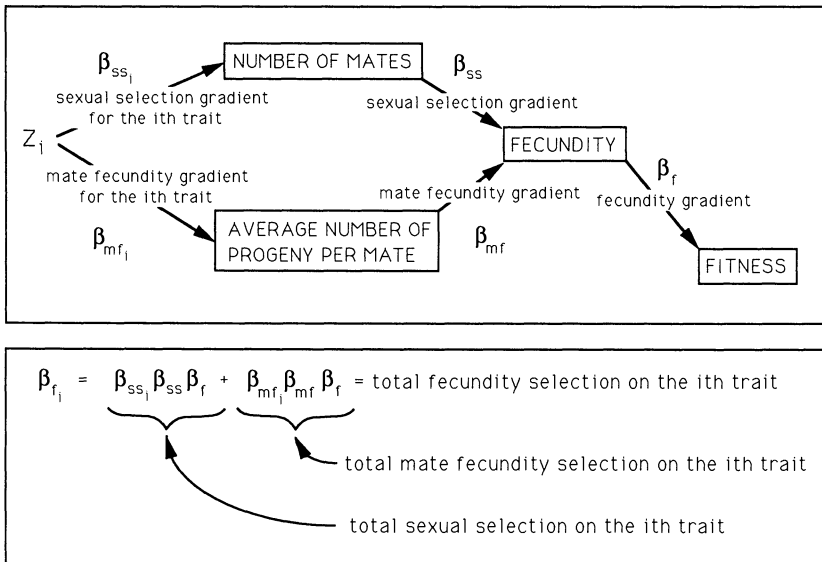


FIG. 6.—Sexual selection as a component of fecundity selection. *Top*, the parts of fecundity selection on a phenotypic trait, z_i , are represented as a path diagram. *Bottom*, the algebraic relationship between total fecundity selection and its parts is illustrated.

ual adult females, columns represent adult males, and entries correspond to number of offspring for a particular pair of parents (Arnold and Duvall 1994; M. S. Webster, S. G. Pruett-Jones, D. F. Westneat, and S. J. Arnold, unpublished manuscript). In a hermaphroditic population, the parental table takes the same form, but each adult occurs as both a row and a column label. To tabulate the mating success of an individual, we count the number of nonempty entries in its column (or row). To tabulate an individual's average mate fecundity, we compute the average of the entries in its column (or row). Consequently, for each individual, the product of mating success and average mate fecundity gives that individual's total fecundity, the sum of its column (or row) entries. Of course, approximations of mating success, average mate fecundity, and total fecundity could be obtained in other ways. Whatever approach is used, the aim is to estimate mating success and average mate fecundity on an individual basis so that they define total fecundity (i.e., so that, in each sex, total fecundity is a mathematical function of only mating success and average mate fecundity).

In species with separate sexes, the sexual selection gradients can be estimated from data on mating success, average mate fecundity, and total fecundity for individuals of each sex. The goal is to isolate the effect of number of mates on fecundity by using partial regression. Thus, we would compute the partial regression of fecundity on number of mates, holding two kinds of variables constant. The first of these is the average fecundity of mates. The rationale for this part of the partial regression calculation can be seen in figure 6. If we do not hold average mate fecundity constant, the direct effect of mate number on fecundity (i.e., the

sexual selection gradient) may be distorted because of a correlation between mate number and average mate fecundity. The second kind of variable to be held constant is longevity or life span. In other words, we need to hold constant the time interval over which mating success and fecundity is assessed. Otherwise, estimates of mate number and fecundity may be distorted by differences in longevity, life span, and so forth (Koenig and Albano 1986). Such distortions can also affect the sexual selection gradient.

In hermaphrodites, one needs to have data on mating success, average mate fecundity, and total fecundity in both sexes in order to estimate a sexual selection gradient for either sex. Thus, to compute the female sexual selection gradient, we need to hold constant the following attributes: male mating success, the average mate fecundity component of male fecundity, as well as the average mate fecundity component of female fecundity, and life span.

