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MATE DENSITY, PREDATION RISK, AND THE SEASONAL SEQUENCE OF MATE CHOICES: A DYNAMIC GAME

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Abstract.—We describe and analyze a computer-simulation model of mate choice, featuring two different quality groups (based on offspring per mating) in each sex. Mating between quality groups results from two-dimensional random encounter and mutual assent, where assent reflects an attempt to maximize expected lifetime reproductive success, E(LRS). Premating predation (via random encounter with predators) and other mortality also influence E(LRS). Given potentially conflicting optimal choices, the model finds the evolutionarily stable patterns of choosiness for the four quality groups. When there are multiple mating episodes by individuals through the season, the resulting dynamic game is solved to obtain a seasonal pattern of mate choice and reproduction. The model generates seven different mating patterns among quality groups. These patterns imply different opportunities for selection, as indicated by the variance components of normalized lifetime reproductive success, var(LRS). The changes in E(LRS), var(LRS), and mating patterns in response to different densities of predators and of potential mates are explored in detail. Decreasing predation risk or increasing mate availability tends to increase E(LRS), choosiness, and assortative mating. Var(LRS) and thus the opportunity for selection for mate quality is highest at intermediate densities of predators and of potential mates. When density remains constant throughout the mating season, choosiness increases late in the season, a time at which less of the potential E(LRS) is jeopardized by the greater predation risk associated with choosiness. Reproductive success of the low-quality group of the less choosy sex is particularly sensitive to changes in density and other parameters. When seasonal density patterns of predators and potential mates are predictable, these low-quality individuals should do better and may thus be more numerous when mate densities are high and predator densities are low, or when predator densities are high and mate densities are low, than for other combinations of relative densities.

Natural selection shapes many behaviors in animals, including the choice of mates (Darwin 1871). If the numbers of offspring expected from a mating, or the risk associated with obtaining the mating and the subsequent offspring, differ among potential mates, then selection should favor the ability to discriminate and respond appropriately (Janetos 1980; Bateson 1983; Partridge and Halliday 1984).

A considerable amount of recent empirical work has focused on mate choice and on the phenomena that influence and constrain choices. Mate choice has been demonstrated both in males (see, e.g., Sargent et al. 1986; Thornhill and Gwynne 1986) and in females (see, e.g., Sargent and Gebler 1980; Sargent 1982); in many cases, reproductive success depends on mate choice (see, e.g., Crocker

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and Day 1987; Simmons 1987). Though mate choice need not be adaptive to permit coevolution between mate preferences and the chosen traits (Lande 1980; Kirkpatrick 1982, 1987; Bradbury and Andersson 1987), in this article we restrict our attention to *adaptive mate choice* in both sexes. We assume that both sexes vary in reproductive quality and that offspring number and survival are determined by the combined reproductive quality of the parents. Such parental contributions to offspring may be genetic, environmental, or a combination.

Our study focuses on environmental contributions to the fitness of offspring. These may include propagule number and size in females, nuptial gifts and high-resource or low-predation-risk territories in males, and parental care in both sexes. Though the model is also applicable to heritable fitness contributions, the possible importance of these in nature is currently a source of considerable controversy (see, e.g., Partridge 1980; Boake 1986; Woodward 1986; Kirkpatrick 1987; Taylor et al. 1987; Moore and Moore 1988). We refer to the total contribution that a potential mate can make to the fitness of its offspring as its *reproductive quality*.

Mate choice can result in assortative mating (e.g., size-assortative mating; Thompson and Manning 1981; Rubenstein 1987). When the chosen trait correlates with reproductive quality, this generates assortative mating on reproductive quality as well. In this article, we model how mate choice and assortative mating based on reproductive quality depend on three factors over a breeding season: mate density, operational sex ratio, and predation risk.

Though these three factors are rarely studied in concert, some information is available about the effects of each. The densities of potential mates over the mating season are known to influence the type of mating system (Parker 1970; Wells 1977; Thornhill 1984; McLain and Boromisa 1987), but density data have been obtained only infrequently in mate-choice studies. The central importance of the operational sex ratio (Wade 1979; Fincke 1982; Hubbell and Johnson 1987) is perhaps more widely appreciated than that of density. In fact, differences in postmating latency alone may alter the operational sex ratio and the variances of reproductive success, whether or not mate choice or overt intrasexual competition is involved (Sutherland 1985; Hubbell and Johnson 1987). Finally, searching for mates has been shown to be dangerous (McCauley and Lawson 1986; Gwynne 1987), even to the point of skewing the sex ratio or inhibiting the mating activities of the vulnerable sex. In extreme cases, predation may retard or counteract sexual selection (Endler 1978, 1983, 1987; Belwood and Morris 1987).

To date, there have been relatively few modeling analyses of environmentally based mate choice. Most of these (i.e., Parker 1979; Janetos 1980; Losey et al. 1986; Hubbell and Johnson 1987) have considered mate choice an optimization problem for each sex separately. Taking account of the potential for each sex to constrain choices by the other generates a game, which can be solved as a standard optimization problem only when one sex can be assumed to mate indiscriminately (Parker 1983). The application to mating tactics of the terminology and methods of game theory and the theory of evolutionarily stable strategies (see Maynard Smith 1982) is recent (Cade 1980; Dawkins 1980; Rubenstein 1980) but well established (Dominey 1984).

In this article, we present the derivation and computer-simulation analysis of a dynamic-game model of mate choice in which there are two discrete quality categories of potential mates in each sex. Dynamic games are dynamic-programming formulations for which the strategy within each time step is determined by the outcome of a game. In a dynamic program, the strategy for each step in a temporal sequence of discrete time steps is optimized, subject to constraints imposed by previous choices of strategy. (For a thorough review of dynamic programming in behavioral ecology, see Mangel and Clark 1988.) Dynamic-game analyses in ecology include those of Schaffer (1977), Enquist and Leimar (1983), Vincent and Brown (1984), Mäkelä (1985), and Houston and McNamara (1987). We focus here on establishing the conditions under which individuals in each of the two quality categories should be choosy or indiscriminate in choosing mates, both for isolated mating episodes and for a seasonal sequence of such episodes. The resulting stable mating patterns, presence or absence of assortative mating, expected lifetime reproductive success (hereafter, E(LRS)), and normalized variance of LRS (hereafter, var(LRS)) within each sex are obtained.

E_x(LRS) and var_x(LRS) indicate the fitness and the opportunity for selection in the specified sex x, respectively (Arnold and Wade 1984*a*, 1984*b*). (Expressions used to calculate E_x(LRS) and var_x(LRS) are presented in App. A.) We use them in this article, with the other responses noted above, to compare and interpret the model's behavior under different ecological conditions. In particular, we attempt to establish (1) the seasonal patterns of mating and of reproductive success expected for organisms capable of repeated reproduction during a breeding season and (2) the extent to which single-episode and seasonal patterns reflect premating predation risk and the availability of potential mates.

In the next section, we describe the structure of the model. We then present results for single mating episodes, emphasizing the effects of mate densities and predators, followed by results for seasonal sequences of mating episodes. Next, we apply the model to three case studies from the literature, obtaining good qualitative agreement with empirical results and some additional insights into the biological interactions. We conclude with a general discussion and some testable predictions and hypotheses derived from the analysis.

MODEL STRUCTURE

Overview

The assumptions listed in table 1 ensure tractability while retaining considerable generality. Each individual's lifetime consists of a series of mating episodes in a single mating season. Over evolutionary time, natural selection is assumed to steer mate choice in each episode toward maximizing the expected number of offspring for the remainder of the individual's lifetime. Choosiness in a given episode generally increases the risk of mortality, jeopardizing potential reproduction in that episode and in all subsequent episodes. Establishing the optimal sequences of mate choice should thus be formulated as a dynamic-programming problem. Because the best strategy in a given episode depends in part on the best

TABLE 1

ASSUMPTIONS OF THE MODEL

Densities:
1. Densities of potential mates and of predators remain constant throughout each mating episode.
2. During successive mating episodes, densities of potential mates and of predators are independent of mating, predation, and mortality in other episodes.

Mating and predation dynamics:
3. Lifetime reproductive success is determined within a single mating season.
4. Frequencies of mating and predation are determined by two-dimensional random encounter.
5. Mating (with consequent reproduction) and predation are instantaneous.
6. Searching for mates entails at least as much risk of predation as not searching for mates.

Access to mates:
7. No matings are forced.
8. There is no interference or sperm competition for mates.

Mate quality:
9. Mate qualities within each sex can be represented as two discrete categories.
10. Qualities of the quality groups are constant throughout the season.
11. Mate quality is instantaneously and infallibly assessed.
12. For matings of each quality-group combination, the number of offspring produced is directly proportional to the number of matings.

Quality-specific choice patterns:
13. All individuals within a quality group are identically choosy, and this degree of choosiness remains constant during a given mating episode.
14. Quality groups combine to exhibit choice patterns in each mating episode that are stable with respect to alternative patterns and that maximize the expected number of offspring from the beginning of that episode to the end of the mating season, subject to this stability constraint.

strategies for the future, the optimal strategy must be found in a reverse-cumulative way. The first step is to calculate the best strategy for the final episode. The second step calculates the optimal strategy for the second-to-last episode, taking into account the extent to which this strategy influences the potential payoff in the last episode. Expected reproductive success for the final two episodes is then used to calculate the optimal strategy for the third-to-last episode, and so on. Because the mate choices made by individuals in each of the four categories during an episode are constrained by choices made by individuals in other categories, we follow a game-theoretic approach to finding the best available strategies for each category. (These categories are designated here as "quality groups.") Actual mating and predation frequencies within mating episodes are calculated as random encounters in two dimensions within a finite area; these frequencies help determine the expected numbers of offspring from which the stable combination of strategies for a particular episode is obtained. These manipulations and calculations are carried out in a computer program, which allows the implications of a large number of parameters to be efficiently studied.

The Seasonal Sequence of Mating Episodes

The mating season is taken to be a sequence of cycles, each composed of a mating episode followed by a nonmating period. The sexes may differ in the frequency with which individuals can participate in mating episodes and in the number of matings possible within a given episode (see fig. 1).

