MEASURING THE EFFECTS OF PAIRING SUCCESS, EXTRA-PAIR COPULATIONS AND MATE QUALITY ON THE OPPORTUNITY FOR SEXUAL SELECTION

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Abstract.—Sexual selection can act through variation in the number of social mates obtained, variation in mate quality, or variation in success at obtaining extra-pair fertilizations. Because within-pair fertilizations (WPF) and extra-pair fertilizations (EPF) are alternate routes of reproduction, they are additive, rather than multiplicative, components of fitness. We present a method for partitioning total variance in reproductive success (a measure of the opportunity for selection) when fitness components are both additive and multiplicative and use it to partition the variance into components that correspond to each mechanism of sexual selection. Computer simulations show that extra-pair fertilizations can either increase or decrease total variance, depending on the covariance between within-pair and extra-pair success. Simulations also suggest that for socially monogamous species, extra-pair fertilizations have a greater effect than variation in mate quality or pairing status on the opportunity for selection. Application of our model to data gathered for a population of red-winged blackbirds (*Agelaius phoeniceus*) indicates that most of the variance in male reproductive success was attributable to within-pair sources of variance. Nevertheless, extra-pair copulations increased the opportunity for selection because males varied both in the proportion of their social young that they sired and in the number of extra-pair mates that they obtained. Furthermore, large and positive covariances existed between the number of extra-pair mates a male obtained and both social pairing success and within-pair paternity, indicating that, in this population, males preferred as social mates also were preferred as extra-pair mates.

Key words.—*Agelaius phoeiceus*, components of fitness, extra-pair copulations, mate quality, opportunity for selection, red-winged blackbirds, sexual selection, variance in reproductive success.

Many behavioral and morphological traits of organisms appear useful only in competition for mates. A complete understanding of the evolution of such traits thus requires investigating that evolutionary process that operates through individual differences in mating and/or fertilization success, a process that Darwin (1871) termed "sexual selection." The opportunity or potential for sexual selection to operate is proportional to variance in mating success (Crow 1958, 1991; Payne 1979; Wade 1979; Wade and Arnold 1980; Arnold and Wade 1984a): when all individuals in the population obtain roughly the same number and quality of mates, sexual selection will be weak; when a few individuals obtain many mates and others go unmated, sexual selection can potentially be very strong. Various authors have pointed out that random (chance) variation can contribute to the opportunity for selection (Houck et al. 1985; Sutherland 1985; Koenig and Albano 1986; Grafen 1987; Hubbell and Johnson 1987; Cabana and Kramer 1991) and that care must be taken in comparisons between populations and species (Trail 1985; Downhower et al. 1987). Subject to these limitations, selection opportunities are useful for comparing the potential for sexual selection in different habitats or years and among species (Payne 1984; Fincke 1986; Conner 1988; McDonald 1989; Pruett-Jones and Pruett-Jones 1990; Wade and Pruett-Jones 1990; Clayton et al. 1992). Furthermore, such indices can provide preliminary information leading to experimental analyses of specific hypotheses (Anholt 1991).

Traditionally, most studies of sexual selection have used

the number of social mates (i.e., the number of females associated with a male during the breeding period) or number of observed copulations as a measure of mating success. However, variance in reproductive fitness can also arise from at least two additional sources (Mock and Fujioka 1990). First, some males may attract higher quality females that breed earlier in the season and/or produce more young per attempt (Darwin 1871; Kirkpatrick et al. 1990). Several empirical studies have demonstrated that females in better condition and/or those females breeding earlier in the season have higher reproductive success (e.g., Howard 1979; Perrins and Birkhead 1983; Howard and Kluge 1985; Price et al. 1988; Rosenqvist 1990), and that such females sometimes exhibit mating preferences for males with certain phenotypic traits (e.g., O'Donald 1980; Gwynne 1981; Price 1984; Burley 1986; Sargent et al. 1986; Côté and Hunte 1989; Møller 1990, 1991; Norris 1990; Wiegmann et al. 1992). Second, both males and females may copulate with individuals other than their own social mates (Hanken and Sherman 1981; McCracken and Bradbury 1981; Gross 1982; Westneat et al. 1990; Birkhead and Møller 1992). Although common in many species, such extra-pair copulations can be very difficult to observe. Extra-pair copulations could potentially produce extreme variance in male reproductive success and correspondingly strong sexual selection, because they can effectively produce a genetically promiscuous system even when a population is socially monogamous (Gowaty 1985; Westneat et al. 1990).

The number of observed mates might thus be a poor indicator of male reproductive success (Gibbs et al. 1990), and

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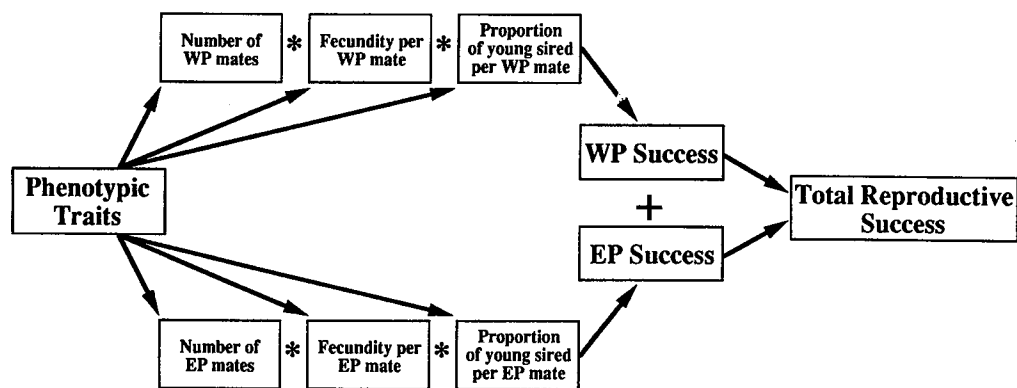
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FIG. 1. Flow chart illustrating components that combine to determine an individual's total reproductive success. Arrows indicate the effects of phenotypic traits can have different components and, eventually, on total reproductive success. Note that the within-pair (WP) path to total reproductive success is separate from the extra-pair (EP) path, indicating that WP success and EP success are additive components of fitness.

hence a poor currency for evaluating the opportunity for sexual selection. Nevertheless, at present the effects of varying mate quality and extra-pair fertilizations on the opportunity for sexual selection are unclear (Mock and Fujioka 1990). The combined effect of these factors might increase or decrease the opportunity for sexual selection relative to that suggested by the number of social mates alone (see below). Furthermore, present statistical techniques for partitioning the opportunity for selection rely on fitness components being multiplicative (Arnold and Wade 1984ab), whereas reproduction gained through extra-pair mates (extra-pair fertilizations, EPF) should be added to that gained through social mates (within-pair fertilizations, WPF). This additivity arises because a male can simultaneously pursue WPF and EPF (fig. 1); they are not separate "episodes of selection" (Arnold and Wade 1984a,b). Other means of reproduction, such as intraspecific brood parasitism, also entail additive components of fitness. To determine the selective effects of these events or to compare effects across populations, a method for assessing the relative contributions of additive components to total variance in reproductive success is needed.