Another important technical point is that mating success and average mate fecundity ideally should have an additive, rather than a multiplicative, relationship to fecundity. A logarithmic transformation of both mating success and average mate fecundity can be used to achieve this additive relationship. Also, an arbitrarily small positive constant can be added to all values before taking logarithms to avoid problems with zero values. The reason for the logarithmic transformation is that the multiple-regression equations assume an additive relationship between predictor variables. Wright (1968) discusses logarithmic transformations and other ways to deal with the additivity assumption. If selection is weak, for example, an additive approximation can be used without resorting to a logarithmic transformation (Lande 1980; Morgan 1994).

Other procedural aspects of estimating selection coefficients with multiple regression are discussed elsewhere (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987; Phillips and Arnold 1989). Perhaps the most important point to remember in using the technique is that selection coefficients can be incorrectly estimated if correlated characters that are themselves targets of selection are left out of the analysis.

The estimated sexual selection gradient can be standardized in various ways. Thus, the gradient can be divided by average total fecundity so that it represents the partial regression of relative total fecundity on mating success. With this standardization, the gradient indicates the extent to which average mating success is directly shifted by fecundity selection. That shift can also be standardized so that it is expressed in units of phenotypic standard deviation, by multiplying it by the standard deviation of mating success (Lande and Arnold 1983).

In species with separate sexes, the other parts of sexual selection on a trait also can be estimated by partial regression. For example, consider the sexual selection gradient for the i th phenotypic trait (fig. 6). To estimate this gradient, we would compute the partial regression of mating success on the i th trait, holding constant all other traits. For this computation, longevity or life span should also be held constant, if differences in such variables affect the value of mating success. The fecundity gradient (fig. 6) could be estimated by computing the partial regression of fitness (ideally estimated as a lifetime count of progeny) on fecundity, while holding life span, and so forth, constant. Finally, the total sexual

selection gradient for the i th trait could be estimated by taking the product of the three gradients just described (fig. 6) or computing the partial regression of fitness on the i th trait, holding constant all other phenotypic traits, average mate fecundity, and life span (or longevity, etc.).

In a hermaphrodite, the estimation of the sexual selection gradient for a particular trait involves some additional statistical considerations. Thus, to compute the female sexual selection gradient for the i th trait, we would need to hold constant male mating success and the average mate fecundity of males, as well as the average mate fecundity of females, the values of all other phenotypic traits, and life span.

CONCLUSION

The particular relationship between fecundity and mating success that Bateman (1948) documented in fruit flies has been widely assumed to be universal. This assumption of universality is almost certainly false. A variety of relationships between fecundity and mating success undoubtedly prevails in both plants and animals. Consequently, females may experience sexual selection in certain mating systems. The existence of sexual selection in female animals has been neglected, and the existence of sexual selection on female function in hermaphroditic plants has been almost totally ignored. A regression view of selection could be used to focus empirical work on both of these important, unresolved issues.

ACKNOWLEDGMENTS

I am grateful to E. Charnov, D. Duvall, M. Morgan, and D. Schemske for helpful discussions (and disagreements); to D. Duvall, L. Houck, and P. Wilson for useful comments on the manuscript; and to M. Turelli for help with graphics. H. B. Shaffer and the Section of Evolution and Ecology at the University of California, Davis, were my gracious hosts during the preparation of this manuscript. National Science Foundation grant BSR 9119588 also supported the preparation of this manuscript.

LITERATURE CITED

- Arnold, S. J. 1983. Morphology, performance and fitness. *American Zoologist* 23:347–361.
———. 1986. Limits on stabilizing, disruptive, and correlational selection set by the opportunity for selection. *American Naturalist* 128:143–146.
———. 1994. Is there a unifying concept of sexual selection that applies to both plants and animals? *American Naturalist* 144(suppl.):S1–S12.
Arnold, S. J., and D. Duvall. 1994. Animal mating systems: a synthesis based on selection theory. *American Naturalist* 143:317–348.
Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.
Baylis, J. R. 1981. The evolution of parental care in fishes, with reference to Darwin's rule of sexual selection. *Environmental Biology of Fishes* 6:223–251.
Campbell, D. R. 1989. Measurements of selection in a hermaphroditic plant: variation in male and female pollination success. *Evolution* 43:318–334.