Though the strategies chosen by each quality group can influence the survival

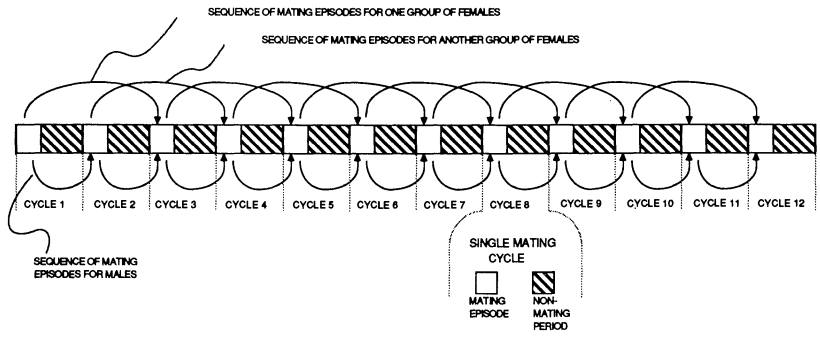


FIG. 1.—Default (or standard) sequence of 12 mating cycles, and sequences of mating episodes in which individual males and females participate. In the default, mating episodes last half as long as intervening nonmating periods.

of individuals through the season, we assume that the densities of each quality group in each mating episode remain constant and thus independent of within-episode survival. (The densities are assumed to be maintained by recruitment that is not explicitly represented in the model.) This allows us to represent the seasonal sequence of matings and reproduction using a dynamic-programming formulation (see Mangel and Clark 1986, 1988) without explicit state variables. Let $\epsilon(t, m)$ be the expected cumulative reproduction by an individual within some quality group beginning at cycle t of m total mating cycles in the season. Thus, $\epsilon(t, m)$ is the total amount of reproduction achieved in the current mating cycle t plus the amount achieved in the $m - t$ subsequent mating cycles. Let $\mu(t)$ be the expected number of matings by an individual during cycle t. Let $\rho(t)$ be the expected number of offspring produced per mating during t. And let $\sigma(t)$ be the chance of surviving the mating cycle t. Then,

$$\epsilon(t, m) = \mu(t)\rho(t) + \sigma(t)\epsilon(t + 1, m). \quad (1)$$

The system of equations implied by this recursion relation can be solved by beginning with the final step (i.e., $t = m$). Since $\epsilon(m + 1, m) \equiv 0$ (i.e., no reproduction can occur with no mating cycles left), it follows that

$$\epsilon(m, m) = \mu(m)\rho(m). \quad (2)$$

Along with reproduction and survival during the penultimate cycle, $\epsilon(m, m)$ yields $\epsilon(m - 1, m)$, and so forth, moving backward through the mating cycles until the expected reproduction over all m cycles, $\epsilon(1, m)$, is found.

To calculate the optimal strategy for a given cycle, we therefore must first calculate optimal strategies and expected reproductive success for later cycles. Procedures for assessing optimal strategies and expected reproductive success for a given cycle are described below.

Stability within Each Mating Episode

Within mating episodes, all members of each quality group are assumed to be choosy (i.e., to mate only with high-quality mates encountered) or all are assumed

to be indiscriminate (i.e., to mate with any high- or low-quality mates encountered), depending on which maximizes expected reproduction through the rest of the season. Individuals do not alter their choosiness within an episode but can alter choosiness between episodes. The choice of being discriminate or indiscriminate may be constrained by the choices of individuals in other quality groups; this sometimes precludes choosiness by low-quality individuals and prevents some otherwise-conceivable mating patterns. The actual tactics used are those for which no individual in a quality group can improve its fitness by altering its own choosiness. This kind of stability is referred to as "evolutionary stability" because it specifies the conditions under which a mutant alternative strategy (or behavioral phenotype) would be unable to invade the population. The corresponding strategies are known as *evolutionarily stable strategies* if they are frequency-dependent (see Maynard Smith 1982). Since maintaining constant densities in the present model prevents frequency dependence, we simply refer to strategies that prevent other strategies from persisting and spreading in the population as *stable*.

Figure 2 depicts the seven possible combinations of mating patterns among the four quality groups and the transitions among the patterns by which quality groups might increase their expected reproduction. Every individual profits most from high-quality mates. But since there are assumed to be no forced matings, high-low matings happen if and only if they increase expected reproduction for high-quality mates, that is, when their increased risk of mortality and of failing to find a mate as a result of choosiness could not be offset by a consistently high reproductive payoff per mating. Otherwise, high-quality individuals discriminate. For example, the uppermost pattern in figure 2 (both high-quality groups are choosy, and low-quality individuals must therefore mate with each other) is stable when neither high-quality females nor high-quality males can increase expected reproduction by mating indiscriminately.

To determine the stable mating pattern or patterns in an episode, we calculate the expected reproduction until the season's end for each quality group and each mating pattern. We then start separately from each of the seven patterns, allowing each quality group to alter its choosiness according to the transition scheme of figure 2 whenever this would increase its expected reproduction. Thus, a pattern from which the transition scheme allows no improvement is stable.

Frequencies of Random Encounters

The expected number of offspring produced and the survival during a mating cycle for each quality group in each mating pattern is calculated by letting both mating and predation result from random encounters in two dimensions. (Though this method of generating encounters may not fit any natural situation precisely, we expect it to fit many situations at least approximately, and it keeps the model structure as simple and as general as possible.) In this case, the relative velocity of two potential mates or of a potential mate and a predator equals the square root of the summed squares of the velocities of each (Koopman 1956). The frequency of encounters is the product of the reactive distance D (the diameter of a circle within which a predator or a mate at the center can just detect its prey

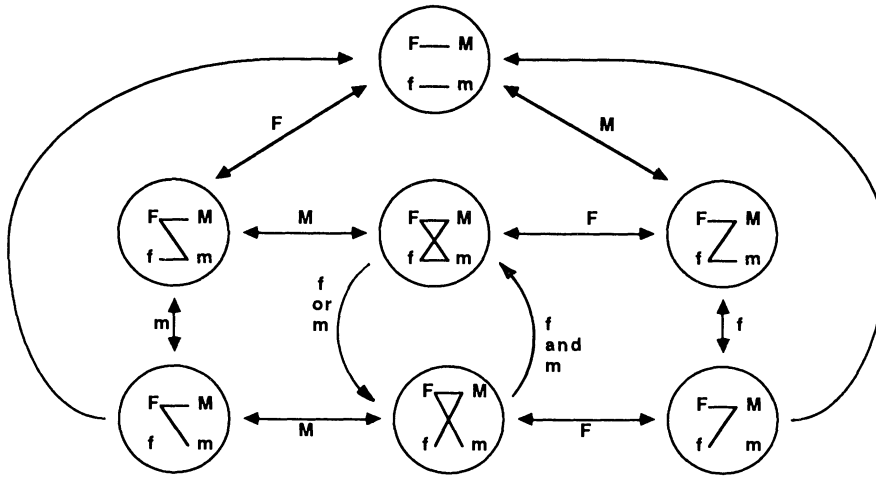


FIG. 2.—Transitions among the seven mating patterns. For each pattern, capital letters indicate high-quality mates and lowercase letters indicate low-quality mates. F (or f) and M (or m) denote the sexes. Lines join quality groups between which matings can occur; they thus imply different combinations of choosiness or indiscriminate mating. We use the line arrangements within each of the seven mating patterns of this figure as abbreviated symbols for the patterns: $\overline{\underline{\ }}$, F and M are both choosy; Σ, F and m are indiscriminate, and M is choosy; $\overline{\mathrm{X}}$, all quality groups are indiscriminate; Z, F is choosy, and M and f are indiscriminate; Υ, F is indiscriminate, and M and m are choosy; X, F and M are indiscriminate, and f and m are choosy; 7, F and f are choosy, and M is indiscriminate. The mating patterns in the figure are connected by arrows indicating how a shift in choosiness by the quality group(s) on the arrow shifts the pattern. The patterns are stable when none of the possible shifts increases the expected number of offspring for the quality group(s) capable of triggering the shift.

or another mate at the periphery), the densities N of the two groups encountering each other, and the relative velocity V. When the densities are expressed as numbers of individuals within the entire mating arena, then the encounter frequency is inversely related to the area A of the mating arena. For example, the frequency of encounters C_{FM} between high-quality females F and males M (encounters $\times$ time^{-1} $\times$ arena^{-1}) is

$$C_{FM} = D_{FM}N_F N_M (V_F^2 + V_M^2)^{1/2}/A\,. \tag{3}$$

Since the encounters are random, the time until the next encounter is distributed according to a negative-exponential probability density function (i.e., zero-order Poisson), and its mean—the expected time until the next encounter—is simply the inverse of the encounter frequency (see Pielou 1977). Since our model is deterministic, we use these expected times as the actual times between encounters.

Quality-group densities remain constant throughout each episode (as in Hubbell and Johnson 1987). The focal individuals are assumed to participate from the beginning of the episode and are removed after each encounter with a predator or with a singly mating individual, but they are replaced by nonfocal individuals to maintain constant densities. Simultaneous assessment of "background mortality"

(i.e., mortality unrelated to predator density) necessitates obtaining implicit solutions for the times until encounter. Following each mating episode is a nonmating period (16 h in the default run), during which background mortality may continue.

Thus, by stepping through the mating episode encounter by encounter, removing and replacing individuals as necessary, and keeping track of each death and mating, we can calculate the expected reproduction by an individual for each pattern and quality group. We then determine which mating pattern or patterns are stable, and these provide entries for equation (1), from which the entire stable seasonal sequence is eventually constructed.

The Computer Program and Its Default Parameter Set

The model has been implemented as a computer program in Pascal (see fig. 3) and run on an 80286-based microcomputer. Though the default parameter values given dimensions in table 2 probably best apply to a small isolated population of insects, the actual numbers used also apply reasonably well to other populations when distance and time are rescaled appropriately.

In the default run, we depict a typical case in which males are capable of mating once during each episode but females can mate only once in alternate episodes and thus invest more in each mating. The operational sex ratio at the beginning of each episode is therefore two males for each female, as expected with an actual 1:1 sex ratio biased by the assumed frequencies of participation in mating episodes. Through the season, predator density remains constant, but densities of the potential mates rise to an early peak and then decline. Mate quality is assumed to contribute multiplicatively to the number of offspring per mating, and the total range of offspring per mating for two low-quality mates versus two high-quality mates is a factor of two (i.e., one offspring per mating vs. two offspring per mating). As is often the case in nature, males move faster in seeking mates than do females (here, twice as fast). Speeds and reactive distances are chosen to spread mating encounters over much of the mating episode. Background mortality removes about 14% of the population per mating cycle, more than the increment of mortality from predation on females. However, because males move faster and tend to take longer, on the average, than females to find a mate, this background mortality loss is less than the predation increment for males.