In this paper, we present a general method for partitioning total variance in reproductive success into component parts that are both additive and multiplicative. This method can be applied to many situations in which some fitness components are additive; here we use it to examine factors affecting the opportunity for sexual selection. To do so, we divide total variance in reproductive success into variance in (1) the number of social and extra-pair mates, (2) the proportion of each mate's young that a male sires, and (3) the quality, in terms of mate fecundity and/or parental abilities, of social and extra-pair mates. Analyses of field data and results from simulations show that estimates of the variance in male reproductive success based on the number of social mates can significantly under- or overestimate actual variance and that interactions among components can have a large effect on the opportunity for sexual selection.

THE MODEL

Male reproductive success can be partitioned into a number of component parts (fig. 1). We define total male reproductive success (T) as the number of young sired during a breeding season. This total is the sum of two components: the number of young that a male sires with his social mates (social fecundity, W) and the number of young that he sires with the social mates of other males (nonsocial fecundity, E)

$$T = W + E. \tag{1}$$

For additive components, the total variance is the sum of the variances of each component plus twice the covariance between them

$$\text{Var}(T) = \text{Var}(W) + \text{Var}(E) + 2\,\text{Cov}(W, E), \tag{2}$$

where the "Var" terms refer to the variance in each component, and $\text{Cov}(W, E)$ is the covariance between a male's within- and extra-pair fertilization (EPF) success.

This expression for the total variance in male fertilization success can be partitioned further. Variation in both the within- and extra-pair components might arise either because some males obtain more mates than others, or because some males sire more young per mate. Therefore, each component of reproductive success in equations (1) and (2) can be partitioned into a component due to the number of mates obtained (M_w or M_e, for the number of social or extra-pair mates, respectively) and a component representing the number of young sired per mate (Y_w or Y_e, for number of young produced by within-pair and extra-pair mates, respectively). Thus,

$$W = M_w Y_w \tag{3}$$

and

$$E = M_e Y_e \tag{4}$$

Substituting equations (3) and (4) into equations (1) and (2) yields

$$T = M_w Y_w + M_e Y_e \tag{5}$$

and

$$\text{Var}(T) = \text{Var}(M_w Y_w) + \text{Var}(M_e Y_e)$$
$$+ 2\,\text{Cov}(M_w Y_w, M_e Y_e). \tag{6}$$

Using equation (6) of Bohrnstedt and Goldberger (1969), the

first two variance terms in equation (6) can be partitioned into their component parts

$$\text{Var}(M_w Y_w) = \bar{Y}_w^2 \text{Var}(M_w) + \bar{M}_w^2 \text{Var}(Y_w)$$
$$+ 2\bar{M}_w \bar{Y}_w \text{Cov}(M_w, Y_w) + D_w \quad (7)$$

and

$$\text{Var}(M_e Y_e) = \bar{Y}_e^2 \text{Var}(M_e) + \bar{M}_e^2 \text{Var}(Y_e)$$
$$+ 2\bar{M}_e \bar{Y}_e \text{Cov}(M_e, Y_e) + D_e, \quad (8)$$

where the $\bar{M}_i$ and $\bar{Y}_i$ terms are mean values, and each D_i value denotes a remainder (see below). The covariance term in equation (6) can likewise be partitioned into its component parts (Bohrnstedt and Goldberger 1969, eq. 14)

$$\text{Cov}(M_w Y_w, M_e Y_e)$$
$$= \bar{Y}_w \bar{Y}_e \text{Cov}(M_w, M_e) + \bar{M}_e \bar{Y}_w \text{Cov}(M_w, Y_e)$$
$$+ \bar{M}_w \bar{Y}_e \text{Cov}(M_e, Y_w) + \bar{M}_w \bar{M}_e \text{Cov}(Y_w, Y_e) + D_{we}. \quad (9)$$

By substituting equations (7) through (9) into equation (6), we obtain an expression that partitions the total variance in male reproductive success into ten component parts (variances of four fitness components plus their associated covariances)

$$\text{Var}(T) = \bar{Y}_w^2 \text{Var}(M_w) + \bar{M}_w^2 \text{Var}(Y_w)$$
$$+ \bar{Y}_e^2 \text{Var}(M_e) + \bar{M}_e^2 \text{Var}(Y_e)$$
$$+ 2\bar{M}_w \bar{Y}_w \text{Cov}(M_w, Y_w) + 2\bar{M}_e \bar{Y}_e \text{Cov}(M_e, Y_e)$$
$$+ 2\bar{Y}_w \bar{Y}_e \text{Cov}(M_w, M_e) + 2\bar{M}_e \bar{Y}_w \text{Cov}(M_w, Y_e)$$
$$+ 2\bar{M}_w \bar{Y}_e \text{Cov}(M_e, Y_w)$$
$$+ 2\bar{M}_w \bar{M}_e \text{Cov}(Y_w, Y_e) + D_T, \quad (10)$$

where $D_T = D_w + D_e + D_{we}$.

The remainder terms (D_w, D_e, D_{we}, and D_T) reflect multivariate skewness and products of variances and covariances. If, for example, the distributions of M_w, M_e, Y_w, and Y_e are multivariate normal, then there is no multivariate skewness and the remainder terms can be estimated by products of variances and covariances (Bohrnstedt and Goldberger 1969, eqs. 6 and 13). However, some skewness will probably be present in the actual data. The magnitude of the remainder terms may be computed by subtraction. For example, D_w can be computed by evaluating Var $(M_w Y_w)$ using values of $M_w Y_w$ for each individual and the standard formula for variance, then computing each of the first three terms on the right side of equation (7) and subtracting their sum from the computed value of Var$(M_w Y_w)$. The remainder terms are present in equations (7) to (10) because total variance is not a simple sum of its component variances and covariances; higher order terms (the products of variances and covariances) and skewness in the data also contribute to the total. Unfortunately, these effects may be difficult to interpret biologically, and in our formulation they are collected together as remainder terms. If the net effect of the higher order terms on total

variance is significant, the remainder terms will be large relative to other variance components. Nevertheless, even when higher order effects are substantial, the above formulation allows one to calculate the direct contribution of each component of fitness (e.g., Var$[M_w]$) to the total.

To obtain the standardized variance in reproductive success and its components, each of the terms in equation (10) can be divided by the squared mean of reproductive success ($\bar{T}^2$). The standardized variance is equal to the opportunity for selection, and each standardized component gives the contribution of that component to the total opportunity (Arnold and Wade 1984a).