- Charlesworth, B. 1993. Natural selection on multivariate traits in age-structured populations. *Proceedings of the Royal Society of London B, Biological Sciences* 251:47–52.
- Charlesworth, D., and B. Charlesworth. 1987*a*. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* 18:237–268.
- . 1987*b*. The effect of investment in attractive structures on allocation to male and female functions in plants. *Evolution* 41:948–968.
- Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences of the USA* 76:2480–2484.
- . 1982. *The theory of sex allocation*. Princeton University Press, Princeton, N.J.
- Charnov, E. L., J. Maynard Smith, and J. J. Bull. 1976. Why be a hermaphrodite? *Nature (London)* 263:125–126.
- Clutton-Brock, T. H., and A. C. J. Vincent. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature (London)* 351:58–60.
- Crow, J. F. 1958. Some possibilities for measuring selection intensities in man. *Human Biology* 30:1–13.
- Darwin, C. 1854. *A monograph on the sub-class Cirripedia, with figures of all the species. The Balanidae (or sessile Cirripedes); the Verrucidae, &c.* Ray Society, London.
- . 1871. *The descent of man, and selection in relation to sex*. J. Murray, London.
- . 1874. *The descent of man, and selection in relation to sex*. 2d ed. J. Murray, London.
- . 1877. *The different forms of flowers on plants of the same species*. J. Murray, London.
- Davies, N. B. 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Animal Behaviour* 33:628–648.
- Downhower, J. F., and K. B. Armitage. 1971. The yellow-bellied marmot and the evolution of polygamy. *American Naturalist* 105:355–370.
- Falconer, D. S. 1989. *Introduction to quantitative genetics*. 3d ed. Longman, Harlow, U.K.
- Fischer, E. A. 1980. The relationship between mating system and simultaneous hermaphroditism in the coral reef fish, *Hypoplectrus nigricans* (Serranidae). *Animal Behaviour* 28:620–633.
- . 1981. Sexual allocation in a simultaneously hermaphroditic coral reef fish. *American Naturalist* 117:64–82.
- Ghislen, M. T. 1969. The evolution of hermaphroditism among animals. *Quarterly Review of Biology* 44:189–208.
- Gibbs, H. L., P. J. Weatherhead, P. T. Boag, B. N. White, L. M. Tabak, and D. J. Hoysak. 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. *Science (Washington, D.C.)* 250:1394–1397.
- Gromko, M. H., M. E. A. Newport, and M. G. Kortier. 1984. Sperm dependence of female receptivity to remating in *Drosophila melanogaster*. *Evolution* 38:1273–1282.
- Gwynne, D. T. 1984. Courtship feeding increases female reproductive success in bushcrickets. *Nature (London)* 307:361–363.
- Gwynne, D. T., and L. W. Simmons. 1990. Experimental reversal of courtship roles in an insect. *Nature (London)* 346:172–174.
- Haig, D., and M. Westoby. 1988. On limits to seed production. *American Naturalist* 131:757–759.
- Halliday, T., and S. J. Arnold. 1987. Multiple mating by females: a perspective from quantitative genetics. *Animal Behaviour* 35:939–941.
- Heath, D. J. 1977. Simultaneous hermaphroditism: cost and benefit. *Journal of Theoretical Biology* 66:363–373.
- Hrdy, S. B. 1977. *The langurs of Abu*. Harvard University Press, Cambridge, Mass.
- Jarne, P., and D. Charlesworth. 1993. The evolution of selfing rate in hermaphrodite plants and animals. *Annual Review of Ecology and Systematics* 24:441–466.
- Jarne, P., B. Delay, C. Bellec, G. Roizes, and G. Cuny. 1992. Analysis of mating systems in the schistosome-vector hermaphrodite snail *Bulinus globosus* by DNA fingerprinting. *Heredity* 68:141–146.
- Kingsolver, J. G., and D. W. Schemske. 1991. Path analysis of selection. *Trends in Ecology & Evolution* 6:276–280.
- Koenig, W. D., and S. S. Albano. 1986. On the measurement of sexual selection. *American Naturalist* 127:403–409.

- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33:402–416.
- . 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:292–305.
- . 1982. A quantitative genetic theory of life history evolution. *Ecology* 62:607–615.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Li, C. C. 1975. *Path analysis: a primer*. Boxwood, Pacific Grove, Calif.
- Lloyd, D. G. 1972. Breeding systems in *Cotula* L. (Compositae, Anthenideae). I. The array of monoclinal and diclinal systems. *New Phytologist* 71:1181–1194.
- . 1987a. Allocations to pollen, seeds and pollination mechanisms in self-fertilizing plants. *Functional Ecology* 1:83–89.
- . 1987b. Benefits and costs of biparental and uniparental reproduction in plants. Pages 233–252 in B. Levin and R. Michod, eds. *The evolution of sex: an examination of current ideas*. Sinauer, Sunderland, Mass.
- Maynard Smith, J. 1971. What use is sex? *Journal of Theoretical Biology* 30:319–335.
- McCracken, G. F., and R. K. Selander. 1980. Self-fertilization and monogenic strains in natural populations of terrestrial slugs. *Proceedings of the National Academy of Sciences of the USA* 77:684–688.
- Meagher, T. R. 1986. Analysis of paternity within a natural population of *Chamaelirium luteum*. I. Identification of most-likely male parents. *American Naturalist* 128:199–215.
- . 1991. Analysis of paternity within a natural population of *Chamaelirium luteum*. II. Patterns of male reproductive success. *American Naturalist* 137:738–752.
- Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* 41:1149–1161.
- Morgan, M. T. 1992a. The evolution of traits influencing male and female fertility in outcrossing plants. *American Naturalist* 139:1022–1051.
- . 1992b. Attractive structures and the stability of hermaphroditic sex expression in flowering plants. *Evolution* 46:1199–1213.
- . 1994. Models of sexual selection in hermaphrodites, especially plants. *American Naturalist* 144(suppl.):S100–S125.
- Phillips, P. C., and S. J. Arnold. 1989. Visualizing multivariate selection. *Evolution* 43:1209–1222.
- Queller, D. C. 1983. Sexual selection in a hermaphroditic plant. *Nature (London)* 305:706–707.
- Ridley, M. 1988. Mating frequency and fecundity in insects. *Biological Reviews of the Cambridge Philosophical Society* 63:509–549.
- Schoen, D. J., and M. DuBuc. 1990. The evolution of inflorescence size and number: a gamete-packaging strategy in plants. *American Naturalist* 135:841–857.
- Snow, A. A. 1986. Pollination dynamics in *Epilobium canum* (Onagraceae): consequences for gametophytic selection. *American Journal of Botany* 73:139–151.
- Stacey, P. B. 1982. Female promiscuity and male reproductive success in social birds and mammals. *American Naturalist* 120:51–64.
- Stanton, M. L., A. A. Snow, and S. N. Handel. 1986. Floral evolution: attractiveness to pollinators influences male fitness. *Science (Washington, D.C.)* 232:1625–1627.
- Strathmann, R. R., M. F. Strathmann, and R. H. Emson. 1984. Does limited brood capacity link adult size, brooding, and simultaneous hermaphroditism? a test with the starfish *Asterina phylactica*. *American Naturalist* 123:796–818.
- Sutherland, W. J. 1985. Measures of sexual selection. *Oxford Surveys in Evolutionary Biology* 2: 90–101.
- Thornhill, R. 1976. Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta: Mecoptera). *American Naturalist* 110:529–548.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, ed. *Sexual selection and the descent of man, 1871–1971*. Aldine, Chicago.
- Wade, M. J., and S. J. Arnold. 1980. The intensity of sexual selection in relation to male behaviour, female choice, and sperm precedence. *Animal Behaviour* 28:446–461.

- Warner, R. R., D. R. Robertson, and E. G. Leigh, Jr. 1975. Sex change and sexual selection. *Science* (Washington, D.C.) 190:633–638.
- Willson, M. F., and N. Burley. 1983. *Mate choice in plants*. Princeton University Press, Princeton, N.J.
- Wilson, P., J. D. Thompson, M. L. Stanton, and L. P. Rigney. 1994. Beyond floral Batemanism: gender biases in selection for pollination success. *American Naturalist* 143:283–296.
- Wright, S. 1934. The method of path coefficients. *Annals of Mathematical Statistics* 5:161–215.
- . 1968. *Evolution and the genetic of populations*. Vol. 1. Genetics and biometric foundations. University of Chicago Press, Chicago.
- Yampolsky, C., and H. Yampolsky. 1922. Distribution of sex forms in the phanerogamic flora. *Bibliotheca Genetica* 3:1–62.
- Young, H. J., and T. P. Young. 1992. Alternative outcomes of natural and experimental high pollen loads. *Ecology* 73:639–647.