RESULTS

Single Mating Episode

When the MateChoice program is run to simulate a single mating episode (and otherwise with the default parameter values in table 2), the stable mating pattern is $\overline{\overline{}}$ (symbolizing the uppermost mating pattern in fig. 2), implying strong positive assortative mating. In this case, high-quality males and females produce the most offspring when they mate only with each other; low-quality males and females must mate with each other if they are to mate at all. Because densities are relatively high and animals that mate or die are replaced in the mating pool, most of

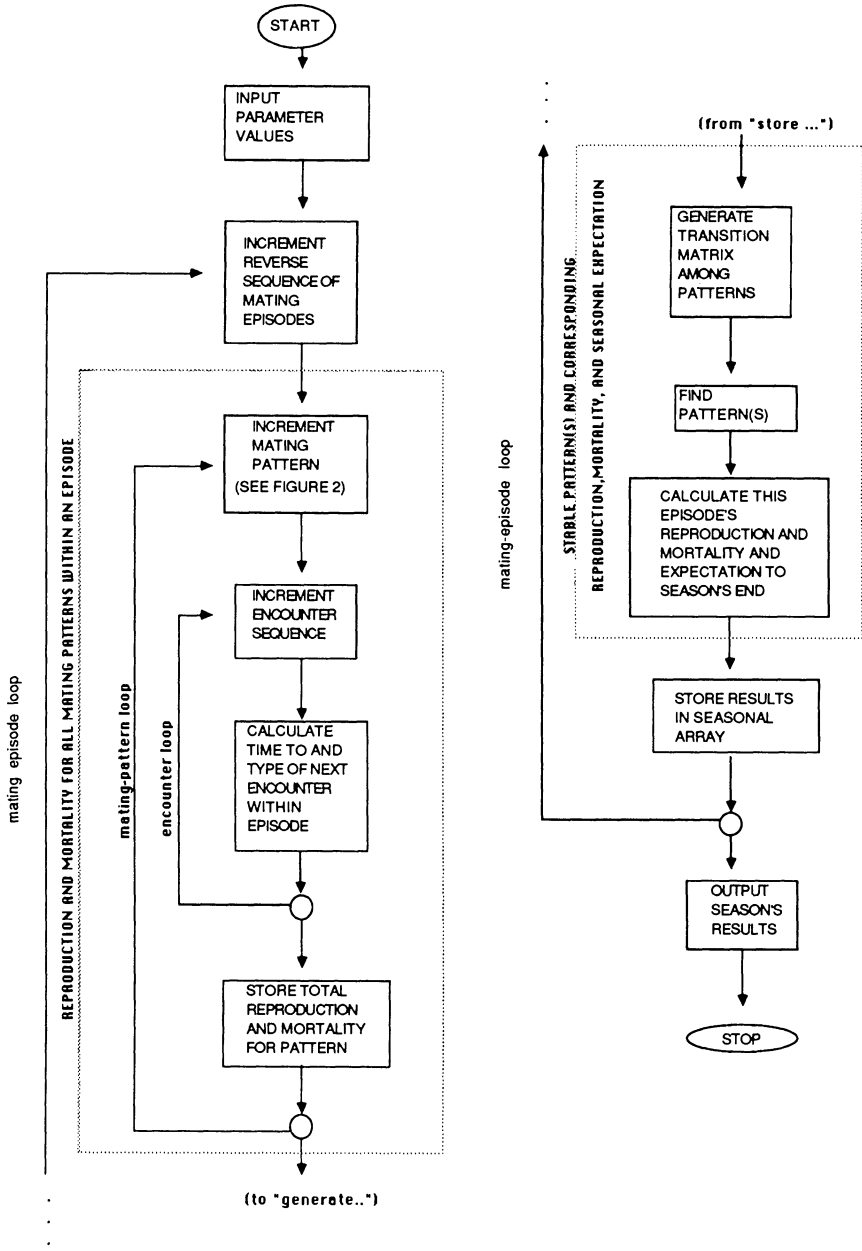


FIG. 3.—Flow diagram of the Pascal computer program MateChoice that implements the model presented here.

TABLE 2

PARAMETERS OF THE MODEL

SYMBOL	PARAMETER	DEFAULT MAGNITUDE	CASE STUDIES*			UNITS†
			SS	K	TF	
m	Mating episodes per season	12	1	1	1	Episodes season^{-1}
T	Duration of mating episode	480	24	960	360	Time
A	Size of mating arena	1	1	1	100	Length^2
N_F, N_f	Average density of females per quality group‡	50	50	50	100	Females arena^{-1}
N_M, N_m	Average density of males per quality group‡	100	150	100	600	Males arena^{-1}
N_P	Density of predators	10	5	10	1	Predators arena^{-1}
V_F, V_f	Speed of females	.01	0	.01	.002	Length time^{-1}
V_M, V_m	Speed of males	.02	.01	0	0	Length time^{-1}
V_P	Speed of predators	0	.05	.1	.025	Length time^{-1}
D_F, D_f	Reactive distance of females to mates	.005	0	.01	1§	Length female^{-1}
D_M, D_m	Reactive distance of males to mates	.01	.01	0	0	Length male^{-1}
D_{PF}, D_{Pf}	Reactive distance of predators to females	.01	0	.002	0	Length predator^{-1}
D_{PM}, D_{Pm}	Reactive distance of predators to males	.01	.02	.01	2	Length predator^{-1}
B	Background mortality rate of mates	.0001	.0002	.0002	.0002	Time^{-1}
M_F, . . . , M_m	Nonmating mortality rate of mates (above background)	.0001	.0002	.0002	.0002	Time^{-1}
n_F, n_f	Nonmating period for females per mating episode	5	8	2	23	Dimensionless
n_M, n_m	Nonmating period for males per mating episode	2	2	2	3	Dimensionless
R_{FM}	Offspring per mating (both mates of high quality)	2	3.6	4.5	2.4	Offspring mating^{-1}
R_{Fm}, R_{fM}	Offspring per mating (high-low pairs)	1.414	3, 1.2	3, 1.5	2, 1.2	Offspring mating^{-1}
R_{fm}	Offspring per mating (both mates of low quality)	1	1	1	1	Offspring mating^{-1}
F_F, F_f	Maximal mating frequency per episode for females‖	1	1	1	1	Matings episode^{-1}
F_M, F_m	Maximal mating frequency per episode for males‖	1	1	1	1	Matings episode^{-1}
L_F, L_f	Interval between mating episodes for females	2	3	1	6	Cycles (see fig. 1)
L_M, L_m	Interval between mating episodes for males	1	1	1	1	Cycles (see fig. 1)

* The three studies are considered in the text: SS, snapping shrimp (Knowlton 1980); K, katydids (Gwynne 1985); TF, túngara frog (Ryan 1985).

† For microveliids, tiny semiaquatic bugs, the appropriate units of time and length are 1 min and 1 m, respectively; for the case study SS, they are 20 min and 5 m; for K, 0.5 min and 1 km; for TF, 1 min and 1 m. For example, for the speed of female katydids, the units of length per time are (1 km) (0.5 min)$^{-1}$, or 2 km min^{-1}; multiplying by 0.01 yields a parameter value of 0.02 km min^{-1}.

‡ For each quality group, there are actually m densities, which make up the seasonal density patterns. In the default run, densities peak early and then decline.

§ Varied from 0.0625 m to 1.6 m; see the text for additional details.

‖ Mated individuals may leave the mating pool (encounter frequency = 1), or they may remain until they die or the episode ends (repeated mating).

TABLE 3

EXPECTED REPRODUCTION FOR EACH MATE-QUALITY GROUP AND MATING PATTERN

	MATING PATTERN*						
QUALITY GROUP	⚌	Z	7	Σ	ϒ	X	X
High-quality females, F	P_1	P_1	P_1	P_2	P_2	P_2	P_2
Low-quality females, f	P_3	P_4	P_5	P_3	P_6	P_4	P_5
High-quality males, M	P_7	P_8	P_8	P_7	P_7	P_8	P_8
Low-quality males, m	P_9	P_9	P_{10}	P_{11}	P_{12}	P_{11}	P_{12}

* The pattern connects females (left corners) with males (right corners) and high-quality individuals (top corners) with low-quality individuals (bottom corners); for example, in the third pattern (7), high-quality males mate with females of either high or low quality. The densities within quality groups are assumed to remain constant during the mating episode. Reproductive payoffs having the same subscript are necessarily equal.

the individuals in both sexes present at the beginning of the episode manage to mate. As a result, E(LRS) is similar for the two sexes (females, 1.43; males, 1.26), despite the operational sex ratio of 2 males: 1 female. Moreover, var(LRS) is fairly low and equal for the two sexes (0.11, where the maximum possible var(LRS) with the quality groups equally abundant is 1; see eq. [A2]).

By altering the parameter values, we obtain all of the seven possible mating patterns illustrated in figure 2. We note that three of these (⚌, Z, and Σ) imply positive assortative mating but that the assortment by quality is weaker in the latter two cases as a result of the indiscriminate mating by two of the four quality groups. One of the patterns (X) implies weakly negative assortative mating; strong negative assortative mating (X) is of course impossible under the assumptions of the model (table 1), because matings with high-quality mates are always advantageous. The other three patterns (7, ϒ, and X) imply no assortative mating, but the first two of them imply for one sex that mated individuals are of higher quality than unmated individuals; the other of these (X) is the completely indiscriminate mating pattern. When animals that mate or die are replaced in the potential-mates pool, as in the model presented here, only one pattern can be stable; multiple stable mating patterns are impossible (see tables 3, 4; App. B).

Mate Density

A series of single-episode simulations illustrates the implications of mate densities (fig. 4; note that female densities are varying in proportion to the male densities here). In general, increased mate density results in more discriminate mating. At densities below about 42 males (and 21 females) per mating arena (the area in which encounters can be considered random, expressed as length^{-2}), encounters between potential mates are sufficiently infrequent that indiscriminate mating by both sexes is the stable outcome. In this region of densities, E(LRS) is strongly related to density for both sexes, and var(LRS) is low and constant (♀ = ♂ = 0.03). At intermediate densities (42–110 males × length^{-2}), both female quality groups mate exclusively with high-quality males, preventing low-quality males from mating altogether. This ensures maximal var(LRS) for males, but var(LRS)

TABLE 4

THE CONTRADICTIONS OF ASSERTING THAT ANY TWO NONADJACENT MATING PATTERNS ARE BOTH STABLE

All Possible Nonadjacent Pairs of Stable Mating Patterns	Contradiction
⚌, ⧖	$\Sigma \rightarrow \overline{=} \Rightarrow P_1 > P_2$; $Z \rightarrow \overline{\Sigma} \Rightarrow P_2 > P_1$
⚌, ⧗	$Z \rightarrow \overline{=} \Rightarrow P_7 > P_8$; $\Upsilon \rightarrow \overline{\Sigma} \Rightarrow P_8 > P_7$
ϒ, ⚌	$\Upsilon \not\rightarrow \overline{=} \Rightarrow P_2 > P_1$; $\Sigma \rightarrow \overline{=} \Rightarrow P_1 > P_2$
ϒ, 7	$\Upsilon \not\rightarrow \overline{=} \Rightarrow P_2 > P_1$; $\overline{\Sigma} \rightarrow 7 \Rightarrow P_1 > P_2$
ϒ, Z	$\overline{\Sigma} \rightarrow \Upsilon \Rightarrow P_7 > P_8$; $\overline{=} \rightarrow Z \Rightarrow P_8 > P_7$
Σ, ⧗	$\overline{\Sigma} \rightarrow \Sigma \Rightarrow P_7 > P_8$; $7 \rightarrow \overline{\Sigma} \Rightarrow P_8 > P_7$
Σ, 7	$\overline{=} \rightarrow \Sigma \Rightarrow P_2 > P_1$; $\overline{\Sigma} \rightarrow 7 \Rightarrow P_1 > P_2$
Σ, Z	$\overline{\Sigma} \rightarrow \Sigma \Rightarrow P_7 > P_8$; $\overline{=} \rightarrow Z \Rightarrow P_8 > P_7$
Z, ⧗	$\overline{\Sigma} \rightarrow Z \Rightarrow P_1 > P_2$; $7 \rightarrow \overline{\Sigma} \Rightarrow P_2 > P_1$
7, ⚌	$7 \not\rightarrow \overline{=} \Rightarrow P_8 > P_7$; $\Sigma \rightarrow \overline{=} \Rightarrow P_7 > P_8$
⧖, ϒ	$\Sigma \rightarrow \overline{\Sigma} \Rightarrow P_8 > P_7$; $\overline{\Sigma} \rightarrow \Upsilon \Rightarrow P_7 > P_8$
⧖, 7	$Z \rightarrow \overline{\Sigma} \Rightarrow P_2 > P_1$; $\overline{\Sigma} \rightarrow 7 \Rightarrow P_1 > P_2$

NOTE.—The expected reproduction for each mate-quality group and mating pattern is specified in table 3. The densities within quality groups are assumed to remain constant during the mating episode. $\rightarrow$ indicates a transition required for the stable pattern; $\Rightarrow$ indicates logical implication; $\not\rightarrow$ indicates a transition inconsistent with the stable pattern.

