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ANIMAL MATING SYSTEMS: A SYNTHESIS BASED ON SELECTION THEORY

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Abstract.—Following principles used by A. J. Bateman, we identify the relationship between fecundity and mating success as the central feature in the operation of mating systems. Using selection theory from the field of quantitative genetics, we define the sexual selection gradient as the average slope of the relationship between fecundity and mating success and show how it can be estimated from data. We argue that sexual selection gradients are the key to understanding how the intensity of sexual selection is affected by mate provisioning, parental investment, and sex ratio.

We lack a conceptual framework that integrates the various perspectives on the evolution of mating systems despite a series of seminal contributions over the past few decades (e.g., Orians 1969; Trivers 1972; Emlen and Oring 1977; Wells 1977; Alcock 1980; Kluge 1981; Thornhill and Alcock 1983; Verrell 1989; Clutton-Brock 1991; Gwynne 1991). Such an integration would facilitate connections between the many disparate theoretical contributions in this area, formal links with evolutionary theory, stronger empirical analyses with more tightly defined variables, and phylogenetic comparisons. The aim of this article is to attempt such an integration, with a special focus on the connection between mating systems and selection theory.

Key contributions in mating system theory seem disconnected because they deal only with particular aspects of selection. For example, Bateman's (1948) important article deals with the relationship between fecundity and mating success and why that relationship differs between males and females. The relationship between fecundity and mating success is in turn modified by nuptial gifts (see, e.g., Thornhill 1976) and by parental investment (see, e.g., Trivers 1972). Some of Bateman's conclusions dealing with the variance of mating success were later formalized in other work (Wade 1979; Wade and Arnold 1980). Parker (1978), Baylis (1981), and Sutherland (1985*a*) discussed how mate search and handling times affect mating success. And yet other workers have sought the environmental and social causes of male and female dispersion patterns and encounter rates

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and their relations to the potential for monopolization of mates (Orians 1969; Emlen and Oring 1977; Alcock 1980; Thornhill and Alcock 1983; Vehrencamp and Bradbury 1984; Ims 1988; Sullivan 1989; Graves and Duvall 1990; Schwagmeyer 1990; Davies 1991). How can these disparate contributions be pulled together?

An additional challenge is provided by recent advances in molecular genetics. Techniques such as DNA fingerprinting promise routine diagnosis of paternity and maternity in natural populations (see, e.g., Gibbs et al. 1990). The fruits of such diagnosis, applied to a large sample of progeny in a population, can be visualized as a *parental table* with rows and columns representing, respectively, potential mothers and fathers and with entries representing the number of progeny produced by each possible parental combination. We depart from some past attempts at conceptualization of mating systems by seeking a framework that makes full and explicit use of the data inherent in the parental table. Clutton-Brock and Vincent (1991), for example, use only the most extreme male and female parent in a population sample to characterize the mating system. Their approach is ad hoc and at best a shortcut. Our approach is to seek concepts that make full use of the data that are becoming available as molecular genetics sweeps into behavioral ecology and to anchor those concepts in formal selection theory.

Concepts of selection used in the field of quantitative genetics enable us to see connections between the key variables that dominate discussions of mating systems (mating success, parental investment, mate monopolization, nuptial gifts, rates of mate encounter, etc.). Selection can be viewed as a statistical relationship between traits (the measurable attributes of individuals) and fitness (Lande and Arnold 1983). The characters that affect fitness can be arranged in a hierarchy (Falconer 1989). A useful ordering of traits that affect male fitness (measured as a progeny count) at a particular age is shown in figure 1. In the first rank are the primary components (fecundity and mortality) of age-specific fitness, the principal traits in discussions of life-history evolution. In the second rank are the proximate determinants of age-specific fecundity and mortality. To analyze mating systems we have found it convenient to recognize mating success and fecundity per mate as the proximate determinants of age-specific fecundity. In the third rank are the primary determinants of mating success and mate fecundity (e.g., mate-cycling time, mate persuasive ability, nuptial gifts, and parental investment). Finally, in the fourth rank are traits that influence the third rank (e.g., mate search time, male weaponry, courtship pheromones, and other tools of mate persuasion) and that may affect age-specific mortality. A diagram analogous to figure 1 could be drawn for females.

Variables in the ranks closer to fitness can be defined so that they have easily specified relations to fitness. Standard demographic theory specifies the relationships between age-specific fecundity and mortality and lifetime fitness and so characterizes the selection that acts on those fitness components. As we move farther away from fitness to characterize the primary determinants of age-specific fecundity, we retreat from generality because the relationship between primary determinants and fecundity changes in different types of mating system. Nevertheless, the relationship between mating success and fecundity emerges as a key

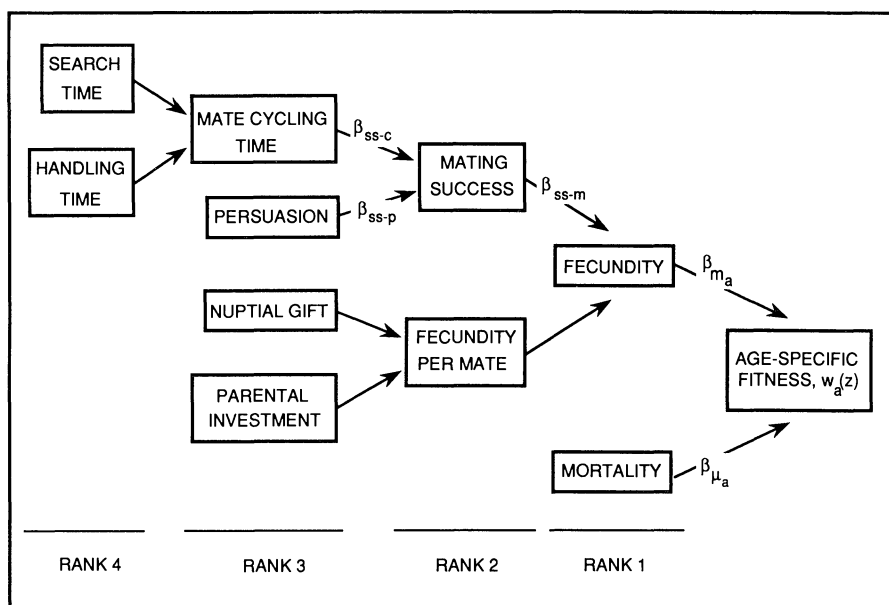


FIG. 1.—A hierarchy of traits that affect age-specific fitness of males, displayed as a path diagram. The symbols on paths denote selection coefficients known as selection gradients and are defined in the text. For simplicity, residual contributions to fecundity, fecundity per mate, and mating success are not indicated on the diagram.

component of selection in mating systems, and so, as an important target of empirical studies.

In the sections that follow we analyze selection as it operates in mating systems, beginning close to fitness itself and then working outward in the trait hierarchy (fig. 1) toward traits that classically have been considered sexually selected (e.g., male weaponry and agents of mate persuasion; Darwin 1871). We begin with a review of phenotypic selection in age-structured populations (Lande 1982) so that we can use those results to address the problem of measuring selection in animals that breed over a series of seasons. We then focus on the relationship between mating success and fecundity, a primary component of sexual selection. We use a series of models to explore that relationship in a variety of mating systems (e.g., systems with and without nuptial gifts and parental care). Our goal is to analyze the potential contribution of various factors to sexual selection.

SELECTION THEORY

Evolution depends on both inheritance and selection. A useful formalization of this statement is provided in the field of quantitative genetics, which deals with the per-generation change in multiple traits each affected by many genes. The change in the means of multiple traits from one generation to the next can be predicted from a standard equation from quantitative genetics,

$$\Delta \bar{z} = G\beta, \quad (1)$$

in which the element $\Delta\bar{z}_i$ of the column vector $\Delta\bar{\mathbf{z}}$ is the per-generation change in the mean of the i th trait; \mathbf{G} is a symmetric matrix of additive genetic variances and covariances (with additive genetic variances as diagonal elements and additive genetic covariances as off-diagonal elements); and $\boldsymbol{\beta}$ is a column vector of selection coefficients in which β_i represents the force of directional selection acting directly on the i th trait (Lande 1979). The selection coefficients, $\boldsymbol{\beta}$, are known as *selection gradients* and are each equivalent to a partial regression of relative fitness on a trait, with other traits held constant,

$$\boldsymbol{\beta} = \mathbf{P}^{-1} \mathbf{s}, \quad (2)$$

with \mathbf{P} representing the phenotypic variance-covariance matrix of the traits before selection (Lande and Arnold 1983) and with the selection differential

$$\mathbf{s} = \text{COV}[w(\mathbf{z}), \mathbf{z}], \quad (3)$$

a column vector of covariances between relative fitness, $w(\mathbf{z})$, and the traits, \mathbf{z} (Robertson 1966). Thus, the relationship between relative fitness and the traits can be represented as a multiple regression equation,

$$w(\mathbf{z}) = c + \beta_1 z_1 + \beta_2 z_2 + \dots + \beta_n z_n + \epsilon, \quad (4)$$

in which c is a constant, z_i is the value of the i th phenotypic trait, and ϵ is an error term. Equation (4) may be visualized as a path diagram (Wright 1934, 1968; Li 1975) (fig. 2a).