Our model can be modified easily to examine particular relationships. For example, suppose one wanted to focus on the relationship between the total number of extra-pair young sired and various components of within-pair success. This can be done by collapsing the extra-pair portion of equation (6) to a single term (E = the total number of young sired through EPF), such that the fitness of a male can be written as

$$T = M_w Y_w + E. \quad (11)$$

Variance in male reproductive success then becomes

$$\text{Var}(T) = \text{Var}(M_w Y_w) + \text{Var}(E) + 2\text{Cov}(M_w Y_w, E). \quad (12)$$

which, using the results of Bohrenstedt and Goldberger (1969), can be expanded to yield

$$\text{Var}(T) = \bar{Y}_w^2 \text{Var}(M_w) + \bar{M}_w^2 \text{Var}(Y_w) + \text{Var}(E)$$
$$+ 2\bar{Y}_w^2 \text{Cov}(M_w, E) + 2\bar{M}_w^2 \text{Cov}(Y_w, E)$$
$$+ 2\bar{M}_w \bar{Y}_w \text{Cov}(M_w, Y_w) + D_T. \quad (13)$$

Each variance term in equation (13) corresponds to one of the factors thought to contribute to the opportunity for sexual selection: number of social mates (M_w), number of young sired per social mate (Y_w), and fertilizations gained through extra-pair copulations (E). Similarly, the covariance terms represent all of the possible associations or trade-offs that might exist between these components of fitness. Other modifications of the general model, which can highlight relationships among different components of interest, are possible.

One important modification is to include the effects of both extra-pair copulations and mate quality. The effects of mate quality can be added by partitioning the number of young fertilized per mate (Y_w or Y_e) into two multiplicative parts: the average number of young produced by each mate (N_w or N_e) and the proportion of those young fertilized by the male (P_w or P_e). By substitution into equation (5), we have the following expression for male reproductive success

$$T = M_w N_w P_w + M_e N_e P_e \quad (14)$$

From equation (6), we have

$$\text{Var}(T) = \text{Var}(M_w N_w P_w) + \text{Var}(M_e N_e P_e)$$
$$+ 2\text{Cov}(M_w N_w P_w, M_e N_e P_e). \quad (15)$$

By replacing Y_w with $N_w P_w$ and Y_e with $N_e P_e$ in equation

TABLE 1. Terms in the expanded model and their biological interpretation.

Term	Interpretation
Within-pair sources of variance	
$\bar{N}_w^2\bar{P}_w^2\text{Var}(M_w)$	variance in number of social mates
$\bar{M}_w^2\bar{P}_w^2\text{Var}(N_w)$	variance in number of young per social mate (social mate quality)
$\bar{M}_w^2\bar{N}_w^2\text{Var}(P_w)$	variance in proportion of social mates' young sired
Extra-pair sources of variance	
$\bar{N}_e^2\bar{P}_e^2\text{Var}(M_e)$	variance in number of extra-pair females mated
$\bar{M}_e^2\bar{P}_e^2\text{Var}(N_e)$	variance in number of young per extra-pair mate (extra-pair mate quality)
$\bar{M}_e^2\bar{N}_e^2\text{Var}(P_e)$	variance in proportion of extra-pair mates' young sired
Covariance terms	
$2\bar{M}_w\bar{N}_w\bar{P}_w^2\text{Cov}(M_w, N_w)$	covariance between number and quality of social mates
$2\bar{M}_w\bar{N}_w^2\bar{P}_w\text{Cov}(M_w, P_w)$	covariance between number of social mates and proportion of young sired in nest of each
$2\bar{M}_w^2\bar{N}_w\bar{P}_w\text{Cov}(N_w, P_w)$	covariance between social mate quality and proportion of social young sired
$2\bar{M}_e\bar{N}_e\bar{P}_e^2\text{Cov}(M_e, N_e)$	covariance between the number and quality of extra-pair mates
$2\bar{M}_e\bar{N}_e^2\bar{P}_e\text{Cov}(M_e, P_e)$	covariance between number of extra-pair mates and proportion of their young sired
$2\bar{M}_e^2\bar{N}_e\bar{P}_e\text{Cov}(N_e, P_e)$	covariance between extra-pair mate quality and proportion of their young sired
$2\bar{N}_w\bar{P}_w\bar{N}_e\bar{P}_e\text{Cov}(M_w, M_e)$	covariance between number of social and extra-pair mates
$2\bar{N}_w\bar{P}_w\bar{M}_e\bar{P}_e\text{Cov}(M_w, N_e)$	covariance between number of social mates and quality of extra-pair mates
$2\bar{N}_w\bar{P}_w\bar{M}_e\bar{N}_e\text{Cov}(M_w, P_e)$	covariance between number of social mates and proportion of young sired in nests of extra-pair mates
$2\bar{M}_w\bar{P}_w\bar{N}_e\bar{P}_e\text{Cov}(N_w, M_e)$	covariance between quality of social mates and number of extra-pair mates
$2\bar{M}_w\bar{P}_w\bar{M}_e\bar{P}_e\text{Cov}(N_w, N_e)$	covariance between quality of social and extra-pair mates
$2\bar{M}_w\bar{P}_w\bar{M}_e\bar{N}_e\text{Cov}(N_w, P_e)$	covariance between social mate quality and proportion young sired in nests of extra-pair mates
$2\bar{M}_w\bar{N}_w\bar{N}_e\bar{P}_e\text{Cov}(P_w, M_e)$	covariance between proportion of social young sired and number of extra-pair mates
$2\bar{M}_w\bar{N}_w\bar{M}_e\bar{P}_e\text{Cov}(P_w, N_e)$	covariance between proportion of social young sired and quality of extra-pair mates
$2\bar{M}_w\bar{N}_w\bar{M}_e\bar{N}_e\text{Cov}(P_w, P_e)$	covariance between proportion of young sired in nests of social and extra-pair mates

TABLE 2. Summary of computer simulations

Simulation number	Case	No. social mates/ male	Number of young per female	Number EPF young*	Source pool for EPF females†
1	a	1	4	2	all females
1	b	1	4	2	mates of non-EPF males
1	c	1	4	2	mates of EPF males
2	a	1–3	4	2	all females
2	b	1–3	4	2	mates of monogamous males
2	c	1–3	4	2	mates of polygynous males
3	a	1	4	2	all females
3	b	1	3, 4, or 5	2	all females
3	c	1	2, 4, or 6	2	all females

* Number of young sired per extra-pair copulation (EPF).
† Pool of females from which extra-pair mates ("EPF females") were selected randomly for each male obtaining an extra-pair copulation ("EPF males").