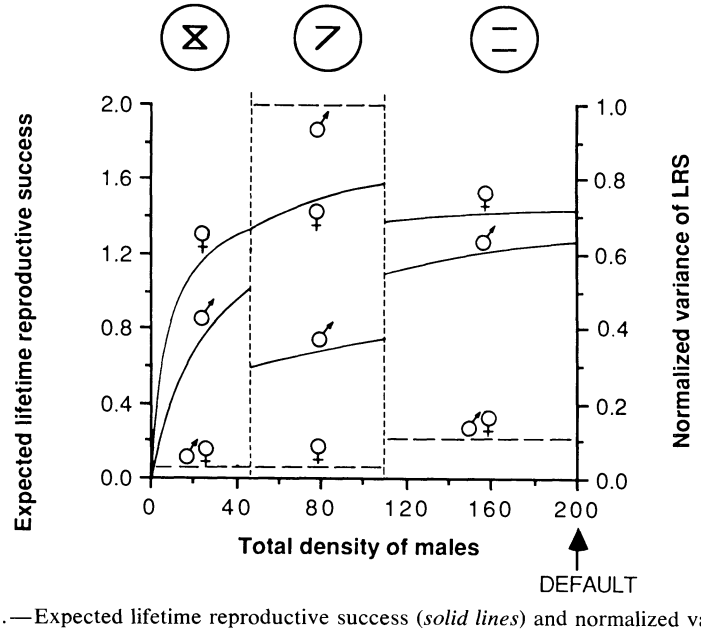


FIG. 4.—Expected lifetime reproductive success (*solid lines*) and normalized variance of LRS (*dashed lines*) for males and females vs. total density of males (which occurs at twice the total density of females). The mating season here consists of a single episode; except for this and the indicated variation in mate densities, all parameters retain their default values (table 2).

for females remains low. At these and higher densities, E(LRS) for each sex is only weakly related to mate densities, except for discontinuities at the boundaries of the density regions. At male densities above 110 males $\times$ length^{-2}, strong positive assortative mating decreases male var(LRS) sharply but increases female var(LRS) somewhat ($\varphi = \sigma = 0.11$).

The trend from the $\bar{X}$ pattern at low mate densities to $=$ at high mate densities, with one or more intermediate patterns featuring high var(LRS) by the less choosy sex, applies quite generally for all of the parameter combinations we have tried. When neither sex is choosier (i.e., when parameter values are identical for the two sexes), however, no patterns intermediate between $\bar{X}$ and $=$ are observed (see table 5, case 31; App. C).

Predation

Four series of single-episode simulations indicate the effects of premating predation (fig. 5). Increasing the density of predators (and thus the intensity of predation) generally decreases E(LRS), more sharply at low predator densities and less sharply toward higher predator densities. As in figure 4, there are discontinuities between the density regions characterized by different stable mating patterns; but along a predator-density axis, the choosiest pattern is found at the lowest densities, and the indiscriminate pattern ($\bar{X}$) is found at the highest densities. The same values of var(LRS) are associated with the same mating patterns in figure 5 as in figure 4. This yields maximal var(LRS) for males at intermediate predator densities (fig. 5), just as for intermediate mate densities (fig. 4).

When potential mates respond to higher predator densities by slowing their own mate-searching movements, the boundaries of the predator-density regions associated with each mating pattern shift to the left (fig. 5*b;* cf. fig. 5*a*). In other words, the behavioral predator-avoidance response by potential mates tends to reduce the mating choosiness for a given predator density. At some predator densities, the speed reduction clearly reduces E(LRS) (e.g., males at 0.4 predators $\times$ length^{-2}); at other predator densities, the result is considerably higher E(LRS) (e.g., males at 1.2 predators $\times$ length^{-2}). The predator densities of maximal male var(LRS) shift to the left with the pattern boundaries.

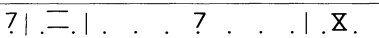
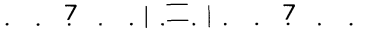
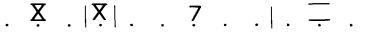
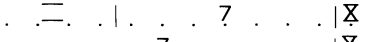
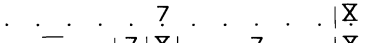
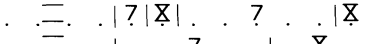
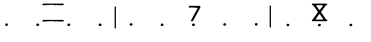
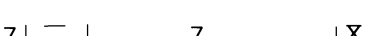
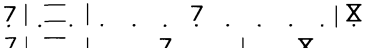
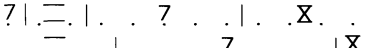
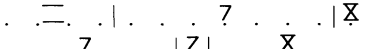
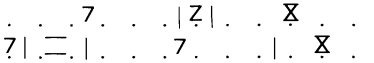
When higher predator densities are assumed to result in lower densities of potential mates, even stronger leftward shifts of the mating-pattern boundaries are observed (fig. 5*c*). In this case, E(LRS) generally decreases more sharply with increasing predator densities than in the previous cases (figs. 5*a,b*), except at high predator densities.

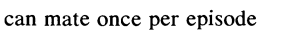
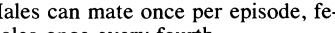
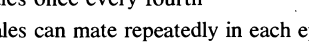
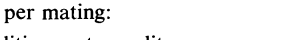
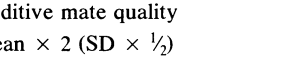
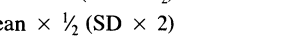
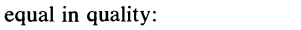
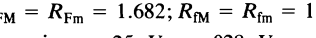
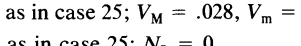
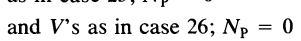
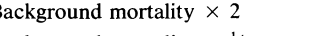
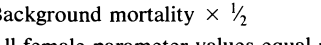
Sequential Mating Patterns and Seasonal Trends

We now turn our attention to mating seasons consisting of a sequence of mating episodes that may differ in the densities of available mates, of predators, or of both. Under these circumstances, expected payoffs for different mating strategies depend on mortality and reproductive success in both the current and future episodes. Thus, as a season progresses and the number of remaining episodes decreases, the optimal choosiness may change even if all else stays the same. We attempted to deal systematically with this complex situation by performing a

TABLE 5

SENSITIVITY ANALYSIS OF THE MODEL OVER TWELVE SUCCESSIVE MATING EPISODES

PARAMETER MODIFICATION (If Any)	MATING PATTERNS BY EPISODE*	E(LRS)†				var(LRS)	
		F	f	M	m	Females	Males
1. None (default)		5.83	3.82	7.55	.57	.05	.74
Mate densities:							
2. Mate density × 2		6.18	3.66	8.91	**2.94**	.07	**.26**
3. Mate density × ½		5.28	3.73	6.02	**.00**	.03	1.00
4. Mate densities constant through season		5.83	4.05	7.13	**.00**	.04	1.00
5. Mate densities peak in mid-season		5.48	3.73	5.99	**.01**	.04	1.00
6. Mate densities peak in late season		4.31	2.99	**2.87**	**1.42**	.04	**.17**
Predator densities:							
7. Predator density × 2		5.33	3.77	6.05	**.00**	.03	1.00
8. Predator density × ½		6.13	3.62	8.85	**2.94**	.07	**.25**
9. Predators peak in first episode		5.64	3.99	6.83	**.00**	.03	1.00
10. Predators peak in mid-season		5.78	3.38	7.68	**2.96**	.07	**.20**
11. Predators peak in last episode		6.02	3.54	8.77	**3.06**	.07	**.23**
Movement and reactive distance:							
12. Mate speed × 2		5.86	3.85	7.58	**.22**	.05	.89
13. Mate speed × ½		5.72	3.75	7.46	.94	.05	.60
14. Mate reactive distance × 2		6.18	3.66	8.91	**2.94**	.07	**.26**
15. Mate reactive distance × ½		5.27	3.73	6.02	**.00**	.03	1.00
16. Mobile predator (speed = .01)		5.61	3.67	7.32	.50	.05	.76
17. Predator's reactive distance × 2		5.33	3.77	6.05	**.00**	.03	1.00
18. Predator's reactive distance × ½		6.13	3.62	8.85	**2.94**	.07	**.25**

Mating cycle:							
19. All can mate once per episode		10.05	5.83	8.91	**2.94**	.07	**.26**
20. Males can mate once per episode, females once every fourth		3.49	2.46	6.02	**.00**	.03	1.00
21. Males can mate repeatedly in each episode		5.83	4.12	**34.42**	**.00**	.03	1.00
Offspring per mating:							
22. Additive mate quality		5.83	4.37	7.67	.31	**.02**	.85
23. Mean × 2 (SD × ½)		9.98	**8.29**	13.62	**.02**	**.01**	1.00
24. Mean × ½ (SD × 2)		3.77	**1.36**	4.64	.78	**.22**	.51
All males equal in quality:							
25. $R_{FM} = R_{Fm} = 1.682$; $R_{fM} = R_{fm} = 1.189$		5.20	2.19	6.35	**6.35**	**.17**	**.00**
26. R's as in case 25; $V_M = .028$, $V_m = .014$		5.21	2.20	6.27	**6.49**	**.17**	**.00**
27. R's as in case 25; $N_P = 0$		5.51	**.28**	9.73	**9.73**	**.82**	**.00**
28. R's and V's as in case 26; $N_P = 0$		5.51	**.63**	9.93	**9.50**	**.63**	**.00**
Others:							
29. Background mortality × 2		4.08	2.66	5.44	.46	.05	.72
30. Background mortality × ½		7.44	4.91	9.32	.63	.04	.77
31. All female parameter values equal male values		9.32	5.35	9.32	**5.35**	.08	**.08**

* Each dot represents one episode in temporal sequence from the first to the twelfth.

† Boldface values differ from corresponding default values by more than a factor of two.