Relative fitness in a population that is neither increasing nor decreasing in numbers is simply the number of progeny (commonly counted at the zygote stage) produced in a lifetime, scaled so that its mean is one. We shall, however, be concerned with populations in which this simple progeny count concept of lifetime fitness is complicated for two reasons: population size may be changing, and each mature individual may reproduce over a sequence of breeding seasons (or ages). Fitness in such populations has been analyzed by Charlesworth (1980) and Lande (1982), building on the demographic theory of Lotka (1956), Fisher (1958), and Keyfitz (1968). The relative fitness of the phenotypic class \mathbf{z} at a particular age a , $w_a(\mathbf{z})$, is the product of the probability of survival to age a , $l_a(\mathbf{z})$, and fecundity at age a , $m_a(\mathbf{z})$:

$$w_a(\mathbf{z}) = l_a(\mathbf{z}) m_a(\mathbf{z}). \quad (5)$$

The intrinsic rate of increase for the population, r , is defined by the equation

$$\sum_{a=0}^{\omega} e^{-ra} l_a(\mathbf{z}) m_a(\mathbf{z}) = 1,$$

in which ω is the age at the last reproduction, and it is assumed that reproduction is concentrated into a brief breeding season each year (Leslie 1966). In a population that may be increasing or decreasing, lifetime fitness is a weighted sum of the expected number of progeny that are produced at each age:

$$w(\mathbf{z}) = \beta_{w_0} w_0(\mathbf{z}) + \beta_{w_1} w_1(\mathbf{z}) + \dots + \beta_{w_\omega} w_\omega(\mathbf{z}), \quad (6)$$

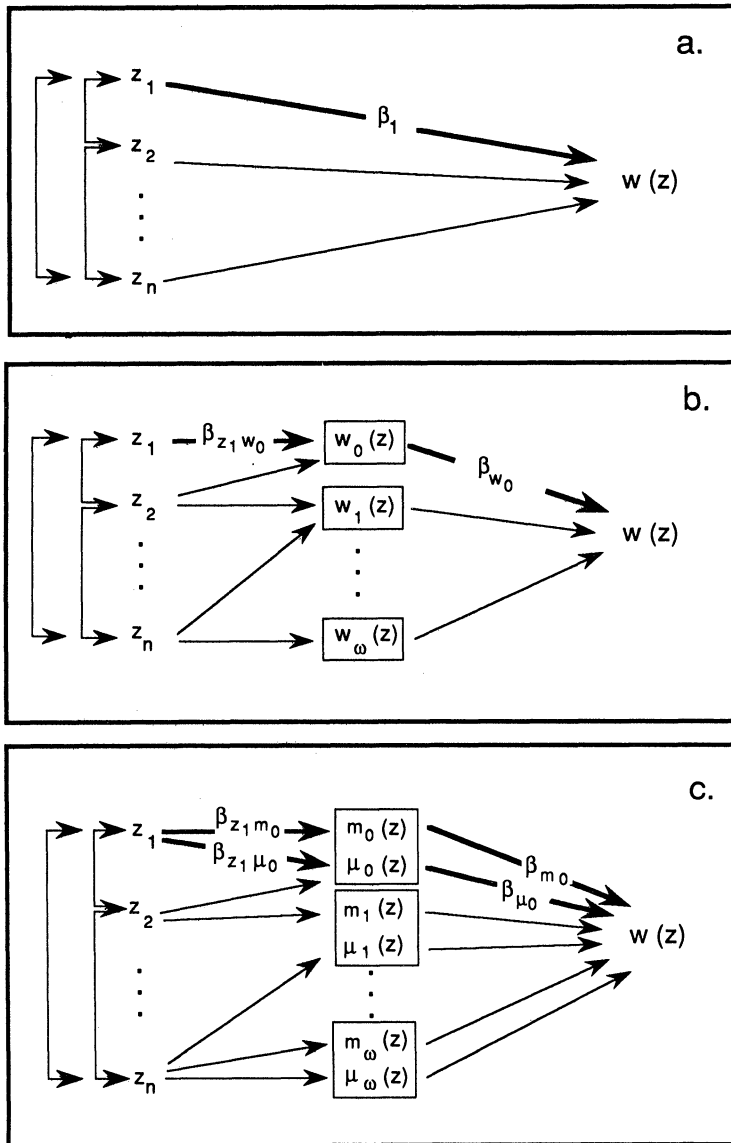


FIG. 2.—Path diagrams illustrating the decomposition of lifetime selection into parts representing age-specific fecundity and mortality selection. The *double-headed arrows* represent phenotypic covariances between phenotypic traits, denoted z_1, z_2, \dots, z_n . *a*, Path diagram representing the multiple regression of lifetime fitness, $w(z)$, on the phenotypic traits. Direct paths from the traits to lifetime fitness are total selection gradients (e.g., β_1). For simplicity, a residual effect on lifetime fitness is not indicated. *b*, Path diagram showing the decomposition of total selection on each trait into paths representing age-specific selection. $w_a(z)$, Fitness at age a . For simplicity, residual effects on age-specific fitness are not shown. *c*, Path diagram showing the decomposition of age-specific selection on each trait into paths representing age-specific fecundity and mortality selection. $m_a(z)$, Fecundity at age a ; $\mu_a(z)$, mortality at age a . For simplicity, residual effects on age-specific fecundity and mortality are not indicated.

in which

$$\beta_{w_a} = e^{-ra}/T, \quad (7)$$

with T denoting the generation time, or mean age of reproducing parents (Lande 1982). The coefficients β_{w_a} are the selection gradients for age-specific fitnesses. Multiple regression equation (6) may be visualized as a path diagram (fig. 2*b*). We see from equations (6) and (7) that, in a growing population ($r > 0$), progeny produced at early ages receive more weight in the tally of lifetime fitness than progeny produced at later ages (when the population is larger).

RESULTS

Selection within a Season as a Component of Lifetime Selection

Many empirical studies of mating systems are conducted in a single breeding season and focus on fecundity relationships. Consequently, it is important to consider the relationship between fecundity in a particular season (at a particular age) and lifetime fitness. Lande (1982) has shown that the lifetime fitness of a particular phenotypic class may be represented as a weighted sum of age-specific fecundity, $m_a(\mathbf{z})$, and mortality terms, $\mu_a(\mathbf{z})$:

$$w(\mathbf{z}) = \sum_{a=0}^{\omega} [\beta_{m_a} m_a(\mathbf{z}) + \beta_{\mu_a} \mu_a(\mathbf{z})], \quad (8)$$

with

$$\beta_{m_a} = e^{-ra} \bar{w}_a / T \bar{m}_a, \quad (9a)$$

and

$$\beta_{\mu_a} = - \sum_{y=a}^{\omega} e^{-ry} \bar{w}_y / T, \quad (9b)$$

in which \bar{w}_a is the average over all phenotypic classes of age-specific fitness, $w_a(\mathbf{z})$, and \bar{m}_a is the average over all phenotypic classes of age-specific fecundity, $m_a(\mathbf{z})$ (Lande 1982). Equation (8) may be represented by the path diagram shown in figure 2*c*. Selection coefficients for age-specific fecundity and mortality selection on each trait in \mathbf{z} may be obtained by substituting equation (8) into equation (3), using the definition of partial regression coefficients (Kendall and Stuart 1979, p. 346),

$$\beta_{zm_a} = \mathbf{P}^{-1} s_{m_a} \quad (10a)$$

and

$$\beta_{z\mu_a} = \mathbf{P}^{-1} s_{\mu_a}, \quad (10b)$$

in which s_{m_a} is the vector of covariances between fecundity at age a and the traits and s_{μ_a} is the vector of covariances between mortality at age a and the traits. Referring to figure 2*c*, we see that these coefficients represent the direct paths

from the traits to age-specific fecundity and mortality. Using equation (2), we find that total selection on a trait, z_i , can be represented as a sum of age-specific fecundity and mortality selection coefficients:

$$\beta_i = \sum_{a=0}^{\omega} [\beta_{z_i m_a} \beta_{m_a} + \beta_{z_i \mu_a} \beta_{\mu_a}]. \quad (11)$$

Thus, total selection on a trait can be viewed as a sum of direct paths connecting the trait to lifetime fitness. Along any path (e.g., from z_1 to $m_0(\mathbf{z})$ to $w(\mathbf{z})$), selection can be viewed as a product of selection gradients (e.g., $\beta_{z_1 m_0} \beta_{m_0}$). Furthermore, the selection gradients for age-specific fecundity and mortality, β_{m_a} and β_{μ_a} , represent the final common paths to fitness for selection that acts at any age.

In the sections that follow we shall concentrate on selection that acts on a cohort of animals within a particular breeding season. Actual data that would mesh with these conceptualizations would consist of observations of phenotypic traits (mate search time, mate-handling time, etc.), components of fecundity (number of mates and their average fecundity), and fecundity and mortality on each individual in a sample from a cohort. In many actual data sets age is unknown or, if known, some cohorts may be small in number. In the Discussion section we shall take up these problems. For the moment, our focus is selection that acts on a set of like-aged individuals in a single breeding season. Accordingly, in the sections that follow we will subscript fecundity with symbols that denote males or females, rather than age.

Effects of Mating Success on Fecundity within a Season

The contributions of age-specific fecundity and mortality to lifetime fitness can be viewed as selection gradients and can be estimated from a life table (eq. [9]). Selection on fecundity at a particular age is simply a function of average relative fitness at that age, the growth rate of the population, and generation time (eq. [9a]). The selection gradient for fecundity at a particular age represents the final common path for selection on all those traits that affect fecundity (fig. 2c).

The number of mates that bear the progeny of an individual male or sire the progeny of an individual female is more directly related to fitness than a simple count of all mating partners. For this reason, we will refer to the number of mates that sire or bear progeny as *mating success* (Wade and Arnold 1980). When we consider mating systems, the most important attribute affecting fecundity is mating success.

Mating success, fecundity, and sexual selection gradients.—The relationship between mating success and fecundity is a critical aspect of the mating system for several reasons. First, this relationship represents the final common path to fitness for all sexually selected traits. Consequently, it represents an important parameter in empirical studies of sexual selection. Second, the differences between males and females in the effect of mating success on fecundity provide a quantitative way of predicting the form of the mating system. And, third, the

functions relating male and female fecundity to mating success provide a way of viewing the effects of mate provisioning and parental investment.

Bateman (1948) stressed the importance of the correlation between mating success and fecundity. In male *Drosophila* this correlation was strong, but in females it was weak. Bateman viewed the higher variance of mating success in males as a mere sign of sexual selection, but he viewed the stronger correlation in males between mating success and fecundity as the cause of sexual selection. To make an explicit connection to selection theory it will be useful to focus on the regression of fecundity on mating success, which is the number of additional progeny to be expected from each additional mate, rather than on the correlation.