(10), and using the results of Bohrenstedt and Goldberger (1969), each of the variance and covariance terms in equation (15) can be expanded to their component parts

$$\text{Var}(T) = \bar{N}_w^2\bar{P}_w^2\text{Var}(M_w) + \bar{M}_w^2\bar{N}_w^2\text{Var}(P_w) + \bar{M}_w^2\bar{P}_w^2\text{Var}(N_w)$$
$$+ \bar{N}_e^2\bar{P}_e^2\text{Var}(M_e) + \bar{M}_e^2\bar{N}_e^2\text{Var}(P_e) + \bar{M}_e^2\bar{P}_e^2\text{Var}(N_e)$$
$$+ \Sigma \text{ (Covariance Terms)} + D_T. \qquad (16)$$

The full list of the 15 covariance terms is shown in table 1. In this case, the resulting expression consists of 21 terms, each of which has a biological interpretation (table 1). As above, Var(T) and its components parts can be standardized by dividing both halves of equation (16) by $(\bar{T}^2)$. Partitioning the standardized variance into all of its component parts allows one to calculate the contribution of WPF, EPF, and mate quality to the opportunity for sexual selection. Thus, the relative importance of each of these three potential mechanisms of sexual selection can be determined.

APPLICATIONS OF THE MODEL

This model of fitness components has both theoretical and empirical benefits. Analysis of particular interactions using contrived scenarios can contribute to theory regarding the operation of sexual selection. In addition, as described above, the model can help generate hypotheses in a particular empirical case, either a priori or after some initial data have been gathered. Below, we explore some details of both of these uses of the model.

Example Simulations

Computer simulations can be useful in generating new theory, as well as illustrating potential empirical uses. We used a Monte Carlo simulation to calculate the variance in male reproductive success in several different situations. For these simulations, we varied the number of social and/or extra-pair mates that each male in the population obtained. We repeated each simulation 1000 times to obtain mean values for each parameter of interest. Table 2 summarizes the parameter val-

ues used for each set of simulations. All variances, covariances, and means were calculated using only those individuals with a defined value for the fitness component of interest (e.g., individuals that did not obtain an extra-pair fertilization were not included in the calculation of mean extra-pair paternity, P_e); this method is analogous to the "independent" method of Koenig et al. (1991).

In the first set of simulations, we investigated the influence of extra-pair copulations on the variance in male success in a socially monogamous species. We assumed a balanced sex ratio (50 males and 50 females) and no variation in female fecundity (brood size = 4). Thus, in the absence of extra-pair copulations, variance in male reproductive success was 0. We explored the influence of extra-pair fertilizations (EPF) in three different cases. In the first (case 1a), each EPF male "copulated" once with a female randomly selected (with replacement) from the pool of 49 females socially bonded to other males. Each extra-pair copulation resulted in two EPF (i.e., two of that female's four offspring were assigned to the EPF male rather than to the female's social mate). If all of a female's young were assigned to extra-pair males, she was removed from the pool of potential extra-pair mates. In this case, there was no trade-off between the pursuit of extra-pair copulations and other components of fitness, and the effect of EPF was to progressively increase the standardized variance in male reproductive success as the proportion of males gaining EPF increased (fig. 2a).

The second case (case 1b) was similar to the first, except that females involved in extra-pair copulations were randomly drawn from the pool of females paired to males who did not obtain EPF. This case simulated a situation in which a male's ability to obtain EPF is correlated with his within-pair paternity, either because such males are better able to guard their mates or because females paired to less-preferred males actively seek extra-pair copulations whereas females paired to highly preferred males do not. In this case, the standardized variance in male reproductive success increased dramatically as the number of males obtaining EPF increased (fig. 2a). An analysis of the covariance components showed that there was a positive covariance between a male's success in obtaining EPF (M_e; either 0 or 1) and the proportion of his own social mate's young that he sired (P_w; fig. 2b).

In the final monogamy case (case 1c), males gained EPF only with the mates of other EPF males (i.e., EPF females were randomly selected from the pool of females socially paired to males who obtained an extra-pair copulation). This simulated a negative trade-off between a male's pursuit of EPF and his ability to guard his own social mate. In this case, the variance in male reproductive success also increased with the proportion of males gaining EPF, but only moderately relative to the previous cases (fig. 2a). This was because a negative covariance existed between the number of extra-pair mates that a male obtained (M_e) and the proportion of his social mate's young that he sired (P_w; fig. 2b), effectively reducing the increase in total variance. This covariance reached its minimum (largest negative value) when approximately half of the males in the population were seeking EPF, at which point the variance in male mating success was less than half of its value when any female could participate in extra-pair copulations (case 1a).
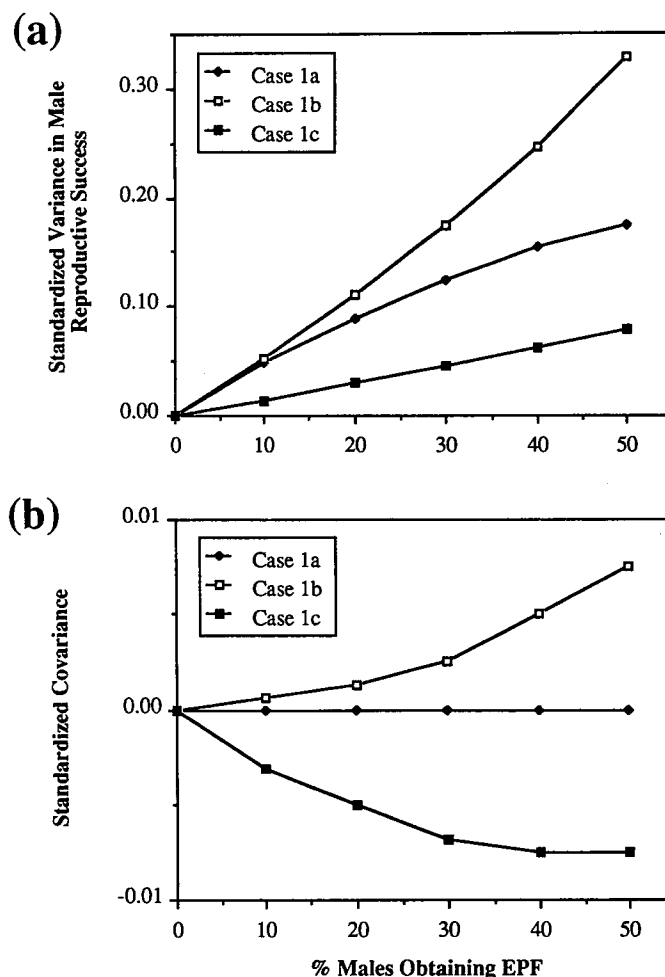

FIG. 2. Results of monogamy simulations. Shown are the percent of males in the population obtaining extra-pair fertilizations versus (a) standardized variance in male reproductive success (total variance divided by mean reproductive success squared) and (b) the standardized covariance between the number of extra-pair females a male sires young with (M_e) and the proportion of his social mate's young that he sires (P_w). In case 1a (filled diamonds), extra-pair females were randomly chosen from the pool of all females in the population. In case 1b (open squares), extra-pair females were randomly chosen from the social mates of males who did not obtain an extra-pair fertilization (EPF). In case 1c (closed squares), extra-pair females were randomly selected from the social mates of males who did obtain an extra-pair fertilization (EPF) (see text for details).