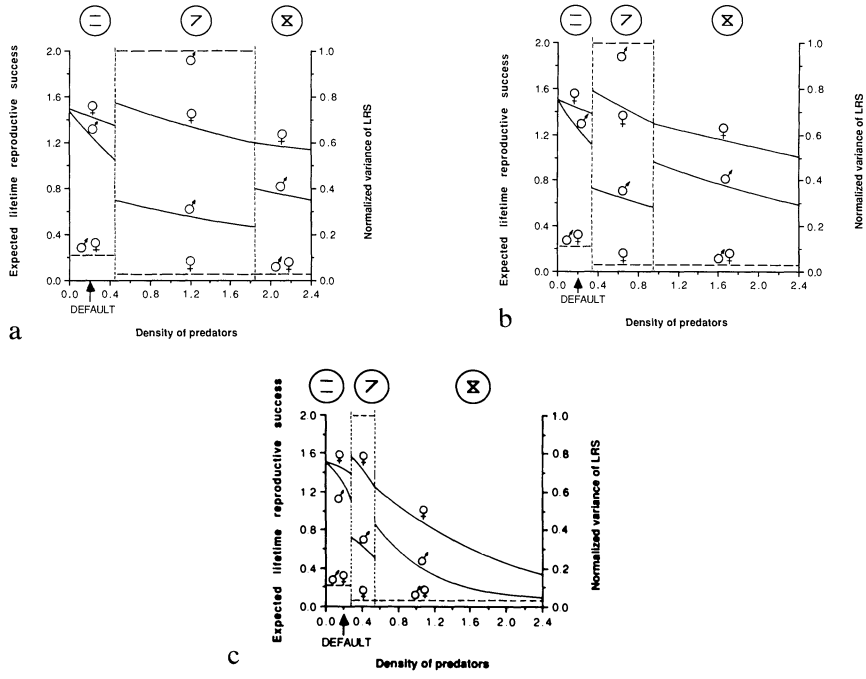


FIG. 5.—Expected lifetime reproductive success (*solid lines*) and normalized variance of LRS (*dashed lines*) for males and females vs. predator density. The mating season consists of a single mating episode; except for this, the indicated variation in predator densities, and other differences noted below, the parameters retain their default values (table 2). *a,* Simulation with parameter changes. *b,* Simulation in which movement speed of potential mates is inversely related to predator density (i.e., when predator density is twice its default value, movement speeds of potential mates are all half their default values). *c,* Simulation in which densities of potential mates are inversely related to predator density (as for movement speed in *b*).

sensitivity analysis based on the default parameter set of table 2. The procedures, rationale, and results of this analysis are presented in Appendix C. Briefly, these results, mainly for populations having a sharp peak in densities of potential mates during the mating season, indicate that the seasonal sequence of stable mating patterns can shift considerably in response to factor-of-two changes in the model's parameters. In addition, the E(LRS) of the low-quality group within the less choosy sex (males, in this case) is exceedingly sensitive to these parameter changes, as is the var(LRS) in the same sex. Within a season, choosiness tends to be strongest during the episodes with the highest densities of potential mates. For seasonally constant densities of potential mates, choosiness is generally strongest toward the season's end.

Figure 6 shows the expected reproductive success and its normalized variance for focal individuals from the beginning of a given episode until the end of a 12-episode mating season. These results can be interpreted in three biologically different ways: (1) the seasonal changes in expectations for a given individual;

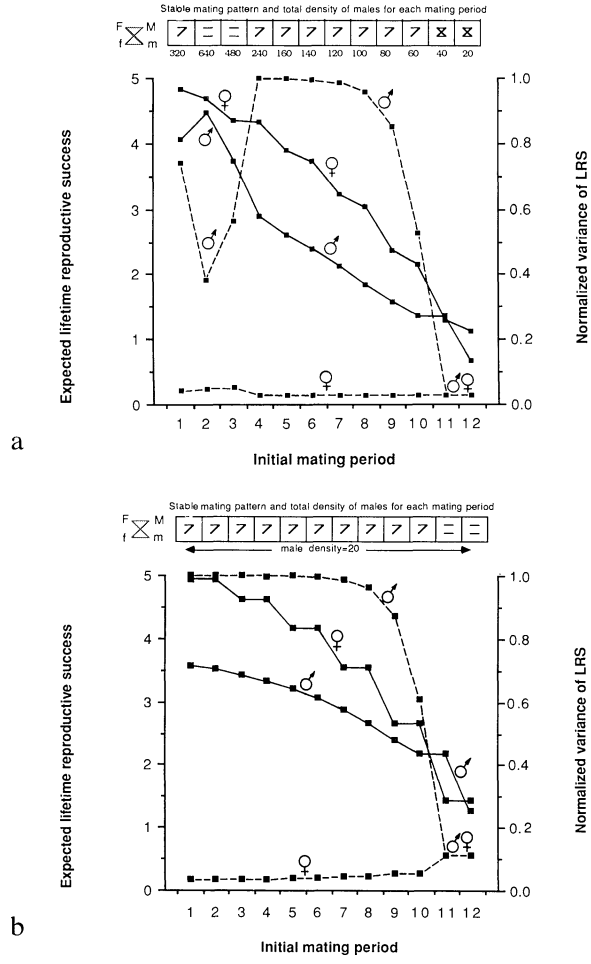


FIG. 6.—Expected lifetime reproductive success (*solid lines*) and normalized variance of LRS (*dashed lines*) for males and females vs. initial mating period. The mating season consists of 12 mating episodes. Plotted values are for individuals joining the mating season in progress at any episode and continuing until the end of the season; or, equivalently, these are expectations through the end of the season for individuals that have reached any particular episode. The parameters retain their default values (table 2) except as indicated below. *a*, Default simulation. *b*, Simulation with constant densities of potential mates throughout the season.

(2) expectations for individuals entering the mating pool at different points in the season; and (3) effects on all individuals of shortening or lengthening the mating season.

The default simulation is illustrated in figure 6*a*. The mate-density schedule indicated above the graph describes an early peak, followed by a sharp and then gradual decline to low densities. The resulting sequence of stable mating patterns includes two $\frac{7}{7}$ patterns high on the peak, with 7 at intermediate densities, and

two X patterns in the lowest-density episodes at the season's end. Female seasonal E(LRS) declines monotonically as individuals wait until later to begin their reproductive season; the weak slope oscillations with a cycle period of two time steps for female E(LRS) reflect the alternate-episode mating of females in these simulations. Interestingly, male E(LRS) is higher for individuals initially attempting to mate during the second episode rather than the first. This is because during the first episode, with its 7 mating pattern, low-quality males are entitled only to mortality, not to mating. This reduced LRS for low-quality males is enough to offset the high initial LRS for high-quality males. After episode 2, overall male E(LRS) (and the LRS for each male quality group, as well) declines monotonically. Though female var(LRS) remains quite low over the season, male var(LRS) begins at intermediate values (under the influence of pattern $\overline{\overline{}}$), rises to the maximum during most of the postpeak 7 period, and then declines to low levels with the onset of late indiscriminate mating.

When mate density remains constant throughout the entire mating season (fig. 6*b*), the sequence of stable mating patterns is strikingly different: the 7 pattern persists until the final two episodes, when the $\overline{\overline{}}$ pattern appears. (Near the end of the season, choosiness at constant densities tends to increase, because less of the season's mating potential is jeopardized by choosiness that lengthens exposure to premating predation.) Female E(LRS) is exactly the same in each consecutive pair of episodes, because mate densities and mating histories are identical. Male E(LRS) declines more smoothly, down to the two $\overline{\overline{}}$ patterns, where low-quality males are also suddenly able to contribute offspring. Note that male var(LRS) begins at a maximum, finally declining as the $\overline{\overline{}}$ patterns become increasingly important over the fewer remaining episodes; female var(LRS) remains low throughout.

Three Case Studies

Snapping shrimp.—Knowlton (1980) presented "circumstantial" evidence that the extent of evolution in response to sexual selection acting on males of the snapping shrimp *Alpheus armatus* depends on the intensity of predation. (Similar ideas and results have been explored by Endler [1978, 1983] with guppies.) These shrimp defend anemones (which provide protection from predators) from conspecific shrimp of the same sex. Females have a 3-wk reproductive cycle associated with molting, but males are capable of mating more often. To locate and inseminate other females, however, males must migrate between anemones, exposing themselves to fish and other predators.

We chose parameter values intended to mimic Knowlton's high- and low-predation sites. In each case, we simulated a single mating episode and assumed that the results indicate LRS, since we have no evidence that density fluctuates significantly and predictably through time. For convenient parameters for the snapping shrimp system, we chose 20 min as the unit of time and 5 m as the unit of length.

The parameter magnitudes are listed in table 2. Using Knowlton's regression of egg number per clutch on female length and her figure 1, we divided females into two groups differing in quality by a factor of 3. Males apparently differ little

in their potential contribution to reproductive success (Knowlton 1980), but larger males may help defend the anemone more effectively from intruders like commensal crabs (Knowlton 1978). We arbitrarily chose the factor 1.2 as the ratio of offspring per mating for the two male quality groups. We calculated offspring per mating for both sites as the product of the qualities of the two mates. The operational sex ratio was taken to be 3♂ : 1♀, within the range suggested by Knowlton (1980).

Since adult females seldom move between anemones, their speed and susceptibility to predators were set to zero. At low-predation sites (≤ 5 predators $\times$ [5 m]$^{-2}$), male speed was set at $\frac{1}{5}$ of the predator's; at higher predator densities, male speed was assumed to be inversely proportional to predator density (in general agreement with Knowlton's observation of inhibited migration of males between anemones in the presence of abundant predators). We set background mortality to obtain a plausible female mortality rate of about 9% per episode. Reactive distance of predators to males was taken to be 10 times that of males to females. All other parameters retained their default magnitudes (table 2).

In good agreement with Knowlton's results, we found positive assortative mating (⩥ mating pattern) and substantial potential for selection in both sexes ($\text{var}_{♀}$(LRS) = $\text{var}_{♂}$(LRS) = 0.320) when predator density was at or below 5 (5 m)$^{-2}$, but we found indiscriminate mating, with a far lower potential for selection acting on males, for predator densities at or above 20 (5 m)$^{-2}$ ($\text{var}_{♀}$(LRS) = 0.250; $\text{var}_{♂}$(LRS) = 0.009). Knowlton (1980) found much more extensive sexual dimorphism at the low-predation site, where males tended to have larger chelae and spines than did females, but little sexual dimorphism where predation was high. With abundant predators and an unfavorable operational sex ratio, the cost to males of seeking out the most fecund females becomes high. Because males differ little in quality and move little under these conditions, females cannot choose on the basis of quality either, and the male variance of LRS simply reflects the low variance of male quality. (Note the general similarities of these results and those in fig. 5*b*.)

We note that none of the var(LRS) in either pattern ⩥ or ⨯ in this example is attributable to the variance of lifetime mating success, var(LMS), generally known as the "opportunity for sexual selection" (Arnold and Wade 1984*a;* see table 6; App. D). Most of the higher $\text{var}_{♂}$(LRS) in the low-predator simulation here results from the higher variance of the quality of individuals mated, var(MQM), and the rest from the assortative mating, cov(MQI, MQM) (table 6).