The importance of the relationship between mating success and fecundity is that it defines the final common path to fecundity for all sexually selected traits. Selection can be conceptualized as the statistical relationship between a particular trait and fitness. In particular, directional selection on a trait can be quantified as the partial regression of fitness on the trait, with other traits held constant (Lande and Arnold 1983). In a path diagram representation of this argument, directional selection on the trait can be viewed as the direct statistical path from the trait to fitness (figs. 1 and 2). For a trait that has diverse effects on fitness, this direct path can be partitioned into parts that represent components of the total directional selection acting on the trait (Arnold 1983). We can view sexually selected traits as those traits that exert part of their effect on fecundity via their effects on mating success. For such traits, total sexual selection is the direct path that leads from the trait to fecundity via mating success and from fecundity to fitness. Because the final segment of the path from any sexually selected trait to fecundity is the segment from mating success to fecundity (fig. 1), the relationship between mating success and fitness defines a final common path for all sexually selected traits. We will refer to this final common path for sexually selected traits as the *sexual selection gradient*. How would we measure the sexual selection gradients for males and females in a particular population?

Estimating sexual selection gradients.—We will illustrate the steps in the calculation of sexual selection gradients for males and females using Bateman's (1948) data for *Drosophila melanogaster*. Bateman was able to determine the mothers and fathers of about 9,500 individual fruit flies by using visible genetic markers. The resulting data are in many ways comparable to data that could be achieved today with DNA fingerprints. At each trial Bateman placed three or four males together with an equal number of females for a 3- or 4-d period during which all matings and egg laying occurred. Bateman conducted his experiment in six blocks (or series) of four to nine trials. Flies in the last two series showed noticeably higher fecundities than flies in the first two series (presumably because of a change in maintenance conditions), so Bateman pooled series 1–4 separately from series 5–6 for data analysis, and so will we. In series 1–4 a total of 143 males and 143 females were potential fathers and mothers. The fathers could be determined for about 4,759 offspring, and mothers could be determined for about 4,641 offspring (the actual numbers are not given by Bateman but can be estimated from his published data summaries). Likewise for series 5–6, about 4,877 offspring were assigned to 72 potential fathers and about 4,849 progeny were

assigned to 72 potential mothers. Once the assignment of parents has been accomplished, the number of mating partners that produced progeny (mating success) can be determined for each potential parent as well as each parent's total fecundity. Average fecundity as a function of mating success is shown in figure 3. To estimate the sexual selection gradient for each sex, we compute the slope of the least-squares regression line relating fecundity to mating success. In Bateman's series 1–4, the slopes are about 23 offspring per mate for males and 15 offspring per mate for females (fig. 3*a*). In series 5–6, the slopes are about 39 offspring per mate for males and two offspring per mate for females (fig. 3*b*). In other words, in series 5–6, on the average, a male gains 39 offspring for each additional mate but a female gains only two offspring for each additional mate. The sexual selection gradient for males is 1.6 times higher than the sexual selection gradient for females in series 1–4; the male gradient is nearly 17 times higher than the female gradient in series 5–6. Although one can calculate the regression slopes of Bateman's data from his published summaries, statistical tests for male-female differences are difficult without recourse to the raw data. Statistical comparison of regression slopes is described by Sokal and Rohlf (1981) and in many other textbooks.

The evident nonlinearity of female fecundity as a function of mating success (fig. 3*b*) may worry some readers. This function may be curvilinear and asymptotic in females, but that does not invalidate the calculation of a linear regression slope. Our aim is not to describe the relationship between fecundity and mating success with a straight line. If description were the goal, one would try fitting a second- or higher-order polynomial to the data. We do not claim that a straight line fits the female data in figure 3*b* as well as a curved line. Our aim is to estimate the directional selection gradient for mating success. It has been shown (Lande and Arnold 1983) that such gradients are best estimated by a linear regression slope even when the relationship is nonlinear. In other words, we are computing a linear regression slope because it estimates a coefficient of directional selection (the average effect of a change in mating success on fecundity), not because we claim that a straight line is an adequate fit to the data.

The sexual selection gradients we have estimated for Bateman's data apply to the conditions in his experiment and may not prevail in nature. For example, in other experimental studies, the fecundity of female *D. melanogaster* that have mated two or more times is usually not different from the fecundity of females that have mated only once (Lefevre and Jonsson 1962; Boorman and Parker 1976; Prout and Bundgaard 1977; Pulvermacher and Timmer 1977; but see Pyle and Gromko 1978). Thus, under some circumstances there may not be a fecundity premium on multiple mating by female *Drosophila*. In any case, to assess the sexual selection gradient in a natural population one would need to determine the number or proportion of surviving females that do not mate. Because the relationship between female fecundity and mating success is nonlinear in *D. melanogaster*, its average slope (the sexual selection gradient) will vary if the proportions of females in different mating success categories change.

To simplify expressions for sexual selection gradients in the following sections, we will assume that neither mating success nor its determinants (e.g., search and

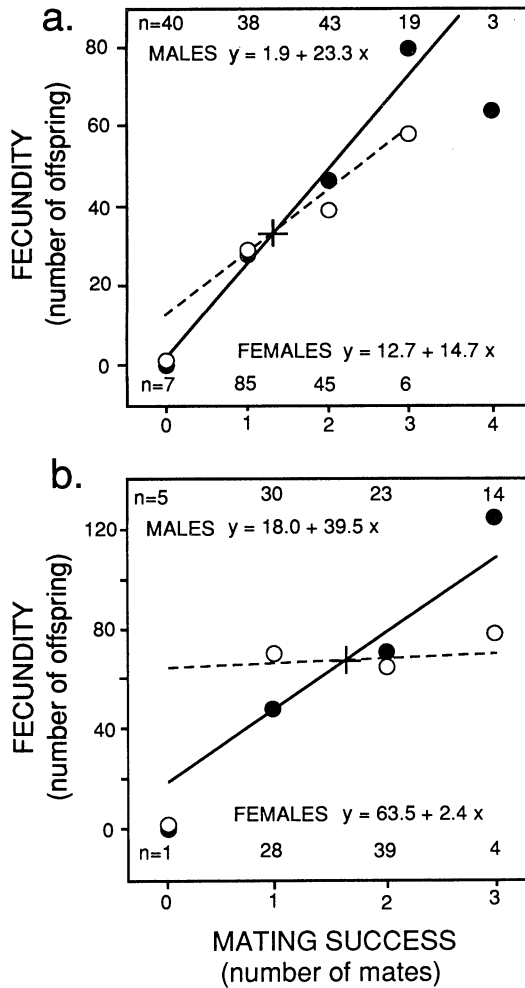


FIG. 3.—Regression analysis of Bateman's (1948) data relating fecundity to mating success in *Drosophila melanogaster*. Average fecundity for males (solid circles) and females (open circles) is plotted as a function of mating success. Sample sizes for males and females are shown, respectively, at the top and bottom of each figure. Weighted, linear regressions of fecundity on mating success are shown for males (solid lines) and females (dashed lines). The bivariate means for males and females coincide in each plot and are indicated with a cross. a, Combined data for series 1–4. b, Combined data for series 5–6.

handling times and persuasion) at a particular age are correlated with mortality at that or later ages. We will then view sexual selection as regressions of mating success on attributes (or of fecundity on mating success) that do not hold mortality constant. Of course, in an analysis of actual data, no such assumption may be necessary. Sexual selection gradients could be computed as partial regressions that take into account effects on mortality.

The Effects of Mate Provisioning and Parental Investment on the Sexual Selection Gradients of Males and Females

Mate provisioning (nuptial gifts) and parental investment are key aspects of the mating system because they affect the sexual selection gradients of males and females. If the male does not care for the offspring, his offspring production may be an ever-increasing function of his mating success. In the absence of any provisioning by her mate, the female may experience no gain in fecundity by mating more than once in a breeding season. Mate provisioning changes her sexual selection gradient, for now with each additional mating she may be able to increase her fecundity. When one or both sexes care for offspring, the relationship between progeny production and mating success may be asymptotic because investment in broods early in the season may compromise the size of broods produced later in the season with other mates. Thus, both mate provisioning and parental investment can affect sexual selection gradients and so produce fundamental differences in how sexual selection operates in males and females.

These ideas can be made more precise by modeling the relationship between fecundity and mating success under various conditions of mate provisioning and parental investment. In the following sections our focus is on selection that operates in an annual species or in a single breeding season of an iteroparous species. We also assume a stationary population with no age structure (or data that have been corrected for age structure). Appendix A lists the variables that we will use. In each of the sections that follow we first make some simplifying assumptions about the mating system so that we can express the average fecundity of males or females as a function of average mating success. We then take the partial derivative of average fecundity with respect to average mating success and equate this partial derivative with the sexual selection gradient. This step relies on results given in earlier articles (Lande 1979; Lande and Arnold 1983), which show the equivalence of partial derivative and partial regression definitions of selection gradients. Consequently, we obtain expressions for sexual selection gradients that involve various key aspects of the mating system (e.g., the average fecundity of the opposite sex and the effects of nuptial gifts and parental care on fecundity). These expressions for sexual selection gradients enable us to identify critical aspects of the mating system that affect sexual selection and to evaluate their contributions.