We also simulated some potential effects of extra-pair copulations in a polygynous species. To generate polygyny, we assigned three social mates to ten males, two social mates to 15 males, and one social mate to 25 males, for a total of 50 males and 85 females. Again, all females were assumed to produce exactly four offspring. We varied the proportion of males obtaining EPF, and EPF males were drawn randomly from the population. One extra-pair mate was randomly chosen for each EPF male and, as above, two of that female's young were assigned to the EPF male. We chose females for extra-pair matings in three different ways. First (case 2a), EPF females were drawn randomly, with replacement, from the pool of all females socially paired to other males. In this case, the standardized variance in male reproductive success
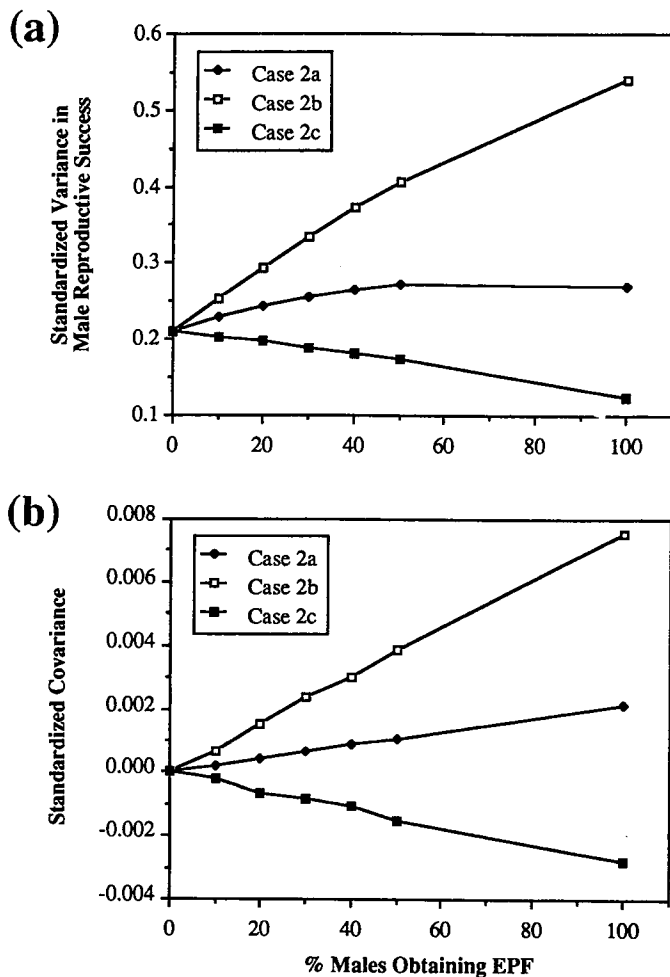
(a)

(b)

FIG. 3. Results of polygyny simulations. Shown are the percent of males in the population obtaining extra-pair fertilizations versus (a) the standardized variance in male reproductive success and (b) the standardized covariance between the number of social mates a male attracts (M_w) and the proportion of their young that he sires (P_w). In case 2a (filled diamonds), extra-pair females were drawn randomly from the pool of all females in the population. In case 2b (open squares), extra-pair females were chosen randomly from the social mates of monogamous males. In case 2c (closed squares), extra-pair females were selected from the mates of polygynous males.

increased as the number of EPF males in the population increased, but only moderately (fig. 3a). Second (case 2b), EPF females were drawn from the pool of females paired to monogamous males, simulating the situation in which certain males were preferred by females as both social mates and extra-pair mates. In contrast to the previous case, this resulted in a large increase in the standardized variance in male reproductive success. This dramatic increase was due to a positive covariance that existed between the number of social mates a male obtained (M_w) and the proportion of their young that he sired $(P_w;$ fig. 3b). Although this covariance was also positive even when EPF females were drawn randomly (case 2a; because a relatively small number of males obtained three social mates), it was three times greater in the latter case, in which females were drawn only from the mates of monogamous males. In the final polygyny simulation (case 2c), EPF
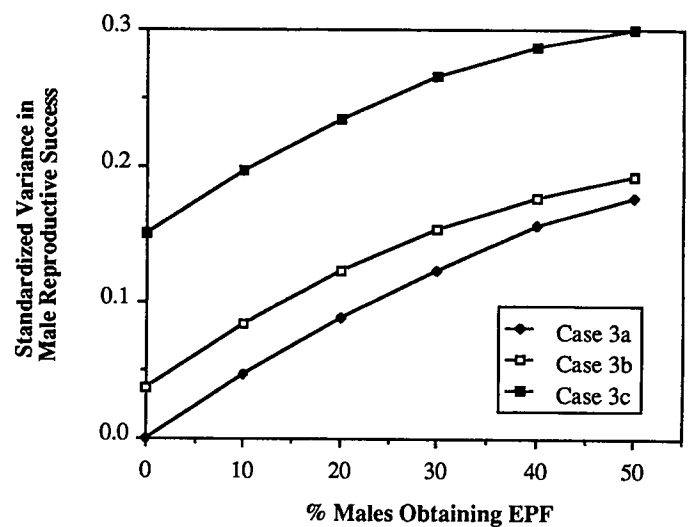

FIG. 4. Results of female quality simulations. Shown are the proportion of males obtaining extra-pair fertilizations versus the standardized variance in male reproductive success when female quality did not vary (case 3a, diamonds), varied moderately (case 3b, open squares), and varied greatly (case 3c, closed squares). See text for details of how female quality was varied. When no males obtain extra-pair fertilization (EPF), variance in male reproductive success is equal to variance in female reproductive success.

females were drawn only from those males having more than one social mate, simulating a trade-off between a male's pursuit of EPF and his ability to guard multiple mates. In this case, the variance in male reproductive success decreased as the proportion of males obtaining an EPF increased (fig. 3a), due to an increasingly negative covariance between M_e and P_w (fig. 3b). Thus, the opportunity for sexual selection in this case was lower than in the situation in which no males obtained EPF.