We emphasize that these results and their interpretation are contingent on differences in male mate quality. Unless males differ in quality by at least a factor of 1.1, there is no assortative mating at low predator densities with these parameter values. We show in Appendix C, however, that differences between males other than quality (e.g., movement speed) can also generate assortative mating at low predator densities. These results underscore the need to measure and account for any differences in quality and other characteristics of males that could ultimately influence LRS.

Katydids.—Gwynne (1985) investigated mating in the katydid *Metaballus* sp., in which males invest about 20% of their body weight in each spermatophore,

TABLE 6

RELATIVE MAGNITUDES OF COMPONENTS OF NORMALIZED VARIANCE OF EXPECTED LIFETIME REPRODUCTIVE SUCCESS BETWEEN QUALITY GROUPS WITHIN SEXES FOR THE SEVEN MATING PATTERNS OF FIGURE 2

MATING PATTERN	COMPONENTS OF var(LRS)					
	var(LMS)	var(MQI)	var(MQM)	cov(LMS, MQI)	cov(LMS, MQM)	cov(MQI, MQM)
—	0*	+	++	0*	0*	++
Z	+	+	+	−(♀), +(♂)	−(♀), +(♂)	+
S	+	+	+	+(♀), −(♂)	+(♀), −(♂)	+
7	0(♀), ++(♂)	+	0	0(♀), +(♂)	0	0
⅂	++(♀), 0(♂)	+	0	+(♀), 0(♂)	0	0
X	0*	+	0	0*	0	0
X	+	+	+	+	−	−

NOTE.—LMS, Mating success per individual of a given sex, mates individual^{-1}; MQI, mate quality of a mating individual of a given sex, offspring (low-quality mate)$^{-1}$; MQM, mate quality of individuals mated, offspring (low-quality mate)$^{-1}$; 0, magnitude zero; 0*, zero, unless quality groups differ in density during an episode; +, magnitude positive and smaller than any ++ magnitudes in the column; ++, magnitude positive and larger than any + magnitudes in the column; −, magnitude negative.

most of which is eaten by the female during copulation. At sites more favorable for spermatophore production (probably those with more food available), the operational sex ratio was probably male-biased (D. T. Gwynne, personal communication). But at a less favorable site, the sex ratio was female-biased, presumably because males spent more time acquiring the energy needed to produce a spermatophore.

To simulate this case, we chose 0.5 min and 1 km as the most convenient units of time and length. Again, we assumed that a single mating episode would yield results indicative of LRS, in the absence of data on katydid densities through the season. The parameter values used to simulate mate choice at the favorable site are shown in table 2. For the unfavorable site, we assumed that half as many males and twice as many females were available for mating.

Reactive distances of predators and females probably differed between the two types of sites, because males used different calls. At favorable sites, males used a longer call that apparently made them easier to locate by both females and predators. At the unfavorable site, males used a shorter call, possibly to reduce their risk of predation; we therefore halved the reactive distances of females and of predators to males in this case. But with the female-biased operational sex ratio, females searched for males somewhat more actively; we therefore doubled the searching speed of these females.

As for the Knowlton (1980) study, Gwynne's (1985) data suggest approximately a threefold difference in offspring per mating for larger versus smaller females. We also take into account that male katydids differ more substantially in potential contributions to offspring, based on differences in spermatophore mass (D. T. Gwynne, personal communication). Background mortality at both sites was $0.0002\ (0.5\ \text{min})^{-1}$. Other parameter values were identical to the default.

Gwynne (1985) observed no choosiness by males at the favorable sites, where they competed for females that probably discriminated among males (D. T. Gwynne, personal communication). The simulation generated a 7 pattern, in good agreement with Gwynne's interpretation. At the unfavorable site, the usual sex roles were reversed, and female katydids competed for the fewer males. Here, the simulation yielded a Σ pattern, again consistent with the empirical study. The realistic shifts in the operational sex ratio and in insect and predator behavior between the simulated sites can indeed trigger a complete sex-role reversal in the model's predictions as well.

In accord with these qualitative results, the opportunity for selection to act on the sexes shifts strongly and oppositely between the two site types: at favorable sites for male spermatophore production, $\text{var}_{\sigma}(\text{LRS}) = 1$ and $\text{var}_{\varphi}(\text{LRS}) = 0.25$; at the unfavorable site, $\text{var}_{\sigma}(\text{LRS}) = 0.04$ and $\text{var}_{\varphi}(\text{LRS}) = 1$. High var(LMS) and covariance between mating success and mate quality, cov(LMS, MQI), are responsible for higher var(LRS) at one of the site types than at the other (see table 6; App. D).

Other simulations of this system show that both sexes should be choosy at both sites when predator densities are lower or when mate densities are higher, and that both should be indiscriminate only when mate densities are considerably lower. Differing mate and predator densities across sites and years should gener-

ate predictable shifts in choosiness by each sex, as in figures 4 and 5, even if resource levels remain relatively constant.

Frogs.—In his study of the túngara frog (*Physalaemus pustulosus*), Ryan (1985) found that females prefer to mate with large males. During the wet season in Panama, sexually mature males return repeatedly to breeding ponds and call for females. The operational sex ratio on any given night is heavily male-biased, averaging 5.5 males per female. Males call for approximately 6 h, but they are preyed on by bats (*Trachops cirrhosus*) attracted to the male's call. Both males and females are occasionally eaten by the South American bullfrog (*Leptodactylus pentadactylus*) and an opossum (*Philander opossum*).

We simulated the túngara frog system by calculating parameters for a single 6-h mating episode, with the unit of time being 1 min and the unit of length 1 m. Male densities six times the magnitude of female densities were used (see table 2), approximating densities found by Ryan (1985). To simulate male-female interactions, we obtained the velocities and reactive distances of males and females by estimating encounter rates from published data (0.003–0.078 encounters m^{-2} min^{-1}; Ryan 1985) and then solving for the velocities and reactive distances using equation (3). Female reactive distance was altered to span this range of encounter rates, and velocities remained constant (see table 2). Bat predation on calling males was simulated by adjusting predator reactive distance in order to match the predation mortality on both classes of males; background mortality was set to the average predation rate from opossums and bullfrogs (Ryan et al. 1981). We assumed high female quality to be twice that of low female quality, since Ryan (1985) showed that females in the upper half of the size range produce roughly twice as many eggs as females in the lower half. With little indication of any substantial variation in male quality, we used quality factors of 1.2 and 1.0, as for the snapping shrimp, above.

At low encounter rates (0.003–0.026 encounters m^{-2} min^{-1}) between potential mates, the model finds that the indiscriminate mating pattern ($\overline{X}$) is stable. At all higher encounter rates in the natural range (0.027–0.078 encounters m^{-2} min^{-1}), all females choose to mate exclusively with high-quality males (7), as consistently observed by Ryan (1985). The mismatch between the model's predictions and Ryan's observations at low encounter frequencies suggests (1) that males may actually differ in quality more than our arbitrary factor of 1.2, (2) that encounter frequencies are actually underestimated in our calculations, or (3) that the animals are behaving suboptimally. This result again emphasizes the importance of documenting and measuring the size-correlated quality differences between males (e.g., ejaculate volume, exposure of mating site to predators).

To examine how predation may structure the mate-choice patterns in túngara frogs, we performed two additional simulations: (1) bat predation on both males and females, and (2) no bat predation. When bat predation was imposed equally on males and females, with all parameters as above, we found that the stable pattern at all encounter rates is indiscriminate mating ($\overline{X}$). When bat feeding on frogs was set to zero, allowing only background frog mortality, we recovered the shift from the complete lack of choosiness ($\overline{X}$) to female choosiness (7) at an encounter rate of 0.026 encounters m^{-2} min^{-1}; but above 0.074 encounters m^{-2}

min^{-1}, we obtained complete assortative mating (⎓) (cf. fig. 4). These results suggest that the higher natural predation on males may largely account for the mating system of túngara frogs.

DISCUSSION

For animals capable of optimal mate choice subject to constraints imposed through choices by the other sex, two quality groups per sex are enough to generate a diverse array of mating patterns and pattern sequences. Though the model's assumptions (table 1) constitute at best a rough caricature of a natural mating system, this approach has provided much information about LRS, var(LRS), and their sensitivity to some measurable biological parameters. We have documented and emphasized the importance of (1) the densities of premating predators and potential mates, (2) postmating latency, through its effects on the operational sex ratio and on the available number of mating episodes, and (3) the sensitivity of the LRS of the low-quality group of the less choosy sex to variation in the mating parameters. Other testable predictions are listed at the end of this section.

Simulations based on the three case studies analyzed above yield mating patterns and trends in var(LRS) generally consistent with data and interpretations in the original studies. These simulation results and the partitioning of var(LRS) described in Appendix D provide some additional insights into the underlying behavioral and evolutionary mechanisms. The model's apparent ability to mimic these cases reasonably well also suggests that some of the natural complexities explicitly ignored in formulating the model (e.g., mating interference) may at least sometimes be of only secondary importance.

To our knowledge, the analysis described in Appendix D represents a unique attempt to partition var(LRS) generated by a mate-choice model into biologically meaningful variance components. (For a similar approach applied to survival, fecundity, and reproductive age, see Brown 1988.) Of the six components in table 6, variance of mating success has received the vast majority of the empirical attention in the literature (see Hafernik and Garrison 1986 and references therein). The other five components involve the magnitudes of mate quality, which are often difficult to assess; yet, a reliable and independent means of measuring quality is clearly essential to a thorough understanding of the basis for mate choice in any particular system. Two of these other components directly express variances of mate quality.

The three covariances especially deserve more empirical attention. The extent to which mating success of a focal individual co-varies with its quality, cov(LMS,MQI), seems to express an important aspect of sexual selection, though the opportunity for sexual selection includes only var(LMS) by definition (Wade and Arnold 1980). Mate choice could maximize LRS by a high mating frequency, perhaps at the expense of accepting lower-quality mates, or by setting high mate standards, possibly lowering mating success somewhat. This suggests that the covariance of mating success and mate quality, cov(LMS,MQM), may sometimes be negative, as associated in table 6 with intermediate levels of choosi-

ness (i.e., patterns Z, S, and X). The final component, the covariance of quality between mates (cov(MQI, MQM)), is a convenient means of expressing the contribution of assortative mating to the overall variance of reproductive success.

A recent article by Hubbell and Johnson (1987) described a mate-choice model and analytical results similar in some respects to ours. Their model considers optimal choosiness by individuals randomly encountering potential mates of two different qualities. (Unlike our approach, however, these choices are assumed to be independent of choices made by the other sex, and thus independent of qualities within the given sex as well, which oversimplifies the problem when both sexes are potentially choosy.) Mating takes place in a single episode. Within the episode, postmating latencies are imposed, and densities remain constant. As for our model, Hubbell and Johnson considered the effects of different survival rates, postmating latencies, probabilities of encounter, and qualities of potential mates. Structurally, their model consists of first-order absorbing Markov chains, based on up to six alternative states in the mating process. Analytical solutions for means and variances of lifetime mating success were obtained.