No nuptial gift or paternal care of offspring.—A simple starting point is a mating system in which the male's fecundity increases linearly with his mating success whereas the female's fecundity fails to increase once she secures a single mate (fig. 4, curve *a*). These circumstances come close to fitting at least some of Bateman's (1948) *Drosophila* data (fig. 3*b*). The female might mate two or more times, but her fecundity does not increase after her first mating. In such systems, a female's multiple mating might, however, affect the progeny count of her mates. Let us imagine a system with multiple paternity in which a male's progeny number by a particular female is simply an inverse proportion of the number of males with whom she has mated. Then the proportion of a female's progeny that a male can expect to sire is $1/H_x$, where H_x is the harmonic mean mating success of

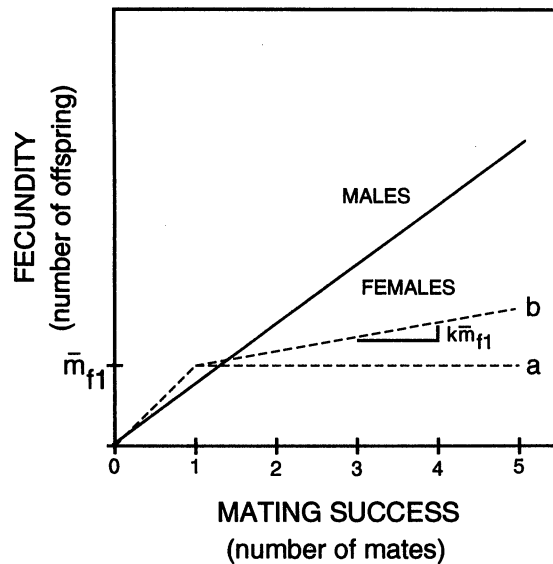


FIG. 4.—Relationships between fecundity and mating success in males and females when only females provide parental care. The relationship of fecundity to mating success is linear in males. The expected number of progeny produced by a female with one mate is \bar{m}_{f1} . When the male provides no nuptial gift, female fecundity does not increase if the female mates more than once (curve *a*). When the male provides a nuptial gift, female fecundity increases by the amount $k\bar{m}_{f1}$ with each mating beyond the first (curve *b*).

females mating one or more times. A discussion of harmonic mean mating success and mixed paternity of broods can be found elsewhere (Wade and Arnold 1980). Let \bar{m}'_f be the average fecundity of females with one or more mates and let \bar{m}_f be the average fecundity of all females. It follows that $\bar{m}'_f = \bar{m}_f/p$, where p is the proportion of females that mate one or more times and bear progeny. Thus, on the average, a male's mate will produce \bar{m}'_f progeny and the average proportion of progeny that the male can expect to sire is $1/H_x$. If it is assumed that there is no correlation between male mating success and mate fecundity, expected fecundity in the male population, \bar{m}_m , is given by the equation

$$\bar{m}_m = \frac{\bar{m}_f \bar{x}_m}{pH_x},$$

where \bar{x}_m is the mean mating success of males. The partial derivative of \bar{m}_m with respect to \bar{x}_m may be termed the male sexual selection gradient, since it indicates how much fecundity is affected by mating success. In the present system, the sexual selection gradient for males, β_{ss-m} , is given by the equation

$$\beta_{ss-m} = \frac{\bar{m}_f}{pH_x}. \quad (12a)$$

In females, the partial derivative of fecundity with respect to mating success is undefined at the bend shown in figure 4 (curve *a*), so it is convenient to view

the sexual selection gradient as the regression of fecundity on mating success. We find that the covariance for all females (mated and unmated) is $(q/p)\bar{m}_f\bar{x}_f$, where q is the proportion of females capable of breeding that do not mate ($q = 1 - p$); \bar{x}_f is the average mating success of all females capable of breeding (mated and unmated). The sexual selection gradient for females, β_{ss-f} , is then given by the equation

$$\beta_{ss-f} = \frac{q\bar{m}_f\bar{x}_f}{p\sigma_{x-f}^2}, \quad (12b)$$

where σ_{x-f}^2 is the variance of female mating success for all females (including the zero class with no mates). Thus, mating failure is a primary cause of sexual selection on females in a mating system with no nuptial gifts and no paternal care of offspring. In such a mating system, sexual selection on females vanishes ($\beta_{ss-f} = 0$) when all females capable of breeding succeed in mating. The other proximate cause of sexual selection on females is the variance of mate number. The variance of the mating success of females diminishes sexual selection on females when there are no nuptial gifts or paternal care.

An inverse relationship between sexual selection and the variance of mating success may seem paradoxical. Indeed, we might consider the relative variance of female mating success ($\sigma_{x-f}^2/\bar{x}_f^2$) to represent the opportunity for sexual selection in females (Houck et al. 1985). However, sexual selection on any female trait is constrained by the relationship shown in figure 4 within the limits set by the opportunity for sexual selection. The average slope of the relationship between female fecundity and mating success decreases with increasing variance of female mating success. This effect of variance of mating success evidently places a tighter limit on sexual selection in females than does the opportunity for sexual selection.

An examination of some special cases suggests that the sexual selection gradient of males will generally be greater than the female gradient in this simple mating system. For example, if all females mate ($q = 0$), the sexual selection gradient of males will always be greater than the female gradient because $\beta_{ss-m} = \bar{m}_f/H_x$ and $\beta_{ss-f} = 0$. When some females fail to mate but no female mates more than once, the sexual selection gradients of males and females are identical (\bar{m}_f/p) because $\bar{x}_f = p$, $\sigma_{x-f}^2 = pq$, and $H_x = 1$. As a third case, consider the gradients of males and females when some females fail to mate, those that do mate may mate more than once, and female mating success follows a Poisson distribution ($\sigma_{x-f}^2 = \bar{x}_f$). Under these conditions $\beta_{ss-f} = q\bar{m}_f/p$ and β_{ss-m} is given by equation (12a). Because the arithmetic mean is greater than the harmonic mean, $\bar{x}_f/p > H_x$, where \bar{x}_f/p is the arithmetic mean mating success of females with one or more mates. Consequently we find that a sufficient condition for the male sexual selection gradient to exceed the female gradient is $(p/q) > \bar{x}_f$, where p/q is the odds that a female in the population will mate at least once. This condition is bound to hold so long as the odds that a female mates are greater than one ($p > 0.5$) and females do not show a strong tendency for multiple mating. For example, if 80% of the females mate at least once ($p = 0.8$), the odds of

mating are four. For our condition to fail, the average female would have to have four or more mates.

Nuptial gifts.—In a variety of animals the female's fecundity is enhanced by materials received from her mate. The female may feed on a prey item presented to her by the copulating male, feed on a portion of the spermatophore, metabolize seminal fluid, or consume the male himself (Thornhill 1976; Thornhill and Alcock 1983; Gwynne 1991). We will consider all such copulatory contributions to female fecundity as nuptial gifts.

The effect of nuptial gifts on the sexual selection gradients of the two sexes can be readily evaluated in a simplified scheme in which the female's expected fecundity is zero if she fails to mate, is \bar{m}_f if she gets one mate, and thereafter increases by an amount $k\bar{m}_f$ with each additional mate (fig. 4, curve *b*). The variable k ranges between zero and one. For example, if $k = 0.2$, the effect of each nuptial gift is to increase the female's clutch size by 20%. We assume that there is no covariance between the size of the nuptial gifts a female receives and her mating success. Using the relationship $\bar{m}_f = \bar{m}_f[(1 - k)p + k\bar{x}_f]$, we find that the covariance between fecundity and mating success for all females (mated and unmated) is $\bar{m}_f[(1 - k)q\bar{x}_f + k\sigma_{x-f}^2]$. So the sexual selection gradient for females is given by the equation

$$\beta_{ss-f} = \frac{\bar{m}_f[(1 - k)q\bar{x}_f + k\sigma_{x-f}^2]}{\sigma_{x-f}^2}. \quad (13)$$

The sexual selection gradient for males is given by equation (12a).

The addition of nuptial gifts to a mating system will increase the intensity of sexual selection on females. Consider mating systems in which all females mate. In the absence of nuptial gifts there is no sexual selection on females (eq. [12b] with $q = 0$), but with nuptial gifts the sexual selection gradient on females is $k\bar{m}_f$ (eq. [13] with $q = 0$). The greater the effect of the nuptial gift on female fecundity, the stronger the sexual selection acting on females.

Although the addition of nuptial gifts to a mating system will increase sexual selection on females, it appears that males will nevertheless experience stronger sexual selection. If we consider the same three special cases that we considered in a mating system that lacks nuptial gifts, we find that sexual selection on males exceeds sexual selection on females under the same sets of conditions. Thus, when all females mate ($q = 0$), we find that the male sexual selection gradient is always greater than the female gradient. When females mate no more than once, the sexual selection gradients of males and females take the same value, \bar{m}_f . Finally, when female mating success is Poisson distributed, a sufficient condition for the male gradient to exceed the female gradient is $(p/q) > \bar{x}_f$, which is easily satisfied. In summary, although we have shown that females will sometimes experience weaker sexual selection than males in a system with nuptial gifts, we have not shown that females always experience weaker sexual selection. It remains to be shown whether plausible circumstances exist under which females experience stronger sexual selection than males. Nevertheless, it is easy to show that females can experience substantial sexual selection and perhaps this demonstration is the more important message for empirical studies.

Parental investment.—In the preceding section we considered male contributions that increased female fecundity. We now turn to parental care and its cost to the parent's subsequent fecundity. Trivers (1972, p. 139) made the provocative suggestion that parental care could be measured by its negative impact on the subsequent reproduction of the parents. He defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving . . . at the cost of the parent's ability to invest in other offspring." We can capture the essential feature of parental investment by considering the sizes of successive broods produced by a female. In a mating system with maternal investment, the female parent invests in her current brood at the cost of reducing the size of her next brood. If males invest, their successive broods would be reduced by a characteristic amount. We can use this characterization to assess the impact of parental investment on sexual selection.

Let the size of the female's $n + 1$ th brood be less than the size of the n th brood by an amount equal to b_f (our measure of maternal investment) times the size of the n th brood: $\bar{m}_{fn+1} = \bar{m}_{fn} - b_f \bar{m}_{fn}$, where $0 < b_f < 1$. For example, when $b_f = 0.2$, successive broods are reduced in size by 20%. Suppose too that each brood is sired by a different mate. The number of progeny in the n th brood (sired by the n th mate) is a binomial series equal to $\bar{m}_{f1}(1 - b_f)^{n-1}$ for $n \geq 1$. The total number of progeny expected from all n mates is the n th partial sum of a geometric series:

$$\bar{m}_f = \frac{\bar{m}_{f1}(1 - c_f^n)}{b_f}, \quad (14)$$

where $c_f = 1 - b_f$. The expected progeny number converges on a limit equal to \bar{m}_{f1}/b_f with increasing number of mates, since $0 < c_f < 1$. For example, if the number of offspring expected from the first mate is $\bar{m}_{f1} = 10$ and parental investment $b_f = 0.2$, then even a female mating with an infinite number of males could have a total of no more than 50 progeny. The family of curves relating fecundity to mating success is shown in figure 5a for the case in which a single mating yields 10 offspring, that is, $\bar{m}_{f1} = 10$.