Finally, we simulated the effect of variation in both female fecundity and EPF success on variance in male reproductive success in a socially monogamous mating system. This simulation was identical to the first monogamy simulation (with EPF females drawn from the entire pool of females in the population), except the number of young that each female produced was allowed to vary. In the first case (case 3a), each female produced exactly four young and the results were identical to case 1a (fig. 4). For case 3b, 15 females produced three young, 20 females produced four young, and 15 females produced five young, for a mean average fitness of four young for both males and females. Overall, the effects of moderate variance in female quality on variance in male reproductive success were small relative to the effects of variance in EPF success (fig. 4). To simulate more extreme variation in female quality (case 3c), we assigned two young to 15 females, four young to 20 females, and six young to the final 15 females. Once again, mean male and female reproductive success were equal to four young, but the variance in female quality was four times that in case 3b. Under these circumstances, variance in male reproductive success was approximately twice as large as when female quality did not vary (fig. 4). However, the difference between case 3a and case 3c decreased as the proportion of males that obtained EPF increased.

TABLE 3. An example data set for red-winged blackbirds (*Agelaius phoeniceus*).* Each entry gives the number of each female's offspring that a male sired through within-pair (W) or extra-pair (E) routes.

Females	BCCX W	BCCX E	CXRY W	CXRY E	RXRG† W	RXRG† E	XCGC W	XCGC E	XYGB W	XYGB E	XGBR W	XGBR E	CYXR W	CYXR E	Total
GGXBf	2	—	—	1	—	0	—	0	—	0	—	0	—	0	3
XRXCf	—	0	4	—	—	0	—	0	—	0	—	0	—	0	4
BXCRf	—	0	4	—	—	0	—	0	—	0	—	0	—	0	4
CRXYf	—	0	—	0	2	—	—	2	—	0	—	0	—	0	4
RXRGf	—	0	—	0	4	—	—	0	—	0	—	0	—	0	4
GXYRf	—	0	—	0	—	1	0	—	—	1	—	0	—	0	2
XCGC	—	0	—	0	—	0	—	0	4	—	—	0	—	0	4
NOBAf	—	0	—	0	—	0	—	0	—	0	4	—	—	0	4
BCCXf	—	0	—	0	—	0	—	0	—	0	1	—	—	2	3
RYGXf	—	0	—	0	—	0	—	0	—	0	—	0	4	—	4
UMf1	—	0	—	0	—	0	—	0	—	0	—	0	0	—	0
UMf2	—	0	—	0	—	0	—	0	—	0	—	0	0	—	0
UMf3	—	0	—	0	—	0	—	0	—	0	—	0	0	—	0
M_w	1	—	2	—	2	—	1	—	1	—	2	—	4	—	
N_w	3	—	4	—	4	—	2	—	4	—	3.5	—	1	—	
P_w	2/3	—	8/8	—	6/8	—	0/2	—	4/4	—	5/7	—	4/4	—	
W_{tot}	2	—	8	—	6	—	0	—	4	—	5	—	4	—	
M_e	—	0	—	1	—	2	—	1	—	1	—	0	—	1	
N_e	—	—	—	3	—	3	—	4	—	2	—	—	—	3	
P_e	—	—	—	1/3	—	2/6	—	2/4	—	1/2	—	—	—	2/3	
E_{tot}	—	0	—	1	—	2	—	2	—	1	—	0	—	2	
T	2		9		8		2		5		5		6		

* A subset of data originally reported in Westneat (1993).

† Second extra-pair mate of male RXRG not shown.

Applying the Model to Field Data

All of the terms derived in the above equations can be calculated from data normally gathered in a field study, combined with genetic data showing actual paternity. Following Arnold and Duvall (1994), we suggest that researchers arrange their data in a parental table: an $f \times m \times 2$ matrix (where f = the number of females, and m = the number of males in the study population), in which the entries are numbers of offspring (table 3). From such a table, the within- and extra-pair reproductive success for each male is merely the sum of the W and E columns for that male, respectively. The number of within-pair mates for each male is the number of entries in his W column, and the number of extra-pair mates is the number of entries in his E column (assuming that the male sires at least one young with each extra-pair mate). Each female's fecundity or reproductive quality is given by the row total for that female. The proportion of a female's young that were sired by a certain male is obtained by dividing the female's total fecundity into the number of her young that were sired by the male. For example, male XGBR in table 3 obtained two social mates and sired 71.4% (five of seven) of the young that those mates produced. The two young produced by female BCCXf not sired by male XGBR were sired by male CYXR, who also sired four young with one social mate and no young with three mates that did not successfully produce any young. Thus, from this table one can compute the variance and covariance terms outlined above.

The data given in table 3 are a subset of data collected during the 1988 season from a population of red-winged blackbirds (*Agelaius phoeniceus*) breeding near Ithaca, New York. For this population, measures of pairing success and female reproductive success were gathered in the field, and the parentage of offspring was determined by DNA fingerprinting (for a description of the study population and methods used, see Westneat [1993]). An analysis of the full 1988 data set (21 males and 36 females) illustrates the value of applying this model to field data (table 4). Of the several fitness components, those pertaining to within-pair success contributed substantially to the total variance in reproductive success, with variance in the number of social mates contributing more than any other single component in this polygynous population. Thus, most of the opportunity for selection was generated by within-pair reproductive success. Variance in extra-pair mating success contributed relatively less to the total variance, indicating that success in siring extra-pair young contributed relatively little to the total opportunity for selection. However, extra-pair matings did contribute to the total opportunity through their effects on within-pair paternity; 35% of the total variance was due to variance in the proportion of young sired by each male with his social mates. Thus, variance in susceptibility to extra-pair fertilization (EPF) appears to create a large opportunity for selection in this population. Of the many covariance terms, most are negligible (account for <5% of the total variance) except the covariances among the within-pair success components and the covariance between the numbers of social and extra-pair mates. The covariances between the number of social mates and within-pair paternity and between the number of social and extra-pair mates are both positive. Indeed, the combined covariance between within- and extra-pair success [Cov(*W*, *E*)] accounted for 20% of the total variance in male reproductive success.