As in our results, Hubbell and Johnson (1987) found more choosiness when survival probabilities and mate-encounter rates were high. But their model generates only chance variation in lifetime mating success, and they suggested that this variance is therefore a poor indicator of the opportunity for sexual selection. In contrast, the var(LRS) and its components generated by our model exclude chance variation and should provide a much better indication of the selection potential. Of course, the effectiveness of sexual selection in actually shaping the evolution of traits chosen by mates depends on the heritability of those traits and perhaps on their genetic correlations with other traits under different selective pressures (see Falconer 1981).

Parker (1983) used an optimal-diet formulation to devise a mate-choice model somewhat similar to ours. Like us, he assumed that willingness by both potential mates is required for mating, that a constant amount of time is invested in each mating and ensuing reproduction, that there is a cost of choice for each sex (which in his model is the time cost of finding an alternative mate and in our model is increased risk of predation or of not finding a mate during the episode), and that an individual has the same quality for all individuals of the opposite sex. Unlike ours, Parker's model includes a continuous distribution of mate qualities, and his analysis is primarily graphical.

For single mating episodes, Parker found three alternative types of stable mating patterns (both sexes indiscriminate, one choosy and the other indiscriminate, and both choosy). As in our results (e.g., table 5, case 24) and those of Hubbell and Johnson (1987), Parker (1983) found that greater variance of mate quality increases choosiness by the other sex. He noted that assortative mating is more likely if the sexes make similar parental investments (see the higher frequency of pattern $\overline{\overline{}}$ in our table 5, case 19) and if search costs are low (table 5, case 8). Parker pointed out that when one sex increases its parental investment, this increases both the costs and the benefits of choosiness by the other sex, making predictions difficult. In our model, greater parental investment (via longer latency) by females reduces male choosiness (table 5, default and cases 19 and 20),

because the longer latency increases male bias in the operational sex ratio without increasing the female's quality (expressed as potential offspring per mating).

Though the model presented and analyzed in this article may prove most useful as a heuristic tool, a considerable number of qualitative predictions have emerged during the analysis. We conclude by listing a few of these.

1. Increased premating predation risk and lower densities of potential mates generally decrease choosiness.
2. When densities of potential mates and of predators are relatively constant late in the mating season, choosiness should increase toward the season's end. Late-season declines in densities of potential mates or increases in predator density tend to mask or reverse the predicted trend.
3. Lifetime reproductive success of low-quality individuals of the less choosy sex and var(LRS) for that sex are extremely sensitive to biological and environmental parameters.
4. Normalized variance of LRS and thus selection for mate quality are greatest at intermediate densities of predators and of potential mates.
5. Low-quality individuals do best and are disproportionately numerous in the mating pool when total densities of potential mates are high and predator densities are low (mating pattern $\overline{\overline{}}$) or when mate densities are low and predator densities are high (pattern $\overline{\underline{X}}$).

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APPENDIX A

Expressions for $E_x(LRS)$ and $var_x(LRS)$

Assume that a given sex x is divided into low- (subscript 1) and high- (subscript 2) quality groups at frequencies f_1 and f_2, such that $f_1 + f_2 = 1$. Then, for sex x, the expected (or mean) lifetime reproductive success, $E_x(LRS)$, and the normalized variance of lifetime reproductive success, $var_x(LRS)$, can be directly calculated from the frequencies and lifetime reproductive successes LRS_1 and LRS_2 of the two quality groups:

$$E_x(LRS) = f_1 LRS_1 + f_2 LRS_2, \tag{A1}$$

and

$$\begin{aligned} var_x(LRS) &= \sum_{i=1}^{2} \{f_i[LRS_i - E_x(LRS)]^2\} \Big/ E_x^2(LRS) \\ &= \frac{f_1 f_2 (LRS_2 - LRS_1)^2}{(f_1 LRS_1 + f_2 LRS_2)^2}. \end{aligned} \tag{A2}$$

The numerator of equation (A2) is the unnormalized variance of LRS, and the denominator (the squared mean) is the normalization term.

APPENDIX B

No Multiple Stable Mating Patterns during a Mating Episode without Depletion of Mates

When the densities of potential mates remain constant during a mating episode (or any other period over which a constant stable mating pattern is to apply), some of the expected reproductive payoffs among mating patterns within mate-quality groups are identical (see table 3). For example, expected reproduction by high-quality females is the same for all patterns in which they are choosy (i.e., they accept only high-quality mates). Mating exclusively with high-quality males must yield the same reproductive payoff (P_1 in table 3) for all three patterns in which high-quality females are choosy (⚌, Z, and 7), because the number of potential male mates remains at the initial density throughout the episode and thus is independent of the males' own degree of choosiness.

A mating pattern is stable only if all possible decision paths leading into the pattern yield higher payoffs than those leading away (see fig. 2). For example, if ⍱ is a stable pattern, then (1) high-quality males have greater reproductive success in ⍱ than in ⊼ (i.e., $P_7 > P_8$ in table 4), (2) low-quality males have greater success in ⍱ than in ⍒ (i.e., $P_{12} > P_{11}$), and (3) high-quality females have greater reproductive success in ⍱ than in ⚌ (i.e., $P_2 > P_1$). Two or more mating patterns can be stable simultaneously only if they all satisfy this rule, which is possible only if the densities of mates are allowed to vary during a mating episode.

Whether or not mates are depleted during a mating episode, adjacent mating patterns in figure 2 for which transitions in both directions hinge on payoffs for one mate-quality group clearly cannot both be stable simultaneously. Except for the special and extremely unlikely instances in which payoffs are exactly the same by accident, one or the other pattern will imply greater reproductive success for the relevant quality group(s). (Consider ⚌ and ⍒, and consult table 4. In general, either $P_1 > P_2$, ⍒ → ⚌, and ⚌ may be a stable pattern or $P_2 > P_1$, ⚌ → ⍒, and ⍒ may be stable; clearly, both cannot be stable simultaneously.) Similar logic applies to all nonadjacent pairs of mating patterns: in the absence of mate depletion within mating episodes, imposing the rule that all paths must lead into both putatively stable mating patterns inevitably leads to contradictions. One of these contradictions is illustrated for each possible nonadjacent pair of mating patterns in table 4.

We conclude that multiple simultaneously stable mating patterns are impossible without mate depletion during the period of mating over which the mating pattern or patterns remain constant. A depletion model that allowed for instantaneously shifting, stable mating patterns would also be unable to produce multiple simultaneously stable patterns. This follows because mate depletion over arbitrarily short time intervals must be negligible, ensuring by the argument presented above that only single stable mating patterns are possible within each short interval.

APPENDIX C

Sensitivity Analysis of the Model

We attempted to clarify the effects and relative importances of the model's parameters in determining seasonal mating patterns, reproduction by quality group, and opportunity for selection, by systematically shifting parameter values relative to the default set (table 2) in a series of simulations (table 5). When possible, quantitative parameters (e.g., mate and predator densities) were shifted both higher and lower by factors of two; qualitative parameters (e.g., presence or absence of seasonal density peaks and their timing) were set to illustrate a diversity of cases.

The resulting sequences of mating patterns are indicated by the symbols illustrated in figure 2. In general, higher mate densities or lower predator densities during an episode

yield greater choosiness and more positive assortative mating (especially the $\overline{=}$ pattern) by potential mates (see also figs. 4–6, noting in particular the corresponding densities of potential mates in fig. 6*a* and 6*b*). Similarly, greater mate speeds or reactive distances or reduced predator speeds or reactive distances increase choosiness.

In these simulations, low-quality males respond to the parameter shifts with dramatic swings in lifetime reproductive success (LRS), whereas the other quality groups generally respond much more weakly. This also implies strong shifts in the normalized variance of male E(LRS), a measure of the opportunity for selection acting on males. As long as predation and background mortality fail to make choosiness too dangerous, the sex with the individuals that encounter potential mates more frequently tends to be choosier. Thus, moderate alterations of mortality rates or encounter frequencies can whipsaw the low-quality group of the less choosy sex between high and low LRS. This interpretation is complicated somewhat by the influence of the relative magnitudes of the offspring-per-mating parameters (greater proportional differences among R's yield more choosiness; see cases 22–28) and by an underlying tendency for choosiness to increase late in the season (see table 2, case 4; fig. 6*b;* and the text).

When the two male groups are set equal in quality (at 1.189, the geometric mean of their default magnitudes), females can no longer be choosy under the assumptions of the model. The resulting sequence of mating patterns (case 25) is the same as the default, except that females were consistently indiscriminate. This drops var_{δ}(LRS) to zero and increases var_{φ}(LRS), because $\top$ replaces $\overline{=}$. To determine whether differences other than quality between male groups could yield assortative mating, we set $V_M = 2V_m$. With predators at the default density (case 26), the velocity difference fails to generate assortative mating. But at sufficiently low predator densities (case 28 vs. 29), the velocity difference results in two episodes of weak assortative mating (Σ), apparently because the risk to slower-moving males of failing to find a mate exceeds the cost of accepting lower-quality mates.

Mating-independent mortality reduces E(LRS) somewhat, as expected, but has no qualitative effect on the sequence of mating patterns. Since predation mortality falls more heavily on the more rapidly moving males and since low-quality males are particularly sensitive to such effects (see above), predation mortality tends to have a greater overall impact on mating patterns and LRS than does nonpredation mortality.

Overall, across this seasonal sequence of mating episodes occurring over a wide range of densities, the sequence of stable mating patterns shifts considerably with changes in parameter values. Moreover, the LRS of the low-quality group of the operationally more numerous sex is sensitive to the parameter values, as is the opportunity for selection in that sex.

APPENDIX D

Partitioning the Normalized Variance of Lifetime Reproductive Success, var(LRS), for the Mating Patterns of Figure 2

In this article, we focus exclusively on the deterministic components of var(LRS) arising from quality differences, ignoring the components arising from accidental details of random encounters with predators and potential mates. The rationale for this approach follows.

1. Though mate quality may or may not be heritable, good luck in attracting mates or avoiding predators certainly is not. Chance variation in reproductive success contributes quantitatively to the empirically observable variance of LRS but should prove less important than quality-related variation in accounting for the responses to selection in natural populations. (For an analysis stressing the implications of chance variations, see Hubbell and Johnson 1987.)

2. This is consistent with our deterministic approach, motivated by the need to keep the analysis tractable and comprehensible, for calculating the timing and numbers of encounters within episodes.

3. Components of variance of LRS attributable to random variation should increase

more slowly than deterministic components over a sequence of mating episodes, since chance evens out somewhat among individuals.