We can solve for the female sexual selection gradient by taking the partial derivative of expected fecundity with respect to average mating success, using equation (14), equating n with \bar{x}_f , and noting that $c_f^{\bar{x}_f} = e^{(\ln c_f)\bar{x}_f}$:

$$\beta_{ss-f} = \frac{\bar{m}_{f1} c_f^{\bar{x}_f} \ln c_f}{-b_f}. \quad (15a)$$

From this equation we can conclude that increasing maternal investment and higher average mating success by females both reduce the intensity of sexual selection on females. Notice in figure 5a that the curves are generally flatter with increasing parental investment (larger b) and with increasing mating success. An equation analogous to equation (14) holds for males if we assume that a male sires all offspring in a brood. If we also assume that each brood is produced by a different female,

$$\beta_{ss-m} = \frac{\bar{m}_{f1} c_m^{\bar{x}_m} \ln c_m}{-b_m}, \quad (15b)$$

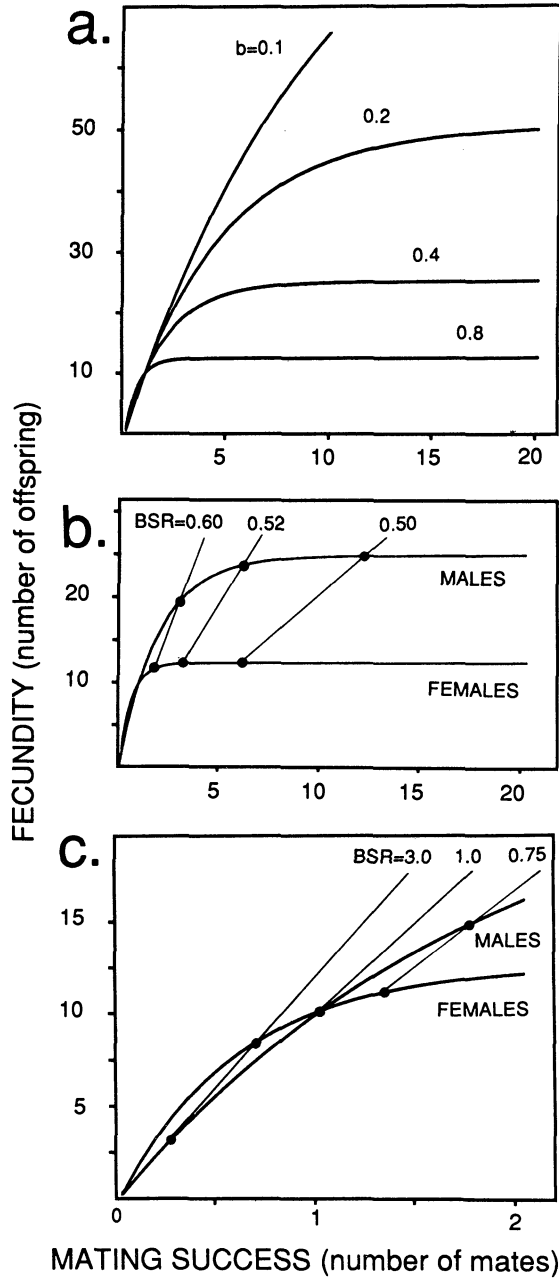


FIG. 5.—Effect of parental investment on relationships between fecundity and mating success. Expected fecundity is plotted as a function of average mating success. Each brood is produced with a different mate. In all cases, the number of offspring in the first brood is 10 ($\bar{m}_{f1} = 10$). *a*, Fecundity as a function of mating success when successive broods are reduced by 10%, 20%, 40%, and 80% ($b = 0.1, 0.2, 0.4, \text{ and } 0.8$). *b*, Fecundity as a function of mating success for a case in which males invest less in offspring than females. Males experience a 40% reduction in the size of successive broods ($b_m = 0.4$) but females experi-

with b_m and c_m possibly taking different values than the corresponding variables in females. As in females, increasing parental investment and higher average mating success reduce the sexual selection gradient.

The sex that invests less in offspring will experience stronger sexual selection. This result is illustrated in figure 5*b* and *c* for a case in which males invest less than females. Notice that the bivariate male and female means for fecundity and mating success must lie on a line that passes through the origin. This constraint arises because the total fecundity of one sex must equal the total fecundity of the other sex owing to the fact that each offspring has one mother and one father. Likewise, the total number of mates that bear the progeny of one sex must equal the total number of mates of the other sex (consider row and column totals in our parental table). Consequently, if we define the breeding sex ratio, BSR, as the ratio of breeding males to females, then $\bar{x}_f = \text{BSR } \bar{x}_m$ and $\bar{m}_f = \text{BSR } \bar{m}_m$. Thus, BSR constitutes a constraint that determines the positions of the male and female means on their respective curves for fecundity versus mating success. The position of the mean in turn specifies the sexual selection gradient for each sex (fig. 5*b*), which is the slope of the curve evaluated at the mean. Notice in figures 5*b* and *c* that the slope is always greater for males than for females. In other words, in a case in which the male invests less in offspring, the male sex always experiences a stronger sexual selection gradient than the female sex. When we reverse the sexual labels, we find that females experience stronger sexual selection than males if they invest less in offspring than males (fig. 6).

In the general case, under the constraint from equation (14) that

$$\bar{x}_f/\bar{x}_m = (1 - c_f^{\bar{x}})b_m/(1 - c_m^{\bar{x}})b_f,$$

the sexual selection gradient for males is always greater than the sexual selection gradient for females when females invest more than males ($b_f > b_m$). A proof by T. Nagylaki of this inequality is given in Appendix B. Likewise, the sexual selection gradient for females is always greater than the sexual selection gradient for males when males invest more than females ($b_m > b_f$). When males and females invest equally ($b_f = b_m$), $\bar{x}_f = \bar{x}_m$ and it is easy to show that the sexual selection gradients are equal for the two sexes.

Our result that the sex with less parental investment experiences stronger sexual selection should be viewed with some caution despite its resemblance to Trivers's (1972) conclusions. In particular, we have assumed that successive broods are produced with different mating partners and that mixed paternity does not prevail within broods. The dependence of our main results on those assumptions needs to be established.

The relationship of BSR to sexual selection deserves additional comment. When males invest less than females in offspring, both sexes experience stronger

ence an 80% reduction ($b_f = 0.8$). Male and female means (*dots*) are constrained to lie at the intersections of the *curves* with a line through the *origin*. Three cases are shown, corresponding to three different breeding sex ratios. *c*, Fecundity as a function of mating success for a case in which males invest less in offspring than females ($b_m = 0.4$, $b_f = 0.8$), showing expected fecundity when average mating success ranges from zero to two.

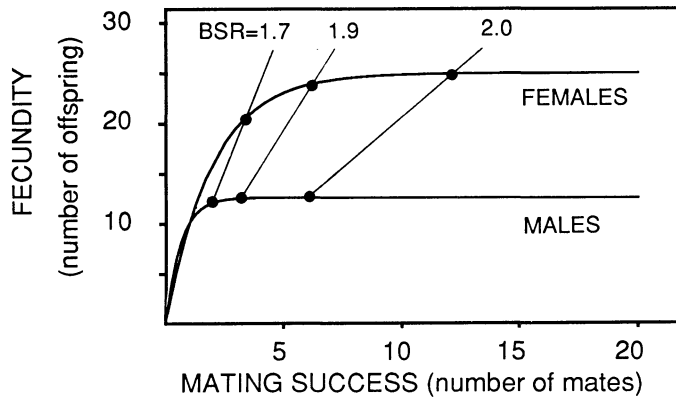


FIG. 6.—Relationships between fecundity and mating success for a case in which females invest less in offspring than males ($b_f = 0.4$, $b_m = 0.8$). Conventions are as in figure 5.

sexual selection (i.e., steeper sexual selection gradients) with increasingly male-biased BSR (fig. 5*b*, *c*). But, when females invest less than males, both sexes experience stronger sexual selection with increasingly female-biased BSR (fig. 6).

Determinants of Mating Success

In the preceding section we focused on how mating success affects the fecundity of males and females. We now move upstream from mating success (to the *left* in fig. 1) and ask how various traits affect mating success, with an emphasis on males. We will proceed by constructing models of mating systems so that we specify the relationship between average mating success and trait averages. We can then solve for the partial derivative of average mating success with respect to the average value of a trait. We will refer to such partial derivatives as sexual selection gradients for the traits in question. The product of such a sexual selection gradient for a particular male trait (e.g., β_{ss-h} , which denotes the sexual selection gradient for mate-handling rate, h) and the male selection gradient that characterizes the mating system (β_{ss-m}) yields the force of sexual selection acting on the trait. As before, we will concentrate on selection acting in a particular breeding season.

An encounter rate approach.—Parker (1978), Baylis (1981), and Sutherland (1985*a*) have argued that the essential difference between the sexes lies in rates of mate encounter and handling. Sutherland (1985*a*; 1985*b*) adapted models from renewal theory (Cox 1962) to characterize the two sexes. We extend Sutherland's approach by incorporating variation in mate handling time and sexual persuasion, as well as variation in time between encounters, and by relating the results to selection theory. By persuasion we mean the probability of mating given encounter. Our variables are summarized in Appendix C.

The following model applies best to mating systems that consist only of finding and processing mates. The model could be applied to systems of female-defense polygyny, competitive-mate-search polygyny, and scramble-competition polygyny (Thornhill and Alcock 1983; Duvall et al. 1991). Territorial systems may not

be well described by the model, which assumes statistical independence of searching and handling.