TABLE 4. Analysis of fitness components for red-winged blackbirds.*

Source	Term	Absolute value	Standardized value†	% total variance
Total variance	Var (T)	9.657	0.492	100.0
Within-pair terms	$\overline{N_w^2}\overline{P_w^2}\mathrm{Var}(M_w)$	4.023	0.205	41.7
	$\overline{M_w^2}\overline{P_w^2}\mathrm{Var}(N_w)$	1.224	0.062	12.7
	$\overline{M_w^2}\overline{N_w^2}\mathrm{Var}(P_w)$	3.403	0.174	35.2
	$2\overline{M_w}\overline{N_w}\overline{P_w^2}\mathrm{Cov}(M_w, N_w)$	−1.474	−0.075	−15.3
	$2\overline{M_w}\overline{N_w^2}\overline{P_w}\mathrm{Cov}(M_w, P_w)$	1.757	0.090	18.2
	$2\overline{M_w^2}\overline{N_w}\overline{P_w}\mathrm{Cov}(N_w, P_w)$	−0.527	−0.027	−5.5
Total within-pair variance	$\mathrm{Var}(W)$	6.691	0.341	69.3
	D_w	−1.715	−0.088	−17.9
Extra-pair terms	$2\overline{N_e^2}\overline{P_e^2}\mathrm{Var}(M_e)$	0.984	0.050	10.2
	$2\overline{M_e^2}\overline{P_e^2}\mathrm{Var}(N_e)$	0.021	0.001	0.2
	$2\overline{M_e^2}\overline{N_e^2}\mathrm{Var}(P_e)$	0.107	0.005	1.1
	$2\overline{M_e}\overline{N_e}\overline{P_e^2}\mathrm{Cov}(M_e, N_e)$	−0.012	−0.001	−0.1
	$2\overline{M_e}\overline{N_e^2}\overline{P_e}\mathrm{Cov}(M_e, P_e)$	−0.110	−0.006	−1.1
	$2\overline{M_e^2}\overline{N_e}\overline{P_e}\mathrm{Cov}(N_e, P_e)$	−0.021	−0.001	−0.2
Total extra-pair variance	$\mathrm{Var}(E)$	0.933	0.048	9.7
	D_e	−0.036	−0.002	−0.4
Within-pair and extra-pair covariance	$2\overline{N_w}\overline{P_w}\overline{N_e}\overline{P_e}\mathrm{Cov}(M_w, M_e)$	1.481	0.076	15.3
	$2\overline{N_w}\overline{P_w}\overline{M_e}\overline{P_e}\mathrm{Cov}(M_w, N_e)$	−0.017	−0.001	−0.2
	$2\overline{N_w}\overline{P_w}\overline{M_e}\overline{N_e}\mathrm{Cov}(M_w, P_e)$	0.368	0.019	3.8
	$2\overline{M_w}\overline{P_w}\overline{N_e}\overline{P_e}\mathrm{Cov}(N_w, M_e)$	0.102	0.005	1.1
	$2\overline{M_w}\overline{P_w}\overline{M_e}\overline{P_e}\mathrm{Cov}(N_w, N_e)$	−0.220	−0.011	−2.3
	$2\overline{M_w}\overline{P_w}\overline{M_e}\overline{N_e}\mathrm{Cov}(N_w, P_e)$	0.168	0.009	1.7
	$2\overline{M_w}\overline{N_w}\overline{N_e}\overline{P_e}\mathrm{Cov}(P_w, M_e)$	0.363	0.019	3.8
	$2\overline{M_w}\overline{N_w}\overline{M_e}\overline{P_e}\mathrm{Cov}(P_w, N_e)$	−0.238	−0.012	−2.5
	$2\overline{M_w}\overline{N_w}\overline{M_e}\overline{N_e}\mathrm{Cov}(P_w, P_e)$	−0.227	−0.012	−2.4
Total WP and EP covariance	$2\ \mathrm{Cov}(W, E)$	1.937	0.099	20.1
	D_{we}	0.157	0.008	1.6
Remainder	D_T	−1.496	−0.076	−15.5

* Data originally reported in Westneat (1993). Total sample included 21 males and 36 females. Full data set, with original calculations available as a spreadsheet upon request.
† Divided by mean reproductive success squared.

Social and Nonsocial Selection on Phenotypic Traits

The statistical model illustrated in figure 1 can also be used to measure directional selection on phenotypic traits. In the simplest application of the model, an investigator might want to measure the amount of directional selection on each trait that is exerted through social mates versus nonsocial mates. The selection gradient (Lande and Arnold 1983) corresponding to selection via social mates can be estimated by computing the partial regression of the number of offspring that a male sires with his social mates, W, on the phenotypic trait in question, holding constant all other phenotypic traits and the number of offspring sired with nonsocial mates, E. Likewise, the selection gradient corresponding to selection via nonsocial mates can be estimated by computing the partial regression of the number of offspring that a males sires with his nonsocial mates, E, on the phenotypic trait in question, holding constant all other phenotypic traits and the number of offspring sired with social mates, W. These selection gradients measure, respectively, the path from a trait to social fecundity (W) and the path from a trait to nonsocial fecundity (E). The path from social fecundity to total fecundity can be estimated as the partial regression of total fecundity, T, on social fecundity, W, holding constant nonsocial fecundity, E. Likewise, the path from nonsocial fecundity to total fecundity can be estimated as the partial regression of total fecundity, T, on nonsocial fecundity, E, holding constant social fecundity, W. Total fecundity selection on a trait via social mates is then the sum of the selection gradient corresponding to the path from the trait to social fecundity plus the selection gradient corresponding to the path from social fecundity to total fecundity. Total fecundity selection on a trait via nonsocial mates is the sum of the selection gradient corresponding to the path from the trait to nonsocial fecundity plus the selection gradient corresponding to the path from nonsocial fecundity to total fecundity. For such partial regressions to accurately represent selection gradients, it is important that total fecundity have a mean of one and that $T = W + E$. An easy way to accomplish this is to divide T, W, and E by average total fecundity before proceeding with statistical calculations. For more discussion of path diagram representations of selection gradients see Arnold (1983, 1994), Arnold and Duvall (1994), and Kingsolver and Schemske (1991).

In a more complicated application of the statistical model (fig. 1), an investigator might want to estimate the selection gradients corresponding to the component parts of social and nonsocial fecundity. In other words, one might want to break the selection gradient corresponding to the path from the trait to social fecundity into three parts, corresponding to the three multiplicative components of W. The method described by Arnold and Wade (1984a,b) can be used for this problem. Koenig et al. (1991) describe and compare two similar methods.

DISCUSSION AND CONCLUSIONS

In this paper, we have extended previous methods for partitioning variance in reproductive success, which have relied on fitness components being multiplicative (Arnold and Wade 1984a,b; Wade and Kalisz 1989; Koenig et al. 1991), to a situation in which fitness components are both additive and multiplicative. We have applied these methods to the case in which males can sire offspring with both social and extra-pair mates. In so doing, we obtained a general equation for variance in male reproductive success that includes the effects of variation in number of social mates, mate quality, and extra-pair copulations. These are the three mechanisms through which sexual selection is generally thought to operate (Darwin 1871; Kirkpatrick et al. 1990; Mock and Fujioka 1990; Møller 1992).