Following Crow (1958) and Arnold and Wade (1984*a*, 1984*b*), we focus on the "opportunity for selection," var(LRS), calculated as the variance of LRS between quality groups within a sex, divided by $[E(LRS)]^2$. To interpret differences among simulations in var(LRS), we note that LRS = (LMS)(MQI)(MQM), where the parenthetical multiplicative factors represent an individual's mating success, its own mate quality, and the quality of its mates, respectively. Taking logarithms of both sides permits the var(log(LRS)) to be readily partitioned into additive components, as suggested by Arnold and Wade (1984*a*, p. 715; see also Brown 1988). Letting lowercase indicate log transformation,

$$\begin{aligned} \text{var(lrs)} = {} & \text{var(lms)} + \text{var(mqi)} + \text{var(mqm)} + 2\,\text{cov(lms, mqi)} \\ & + 2\,\text{cov(lms, mqm)} + 2\,\text{cov(mqi, mqm)}. \end{aligned} \tag{D1}$$

Because qualitative effects of these components are essentially the same for both log-transformed and untransformed values, we simply refer to untransformed values in the text and in most of what follows below. (For var(lms) of males in pattern 7 and of females in pattern ⍱, however, note that low-quality individuals have a mating success of zero, and var(lms) and thus var(lrs) become infinitely large.)

Table 6 indicates the components contributing to var(LRS) for each mating pattern. Variance of lifetime mating success, var(LMS), is often called the "opportunity for sexual selection" (Arnold and Wade 1984*a*); it is the only component contributing to var(LRS) for males in pattern 7 and for females in pattern ⍱. Var(LMS) contributes nothing to var(LRS) for patterns ⩢ and X, unless differences in quality-group densities are large enough to differentiate mating success in the two quality groups.

Variance of quality contributes directly to var(LRS) in most cases. Variance of an individual's mating quality, var(MQI), is the same for all patterns. Variance of the quality of individuals mated, var(MQM), contributes most for the quality-stratified pattern ⩢, somewhat less when quality groups partially overlap in mate qualities, and nothing when there is neither stratification nor overlap.

Among the covariance components, cov(MQI, MQM) measures assortative mating by quality, which (as noted in the text) is strongest in the quality-stratified pattern ⩢ and weaker or zero in the others, except for X, where it is weakly negative. Cov(LMS, MQM) indicates whether individuals mating more frequently also choose better mates (+); or perhaps mating frequency is traded off against mate quality (−, as for one sex in patterns Z and Σ and for both sexes in pattern X). Cov(LMS, MQI) expresses the extent to which being of higher quality co-varies with more frequent mating.

LITERATURE CITED

Arnold, S. J., and M. J. Wade. 1984*a*. On the measurement of natural and sexual selection: theory. Evolution 38:709–719.

———. 1984*b*. On the measurement of natural and sexual selection: applications. Evolution 38:720–734.

Bateson, P., ed. 1983. Mate choice. Cambridge University Press, Cambridge.

Belwood, J. J., and G. K. Morris. 1987. Bat predation and its influence on calling behavior in Neotropical katydids. Science (Washington, D.C.) 238:64–67.

Boake, C. R. B. 1986. A method for testing adaptive hypotheses of mate choice. American Naturalist 127:654–666.

Bradbury, J. W., and M. B. Andersson, eds. 1987. Sexual selection: testing the alternatives. Wiley, Chichester.

Brown, D. 1988. Components of lifetime reproductive success. Pages 439–453 *in* T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.

Cade, W. 1980. Alternative male reproductive behaviors. Florida Entomologist 63:30–45.

Crocker, G., and T. Day. 1987. An advantage to mate choice in the seaweed fly, *Coelopa frigida*. Behavioral Ecology and Sociobiology 20:295–301.

Crow, J. F. 1958. Some possibilities for measuring selection intensities in man. Human Biology 30:1–13.

Darwin, C. 1871. The descent of man, and selection in relation to sex. 2d ed. Burt, New York.

Dawkins, R. 1980. Good strategy or evolutionarily stable strategy? Pages 331–367 *in* G. W. Barlow and J. Silverberg, eds. Sociobiology: beyond nature/nurture? Westview, Boulder, Colo.

Dominey, W. J. 1984. Alternative mating tactics and evolutionarily stable strategies. American Zoologist 24:385–396.

Endler, J. A. 1978. A predator's view of animal color patterns. Evolutionary Biology 11:319–364.

———. 1983. Natural and sexual selection on color patterns in poeciliid fishes. Environmental Biology of Fishes 9:173–190.

———. 1987. Predation, light intensity, and courtship behavior in *Poecilia reticulata* (Pisces: Poeciliidae). Animal Behaviour 34:1376–1385.

Enquist, M., and O. Leimar. 1983. Evolution of fighting behavior: decision rules and assessment of relative strength. Journal of Theoretical Biology 102:387–410.

Falconer, D. S. 1981. Introduction to quantitative genetics. 2d ed. Longman, London.

Fincke, O. M. 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). Behavioral Ecology and Sociobiology 10:293–302.

Gwynne, D. T. 1985. Role-reversal in katydids: habitat influences reproductive behavior (Orthoptera: Tettigoniidae, *Metaballus* sp.). Behavioral Ecology and Sociobiology 16:355–361.

———. 1987. Sex-biased predation and the risky mate-locating behaviour of male tick-tock cicadas (Homoptera: Cicadidae). Animal Behaviour 35:571–576.

Hafernik, J. E., and R. W. Garrison. 1986. Mating success and survival rate in a population of damselflies: results at variance with theory? American Naturalist 128:353–365.

Houston, A. I., and J. M. McNamara. 1987. Singing to attract a mate: a stochastic dynamic game. Journal of Theoretical Biology 129:57–68.

Hubbell, S. P., and L. K. Johnson. 1987. Environmental variance in lifetime mating success, mate choice, and sexual selection. American Naturalist 130:91–112.

Janetos, A. C. 1980. Strategies of female mate choice: a theoretical analysis. Behavioral Ecology and Sociobiology 7:107–112.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. Evolution 36:1–12.

———. 1987. Sexual selection by female choice in polygynous animals. Annual Review of Ecology and Systematics 18:43–70.

Knowlton, N. 1978. The behavior and ecology of the commensal shrimp *Alpheus armatus*, and a model for the relationship between female choice, female synchrony and male parental care. Ph.D. diss. University of California, Berkeley.

———. 1980. Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp. Evolution 34:161–173.

Koopman, B. O. 1956. The theory of search. I. Kinematic bases. Operations Research 4:324–346.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:292–305.

Losey, G. S., Jr., F. G. Stanton, T. M. Telecky, W. A. Tyler III, and the Zoology 691 Graduate Seminar Class. 1986. Copying others, an evolutionarily stable strategy for mate choice: a model. American Naturalist 128:653–664.

Mäkelä, A. 1985. Differential games in evolutionary theory: height growth strategies of trees. Theoretical Population Biology 27:239–267.

Mangel, M., and C. W. Clark. 1986. Towards a unified foraging theory. Ecology 67:1127–1138.

———. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, N.J.

Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.

McCauley, D. E., and E. C. Lawson. 1986. Mating reduces predation on male milkweed beetles. American Naturalist 127:112–117.

McLain, D. K., and R. D. Boromisa. 1987. Male choice, fighting ability, assortative mating and the

intensity of sexual selection in the milkweed longhorn beetle, *Tetraopes tetraophthalmus* (Coleoptera: Cerambycidae). Behavioral Ecology and Sociobiology 20:239–246.

Moore, A. J., and P. J. Moore. 1988. Female strategy during mate choice: threshold assessment. Evolution 42:387–390.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biological Reviews of the Cambridge Philosophical Society 45:525–567.

———. 1979. Sexual selection and sexual conflict. Pages 123–166 *in* M. S. Blum and N. A. Blum, eds. Sexual selection and reproductive competition in insects. Academic Press, New York.

———. 1983. Mate quality and mating decisions. Pages 141–164 *in* P. Bateson, ed. Mate choice. Cambridge University Press, Cambridge.

Partridge, L. 1980. Mate choice increases a component of offspring fitness in fruit flies. Nature (London) 283:290–291.

Partridge, L., and T. Halliday. 1984. Mating patterns and mate choice. Pages 222–250 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 2d ed. Sinauer, Sunderland, Mass.

Pielou, E. C. 1977. Mathematical ecology. Wiley-Interscience, New York.

Rubenstein, D. I. 1980. On the evolution of alternative mating strategies. Pages 65–100 *in* J. E. R. Staddon, ed. Limits to action: the allocation of individual behavior. Academic Press, New York.

———. 1987. Alternative reproductive tactics in the spider *Meta segmentata*. Behavioral Ecology and Sociobiology 20:229–237.

Ryan, M. J. 1985. The túngara frog: a study in sexual selection and communication. University of Chicago Press, Chicago.

Ryan, M. J., M. D. Tuttle, and L. K. Taft. 1981. The costs and benefits of frog chorusing behavior. Behavioral Ecology and Sociobiology 8:273–278.

Sargent, R. C. 1982. Territory quality, male quality, courtship intrusions, and female nest choice in the threespine stickleback, *Gasterosteus aculeatus*. Animal Behaviour 30:364–374.

Sargent, R. C., and J. B. Gebler. 1980. Effects of nest site concealment on hatching success, reproductive success, and paternal behavior of the threespine stickleback, *Gasterosteus aculeatus*. Behavioral Ecology and Sociobiology 7:137–142.

Sargent, R. C., M. R. Gross, and E. P. van den Berghe. 1986. Male mate choice in fishes. Animal Behaviour 34:545–550.

Schaffer, W. M. 1977. Some observations on the evolution of reproductive rate and competitive ability in flowering plants. Theoretical Population Biology 11:90–104.

Simmons, L. W. 1987. Female choice contributes to offspring fitness in the field cricket, *Gryllus bimaculatus* (De Geer). Behavioral Ecology and Sociobiology 21:313–321.

Sutherland, W. J. 1985. Chance can produce a sex difference in variance in mating success and explain Bateman's data. Animal Behaviour 33:1349–1352.

Taylor, C. E., A. D. Pereda, and J. A. Ferrari. 1987. On the correlation between mating success and offspring quality in *Drosophila melanogaster*. American Naturalist 129:721–729.

Thompson, D. J., and J. T. Manning. 1981. Mate selection by *Asellus* (Crustacea: Isopoda). Behaviour 78:178–187.

Thornhill, R. 1984. Alternative female choice tactics in the scorpionfly *Hylobittacus apicalis* (Mecoptera) and their implications. American Zoologist 24:367–383.

Thornhill, R., and D. T. Gwynne. 1986. The evolution of sexual differences in insects. American Scientist 74:382–389.

Vincent, T. L., and J. S. Brown. 1984. Stability in an evolutionary game. Theoretical Population Biology 26:408–427.

Wade, M. J. 1979. Sexual selection and variance in reproductive success. American Naturalist 114:742–747.

Wade, M. J., and S. J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. Animal Behaviour 28:446–461.

Wells, K. D. 1977. The social behaviour of anuran amphibians. Animal Behaviour 25:666–693.

Woodward, B. D. 1986. Paternal effects on juvenile growth in *Scaphiopus multiplicatus* (the New Mexico spadefoot toad). American Naturalist 128:58–65.