Consider a mating system in which males search for mates, attend to the sexual partners they encounter, and then renew their search. We will refer to the interval of time spent searching for successive mates as "search time" and the interval of time spent consorting with, courting, mating, and guarding each mate as the "handling time." Handling is not synonymous with mating, because some fraction of the potential mates that a male courts, consorts with, and so on, will not mate with him. The entire breeding season lasts some length of time, L , and throughout this interval each male spends all his time either searching for or handling mates. Although we assume that each male's searching and handling is not complicated by fighting or other interactions among males, male-male competition can also be considered with the present framework (Duvall et al. 1991). Suppose that male search time, s , has an arbitrary statistical distribution with mean α_s and variance σ_s^2 , and that handling time, h , has an arbitrary but independent distribution with mean α_h and variance σ_h^2 . The average time spent on a potential mate, called mate-cycling time, is $\alpha = \alpha_s + \alpha_h$. The variance of mate cycling time is $\sigma^2 = \sigma_s^2 + \sigma_h^2$. During the breeding season the average male will encounter and handle L/α mates, but not all of these potential sexual partners will mate. Suppose that on the average a proportion, α_p , of the encountered and handled partners actually mate. According to some results from Cox (1962), the expected mating success of a male during a breeding season of length L is

$$\bar{x}_m = \alpha_p L/\alpha. \quad (16)$$

Sutherland (1985a) used a special case of these results in which he assumed a Poisson distribution of search time, no variation in handling time and persuasion, and absolute certainty of mating given encounter ($\alpha_p = 1$).

Selection gradients for search and handling times, and persuasion.—Taking the partial derivatives of expected male mating success with respect to average search time and average handling time, we find that the sexual selection gradients for search time, β_{ss-s} , and handling time, β_{ss-h} , are given by the equation

$$\beta_{ss-s} = \beta_{ss-h} = -\alpha_p L/\alpha^2. \quad (17a)$$

Likewise, the sexual selection gradient for mate-cycling time, β_{ss-c} , is given by equation (17a). Thus, sexual selection favors shorter search and handling times. Selection is strongest on search, handling, and cycling times when the mating season is much longer than the average mate cycling time, $L \gg \alpha$, and when a high proportion of encountered males are persuaded to mate. Similarly, the sexual selection gradient for the persuasion trait, β_{ss-p} , is given by the equation

$$\beta_{ss-p} = L/\alpha. \quad (17b)$$

Likewise, the sexual selection gradients for L and L/α can be obtained by taking first derivatives according to equation (16).

We can use the preceding encounter rate model to evaluate the variance of male mating success. Noting from Cox (1962) that the variance of the number of mates cycled per season is $\sigma^2 L/\alpha^3$ and using the delta technique (Bulmer 1979, p. 79) to account for the contribution of the variance of persuasion, we find that

the variance of mating success is

$$\sigma_{x-m}^2 = \left(\frac{\alpha_p^2 L^2}{\alpha^2} \right) \left[\left(\frac{1}{\alpha L} \right) \sigma^2 + \left(\frac{1}{\alpha_p^2} \right) \sigma_p^2 \right], \quad (18a)$$

assuming statistical independence between cycling time and persuasion.

If we divide equation (18a) by the square of mean mating success ($\alpha_p L / \alpha$), we obtain the variance of relative mating success, I_{x-m} (standardized to a mean of one), which is a useful index of the opportunity for sexual selection (Crow 1958; Wade and Arnold 1980; Arnold 1986):

$$I_{x-m} = \left(\frac{1}{\alpha L} \right) \sigma^2 + \left(\frac{1}{\alpha_p^2} \right) \sigma_p^2. \quad (18b)$$

Thus, the opportunity for sexual selection is increased by a large variance of cycling time (arising from the variance of search and handling times) and persuasion, by a short average cycling time (α_p), a short breeding season, and low average persuasive ability (α). Notice that the effects of short cycling time and a short breeding season are to enhance the contribution of the variance of cycling time to the opportunity for sexual selection, whereas the effect of low average persuasion is to enhance the contribution of the variance of persuasive ability.

If we define the relative variance of the number of mates cycled to be the ratio of absolute variance of the number of mates cycled to the squared mean number of cycled mates ($I_c = \sigma^2 / \alpha L$) and define the relative variance of persuasion, I_p , according to the equation $I_p = \sigma_p^2 / \alpha_p^2$, then we can rewrite equation (18b) as

$$I_{x-m} = I_c + I_p. \quad (18c)$$

Thus, the opportunity for sexual selection is simply the sum of selection opportunities arising from the mate-cycling and persuasion processes.

Covariance between the number of mates cycled in a season and persuasive ability is easily included in the above results. This covariance is likely to be positive (e.g., large males cycle more mates and also have higher persuasive ability), but negative covariance (denoting a phenotypic trade-off) is also conceivable. If we relax the assumption of zero covariance, equation (16) is approximately correct, as are equations (18) with the addition of a covariance term. The effect is to add a factor of $(2\alpha / L\alpha_p) \sigma_{cp}$ inside the large brackets on the right side of equation (18a) and to the right sides of equations (18b) and (18c), where σ_{cp} denotes the covariance between the number of mates cycled and persuasive ability. Thus, positive covariance increases the opportunity for sexual selection (by enhancing the variance of mating success), whereas negative covariance decreases the selection opportunity.

DISCUSSION

Toward a General Theory of Mating Systems

Emlen and Oring (1977) have provided the most influential contribution to contemporary thinking about the evolution of mating systems. They viewed the

degree to which mates could be monopolized as the primary proximate determinate of the mating system and sought to explain monopolization in terms of the spatial distribution of resources and the temporal availability of mates. The elements in their scheme (operational sex ratio [OSR], environmental potential for polygyny, variance of reproductive success, intensity of sexual selection, and parental investment) continue to dominate discussions of mating systems. While most workers have continued to operate in the conceptual framework provided by Emlen and Oring, reliance on their framework is not without its frustrations: some key variables are undefined (e.g., intensity of sexual selection and environmental potential for polygamy) and verbal arguments unsupported by formal theory are used to draw connections between variables. This lack of support can create a false or inaccurate sense of connection between theory, hypothesis, and predictions. Consequently, it has been difficult to translate the Emlen and Oring framework into a program of precise field research and to test the veracity of their arguments. For example, most workers are convinced that the operational sex ratio and parental investment are key features of mating systems, but how can we evaluate their relative contributions? Thus, a primary contribution of the present article is to define key variables, so that they can be both measured and evaluated, and to seek interconnections between variables using a formal theory for the operation of sexual selection. The looseness of Emlen and Oring's (1977) framework means that some of their conclusions may not stand up to more detailed scrutiny. The claim of a pivotal role for the operational sex ratio is a case in point. "To understand the intensity of sexual selection it is not the overall population ratio of males to females that is of importance but rather . . . the operational sex ratio" (Emlen and Oring 1977, p. 216). Despite its accessibility in field studies, OSR may not be the most useful characterization of sex ratio in the analysis of mating systems. In a simulation study, Ims (1988) found that OSR was a poor predictor of the variance of male mating success in systems with mate searching and guarding. In our characterization of sexual selection, it is the BSR, rather than OSR, that plays a key role. The importance of BSR is that it constitutes a constraint on the means of mating success in males and females and so constrains the magnitude of sexual selection gradients. The importance of OSR may lie in its connections to BSR. Those connections need to be determined as well as the formal relationship between OSR and sexual selection.

The present contribution is less successful in responding to the central challenge posed by Emlen and Oring (1977): predicting the form of the mating system from the spatial and temporal distribution of resources. The key question is how these ecological distributions affect the patterns of encounter between males and females (see, e.g., Vehrencamp and Bradbury 1984). We have explored some patterns of mate encounter and evaluated the importance of persuasion, but we have not tied those encounter rate models to the statistics of resource dispersion. Simulation models (e.g., Ims 1988; Duvall et al. 1991) represent a start in this direction, however. Another promising approach, which seems not to have been explored, would be to assess the impact of ecological factors, such as resource availability and dispersion, on relationships between fecundity and mating success and hence on sexual selection gradients.

Which Sex Competes for the Other?

This question has been answered by pointing to the size of gametes in males and females, or to sexual differences in parental investment, gamete cycling time, or variance of mating success (Bateman 1948; Williams 1966; Trivers 1972; Baylis 1981; Thornhill 1986; Gwynne 1991). But, before we seek an answer, we must ask what we mean by one sex competing for the other. We take this as a question that asks, Which sex experiences the strongest sexual selection? Phrased in these terms, the issue is the proximate one of characterizing sexual selection in prevailing mating systems, rather than the ultimate issue of phylogenetic origins of sex differences. The popular message from Bateman's (1948) article deals with the ultimate issue (differences in sex role reflect differences in gamete size), but perhaps the more useful message in this article deals with the proximate issue of which sex experiences stronger sexual selection. Bateman's (1948, p. 367) neglected argument was that males are inherently subject to stronger selection than females because of "the greater dependence of the fertility of males on frequency of insemination." A major goal of the present article is to relate Bateman's argument to formal selection theory. We show that the dependence of fecundity on mating success represents the force of selection on mating success and also the final common path for sexual selection on any trait. We call this final common path the sexual selection gradient. Males will experience stronger sexual selection than females when their sexual selection gradient is steeper. Males will compete for females when their sexual selection gradient is steeper, because male traits that influence competition for mates will have a greater impact on fecundity than comparable traits in females.

Trivers (1972) portrayed the sexual differences in the costs of parental investment by plotting parental investment as a function of the number of offspring produced. This portrayal does little to illuminate his argument. Furthermore, this visualization is not easily translated into a program of quantitative field research, and conceptual connections to sexual selection are a few steps removed from the plot (but see Thornhill 1986; Gwynne 1991). A more revealing portrayal of the costs of parental investment is obtained by plotting the number of offspring produced as a function of mating success (fig. 5). With this plot, Trivers's argument becomes clear and connections to Bateman's (1948) contribution are transparent. Furthermore, the plot has a straightforward connection to sexual selection theory. The cost of parental investment is that successive clutches are progressively smaller in size. When parental resources are limited, investment in the present clutch reduces the parent's ability to invest in the next clutch and consequently it is smaller in size. The negative effect of parental investment is to pull down expected total fecundity as the average number of mates is increased. (The benefit of parental investment is an increase in offspring survival.) Because of this negative effect, the sex that invests less in offspring will experience stronger sexual selection (i.e., a steeper sexual selection gradient).