Our variance model can be used to examine both the potential effects of various fitness components on the opportunity for selection and the extent to which different mating activities conflict with each other. We have briefly explored these applications of the model. Although it is tempting to assume that processes such as extra-pair copulations, sperm competition, and mate quality will automatically increase the variance in male reproductive success, as demonstrated in our simulations the actual variance will depend on relationships among fitness components. If, for example, a strong trade-off exists between within-pair success and extra-pair success, such that their covariance is large and negative, then the opportunity for selection could approach 0 even if significant variance exists in both of the components (e.g., fig. 3a, case 2c). If, however, the covariance is positive, then the total opportunity for selection can be much higher than the simple sum of variances (e.g., case 2b).

Although the purpose of our simulations was illustrative, they indicate that the effects of extra-pair copulations on the opportunity for selection can be substantial in some cases. For socially monogamous species, both variance in the number of social mates (if the sex ratio is unbalanced) and variance in female quality have been thought to produce the opportunity for sexual selection (Darwin 1871; Price 1984; Kirkpatrick et al. 1990; Mock and Fujioka 1990). However, our analysis suggests that variance in the number of extra-pair mates could potentially have much greater effects than either of these other fitness components (see fig. 4). For number of social mates, the opportunity for sexual selection will be small unless the adult sex ratio is strongly biased toward males. Similarly, if the sex ratio is not biased, and if males do not pursue extra-pair fertilization (EPF), then variance in male reproductive success is equal to variance in female re-

productive success and is constrained by the number of young that a successful female can raise; unless female fecundity varies substantially, variance in male reproductive success will be small. In contrast, there may be few constraints on the maximum number of extra-pair young that a male can sire, depending on the time necessary to obtain an EPF and the breeding synchrony of females (Westneat et al. 1990). At the extreme, it is possible to envision a socially monogamous species in which a small number of males sire extra-pair young with many females and the variance in male reproductive success approaches that seen in lekking species (e.g., Mulder et al. 1994). Clearly, additional simulations are needed to define the range of possible relationships among components and their effects on total variance.

In addition to the theoretical analyses discussed above, our method has two general applications for field workers. First, through explicit consideration of possible components of fitness and the covariances among them, an investigator can organize hypotheses in an initially unbiased manner. Data analyses would then provide the basis for future, more experimental investigation of specific hypotheses, perhaps in a hierarchical fashion from most to least important. Indeed, one major benefit of applying this model to field data is that new hypotheses are generated. For example, one term in the model is the association between the number of extra-pair mates and the paternity in each extra-pair mate's brood. Initially, this might seem a relatively obscure and unimportant component to consider, yet because it exists in the expanded model, one is forced to consider under what circumstances this term might be important. In a synchronously breeding population, male sperm counts might decline with increased number of extra-pair mates (Birkhead and Møller 1992), leading to reduced probability of fertilization per extra-pair mate and reduced within-brood paternity. Although this hypothesis could be generated through other avenues (e.g., careful field work), the advantage of deriving equations for the components of fitness is that it provides a systematic framework for listing potential hypotheses from the start.

Second, and more importantly, the standardized variance and covariance components measure the magnitude of each component's effect on total variance, allowing an investigator to determine which components have the greatest effect on the opportunity for selection. Such an examination will provide preliminary evidence to focus on particular types of mating events and the phenotypic traits associated with them. For example, in the case of red-winged blackbirds breeding in New York, the effect of within-pair reproductive success on the opportunity for sexual selection is seven times greater than the effect of extra-pair reproductive success (table 4). This suggests that, for this population, researchers interested in sexual selection should focus their attention on the effects of male traits on the ability to obtain and guard social mates rather than on the ability to obtain EPF. Similarly, particularly large covariance terms represent potentially interesting and important associations between fitness components; the behavioral and/or ecological mechanisms that underlie these covariances require empirical study. In the case of red-winged blackbirds, our preliminary analysis (table 4) indicates that males that have many social mates also have many extra-pair mates and high within-pair paternity (compare with Gibbs et

al. 1990). Westneat (1993) explores some of the possible explanations for these relationships. Finally, some covariance terms might be surprisingly small. Although different mating activities, such as the pursuit of social and extra-pair mates, are expected to present conflicting demands on an individual's time and energy, selection should favor mechanisms that minimize trade-offs between fitness components.

Some practical issues might arise when researchers attempt to apply this model to field data. Some of these issues are common to any study that examines reproductive success, whereas others are specific to the approach we present in this paper. First, in most field studies, not all individuals in the population will be sampled, such that some males will have sired unsampled young. If only a portion of the total population has been sampled, then the number of sampled young sired by unsampled males gives an estimate of the number of young that sampled males have sired outside of the main study area. If this number is large, then estimates of male reproductive success might be quite inaccurate. Researchers faced with a large number of young that cannot be accounted for might be able to restrict their analysis to a core group of males and ignore those near the edge of the study area. Second, it is often difficult to know the number of extra-pair females that a male copulates with, as some copulations may not lead to fertilization. One approach, adopted in this paper, is to operationally define extra-pair mates as those females who produce young sired by the male in question. Alternatively, one could collapse extra-pair reproductive success to a single term (e.g., eq. [11] to [13]). Although this approach sacrifices detailed description of potentially interesting interactions, it would not require accurate measures of number of extra-pair mates. Finally, the variance and covariance terms in this model can be calculated in several different ways (e.g., Arnold and Wade 1984b; Kalisz 1986; Koenig and Albano 1987; Conner 1988; Wade and Kalisz 1989). In this paper, we have calculated all components using only those individuals who had non-zero fitness in the previous episode of selection (see above), as this method gives the effect of each component independent of the others. For example, individuals who did not obtain any extra-pair mates were excluded from the calculation of variance in extra-pair mate quality. Other approaches, and their relative benefits, are discussed by Koenig et al. (1991).

We have applied our variance model to the case in which individuals pursue copulations with both social and extra-pair mates. The model is also applicable to other situations in which fitness components are both additive and multiplicative. One example is the case of organisms that live through several successive and distinct breeding seasons. In this case, fitness components describing success within each season could be multiplicative, whereas the success within each season should be summed to give total reproductive success (Arnold and Duvall 1994). Note also that the general model can be modified to fit different situations or questions of interest (e.g., eq. [13]). Furthermore, a researcher may have good a priori reasons to suspect that several terms in the general model are negligible (e.g., if the study species is monogamous with a balanced sex ratio), or may have a narrowly defined question in mind, such that several of the terms could be ignored.

Standardized variance in reproductive success gives the upper limit for the strength of selection that can act on phenotypic traits. Detailing the contribution of various fitness components to total variance in reproductive success reveals both important sources of variance and potentially interesting interactions among them. Careful correlational studies (e.g., the measurement of selection gradients, see above) and/or experimental manipulations are then needed to determine the extent to which the potential for selection is realized (Koenig and Albano 1986; Grafen, 1987, 1988). In our view, an analysis of the opportunity for selection is an initial step, rather than the last, in a detailed study of sexual selection.

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