Mating System Characterized by Relationships between Fecundity and Mating Success

We can characterize mating systems on the basis of the relationship between fecundity and mating success in males and females. The relationship might be

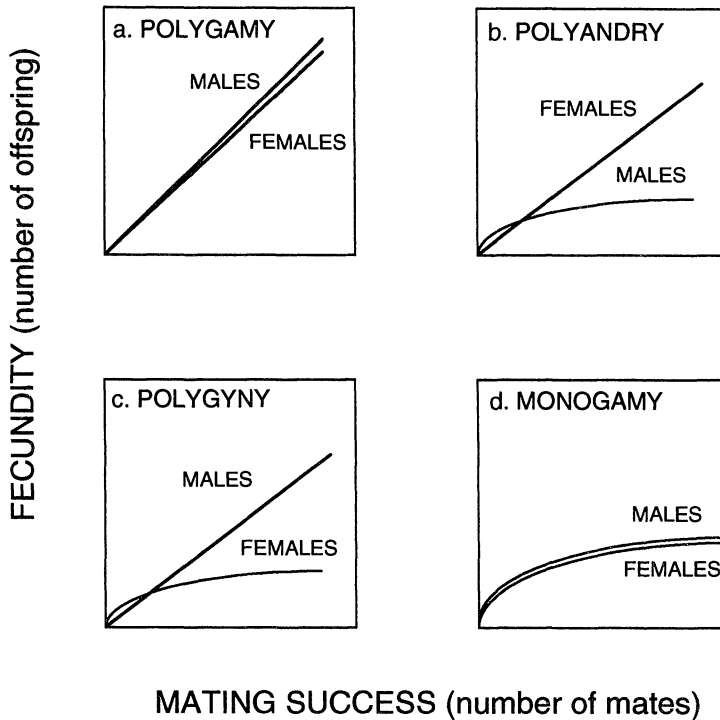


FIG. 7.—Expected associations between the type of mating system and the relationships between fecundity and mating success of males and females.

increasing or asymptotic (fig. 7) in either sex. For example, fecundity might be an increasing function of mating success in both sexes (see, e.g., fig. 7*a*). In this case, we might expect a polygamous mating system in which the average male has multiple mates and so does the average female. Alternatively, in both sexes fecundity might reach an asymptote with one mating (fig. 7*d*). In this case, there is no advantage to additional matings after the first, and so we expect a monogamous mating system. Two final cases arise when one sex shows a steadily increasing association between fecundity and mating success while the other sex shows an asymptotic relationship. If the male function is increasing while the female function is asymptotic, we expect a polygynous mating system (fig. 7*c*). If the male function is asymptotic while the female function is increasing, we expect a polyandrous mating system (fig. 7*b*). In fact, Ridley (1988) has discovered a striking tendency for female fecundity to increase with mating success in polyandrous insects but has found no such tendency in monogamous insects.

The relationships between fecundity and mating success also enable us to decide which sex will experience the strongest sexual selection. When the curves are identical for males and females (fig. 7*a*, *d*), both sexes will experience the same strength of sexual selection (i.e., identical sexual selection gradients). If the curve of fecundity versus mating success of one sex is always steeper than

the curve of the other sex, that sex will experience stronger sexual selection. If the mating system is polyandrous, with curves like those in figure 7*b*, females will experience stronger sexual selection than males. If the mating system is polygynous, with curves like those in figure 7*c*, males will experience stronger sexual selection. When both sexes show parental investment, the sex that invests less will experience stronger sexual selection (figs. 5 and 6).

Variance of Mating Success and Reproductive Success

A sexual difference in the variance of mating success is best viewed as a sign of sexual selection (Bateman 1948). It is not an infallible diagnostic of the mating system. Sutherland (1985*a*) argued that chance alone could produce a larger mating success variance in males if males had a shorter average mate-handling time. We have extended Sutherland's encounter rate approach by permitting variation in mate-handling time (time devoted to the act of mating, mate guarding, etc.) and in persuasion (the probability of successful mating given an encounter). Using this more general model, we show that the contribution of random processes to the variance of male mating success may be important or trivial depending on the importance of the deterministic processes of mate handling and persuasion. The utility of the variance of mating success as a measure of the opportunity for sexual selection on males (Wade 1979; Wade and Arnold 1980; Arnold and Wade 1984) depends on whether it reflects intrinsic differences among males in mating success (arising, e.g., from differences in handling time and persuasion). Fitting a Poisson or binomial distribution to data on mating success (Sutherland 1985*a*) is a weak way to exclude the possibility of intrinsic differences, for intrinsic differences might be Poisson or binomially distributed. A more useful approach is to test for the contribution of intrinsic differences among males by comparing the among- and within-male variances of mating success (Houck et al. 1985).

Sutherland (1985*b*) has proposed a variety of measures of sexual selection based on the parameters in an encounter rate model. These measures are of limited usefulness, however, because they are based on the unlikely supposition that males do not differ intrinsically in mate-handling time or persuasive ability.

In this article we have focused on the relationship between fecundity and mating success in males and females and only secondarily on the sexual difference in mating success or fecundity variation. When we plot fecundity as a function of mating success, the two marginal distributions portray variation in fecundity and mating success. The two distributions are tied together by the relationship of fecundity and mating success. Variation in mating success and fecundity in the two sexes are revealing aspects of the mating system (Wade and Arnold 1980; Clutton-Brock 1983, 1988), but the relationships of fecundity and mating success are more fundamentally important because of their more direct relationship to the action of sexual selection.

Age and Season Effects on Selection

Our consideration of sexual selection in relation to demography (eqq. [5]–[11]), enables us to evaluate the merits and limitations of various actual data sets. As a first case, suppose we have data on various traits, mating success, and fecundity

for each individual in our sample. We have these data for only a single breeding season, but we know the age of each individual. With such data we can estimate selection gradients for each age class (within each sex). We can also test for the heterogeneity of these multiple regression slopes across ages by ANCOVA. If we find evidence of homogeneity of slopes, we can pool data across ages and estimate a common selection gradient.

As a second case, we can imagine a similar data set in which ages are unknown. Most data sets are of this kind. In this case we cannot test for age-specific differences in selection. We can ignore age and estimate selection gradients, but these gradients may not be characteristic of any particular age. We also have no way of evaluating their relationship to lifetime selection.

As a third case, we can imagine following a cohort throughout life, over a succession of breeding seasons, and scoring the attributes in question (traits, mating success, fecundity, etc.) in each breeding season. With such data we can estimate selection gradients for each season and make comparisons across seasons. But, because age is confounded with breeding season, we will not know whether any changes in selection represent true age effects or season-to-season changes in the environment. We can, however, estimate lifetime selection on various attributes by using equation (6) to compute lifetime fitness and equation (4) to estimate lifetime selection gradients. Furthermore, we could partition that total selection into age-specific (or season-specific) effects on fecundity and mortality using equation (11). All of these selection estimates, however, may be characteristic of only the cohort in question and the particular seasonal series of environments that it encountered. Nevertheless, the evolutionary inferences we can make are considerably greater than in the first two cases.

As a final and best case, we can imagine following multiple cohorts throughout their lifetimes. With such data, we could escape from some of the limitations of the third case. In particular, we could in principle tease apart the effects of age and season on selection.

Murray (1984) has considered the problem of selection in age-structured populations in a discussion of the evolution of mating systems. Murray follows Fisher's (1958) approach of assigning a fixed Malthusian parameter to each phenotypic class. The problem with this approach is that a phenotypic class cannot have a fixed per capita birth rate and death rate when the genotypic and hence phenotypic composition of the population is changing under selection (Charlesworth 1980). The approach adopted in this article follows Charlesworth (1980) and Lande (1982) in making the Malthusian parameter (r) a property of the whole population rather than an attribute of individual phenotypic classes or genotypes. Furthermore, Murray (1984) represents selection by taking the ratio of lifetime progeny production for two phenotypic classes. We see, however, from Lande's (1982) results, that we need to weight the contribution of progeny produced at each age by the growth rate of the population and its generation time (eqq. [6]–[7]). Even when this more exact expression for the fitness of each phenotypic class is used, simple ratios of fitness do not describe the impact of selection on a trait. That description is better accomplished with partial regression (eq. [2]). These and other technical problems make Murray's (1984) conclusions difficult to evaluate.

SUMMARY

1. Selection on quantitative traits can be represented by a multiple regression equation and visualized as a path diagram with paths connecting the traits to lifetime fitness. The paths in figures 1 and 2 can be estimated in actual populations as partial regression slopes.

2. The statistical relationship between mating success and fecundity in a particular breeding season is a key aspect of the mating system. We refer to the partial regression slope that characterizes the relationship between fecundity and mating success as the sexual selection gradient. Differences between males and females in sexual selection gradients provide important insights into mating systems.

3. In the absence of nuptial gifts and paternal care of offspring, males generally will experience stronger sexual selection than females because their sexual selection gradient is steeper.

4. Nuptial gifts provided to a female by a male constitute a premium on female mating success. The addition of such gifts to a mating system steepens the sexual selection gradient for females. Consequently, both sexes may experience strong sexual selection.

5. Parental care may depress the size of successive broods produced within a season. Such parental investment may reduce the premium on mating success in one or both sexes. As a consequence, the sex that invests less in offspring will experience stronger sexual selection.

6. Encounter rate models can be used to evaluate the strength of sexual selection on male traits, as well as to evaluate the stochastic aspect of mating success.

7. From the standpoint of evaluating the strength of sexual selection, the breeding sex ratio is a more revealing aspect of mating systems than is the operational sex ratio.

8. A conceptual framework couched in terms of sexual selection gradients explains why one sex competes for the other and can be used to predict the type of mating system.

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APPENDIX A

TABLE A1

SUMMARY OF VARIABLES USED IN MODELS OF MATE PROVISIONING AND PARENTAL INVESTMENT

Variable	Definition
\bar{m}_{f1}	Average fecundity of females with one mate
\bar{m}'_f	Average fecundity of females with one or more mates
\bar{m}_f	Average fecundity of all females (mated and unmated)
\bar{m}_m	Average male fecundity (average progeny count for males)
\bar{x}_f	Average female mating success (number of males that sire the female's progeny); includes mated and unmated females
\bar{x}_m	Average male mating success (number of females that bear the male's progeny); includes males capable of mating that fail to mate
H_x	Harmonic mean mating success of females with one or more mates
σ_{x-f}^2	Variance of female mating success for all females (including the zero class with no mates)
$\sigma_{x-f}^{\prime 2}$	Variance of mating success among females with one or more mates
β_{ss-m}	Male sexual selection gradient
β_{ss-f}	Female sexual selection gradient
q	Proportion of females capable of breeding that do not mate
k	The effect of a nuptial gift on female fecundity
b_f	Cost of parental investment by females
b_m	Cost of parental investment by males
c_f	$1 - b_f$
c_m	$1 - b_m$
BSR	Breeding sex ratio (ratio of number of breeding males to number of breeding females; includes the zero fecundity class for each sex)
OSR	Operational sex ratio (the average over time of the number of sexually active males to the number of females capable of insemination)

APPENDIX B

PROOF THAT THE SEX THAT INVESTS LESS IN OFFSPRING EXPERIENCES STRONGER SEXUAL SELECTION

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To simplify the notation, we set $c = c_m$, $\gamma = c_f$, $a = \bar{x}_m$, and $\alpha = \bar{x}_f$. These parameters satisfy

$$0 < c, \gamma < 1; \quad a, \alpha > 0; \quad c > \gamma; \quad (\text{B1a})$$

and

$$\frac{\alpha}{a} = \frac{(1 - \gamma^\alpha)(1 - c)}{(1 - c^\alpha)(1 - \gamma)}. \quad (\text{B1b})$$

We wish to prove that

$$c^\alpha(1 - \gamma)\ln(1/c) > \gamma^\alpha(1 - c)\ln(1/\gamma). \quad (\text{B2})$$

The proof falls naturally into several sections.

First, we reduce inequality (B2) to a much simpler inequality. If we use equation (B1b), it is easy to show that inequality (B2) is equivalent to

$$f(c^\alpha) > f(\gamma^\alpha), \quad (\text{B3a})$$

where

$$f(x) = \frac{x}{1-x} \ln \frac{1}{x}, \quad (\text{B3b})$$

and an elementary calculation establishes that $f'(x) > 0$ for $0 < x < 1$. Hence, inequality (B3a) holds whenever

$$c^a > \gamma^\alpha. \quad (\text{B4})$$

Thus, given conditions (B1), the inequalities (B2) and (B4) are equivalent.

Since $c > \gamma$, inequality (B4) obviously holds if $a \leq \alpha$.

If $a = 1$, equation (B1b) simplifies to

$$F(\gamma) \equiv \gamma^\alpha - 1 + \alpha(1 - \gamma) = 0. \quad (\text{B5})$$

Observe that (i) $F(\gamma) \equiv 0$ if $\alpha = 1$ and (ii) $F(1) = 0$. For $0 < \gamma < 1$, the inequality $\alpha \leq 1$ implies $F'(\gamma) \geq 0$, whence $F(\gamma) \leq 0$. Therefore, equation (B5) has no solution in $(0, 1)$ unless $\alpha = 1$. An identical argument demonstrates that $\alpha = 1$ implies $a = 1$.

In view of the last two paragraphs, it will suffice to prove inequality (B4) under the additional restrictions

$$a > \alpha, \quad a \neq 1, \quad \alpha \neq 1. \quad (\text{B6})$$

Second, we investigate the existence of sets (α, a, γ, c) that satisfy conditions (B1) and (B6). We fix (α, a, c) , set

$$p = \frac{\alpha}{a} \left(\frac{1 - c^a}{1 - c} \right), \quad (\text{B7})$$

rewrite equation (B1b) as

$$g(\gamma) \equiv \gamma^\alpha - 1 + p(1 - \gamma) = 0 \quad (\text{B8})$$

and study the existence and uniqueness of solutions of equation (B8) in $(0, 1)$. These solutions, however, may not satisfy $c > \gamma$. We have

$$g(0) = p - 1, \quad g(1) = 0, \quad (\text{B9a})$$

$$g'(\gamma) = \alpha\gamma^{\alpha-1} - p \leq \alpha - p \Leftrightarrow \alpha \geq 1, \quad (\text{B9b})$$

and

$$g''(\gamma) = \alpha(\alpha - 1)\gamma^{\alpha-2} \geq 0 \Leftrightarrow \alpha \geq 1. \quad (\text{B9c})$$

From observations (B9) we obtain seven cases: (i) $p = \alpha$, (ii) $1 < \alpha < p$, (iii) $p < \alpha < 1$, (iv) $\alpha < 1 \leq p$, (v) $p \leq 1 < \alpha$, (vi) $1 < p < \alpha$, and (vii) $\alpha < p < 1$. We conclude easily that in cases i to v equation (B8) has no root in $(0, 1)$, whereas in cases vi and vii it has a unique root in $(0, \gamma_0)$, with

$$g'(\gamma_0) = 0, \quad \gamma_0 = (p/\alpha)^{1/(\alpha-1)} < 1. \quad (\text{B10})$$

Third, we prove that $\alpha > 1$ if and only if $a > 1$. Suppose first that $\alpha > 1$. Then equation (B8) has a solution in $(0, 1)$ if and only if $1 < p < \alpha$ (case vi), which is equivalent to

$$\alpha^{-1} < G(a, c) < 1, \quad (\text{B11a})$$

where

$$G(a, c) = \frac{p}{\alpha} = \frac{1}{a} \left(\frac{1 - c^a}{1 - c} \right). \quad (\text{B11b})$$

Noting that $G(1, c) = 1$ and setting $\lambda = -\ln c$, we find

$$a^2(1-c)e^{\lambda a} \frac{\partial G}{\partial a} = 1 + \lambda a - e^{\lambda a} < 0; \quad (\text{B12})$$

inequalities (B11a) and (B12) imply that $a > 1$.

If $\alpha < 1$, we must have case vii, so $G(a, c) > 1$, whence $a < 1$.

Next, we demonstrate that if $\alpha < a < 1$, then $c < \gamma$, that is, equation (B1b) has no acceptable root. We rewrite equation (B1b) in the form

$$G(a, c) = G(\alpha, \gamma) \quad (\text{B13})$$

and note that if $\alpha < a$, then inequality (B12) and equation (B13) yield

$$G(a, c) > G(a, \gamma), \quad (\text{B14})$$

which means that it will suffice to establish

$$\frac{\partial G}{\partial c} < 0. \quad (\text{B15})$$

We have

$$\psi(c) \equiv a(1-c)^2 \frac{\partial G}{\partial c} = 1 - ac^{a-1} - (1-a)c^a, \quad (\text{B16})$$

whence $\psi(1) = 0$ and

$$\psi'(c) = a(1-a)(1-c)c^{a-2} > 0. \quad (\text{B17})$$

Therefore, $\psi(c) < 0$ for $0 < c < 1$, which proves inequality (B15).

Finally, we posit that $a > \alpha > 1$ and validate inequality (B4). We fix α and γ and suppress dependence on them. From the symmetry of equation (B1b) under the interchange $(a, c) \leftrightarrow (\alpha, \gamma)$ and the uniqueness of the solution of equation (B8), we see that equation (B1b) defines $c = c(a)$ uniquely. We put

$$h(a) = [c(a)]^a - \gamma^\alpha \quad (\text{B18})$$

and observe that $c(\alpha) = \gamma$ is the unique solution of equation (B1b) for $a = \alpha$. Therefore, $h(\alpha) = 0$, and it will suffice to show that $h'(a) > 0$.

Differentiating equations (B18) and (B13) leads to

$$h'(a) = c^a \left(\ln c + \frac{a}{c} \frac{dc}{da} \right) \quad (\text{B19})$$

and

$$\frac{a}{c} H(a) \frac{dc}{da} = (1-c)(ac^a \ln c + 1 - c^a), \quad (\text{B20})$$

where

$$H(a) = c(1 - c^a) - ac^a(1 - c). \quad (\text{B21})$$

Substituting equations (B20) and (B21) into equation (B19) gives

$$H(a)h'(a) = c^a(1 - c^a)(c \ln c + 1 - c) > 0. \quad (\text{B22})$$

It remains only to demonstrate that $H(a) > 0$. We again set $\lambda = -\ln c$ and examine

$$\phi(a) \equiv e^{\lambda(1+a)} H(a) = e^{\lambda a} - 1 - a(e^\lambda - 1) \quad (\text{B23})$$

in the positive quadrant by fixing λ and varying a . We have $\phi(1) = 0$ and, for $a > 1$,

$$\phi'(a) = \lambda e^{\lambda a} - e^\lambda + 1$$

$$> (\lambda - 1)e^\lambda + 1 \quad (\text{B24})$$

$$> (\lambda - 1)(\lambda + 1) + 1 = \lambda^2 > 0.$$

Consequently, $\phi(a) > 0$, and therefore $H(a) > 0$.

This completes the proof of inequality (B2).

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APPENDIX C

TABLE C1

SUMMARY OF VARIABLES USED IN ENCOUNTER RATE MODELS

Variable	Value	Mean	Variance	Standardized Variance
Length of season	L			
Search time	s	α_s	σ_s^2	
Handling time	h	α_h	σ_h^2	
Cycling time	c	α	σ^2	
Number of mates cycled		L/α	$L\sigma^2/\alpha^3$	I_c
Persuasion		α_p	σ_p^2	I_p
Male mating success	x_m	\bar{x}_m	σ_{x-m}^2	I_{x-m}

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